FUNDAMENTALS OF Tropical Freshwater Wetlands

From Ecology to Conservation Management

Edited by

Tatenda Dalu

Ryan J. Wasserman

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Dedication

This book is dedicated to *Professor Olaf Laurence Friedrich Weyl* (1972–2020) who passed away suddenly on the Wolf River in Hogsback, South Africa on the 14th of November 2020. Working predominantly in African freshwater systems, Olaf was a global authority in freshwater and fisheries ecology and invasion biology.

For many of us, we lost a great friend, brother, teacher, and mentor, and his passing left us so much poorer and heartbroken.

. . . ***gone too soon Olaf*** . . .

Front left to right: The late Prof. Olaf L.F. Weyl, Dr. Tatenda Dalu, Prof. Ryan J. Wasserman, Dr. Jaclyn M. Hill and Dr. Richard A. Peel, and Dr. Geraldine C. Taylor and Prof. Michelle C. Jackson with their backs to the camera, during the 2015 research team outing at Thomas Baines, Eastern Cape province of South Africa [Photo by Bruce Ellender].

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Preface

Historical perceptions often viewed wetlands as dangerous and foreboding places. Inaccessible haunts of strange tribes, living outside the reaches of societal norms. Places ripe with disease-carrying insects, and to be put to better use through draining to convert the wastelands to more "productive" use. That was a serious underestimate of the societal importance of wetlands and the ecosystem services that they provide. The image was somewhat improved by international recognition as areas important for wildlife brought about by the "Convention on Wetlands of International Importance especially as Waterfowl Habitat" agreed in the city of Ramsar in Iran by representatives of 18 nations, and signed as an International Treaty on February 3, 1971. The Convention, commonly known as The International Convention on Wetlands (www.ramsar.org), now has 171 contracting parties, covering the majority of countries of the world.

It might be expected that these days wetlands would be widely considered as a global asset of social, economic, and ecological importance. Despite awareness among governments and high-level decision-makers, wetlands continue to be lost through conversion or overexploitation. This diminishes their value for the multiple services they provide, including the provision of goods such as water, fish, and construction materials; as regulators of ecosystem process that can mitigate against climate extremes and carbon loss; as providers of habitats for a diverse range of, including migratory, organisms; and as important recreational and spiritual sites. Yet, wetlands are still subject to multiple direct and indirect pressures, often arising from decisions or policies that can occur far from the wetland itself, and revealing policy contradictions arising from the so called "silo mentalities." Government or international policies, for example, development can contradict those for conservation and are even evident among the recent Sustainable Development Goals adopted in 2015 by 193 Member States of the United Nations.

The diversity and threats to wetland integrity are pronounced in the tropics. It is also in the tropics where wetland structure and function is still in need of considerable further understanding. We can view this in more optimistic terms as an opportunity, also recognizing that it is in the tropics where the largest designated Ramsar sites are, and where there is growth and development of wetland policies and river basin management authorities, that naturally encompass wetlands.

Knowledge of itself does not guarantee wetland protection and wise management but is a necessary underpinning element to that. Surprisingly, then, there is no single textbook dedicated to tropical wetlands. That gap is addressed in this volume on *Tropical Freshwater Wetlands*. The book, comprising 23 chapters, provides a comprehensive overview of topics from physical structure to management. Like wetlands themselves, the book demonstrates diversity, written by authors with direct experience of tropical wetlands across the world. A focus on Africa is most represented, and that of Asia and Australasia least. This provides a motivation for further gathering and sharing of knowledge. Nevertheless, the book is much needed milestone in collating experience on tropical wetlands and providing a stimulus for further work. The volume has been brought together by tireless efforts of Tatenda Dalu and Ryan J. Wasserman and is structured around themes that build from the physical structure, ecosystem processes, biotic composition, and, finally, management.

Following a general overview of tropical wetlands in the introductory chapter by Wasserman and Dalu (2022), the next three chapters lead us through the formation of tropical wetlands (Job et al., 2022) in Chapter 2, Factors Controlling Wetland Formation, and an overview of hydrology and physical and chemical attributes by Deemy et al. (2022a) in Chapter 3, Hydrology, Geomorphology, and Soils: An Overview, and Chapter 4, Physicochemical Environment (Deemy et al. 2022b). Tropical wetlands form under a variety of climate and geomorphological conditions. Appreciating the underlying geomorphology and influence of climate is necessary for understanding wetland processes. This is also needed in adapting management to a changing climate and local human pressures. Hydrology is, self-evidently, a crucial factor for the form and function of wetlands and the multiple wetland types found in the tropics. Pronounced wet and dry season water-level fluctuations are a major defining feature of tropical wetlands, and alterations to hydrology from catchment developments can have dramatic consequences on wetland conditions. The hydrology in turn drives much of the wetland chemistry, as outlined in Chapter 4, Physicochemical Environment. Water retention and its effects on redox potential affect chemical transformations across temporal and spatial scales and with consequences for numerous wetland functions. These influence the very character of the wetland, and the plants and animals that live there. They, in turn, affect vegetation structure, with ecological feedbacks to the chemistry and soil formation. These themes are explored further in Chapter 5, Carbon Sequestration and Fluxes, and Chapter 6, Nutrient Cycling.

With increasing, and much needed, political attention on global shifts in climate, the rates and processes of wetland chemistry drive carbon storage and greenhouse gas retention and emissions. These processes are reviewed by Moyo (2022) in Chapter 5, Carbon Sequestration and Fluxes. Wetlands are a major component of the global carbon cycle and attention to their management is a global issue. Carbon flux relates to nitrogen retention, and more generally nutrient cycling, themes explored by Deemy et al. (2022c) in Chapter 6, Nutrient Cycling. Wetlands are extremely chemically dynamic, with nutrient transformation driven by sediment structure and microbial communities. The consequential occlusion and availability of nutrients drive primary production and trophic dynamics. Open water and sediment biogeochemistry, and linked to redox state, are of fundamental importance for a range of other chemical species such as sulfur and its role in microbial and chemical processes.

Following on from the first section of the book, Biota and Biotic Processes form the second section. The current state of knowledge of the more visible vegetation of tropical wetlands, particularly aquatic macrophytes and woody plants, is reviewed in Chapter 7, Vegetation, by Piedade et al. (2022). The wide range of wetland types in the tropics reveals a diverse assortment of plant adaptation. Flood pulses, extensive range of water chemistry, and soil properties influence majorly tropical wetland plant diversity. Tropical wetland comprises some of the most species-rich and productive ecosystems on Earth. Nevertheless, the number of endemic higher plant species is generally low. As pressures on tropical wetlands increase, the ecosystem services they provide become increasingly evident. Conversion of wetlands to croplands and damming of rivers across the tropics continue to lead to loss and degradation of wetland habitats. The chapter concludes with recognizing the need for stronger administration for the protection and management of many of the world's tropical wetlands and how this can be helped with international financial as well as moral support. Looking at smaller, but no less important, components of the plant Kingdom, in Chapter 8, Phytoplankton Dynamics, Dalu et al. (2022) describe phytoplankton dynamics and the high rates of primary production of tropical wetlands. Although there are no key taxa that occur exclusively in tropical wetlands, the importance of functional groups and the value of some taxa, particularly the diatoms, in monitoring schemes are emphasized.

Chapters 9–11 explore the diversity and habitats of the zooplankton, branchiopods, and macroinvertebrates of tropical wetlands. First, Brendonck et al. (2022a) give an overview of tropical zooplankton, and how each new study can reveal new taxa. While the plankton of some, mainly larger tropical lakes, are well-known knowledge of taxa richness and distribution patterns in smaller water bodies and wetlands is much more limited. Unlike phytoplankton, many zooplankton species are thought to be exclusive to the tropics and subtropics, but what is known about their biogeography is certainly limited by low numbers of taxonomists who have or are currently working in tropical wetlands. Many discoveries await, especially perhaps in small and temporary waters. This applies also to branchiopods, the topic of

Chapter 10, Large Branchiopods, by Brendonck et al. (2022b) and a group prevalent in small and temporary water bodies. The hydrological dynamics of tropical wetlands often mean that temporary waters are important features of the ecosystem (emphasized also in Chapter 8, Phytoplankton Dynamics), and a special feature throughout much of the tropics. In these water bodies, fish are often absent or in low numbers, leading to low predation pressure on potential invertebrate prey. Many temporary or ephemeral pools are isolated in the landscape, and pressures of pollution can be lower than where water bodies are directly connected with upstream surface waters. A consequence of this is that the fauna of those waters such as the branchiopods can have high diversity, with an often unrecognized importance for global conservation. Yet, their isolation also means that many smaller temporary waters are not featured in conservation planning. The very ancient history of large branchiopods has particular value in the study of the biogeography. Many families predate the splitting up of the continents. Subsequent evolution, however, has led to a rich global diversity with many endemics, known only from a restricted region, and areas of the tropics are considered "hotspots" for the group. As they cover all recognized functional feeding groups known from invertebrates, large branchiopods play an important role in ecosystem functioning of temporary wetlands, and services to human communities.

Tropical freshwater macroinvertebrates are relatively better known and more studied than zooplankton or large brachiopods. They are increasingly used as bioindicators of river quality across the tropics, although the methods (and some assumptions) are often rooted in the tradition of northern hemisphere water quality classification schemes. Chapter 11, Macroinvertebrates, by Dube et al. (2022a), reviews the existing knowledge and application of macroinvertebrates, with a focus on those occurring in wetlands in the Afrotropical regions. A high diversity, reflecting the biological production and habitats diversity, of Invertebrates are found in floodplain wetlands throughout the tropics. Insect groups dominate the taxa in permanent wetlands. In the temporary wetlands, many insects disperse to more permanent waters to survive dry periods. Freshwater macroinvertebrates are crucial for ecological processes, and the higher temperatures of the tropics lead to higher turnover rates of organic matter mediated through the invertebrate functional feeding groups. Much remains to be done to provide a better understanding of the distribution and ecology of aquatic tropical invertebrates, and that will lead to a more comprehensive and robust use of invertebrates to support wetland management.

In Chapter 12, Fish, Reichard (2022) outlines taxonomic, functional, and ecological diversity of tropical wetland fishes across diverse regions of the world. The variety of wetland habitats is commensurate with the diversity of fish and their many adaptations. Many of these are the result of adaptive radiation and the evolution of endemic species, often with trophic equivalents across different tropical biogeographic regions. Species diversity of any particular wetland system can, therefore, be very high, and considerably greater than wetland habitats in the temperate zones. The flood pulses inherent of many wetlands are associated with life-history strategies of the fish and, for many species, extensive migrations. Life histories of inland tropical fish range from seasonal breeding availing of the productive flood pulse resulting in high fecundity over brief periods, to all year round production involving low fecundity and intense parental care, best illustrated by the cichlids. A third broad category involves opportunists with rapid maturation rates and adaptation to exploit unpredictable availability of resources. Similar adaptive strategies are reflected in specialized feeding habits of tropical fish, often allowing species packing, where many species with similar modes of behavior can coexist because of small, but ecologically important, differences allowing for resource partitioning. In wetlands, many species can overcome periods of habitat dissection through burrowing into the mud or existing as dormant embryos.

The amphibians and reptiles of tropical wetlands are relatively much less studied than the fishes. Chapter 13, Amphibians and Squamates in Amazonian Flooded Habitats, with a Study on the Variation of Amphibian Assemblages Along the Solimões River, by Moraes et al. (2022) uses a case study of the Solimões River floodplain in Brazil, to complement more general information about the Amazonian distribution of amphibians and squamates (the latter commonly known as scaled reptiles). The flood pulse promotes high species turnover along the flooding gradient. This also increases regional species richness because several amphibians species typically found in open habitats use macrophytes for breeding and, along with several species of lizards and snakes, as refuge during high flood periods. In the Solimões River, species turnover was found to be maximum among localities in the middle reaches. As with other biotic groups in the tropics, much works remain to be done to better document species distribution and understand relationships between diversity and hydrology. For the Amazon, as in many other tropical rivers, planned hydroelectric dams may irreversibly affect the ecology of the wetlands.

The origins of the Ramsar Convention stemmed from a concern of human impact on waterfowl that needed wetlands for permanent and migratory habitat. Many tropical wetlands are vital end-points and intermediary stop-overs for migratory birds, and as seasonal breeding sites associated with flood pulses. A second case study, in Chapter 14, Management of Waterbirds in a Kalahari Pan Ecosystem, by Tarakini et al. (2022), focuses on the waterbirds in the temporary flooded “pans” of the Kalahari, encompassing the Northern Cape of South Africa through Namibia, Botswana, Angola, western Zimbabwe and Zambia, to western and southern Democratic Republic of the Congo. The landscape includes a large spatial network of endorheic pans, which are typically small, circular/oval and shallow forming small closed basins, with no outlet. Water inundation is ephemeral. Collectively known as the Kalahari pan ecosystem, these pan systems are used by about 200 bird species. A major importance of the pans is that they act as an interconnected network for the birds, and for even other less mobile organisms dispersed by wind, or the commonly evoked, hitching a ride on the feet or in the gut of the birds. The arid landscape of the pans makes them vulnerable to intense human or wildlife activities, yet also provides important ecosystem services. Working within sustainable limits of pressures can be a delicate balance, and impact on, and decline of, the pan network as a whole is an increasing threat to the birds. Increasing pressures, accentuated by climate change, include disturbance from livestock, water extraction, pollution, and subsistence level hunting. A more optimistic note is provided from increasing community-based natural resources management (such as the CAMPFIRE in Zimbabwe) in communal areas.

Chapter 15, A Snapshot of Parasites in Tropical and Subtropical Freshwater Wetlands: Modest Attention for Major Players, by Vanhove et al. (2022) deals with a special group of wetland organisms, the parasites. The opening sentence of this Preface referred to how parasites dangerous to human shaped a certain view of tropical wetlands. High mortality of early European settlers to the tropics was often attributed to "swamp fever" (an early colonial view that also largely underplayed the chronic and often lethal effect of parasites on local populations). Despite the capturing of popular imagination, investigations on the diversity of water-borne parasites and their importance for wetland ecology and health of people, animals, and ecosystems have been very much neglected. The ecology of parasites found in wetlands across all taxonomic grouping is very much understudied. This chapter makes in-roads in addressing such a deficit in providing an overview, modestly termed by the authors as a "flavor," of the parasites in tropical wetlands. Using well-chosen examples, this opens up fascinating insights to a much wider perspective of parasitology beyond the more familiar human diseases associated with wetlands and their, predominantly, insect vectors. That broader perspective leads Vanhove et al. (2022) to call for better integrated "One Health," and less narrowly viewed and anthropocentric "us versus them," perspective. Tropical wetlands can provide new models to better understand infectious and environmental hazards and open avenues for greater multidisciplinary engagement in wetland science and management. This will inform how human society uses, and modifies, tropical wetlands.

Many habitats across the globe have been disturbed by invasive species. Tropical wetlands have provided both the source and sink for such species. The impact on tropical wetlands from the alien invasive species is already clear, and with increasing global trade and climate change the risk of spread, and new impacts, will not lessen. This is the topic of Chapter 16, Impacts of Alien Invasive Species on Large Wetlands, by Pegg et al. (2022). That tropical wetlands are such important social-ecological systems make them vulnerable to disturbance that facilitates the introduction and spread of species from outside the region, sometimes from other continents. Often acting in concert with other anthropogenic impacts such as nutrient enrichment, the spread of aggressive aliens—the so-called invasive species—can dramatically change the character of a wetland and affect those dependent on it. Infamous examples are water hyacinth *Eichhornia crassipes*, water cabbage *Salviniamolesta*, Melaleuca tree *Melaleuca quinquenervia*; invertebrates golden apple snail *Pomacea canaliculata* and crayfish *Procambarus clarkii* and *Cherax quadricarinatus*; and vertebrates Nile tilapia *Oreochromis niloticus*, cane toad *Rhinella marina*, and Burmese python *Python molurus bivittatus*. Successful invasive species often exhibit traits that facilitate proliferation in novel environments. Impacts can occur across a range of biological scales: (1) genetic, (2) individual, (3) population, (4) community, and (5) ecosystem level. The damage they cause is through a variety of mechanisms related to the life-cycle and adaptability of the invasive. An impact can be direct, such as clogging waterways and outcompeting native species, or indirect through introducing diseases to native species. Once invasive species are in a wetland, removing them can be extremely difficult and costly. Many methods have been tried, often with uncertain success. Prevention is better than cure and understanding the risk, forecasting potential invaders, employing effective biosecurity measures, and responding rapidly to novel invasions are key means of management.

Building on the previous chapters, Chapter 17, Food Webs, by Cuthbert et al. (2022) introduces the importance of food webs in tropical wetlands and their relationship with hydroperiod. The trophic interactions of tropical wetlands, with frequent high diversity and high rates of species turnover and “boom-bust” dynamics, suggest that tropical wetlands are a much underutilized resource for testing food web and community ecology theories. The connectivity with terrestrial systems indicates the importance of both internal (autochthonous) and external (allochthonous) drivers of food web dynamics. The chapter introduces a range of approaches to the study of trophic interactions that are highly relevant to tropical wetlands, illustrating how better understanding of food webs of tropical wetlands can contribute to both theoretical models and, for example, how stable isotopes can assist wetland management. The spatial and temporal patterns of tropical wetland communities manifest as meta-population and community interactions. This applies across a large range of spatial scales. Gálvez et al. (2022) in Chapter 18, Metacommunity Structure and Dynamics in Tropical Wetlands, the last chapter in the Biota and Biotic Processes section, describe how these patterns, and the processes that connect them, are crucial in organizing tropical wetland communities. Better appreciation and understanding of these patterns, and connectivity across sites, are often critical for wetland conservation. This refers back to Chapter 14, Management of Waterbirds in a Kalahari Pan Ecosystem, on waterbirds and how separated sites are important for the dispersal and maintenance of regional populations. Diversity patterns for a range of taxa operating as meta-populations are facilitated or constrained by environmental variables, such that changes that affect the connection of sites within the network can be important for the entire network.

The final five chapters of the book focus on the conservation and management of tropical wetlands. An overview of the management and challenges of tropical wetlands, setting the scene for the remaining chapters, is provided in Chapter 19, Vegetated Wetlands: From Ecology to Conservation Management, by Irvine et al. (2022). This highlights the need for an integrated and realistic approach. The policies for the protection of tropical wetlands often exist in some form, and there is a wide range of extremely useful information available that can guide management. Often the key difficulties lie with national and local capacity, and the limitation that entails for the production of management plans, even for designated Ramsar sites. The majority of tropical wetlands do not have the benefit of even basic formal management planning, although much can be learnt from traditional social-ecosystem approaches. In the face of increasing pressures on wetlands, often from national food security and development aspirations, and the already presence of the magnifier of climate change, the chapter concludes with a series of recommendations for the future.

The need for effective monitoring of tropical wetlands is further developed by Greenfield (2022) in Chapter 20, Introduction to Wetland Monitoring, who defines wetland monitoring as “the assessment of the abiotic and biotic components within a wetland to assess the current integrity of the wetland system in question.” It can involve the collection and analysis of both biotic and abiotic samples, and the habitats of a wetland. A key point is for managers to decide on the key purpose of monitoring before deciding on what to monitor and the techniques to use. While there is a long history of monitoring wetlands, recent developments covered in the chapter are the use of biomarkers that assess responses of organisms to the exposure of polluting chemicals. The chapter concludes with the recommendation that monitoring programs should evolve and if the data generated are insufficient, then changes should be made with a view to adaptive management.

The use of remote sensing, and recent developments in the technology, to support management and monitoring are picked up in Chapter 21, GIS and Remote Sensing Analytics: Assessment and Monitoring, by Dube et al. (2022b). While GIS has advanced considerably the capacity to map wetlands, spectral and spatial resolutions from satellite data can limit more detailed extraction of wetlands character and status. This limitation can be overcome by using lower-altitude aerial imagery, but this is not feasible owing to the high costs for most tropical wetlands. High-resolution satellite data are available, but at a high cost, so most wetland mapping using remote sensing will have to rely on freely available datasets. The mapping of tropical wetlands, therefore, requires trade-offs between costs and availability of remote sensing data. A promising development is the recent use of integration of radar (e.g., Sentinel 1) and optical (e.g., Landsat) data for improved accuracy of mapping. Future developments will include advanced machine learning techniques, for example, artificial intelligence (AI), cloud-based and big data analytics for repeated and timely monitoring of tropical wetlands. The field is moving fast, which is good news for the monitoring of the world's wetlands.

The policy framework for the protection of tropical wetlands is provided in Chapter 22, Institutional, Policy and Legal Nexus and Implications, by Marambanyika et al. (2022), which outlines how policy, legal, and institutional discrepancies affect wetlands management and conservation. With a focus on southern Africa, it is shown how the approach to wetland protection varies across countries, even though nations signed up to the Ramsar Convention have made a commitment to wetland protection. The chapter makes key points relating to the formal and informal institutional settings that affect wetland management. The discrepancies across formal institutions can be recognized, but there is very scant literature on the link among policy, legislation, and institutional arrangements and the associated implications on wetland management at regional or basin scale. Wetlands are multifunctional systems on which many people depend, but loss and degradation often through commercial or community-led conversion to agriculture, as also illustrated in Chapter 19, Vegetated Wetlands: From Ecology to Conservation Management (Irvine et al., 2022), continue. While there is a need for regional and transboundary assessments, wetland degradation occurs mainly at the scale of individual wetlands and coordination across government departments, including transnational, is often weak. The need for coordination at local scales is also evident, illustrating the need for better connection across tiers of governance. Political interference, lack of awareness of existing policies, and competing interests can make matters more challenging at all tiers. The chapter concludes with a proposed wetland governance framework to enhance the management of wetland. This would harmonize laws that govern wetland protection, establish national wetland policies synchronized at regional level, and strengthen those institutions focusing on wetland management.

The tradition, and some of the misgivings, of modern wetland management is that, by and large, the approach to management has been led by biophysical and policy considerations. Both can be viewed as risking an overly "top-down" approach to wetland conservation and management. Policies across large parts of the world with tropical wetlands have a colonial legacy that determined institutional structures. Scientific endeavor is dominated by richer countries, with their strong academic institutions with access to resources. The world's influential scientific literature is written largely in English. At least recognizing these current realities can help develop future management of tropical wetlands. Traditionally missing in the mainstream wetland discourse has been the voice of the local communities, and their rich culture of living with and depending on wetlands. Chapter 23, Indigenous Peoples' Participation and the Management of Wetlands in Africa: A Review of the Ramsar Convention, by Laltaika (2022) ensures that this is not a gap perpetuated here, although some may perceive a single chapter on *Indigenous peoples' participation and the management of wetlands* is not enough. There are inevitably other areas and regional coverage that would merit more extensive inclusion. This provides an invitation for future research and textbooks on the subject.

The Ramsar Convention has grown to set out a framework for the conservation and "wise use" of wetlands. Attention to local knowledge and participatory approaches to management increases in the reporting and thinking in the implementation of the Convention. However, as Laltaika (2022) notes there is a "paucity of literature… examining the procedural right to participation in relation to Africa's indigenous peoples and local communities when it comes to the designation and management of Wetlands of International Importance or Ramsar Sites." This applies to different degrees across all Ramsar sites. Guided by International law, Chapter 23, Indigenous Peoples' Participation and the Management of Wetlands in Africa: A Review of the Ramsar Convention, addresses the procedural right to public participation and the right of indigenous peoples and local communities. Many indigenous peoples attribute their marginalization in terms that their way of life conflicts with the development priorities of their country. Accentuating this view is that indigenous lifestyles often transverse international political boundaries. The African Charter on Human and Peoples Rights has (re) affirmed "the right to survive as peoples, and to have a say in their own future, based on their own culture, identity, hopes and visions." In reality, this hardly features in wetland management policies. The principle has opened a debate described in the chapter, including the implications this has for the Ramsar Convention, as many wetlands indigenous people are intimately connected with wetlands. Most African countries, for example, do not recognize indigenous peoples' rights within their borders.

The collection of chapters in this volume of *Tropical Freshwater Wetlands* provides for a much needed addition to wetland and conservation resources, and brings out a number of key points and insights that will provide a consolidated body of knowledge for all those interested in the ecology and management of tropical wetlands. Many chapters identify the need for further work in tropical wetlands as a means to provide improved understanding for their conservation and management. There is certainly no shortage of important research and policy questions. Picking up that challenge provides a rich opportunity, especially for the new generations of researchers, policymakers, and wetland managers.

This can only provide better regional capacity for the protection of a natural resource that is important for everyone.

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Chapter 1

Tropical freshwater wetlands: an introduction

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Widely considered as among the most productive ecosystems on Earth, wetlands have been central for human societies throughout history. Forming as a result of a complex interplay between geomorphological, geological, and climatic conditions, wetlands are widespread and diverse environments. Wetlands are so diverse in form and function that the definition of the term "Wetland" needed to be broad enough to suitably encompass the many forms recognized as Wet Lands. To this end, wetlands are defined under the Convention on Wetlands (Ramsar and Iran, 1971) as: "*areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres*." which "*may incorporate riparian and coastal zones adjacent to the wetlands, and islands or bodies of marine water deeper than six metres at low tide lying within the wetlands*".

While this definition is suitably inclusive and perhaps the most widely cited, it is a culmination of numerous discussions, often contentious, some of which are covered in the following articles (Elliott and McLusky, 2002; Ping et al., 1992; Semeniuk, 1987; Tiner 1999). According to Semeniuk and Semeniuk (2004), the consensus on wetlands is that they are "*... an area of land in which the period of waterlogging or inundation is sufficient to develop physical and chemical responses in the soil or sediment*" and that "*the presence of such pedogenic/diagenetically altered soils, together with an abundance of water during the normal growing season, should induce colonisation by recognisable communities of biota adapted to or tolerant of such conditions*".

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1.1 Wetlands importance

Wetlands are important features in many landscapes and are often among the most productive of ecosystems, providing many of the services that society depends on (Fig. 1.1), including habitat for a myriad of wildlife. Through the provision of billions of dollars of essential services every year, these environments also contribute to national and global economies (Barbier, 2011). These valuable wetland functions are the result of their unique natural characteristics. They provide great volumes of food in the form of particulate organic matter, microbes, and plants (phytoplankton, macrophytes) that attract and are used by many animal species for part of or all of their life cycle. Dead organic matter is readily broken down in the water to form small organic particles material which are enriched and are fed on by a large variety of aquatic invertebrates (zooplankton, aquatic insects) and vertebrates (juvenile fish) that are food for larger amphibians, birds, fish, reptiles, and mammals (including humans). The many biotic components are harvested for direct consumption, or as stock for enterprise, facilitating local and even nonlocal economies. Therefore wetland degradation and loss, which generally results in loss of biodiversity, also results in loss of associated ecosystem services, with economic implications (Fig. 1.1). Such degradation

BOX 1.1 Chobe River.

Wetlands have often been important/useful landmarks and boundaries for societies. Even today, wetlands such as rivers often form boundaries between countries. Here the Chobe River serves as the natural border between Botswana and Namibia in Southern Africa (Photo by Russell Brian Tate).

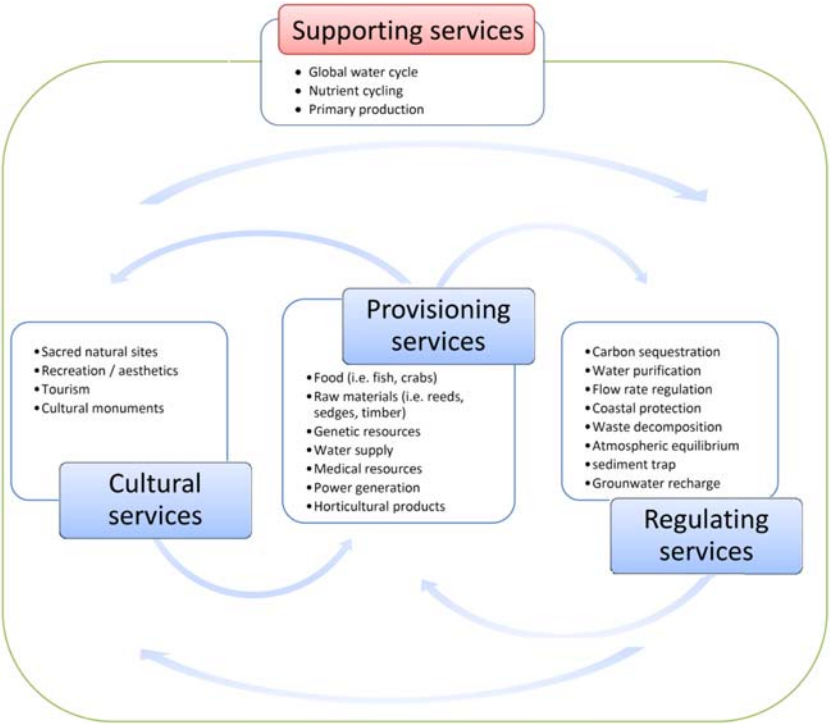

FIGURE 1.1 Ecosystem services provided by wetland ecosystems.

can even have implications for climate. Wetland microbes, plants, and wildlife form an integral part of global cycles for carbon, water, nitrogen, and sulfur, and we now know that atmospheric maintenance through moderation of climate conditions may be an additional function of wetlands (see Irvine et al., 2022, Chapter 19).

Individual wetland systems or types typically do not provide the full range of listed services. This is due to the fact that a particular wetland provides services which are determined by its characteristics and specific factors such as climate, geology, topography, and its size (Jogo and Hassan, 2010; Bassi et al., 2014). As such, prioritization of conservation and management of any one wetland/type can still lead to loss of services in nonprioritized habitats.

1.2 Wetland threats

Wetlands are dynamic and often complex ecosystems which provide a variety of beneficial services to humans and yet remain ecologically sensitive (Turner et al., 2000). Regardless of their sensitivity, wetlands are exploited and overexploitation has consequently led to degradation and loss of these ecosystems

(Skowno et al., 2019; Sievers et al., 2018). Most wetlands are under threat primarily from a variety of human activities (Gren et al., 1994; Dalu et al., 2017).

The remaining natural wetlands cover only a fraction of their original area and have been progressively declining around the world (Table 1.1) through drainage, road construction, agriculture, grazing, mining, de-vegetation, damming flow, dumping, dredging, and urban development, among others. Presently, these activities are particularly pervasive in the tropical areas, given economic development dynamics in these often low- and middle-income regions. Globally, approximately 87% of known inland wetland systems have been lost, with rates of loss having been greatest during the late 20th century (Joosten, 2010; Davidson, 2014). Major declines have also been observed in forested and tropical peatlands during this time (Joosten, 2010; Davidson, 2014). Artificial wetlands (i.e., artificial reservoirs' and rice paddies) have increased since the 1970s, but this is mostly due to conversion of natural wetlands

TABLE 1.1 Extent and area change of natural inland wetland classes.

Inland wetland	Wetland classes (million km^2)	Wetland subclasses[a] (million km^2)	Global area change (%)[b]
Peatlands	4.232		-0.97
Nonforested (bogs, mires, ferns)		3.118	+6.80
Forested		0.696	-25.32
Tropical		1.505	−28.00
Temperate and boreal		3.380	
Marshes and swamps in floodplain	2.530		
Tropical freshwater swamps		1.460	
Forested wetlands	1.170		

Light grey shading indicates no information available.

[a] *Different wetland subclasses are defined according to different criteria and do not necessarily add up to the total figure for the wetland class. The areas provided for temperate/boreal and tropical peatlands are not additive to those for nonforested and forested peatlands; rather, these are two different spatial disaggregations of all Peatlands.*

[b] *Year ranges for % area change vary between sources and wetland classes: peatlands, nonforested peatlands, forested peatlands 1990–2008, tropical peatlands 2007–15.*

Source: Modified from Davidson, N.C., Fluet-Chouinard, E., Finlayson, C.M., 2018. Global extent and distribution of wetlands: trends and issues. Marine and Freshwater Research, 69, 620–627, with permission from CSIRO Publishers.

(Davidson et al., 2018) and these homogenized environments are typically less biodiverse. For example, wetland conversion to rice−paddy fields is among the leading causes of current wetland loss in Asia, estimated at about 5000 km^2 per year (Gopal, 2013). The mounting pressures on wetlands in tropical regions of the world and the small fraction of protected wetlands call for urgent action.

Many populations of wetland dependent species are exhibiting long-term declines and are threatened with extinction based on recent assessments. The International Union for Conservation of Nature (IUCN) Red List highlighted that of the over 19,500 wetland dependent species globally, approximately 25% are threatened with extinction and about 25% and 6% of inland wetland dependent species are globally threatened and critically endangered, respectively, from over 18,000 taxa assessed (Collen et al., 2014; Ramsar Convention on Wetlands, 2018; Table 1.2). At a finer spatial scale, global threat levels of wetland dependent species vary greatly across different regions. Globally threatened freshwater taxa percentages vary between 20% and 37% across different biogeographic realms (i.e., areas with a broadly similar evolutionary history) (Collen et al., 2014), with the highest threats being recorded in the tropics (Boxes 1.3 and 1.4).

1.3 Sustainable use of the remaining wetlands

The sustainable use of wetlands and their management requires proper planning and taking into consideration of the circumstances of all affected parties (see Irvine et al., 2022, Chapter 19; Marambanyika et al., 2022, Chapter 22; Laltaika, 2022, Chapter 23). Thus further research on wetlands provides improved scientific understanding about these ecosystems and consequently helps inform improved management approaches (Ahmed, 2015). Additionally, the empowerment of all users, including landowners, through various programs and training, is crucial in planning the sustainable use of these wetlands. In turn, cooperation from all relevant stakeholders facilitates proper planning for the sustainable use of wetlands. Apart from the legislation, there are several existing programs, supported by both private and public institutions, which assist in safeguarding, rehabilitating, and restoring degraded wetlands. The majority of these programs insists on the sustainable management of wetlands, while also considering the livelihoods of surrounding communities.

Adamus and Stockwell (1983) suggested that scientists and managers dealing with wetlands should recognize three classes of wetland functions when preparing management plans, and these are:

1. hydrologic functions, such as the reduction of flood peak and groundwater recharge/exchange, shoreline, anchoring, and erosion control;
2. water quality improvement processes, which includes sediment accretion or nutrient uptake; and
3. wildlife habitat and food chain support.

BOX 1.2 Wetlands as a source of water supply and biodiversity, facilitating sustainable livelihoods.

Wetlands are a source of water supply and species diversity, fundamental to sustaining livelihoods. From top, left to right: water buffalo in Lake Kaliveli, India [Hamish Appleby, International Water Management Institute (IWMI)]; Mabamba Bay, Kenya (Photo by Kenneth Irvine); water crossing and transportation of cassava in Várzea floodplains, Mamirauá Sustainable Development Reserve, Central Amazônia (Photo by Jochen Schöngart); *Kingsleya* crabs in Várzea floodplains, Mamirauá Sustainable Development Reserve, Central Amazônia (Photo by Jochen Schöngart); cormorant *Nannopterum brasilianus* eating the red-bellied piranha *Pygocentrus nattereri* in Várzea floodplains, Mamirauá Sustainable Development Reserve, Central Amazônia (Photo by Jochen Schöngart); gardening in Sambandou wetlands, Vembe Biosphere Reserve, South Africa (adapted from Dalu and Chauke, 2020 under Creative Commons Attribution 4.0 International License); man with his harvest of *Lotus* flowers from a Sri Lankan wetland (Photo by Hamish Appleby, IWMI); fish market with fish being dried for sale in Kenya (Photo by Kenneth Irvine); women fishing in a wetland in Nepal (Photo by Andrew Reckers, IWMI).

Whereas, Stevens and Vanbianchi (1993) emphasized the development of a wetland inventory for proper management and suggested that this should mainly include data on the presence, extent, condition, characteristics, and functions of wetlands within a selected area. Such data would aid in documenting the wetland status in a given area and support

TABLE 1.2 **Summary of the global threat status (IUCN Red List) of different wetland dependent taxa.**

Wetland dependent taxon	**Globally threatened (%)**[a]	**Critically endangered (%)**
Lycopods and ferns[b]	36***	Unknown
Freshwater vascular plants[c]	17**	4*
Seagrasses	16**	0*
Mangroves	17**	3*
Corals	33***	1*
Nonmarine molluscs[c]	37***	10**
Crabs	32***	5*
Crayfish	32***	10**
Freshwater shrimp	28***	4*
Dragonflies	8*	1*
Fish		
Freshwater fish	29***	5*
Coral reef fish (parrotfish, surgeonfish only)	2*	0*
Amphibians	35***	9*
Reptiles		
Freshwater reptiles	40***	11**
Marine turtles	100***	33***
Waterbirds	18**	3*
Mammals	23**	3*
Wetland dependent megafauna (fish, reptiles, mammals >30 kg)	62***	27***

[a] *IUCN Red List status: Critically endangered, endangered, vulnerable.*
[b] *For Europe only.*
[c] *For some geographic regions only; global threatened colors: *** red > 25%, ** orange 10%–25%, and * green < 10% of the global threatened taxa.*
Source: Adapted from Ramsar Convention on Wetlands, 2018. Global Wetland Outlook: State of the World's Wetlands and Their Services to People. Ramsar Convention Secretariat. Gland, Switzerland.

decisions on more appropriate management approaches. However, Chuma et al. (2012) and Horwitz et al. (2012) suggested that in wetland management decisions, the human communities' connection with the wetlands also need to be taken into consideration and that the human community

BOX 1.3 Examples of wetland degradation from the (sub)tropical regions of the world.

Clockwise, from top right: wetland draining in Intunjambili Wetland, Matobo District, Zimbabwe (Photo by Thomas Marambanyika); rice farming in Pakistan (Photo by Faseeh Shams, IWMI); illegal artisanal mining, Taka forest, Chimanimani, Zimbabwe; fertilizer application to a rice farm in Nepal (Photo by Jim Holmes, IWMI); invasive nonnative water hyacinth *Eichihornia crassipes* and Kariba weed *Salvinia molesta* in Kenya (Photo by Kenneth Irvine); sand mining in Sambandou wetlands (sourced from Dalu and Chauke, 2020).

cannot be separated from the wetlands because of their dependency on services provided by these ecosystems for their well-being. They further suggested that wetland management processes should strive to understand the human communities' situation, hopes, and wishes, thereby sustaining their livelihoods.

1.4 Ramsar wetland classification

The Convention on Wetlands (http://www.ramsar.org) is "*...the intergovernmental treaty that provides the framework for the conservation and wise use of wetlands and their resources*." Also known as the Ramsar Convention, this collection of contracting parties has done much for the international recognition of wetland importance and protection. The mission of the International Convention on Wetlands is for "the conservation and wise use of all wetlands through local and national actions and international cooperation, as a contribution towards achieving sustainable development throughout the world." Under the Ramsar Convention, a classification system for wetland types was developed, providing a broad framework for wetland identification and management. Any collection of work on wetlands would not be complete without mention of this classification system. The "Ramsar Classification System for Wetland Type as approved by Recommendation 4.7 and amended by Resolution VI.5 of the Conference of the Contracting Parties" is discussed in the following sections.

1.4.1 Marine/coastal wetlands

A—Permanent shallow marine waters in most cases less than 6 m deep at low tide; includes sea bays and straits.
B—Marine subtidal aquatic beds; includes kelp beds, sea−grass beds, tropical marine meadows.
C—Coral reefs.
D—Rocky marine shores; includes rocky offshore islands, sea cliffs.
E—Sand, shingle, or pebble shores; includes sand bars, spits, and sandy islets; includes dune systems and humid dune slacks.
F—Estuarine waters; permanent water of estuaries and estuarine systems of deltas.
G—Intertidal mud, sand, or salt flats.
H—Intertidal marshes; includes salt marshes, salt meadows, saltings, raised salt marshes; includes tidal brackish and freshwater marshes.
I—Intertidal forested wetlands; includes mangrove swamps, nipah swamps, and tidal freshwater swamp forests.
J—Coastal brackish/saline lagoons; brackish to saline lagoons with at least one relatively narrow connection to the sea.
K—Coastal freshwater lagoons; includes freshwater delta lagoons.
Zk(a)—Karst and other subterranean hydrological systems, marine/coastal.

1.4.2 Inland wetlands

L—Permanent inland deltas.
M—Permanent rivers/streams/creeks; includes waterfalls.

N—Seasonal/intermittent/irregular rivers/streams/creeks.
O—Permanent freshwater lakes (over 8 ha); includes large oxbow lakes.
P—Seasonal/intermittent freshwater lakes (over 8 ha); includes floodplain lakes.
Q—Permanent saline/brackish/alkaline lakes.
R—Seasonal/intermittent saline/brackish/alkaline lakes and flats.
Sp—Permanent saline/brackish/alkaline marshes/pools.
Ss—Seasonal/intermittent saline/brackish/alkaline marshes/pools.
Tp—Permanent freshwater marshes/pools; ponds (below 8 ha), marshes, and swamps on inorganic soils; with emergent vegetation water-logged for at least most of the growing season.
Ts—Seasonal/intermittent freshwater marshes/pools on inorganic soils; includes sloughs, potholes, seasonally flooded meadows, sedge marshes.
U—Nonforested peatlands; includes shrub or open bogs, swamps, fens.
Va—Alpine wetlands; includes alpine meadows, temporary waters from snowmelt.
Vt—Tundra wetlands; includes tundra pools, temporary waters from snowmelt.
W—Shrub-dominated wetlands; shrub swamps, shrub-dominated freshwater marshes, shrub carr, alder thicket on inorganic soils.
Xf—Freshwater, tree-dominated wetlands; includes freshwater swamp forests, seasonally flooded forests, wooded swamps on inorganic soils.
Xp—Forested peatlands; peatswamp forests.
Y—Freshwater springs; oases.
Zg—Geothermal wetlands.
Zk(b)—Karst and other subterranean hydrological systems, inland.

1.4.3 Human-made wetlands

1—Aquaculture (e.g., fish/shrimp) ponds.
2—Ponds; includes farm ponds, stock ponds, small tanks; (generally below 8 ha).
3—Irrigated land; includes irrigation channels and rice fields.
4—Seasonally flooded agricultural land (including intensively managed or grazed wet meadow or pasture).
5—Salt exploitation sites; salt pans, salines, etc.
6—Water storage areas; reservoirs/barrages/dams/impoundments (generally over 8 ha).
7—Excavations; gravel/brick/clay pits; borrow pits, mining pools.
8—Wastewater treatment areas; sewage farms, settling ponds, oxidation basins, etc.
9—Canals and drainage channels, ditches.
Zk(c)—Karst and other subterranean hydrological systems, human-made.

This broad classification system highlights the diversity of wetland types, and considering that threats to these ecosystems are as diverse as the wetlands themselves, this gives some insight into why managing wetlands can be challenging. Not surprisingly, this diversity also presents some challenges when

BOX 1.4 Global assessment of inland wetland conservation status (Reis et al., 2017, with permission from CSIRO Publishing).

The total global inland seasonal wetlands cover approximately 6.1% of the Earth's land surface (excluding Antarctica), with 88.7% of these being unprotected. Among the 11.3% of the globally protected wetlands, 9.7% are within the IUCN categories I–VI, including 7.1% in the more strictly protected categories I–IV (i.e., areas of stricter protection) and 2.7% in the categories V–VI (i.e., areas that allow economic activities). The remaining 1.5% are designated as Ramsar sites (Table B1.4). It is important to note that inadequate consideration of the freshwater ecosystems ecological functioning when designing terrestrially focused protected areas could compromise the effectiveness of freshwater ecosystems conservation efforts and wetlands in particular (Pittock et al., 2015).

(*Continued*)

TABLE B1.4 Total wetland area summary highlighting the total wetland in protected areas (PA), and the percentage of wetland protection in each geographical unit.

Geographic unit	Total wetland area (km^2 × 10^6)	Total wetland in PA (km^2 × 10^6)	Total % of wetland protection	% of wetland protection per category of PA		
				IUCN I–IV	IUCN V–VI	Ramsar
South America	0.89	0.16	17.82	7.17	9.09	1.56
North America	2.46	0.30	12.24	9.30	0.09	2.00
Central America	0.04	0.01	20.30	14.87	2.82	2.62
Africa	0.74	0.09	12.88	6.18	3.35	3.35
Europe	0.75	0.11	14.93	7.87	4.63	2.42
Asia	4.11	0.33	8.01	5.03	2.26	0.72
Oceania	0.17	0.03	15.49	10.63	3.58	1.28

Source: Adapted from Reis, V., Hermoso, V., Hamilton, S.K., Ward, D., Fluet-Chouinard, E., Lehner, B., et al., 2017. A global assessment of inland wetland conservation status. Bioscience, 67, 523–533.

BOX 1.4 (Continued)

There is a strong association between wetland distribution within a particular landscape and human occupation, with the most significant threats to wetlands being associated with direct or indirect human use of these areas (Gibbs, 2011). Human pressure in wetlands varies widely among geographical units (Fig. B1.4). The low human influence for North America can be attributed to the large area of boreal and Arctic wetlands in Canada and Alaska (Reis et al., 2017).

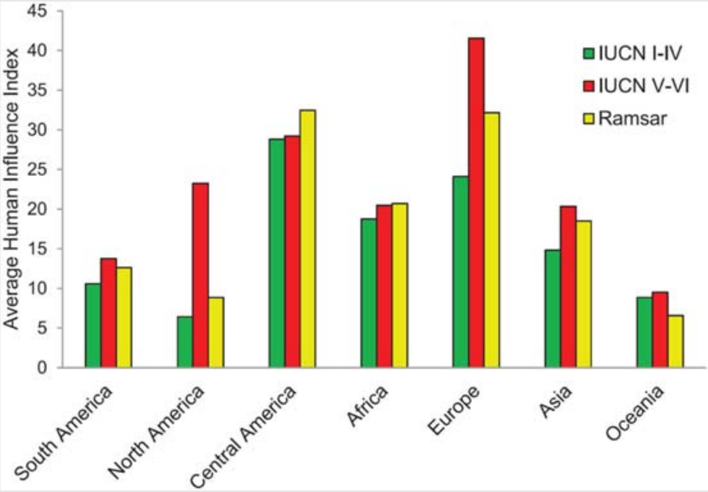

FIGURE B1.4 Human pressure in wetlands within different categories of protected areas, as is indicated by the average Human Influence Index (0, lowest; 100, highest human influence).

attempting to collate relevant information on wetlands, such as we have endeavored to do here. While not the first book on wetlands and likely not the last, *Fundamentals of Tropical Freshwater Wetlands* is among the first to focus exclusively on freshwater wetlands in tropical/subtropical regions (Box 1.5).

1.5 Book structure and content

During the conceptualization stage, the editors were eager to develop a book intended as a practical guide and important educational tool for researchers, managers, and students interested in tropical/subtropical wetlands. It was ultimately decided that the book would deal with natural freshwater wetlands typically found in tropical and subtropical regions. This meant that we needed to exclude marine/estuarine systems, lakes, reservoirs, and other man-made wetlands from the content. As it relates to the *Ramsar Classification System for Wetland Type* presented above, this meant that the book is largely focused on the *Inland Wetland* types. One of the main justifications for the exclusion of certain wetlands types was that there are already great collections of work that

BOX 1.5 Examples of (sub)tropical wetlands from around the world.

Clockwise, from top right: white-water flooded habitats (várzea) at the margin of the Solimões River, western Brazilian Amazonia (Photo by Leandro J.C.L. Moraes); a temporary wetland in the southeast of Zimbabwe, Southern Africa (Photo by Luc Brendonck); Reitboekvlei pan in Northern Kruger National Park, South Africa (Photo by Tatenda Dalu); Nwambi pan in Northern Kruger National Park, South Africa (Photo by Tatenda Dalu); a swamp wetland in a forest in Cameroon, West Africa (Photo by Russell Brian Tate); a swamp habitat from the Kota Damansara Community Forest, Malaysia (Photo by Cyren Wong Zhi Hoong).

deal with these systems, as are there excellent books dealing with wetlands in general, although focused mainly on temperate regions (e.g., Finlayson et al., 2018; Dennison and Berry, 1993; Wetzel, 2001; Finlayson et al., 2016; Perillo et al., 2018). Fig. 1.2 outlines the wetlands of the world, according to

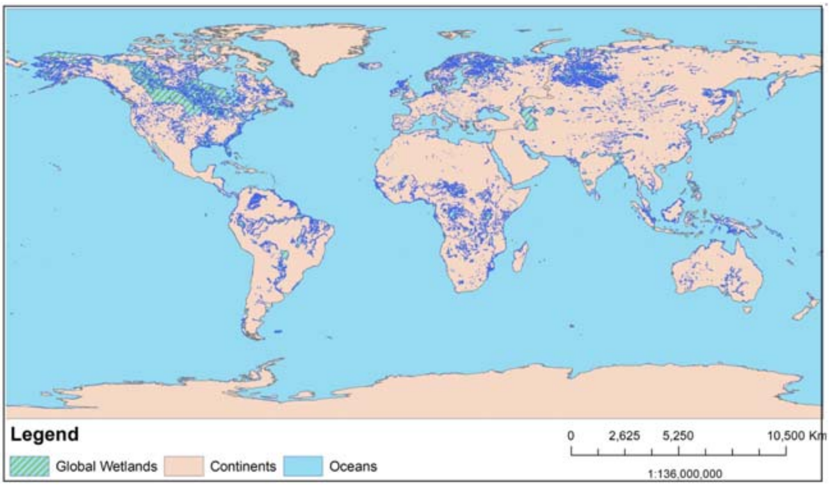

FIGURE 1.2 The Ramsar Wetland Systems of the world. Projection: WGS 84 and data used to create the map were sourced from UNESCO Intergovernmental Hydrological Programme.

the UNESCO Intergovernmental Hydrological Programme and from this figure it is clear that Northern Hemisphere, nontropical systems are well represented, and this is likely at least partly a result of more intensive research in these regions. Knowledge and data generation has been largely skewed toward high latitude wetland systems, particularly in the Northern Hemisphere. While much work has been directed toward wetlands in tropical environments, it is highly likely that as effort increases, the increased inclusion of tropical wetlands as areas of conservation concern will follow.

The next step involved determining the regions to be included as "tropical and subtropical", although this was not as straightforward as one may think. According to the Cambridge Dictionary, the word *Tropics* can be defined as "*the hottest area of the earth, the area on either side of the equator reaching to 23.5 degrees to the north and south*" while the word *Tropical* is defined as "*of or characteristic of the tropics (=the hottest area of the earth)*" (https://dictionary.cambridge.org/). These definitions explicitly place temperature centrally when categorizing "tropical" environments. The Köppen–Geiger climate classification system (see Fig. 1.3), on the other hand, incorporates both temperature and precipitation in its classification, separating the broad descriptors as Tropical, Arid, Temperate, Cold, and Polar climate types, with each further subcategorized (Peel et al., 2007). The updated Köppen–Geiger climate map relied on "*...observed data, rather than experience...*," in order to "*...minimise the number of subjective decisions*" wherever possible (Peel et al., 2007). The result is a complex, useful, and widely employed classification system in teaching and

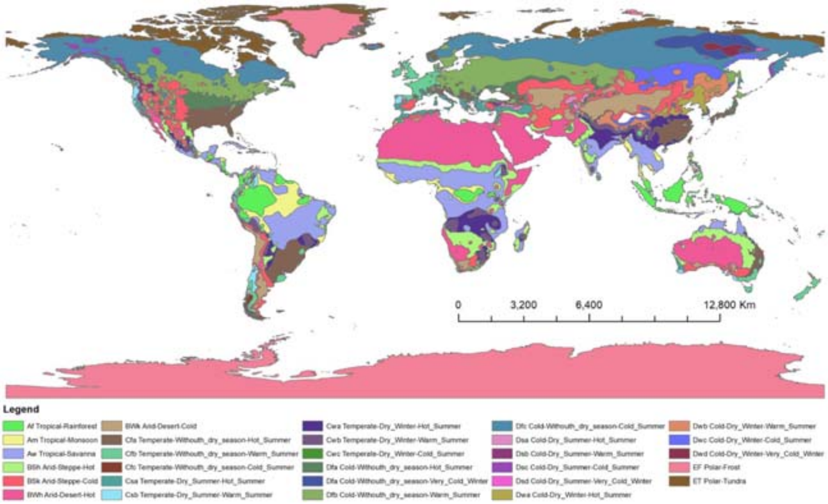

FIGURE 1.3 Modified Koppen–Geigher climate type map of the world. Projection: GCS Bessel 1841.

research. However, with regard to what is explicitly classified as "tropical" using this system, the criteria are that temperature of the coldest month is greater or equal to 18°C, with subcategories (Tropical Rainforest, Tropical Monsoon, and Tropical Savannah) including "*precipitation of the driest month*" and "*mean annual precipitation*." Although present in the original work by Köppen (Köppen 1884), from which the Köppen–Geiger climate classification system has been extensively modified, the "subtropical" designation no longer appears explicitly in the revised system. As such, the strict Köppen–Geiger classification of "tropical" was not followed for this book.

Another classic and widely used system worth mentioning is that of the life zone chart developed by Holdridge (1967) (Fig. 1.4). The three axes used for the barycentric division of the life zones in this chart are "*Precipitation*," "*Biotemperature*," and "*Potential Evapotranspiration*." The life zones are also overlain with the indicators "*Humidity Provinces*," "*Latitudinal Regions*," and "*Altitudinal Belts*." The system has been shown to be particularly reflective of tropical vegetation zones, Mediterranean zones, and boreal zones. This system does, however, still designate drier regions as "*Subtropical/Tropical*" if they fall within the lower latitudes. There are other such climate classification systems, many of which are covered in key reviews (e.g., Sanderson, 1999; Essenwanger, 2001). It is clear that large global patterns exist and that the development of categorization systems can be highly useful for teaching and research purposes. But as outlined in the philosophy behind

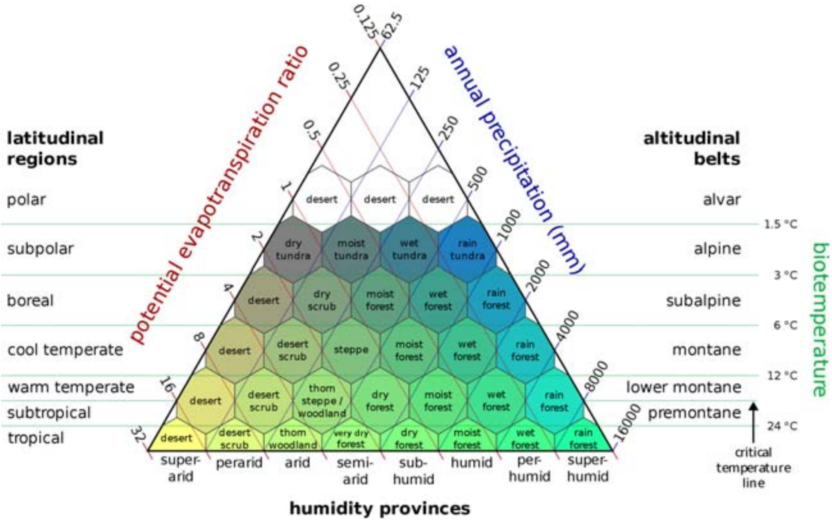

FIGURE 1.4 The modified life zone chart originally developed by Holdridge (1967). *Color image acquired from https://en.wikipedia.org/wiki/Holdridge_life_zones#/media/File:Lifezones_Pengo.svg. Created by Peter Halasz under CC BY—SA 2.5.*

the construction of the Köppen—Geiger climate map, data are key. As such, rather than insisting on the adoption of any one broad system of classification for areas deemed as "tropical" or "subtropical" for this book, we opted to allow the chapter authors freedom to explore topics within their own paradigms in this regard. As the denizens of data in their respective fields, we were confident that local case studies, general patterns, and gap identification across chapters would benefit from this less prescriptive approach.

This volume on *Fundamentals of Tropical Freshwater Wetlands* comprises a collection of 23 chapters, covering a range of relevant topics and authored by specialists working in tropical freshwater environments. While diverse and voluminous, the book is by no means comprehensive. Projects of this nature often involve compromise at various stages from conceptualization through to production, with this volume being no exception. The book does, however, provide considerable coverage of components typically regarded as important in wetland science and management, within the tropical context. As such, we trust the book will be well received by our target audience and hope that it inspires future work, potentially even addressing any gaps and biases associated with this volume. Following this introductory chapter, the book has been organized into three themed sections. The first section covers the abiotic processes theme for tropical wetlands (in order of appearance—Job and Sieben, 2022; Deemy et al., 2022a, b,c; Moyo, 2022). The second section deals with biota (in order of appearance—Piedade et al., 2022; Dalu et al., 2022; Brendonck et al., 2022a,b; Dube et al., 2022a,b; Reichard, 2022; Moraes et al., 2022; Tarakini et al., 2022; Vanhove et al., 2022) and biotic processes (in order of appearance—Pegg et al., 2022; Cuthbert et al., 2022; Gálvez et al., 2022). The final section is a compilation of chapters under the theme of monitoring, conservation, and management (in order of appearance—Irvine et al., 2022; Greenfield, 2022; Dube et al., 2022a,b; Marambanyika et al., 2022; Laltaika, 2022). Chapter content has been overviewed in the Preface section by Kenneth Irvine (Box 1.6).

BOX 1.6 Examples of charismatic fauna associated with (sub)tropical wetlands from around the world.

Clockwise, from top right: a male dragonfly (*Trithemis aurora*) from the Kota Damansara Community Forest, Malaysia (Photo by Cyren Wong Zhi Hoong); a white-lipped floodplain snake (*Lycodonomorphus obscuriventris*) from Banyani pan, Northern Kruger National Park, South Africa (Photo by Chad Keates); a tadpole shrimp *Triops granarius* from a temporary wetland in Save Conservancy, Zimbabwe (Photo by Luc Brendonck); a toad (*Rhinella margaritifera*) perched on herbaceous vegetation in the wetlands of the lower Juruá River, western Brazilian Amazonia (Photo by Leandro J.C.L. Moraes).

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Section 1

Abiotic properties and processes

Chapter 2

Factors controlling wetland formation

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2.1 Introduction

Wetlands form across a wide range of landscapes in response to landform development over geologically long timescales (McCarthy et al., 1997; Tooth et al., 2002; Ellery et al., 2009). The interaction of climate, geology, and geomorphic processes provide the framework and drivers for multiple local hydrological, physiochemical and biotic interactions (De-Campos et al., 2013; Fryirs et al., 2017; Lisenby et al., 2019; Grenfell et al., 2019).

The incorporation of geomorphic perspectives of wetland origin can improve our ability to interpret and predict the natural capacity of different types of wetland to undergo change over time, and complement the assessment of wetland ecological function (Ellery et al., 2009; Fryirs et al., 2017; Lisenby et al., 2019; Grenfell et al., 2019; Wasserman and Dalu, 2022, Chapter 1). This chapter offers a preliminary application of research from the last 20 years, largely on wetlands in drylands, to the range of geologic and landscape settings and geomorphic modes of formation of wetlands in tropical regions.

2.2 Climate

Wetlands exist where there is a local, near-surface water balance for all or part of the year (Mitsch and Gosselink, 2000; Ellery et al., 2009), and therefore, are widespread in high rainfall regions, with an excess of water available in the landscape, such as within the Intertropical Convergence Zone. In terms of Köppen-Geiger climate zones (Kottek et al., 2006), areas along the equator that support tropical rainforest (Af), tropical wet savannah (Aw), and monsoonal (Am) climates (Fig. 2.1) are conducive to wetland development.

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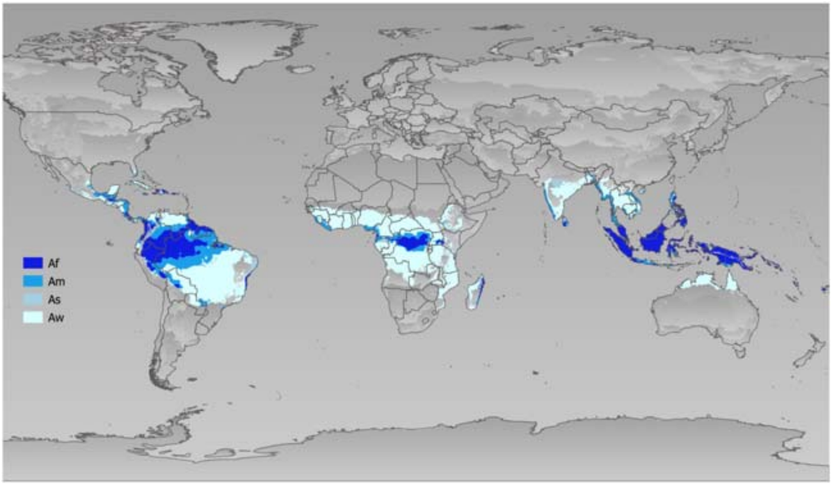

FIGURE 2.1 Köppen-Geiger tropical climate distribution and extent (Af = tropical rainforest; Am = tropical monsoon; Aw = tropical savanna, wet, and As = tropical savanna, dry). *Based on Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World map of the Koppen-Geiger climate classification updated. Meteorologische Zeitschrift, 15, 259–263, vectorized by GeoAfrikana.*

In Northern Australia, characteristic of a wet savannah climate, average annual rainfall is around 1500 m in the Kakadu region. Approximately 90% of rainfall is concentrated in a distinct wet season, inundating floodplains and other wetlands, and this is followed by extreme temperatures and high evaporative loss during the dry season, causing many wetlands to dry out seasonally (Cook, 2004). In Western and Central Africa, extensive tropical rainforest is interspersed with tropical wet savannah and limited areas supporting a monsoonal climate (Fig. 2.1). Although rainfall and temperature are relatively constant, the tropical rainforest still supports distinctive flooded and dry seasons, with water levels accordingly fluctuating markedly. These regions achieve average annual rainfall up to 1500 mm in the central highlands and up to 2000 mm in the Congo basin. South and Central America similarly support extensive tropical rainforest and tropical monsoon climate regions (Fig. 2.1), with large areas of tropical savannah that have well defined dry (beginning of April to end of August) and rainy (beginning of September to end of March) seasons, with an associated 7–10 m change in floodplain water levels between seasons. Average annual rainfall is around 1400 mm in the Pantanal region and up to 2200 mm in the Amazon basin. Malaysia largely presents a monsoonal and tropical rainforest climate. It has the highest average rainfall of all the tropical regions, ranging from just under 3000 mm in some regions to higher than 3000 mm in others, and with relative humidity remaining around 60% for most of the year (Page et al., 2004). Given the high rainfall, approximately four-fifths of the peninsula of Malaysia is estimated to be rainforest or wetland (Kent, 2019).

While the amount of rainfall a climate produces determines how much water there is in the landscape, this water finds its way to a wide variety of lakes, shallow depressional wetlands, rivers, and river-associated wetlands and groundwater (Winter, 1992; Sieben et al., 2021). The range in topographic settings in tropical regions (Figs 2-4) exert a significant influence on wetland morphology and on water moment through the catchment to the wetland. The climate in mountainous areas attracts more cloud formation and higher precipitation due to orographic effects. In South America, for example, the increased water levels during the flood season of the downstream Amazon basin are largely a result of rainfall arising in the Andean highlands (Ellison, 2004). Water has shaped the landscape over millennia, carving valleys and transporting and depositing sediment (Knighton, 1998; Ellery et al., 2009) and influencing landscape and within wetland gradient (Ellery et al., 2009; Grenfell and Ellery, 2009).

Wetlands are low energy environments in low gradient topographic basins, plains and valley floors, and it follows, zones of deposition characterised by net accumulation of sediment and water, and should not typically occur on steep slopes. However, abrupt slope breaks found in landforms of escarpment and steep slopes often create environmental conditions suitable for the discharge of subsurface water which leads to seepage and the formation of wetlands (Montgomery and Dietrich, 1988; Stein et al., 2004). These situations are supported by the presence of a geological substrate with stratified layers or planar surfaces and landforms with slope breaks which facilitate groundwater seepage to the surface. In addition to groundwater, shallow subsurface soil water flowpaths may return to the surface driven by gravity, changes in underlying geology and soil texture within the soil profile and to contribute to slope seepage wetlands (Winter, 1992; Kuenene et al., 2011, 2013; Van Tol et al., 2011).

2.3 Macro-scale controls on wetland formation

Characteristic landforms of the African continent include widespread volcanic activity, as well as rift valleys, subsided basins and uplifted domes resulting from tectonic activity (Moucha and Forte, 2011; Burke, 1996). The western arm of the East African Rift System (supporting Lake Malawi, Lake Tanganyika, and Lake Kivu), and eastern arm (extending from Zambia in the south, throughout Kenya to Lake Turkana in the north) (Fig. 2.2), transect an anomalously high-elevation plateau, which itself distinguishes the continent. The high-elevation plateau and volcanic activity are at the broadest scale attributed to be a response to the upwelling more than 30 million years ago of the African superplume (Moucha and Forte, 2011). This region supports the watershed divide of the Congo and Nile rivers (Fig. 2.2) with the

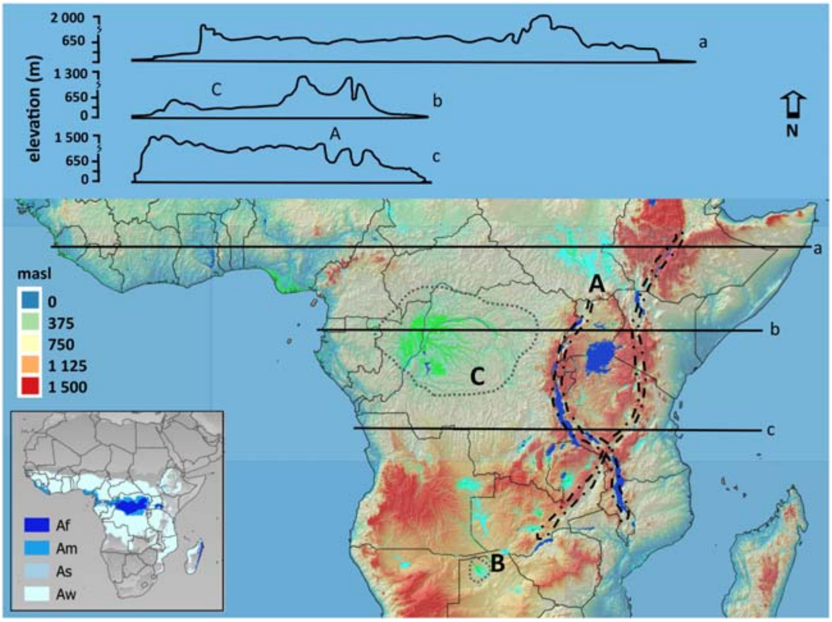

FIGURE 2.2 Generalized topography of the African continent showing (A) East African Rift System (dashed lines), (B) Cuvette Centrale and (C) Okavango Delta. Major wetlands in green (predominantly forested wetland, both peat and non-peat) and light blue (predominantly herbaceous, both peat and non-peat) and lakes (dark blue), *from Gumbricht, T., Román-Cuesta, R.M., Verchot, L.V., Herold, M., Wittmann, F., Householder, E., Herold, N., Murdiyarso, D., 2017. An expert system model for mapping tropical wetlands and peatlands reveals South America as the largest contributor. Global Change Biology. 10.1111/gcb.13689.*

equatorial uplands of Uganda, Rwanda, and Burundi averaging 1500 m asl, mountain peaks reaching to 5100 m asl, and erosional, sediment-laden rivers falling away to the Cuvette basin which extends west of the watershed divide and the Sudd River lowlands (380–450 m asl) in South Sudan (Daly et al., 1992) (Fig. 2.2).

The overall topography of tropical South America is characterized by the Andean Mountain Chain traversing Venezuela, Columbia, Ecuador, Peru, and Bolivia along the western length of the continent, falling away to an overall low gradient over much of the remainder of the South American tropical region. Central America is more mountainous overall with extensive lowlands occurring mostly in the Yucatan peninsula (Fig. 2.3). With elevations reaching to more than 6000 m in places, the Andes at times form two or three parallel ranges (cordillera) bridged by high altitude interplateau areas, at 3500–4500 m asl, supporting diverse wetlands, lakes, and saline pans. The gently rolling plateaus occur at elevations ranging from 500 to 1700 m asl (Fig. 2.3). Wetlands in these upland plateaus are predominantly

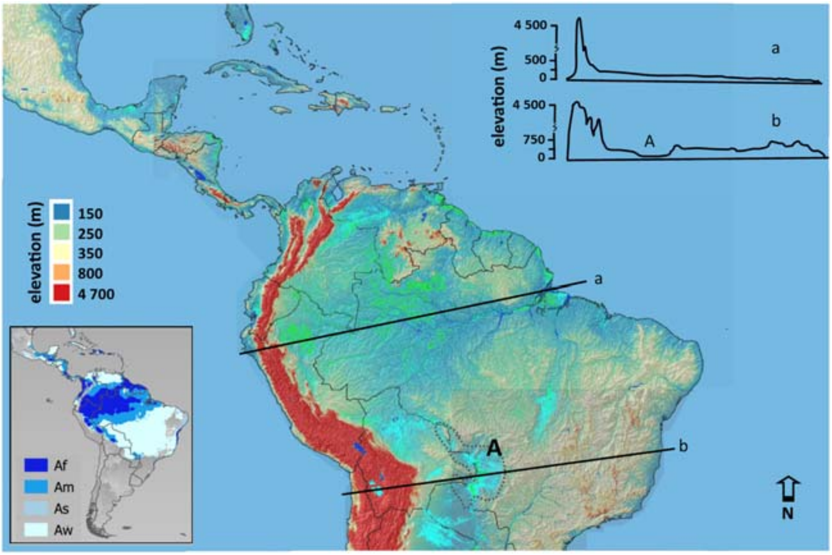

FIGURE 2.3 Generalized topography of Central and South America showing (A) Pantanal. Major wetlands in green (predominantly forested wetland, both peat and non-peat) and light blue (predominantly herbaceous, both peat and non-peat) and lakes (dark blue), *from Gumbricht, T., Román-Cuesta, R.M., Verchot, L.V., Herold, M., Wittmann, F., Householder, E., Herold, N., Murdiyarso, D., 2017. An expert system model for mapping tropical wetlands and peatlands reveals South America as the largest contributor. Global Change Biology. 10.1111/gcb.13689.*

linked to the existence and perenniality of watercourses, groundwater recharge and headwater wetlands (Ellison, 2004) (Fig. 2.3).

South-East Asia presents a complex topography with several continental plates that are mostly occupied by islands. Malaysia, located on the Sunda shelf and is tectonically inactive, supports rocks dating from 540 million years ago, mostly sedimentary. Mountain ranges in Malaysia were formed through orogenesis beginning in the Mesozoic era. A generalized topography of South-East Asia, and in particular Malaysia, indicates a series of mountain ranges rising abruptly from wide, flat coastal plains (Fig. 2.4). The highest peaks range from 2190 m to over 4100 m at Mt Kinabalu, the highest point in Malaysia. Rivers flowing down steep gradients from the high altitudes cut deep gorges, but on reaching the coastal flats they lose energy, slow, and spread out.

2.4 Fluvial forms and processes

Floodplain wetlands are strongly influenced by their inflowing rivers, as well as their wider catchments, from which they receive water as well as dissolved and suspended material, and with which they exchange organisms (Junk, 2002; Deemy et al., 2022), Chapter 3). Levels of weathering and erosion within the

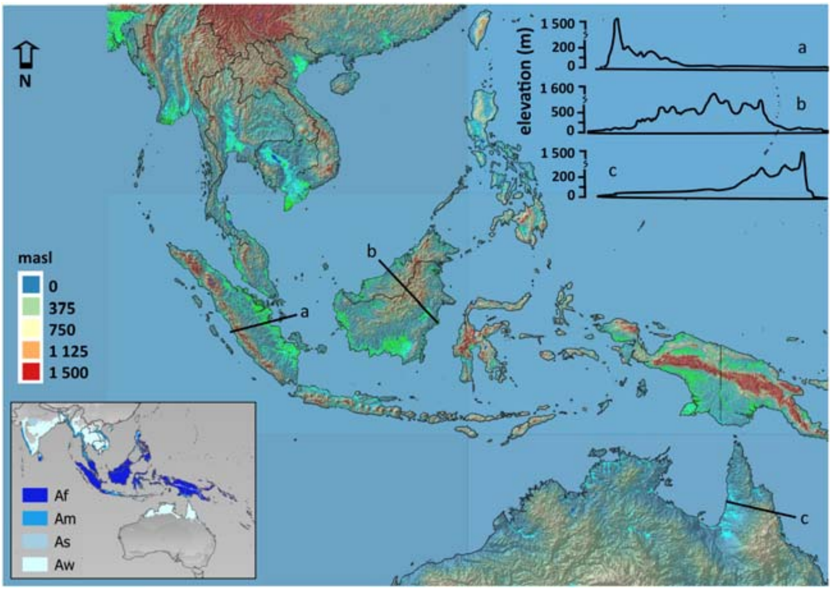

FIGURE 2.4 Generalized topography of South-East Asia and Australia. Major wetlands in green (predominantly forested wetland, both peat and non-peat) and light blue (predominantly herbaceous, both peat and non-peat) and lakes (dark blue), *from Gumbricht, T., Román-Cuesta, R.M., Verchot, L.V., Herold, M., Wittmann, F., Householder, E., Herold, N., Murdiyarso, D., 2017. An expert system model for mapping tropical wetlands and peatlands reveals South America as the largest contributor. Global Change Biology. 10.1111/gcb.13689*

catchment, and variations in catchment connectivity, drainage density and land surface properties, can trigger sediment and biogeochemical cascades, shift river channels or in-channel sediment accumulation that can block outflow and impound water (Grenfell et al., 2009a,b, 2019) and thus shape wetland development (Ellery et al., 2012, 2016). Such geomorphic developments have a great potential to influence wetland type, structure, and function over timescales of decades to millennia (Grenfell et al., 2009a; Grenfell et al., 2009b, 2010, 2019; McCarthy et al., 2011; Ellery et al., 2012).

Base level control, such as sea level or local bedrock outcrops, is widely acknowledged to influence river form (Schumm, 1979; Knighton, 1998) and this has been expanded to wetlands by Tooth et al. (2004), who describe the influence of local bedrock outcrops on the formation of floodplain wetlands where they are located upstream of erosion-resistant dolerite dykes or sills. In these systems, the authors describe excess energy generated within rivers blocked by the erosion-resistant dolerite geology. Unable to flow unimpeded downstream or to cut vertically, river energy was found to laterally plane and shape the valley upstream of the rock barrier, over long timescales ultimately producing a broad, low relief, river valley conducive to supporting extensive wetlands.

Many wetlands in Africa's elevated highlands occupy wide valleys developed on more erodible lithology, occurring upstream of deep and narrow valleys which overlay more resistant lithology (Lidzhegu et al., 2020). Lidzhegu et al. (2020) describe lateral planning during the development of the Kafue floodplain in Zambia, which has a sinuous and low gradient (0.1%) river channel slope and is located on a wide valley overlaying Quaternary sedimentary rocks.

The process of lake and wetland formation due to accumulated sediment blocking river tributaries, also frequently associated with the initiation of peat accumulation and wetland formation, has been described for Lake Nuga-Nuga in Australia (Finlayson and Kenyon, 2007), the Amazon basin (Neller et al., 1992), and for multiple lakes in Papua New Guinea (Chambers, 1987). During flood events, deposition of sediment is focused along the river channel leading to development of natural levees adjacent to the channel. This, combined with sediment-laden inflow leads to the river becoming elevated relative to the rest of the floodplain (Grenfell et al., 2008, 2010; Ellery et al., 2012), creating a depression for lake or wetland formation in the blocked valley behind the levee. With the power of incoming tributary streams reduced, sediment begins to accumulate in the depression created within the tributary, and over time, peat may form in these permanently wet areas (Grenfell et al., 2010; Ellery et al., 2012). Wetlands associated with the Nyaborongo River in Rwanda appear to be similarly driven by a strongly interdependent relationship of sediment and hydrology. The Mugesera/Rweru complex includes more than eight lakes along the Nyabaronga/Akagera River, with the largest being Lake Mugesera at 4000 ha (Fig. 2.5). Dense papyrus vegetation, in this case an ecosystem

FIGURE 2.5 Blocked valleys leading to lake formation, and floodplain wetland within the Mugesera/Rweru complex, Nyabarongo River, Rwanda.

engineer (Ellery et al., 1990, 1995) amplies the geomorphic processes at play on the mainstem river, colonising the open water in the tributary rivers as they join the Nyaborongo and further facilitating sediment deposition thereby performing a key role in the origin and sustained functioning of the lake itself (Projet de Gestion Integree des Ecosystemes Critiques IMCE, 2008; Piedade et al., 2022, Chapter 7).

2.5 Nested spatial scales

The relationship between landscape controls and wetland types soccurs at a range of spatial scales, spatially nested within each other (Fryirs et al., 2017; Grenfell et al., 2019). Understanding and identifying these nested hierarchies of process and form provides essential insight into wetland structure, function and dynamics for management (Grenfell et al., 2019). The Okavango Delta in Botswana, for example, has formed on a subsiding half-graben structure which has provided long-term accommodation space for water and sediment to accumulate and thus ensured the persistence of this system (McCarthy et al., 1997; McCarthy, 2013). Subsequent to the formation of the tectonic depression, fluvial processes transporting unconsolidated Kalahari sediments as bedload have modified the valley floor (McCarthy et al., 1997; Grenfell et al., 2019). As the meandering, more steeply-sloped river channel transitions from the upper panhandle region, it then loses confinement and disperses as an alluvial fan region, characterized by straight river channels, bed aggradation, a flatter river channel slope and overall elevation of the wetlands ranging between 930 and 1000 m asl (McCarthy et al., 1997). Finally, if considered at finer resolution, several types of wetland have formed within the Okavango Delta, due to variations inflow and sediment transport (Grenfell et al., 2019).

The Pantanal is a large plain, spread across western-central Brazil, eastern Paraguay, and eastern Bolivia, approximately 100 m asl and is considered one of the most extensive tropical wetlands in the world. It is located within a natural basin, surrounded by the Planalto Highlands region (Mercante et al., 2011). Where the Paraguay River runs through the Pantanal, the water level may fluctuate between 2 and 5 m, depending on the season. The Pantanal ranges from being flooded, to pockets of water, or temporary lakes, remaining throughout the dry season. Alluvial fans form at locations of loss of confinement as a stream discharges onto a receiving basin of very low gradient. Loss of confinement is generally controlled by geological factors, such as rifting (McCarthy et al., 1997) or a change in lithology, or may simply be due to a landform transition such as confined tributary valley to unconfined trunk floodplain. In the Pantanal, the Paranà River drains a catchment with high rainfall and discharges into a rift valley basin oriented perpendicular to the watercourse, through which the Paraguay River flows. Alluvial fans are characterized by sediment fining from the apex to distal reaches, and have a network of distributary channels, some of which may be abandoned and some of which may be morphodynamically active (Grenfell et al., 2019).

2.6 Timescales of development

In humid settings, wetlands have mostly developed within the last 10–15,000 years following the recession of the late Pleistocene ice sheets (Pajunen, 1996; Greb and DiMichele, 2006), and with changing sedimentation, through dynamic river processes and sediment movement and deposition (Ellery et al., 2009; Fryirs et al., 2017; Lisenby et al., 2019; Grenfell et al., 2019). Some wetlands have initiated independently of rivers in depressions in deglaciated terrain and have changed relatively little over time (Tooth and McCarthy, 2007), while others have evolved from lakes to wetlands, as the Rwanda peatlands formed in paleo-lakes (Pajunen, 1996). Most wetlands have been affected by palaeoclimatic changes as testified by historic floral and faunal evidence within sediment cores and present species composition (Pajunen, 1996; Collen et al., 2014). For instance, during the last glacial period, the surface of the Amazon River floodplain near Manaus was about 20 m lower and its total area considerably smaller than today, because of the lower sea level stage, and the Pantanal mostly dry (Junk, 2002; Müller et al., 1995), while much of North Africa was covered with grasslands along with scattered lakes and wetlands (Carrington et al., 2001). Climate changes over the past 2 million years have influenced wetlands of the Congo basin, in response to expansions and contractions of the polar ice caps, cool dry periods have alternated with warmer, humid periods, causing the forests and wetlands to shrink and expand, with scattered refuges, for example, along the gallery forests and swamps associated with the Congo River (Kadima Kabongo et al., 2011).

2.7 Peat accumulation

Peatlands occur on a multitude of landscape settings but especially those with a low to flat gradient or a basin-shaped topography, where water is stilled and slow to flow away (Rydin and Jeglum, 2006; Ellery et al., 2009). In these settings, near-continuous inundation or saturation and the resultant anaerobic conditions work together to inhibit plant debris decomposition, allowing the accumulation of thick organic deposits (Charman, 2002). Globally, peatlands widely occur in the northern hemisphere where low temperatures inhibit plant decomposition, while in the high temperatures of the tropics it should follow that peat soils are less common, as plants decompose quickly (Joosten and Clarke, 2002; Belyea and Clymo, 2001; Charman, 2002). However, in areas that are waterlogged year-round, and where nutrient levels in the water are low, decomposition can be slowed enough to allow peat to form (Mitsch and Gosselink, 2000; Charman, 2002; Rydin and Jeglum, 2006).

Swamp forest peatlands are widespread in the Central Congo basin and South-East Asia where high rainfall and very high plant productivity in these tropical regions offset the effect of high temperatures, allowing organic matter accumulation to exceed decomposition (Sjögersten et al., 2014). In many cases, conditions of peat formation prevail under conditions where swamp forests develop (Dargie et al., 2017; Kent, 2019).

The fluvial settings described above provide a template for regions of peat accumulation, such as in the Congo basin, braided in a maze of alluvial islands. Water is retained adjacent to river channels within backwater channel and oxbow lake situations. Peat formation requires these low energy situations that are removed from the influence of flooding or surface flow, and from frequent inputs of clastic sediment (Ellery et al., 2009; Rydin and Jeglum, 2006). Dargie et al. (2017) found that approximately 40% of the total extent of Cuvette Centrale wetlands support peat occurring in shallow basins between the main rivers, supporting a continuous layer of peat reaching depths between 6 and 20 m and dated to approximately 10,600 years before present (BP).

Peat swamp forest in Borneo is mostly located in the low-lying and low relief coastal areas, which have been conducive to the development of peat swamp forest since sea level dropped approximately 26,000 years ago (Page et al., 2004; Kent, 2019). The rise in elevation from the sea is typically very gradual, in some areas river source is just 12 m above sea level (Page et al., 2009). Most of the lowland peatlands in Malaysia have developed along the coast behind accreting mangrove coastlines, and are permanently waterlogged, promoting optimal conditions for the accumulation of organic matter as peat (Kent, 2019). The peatlands, frequently forming domes, develop on the alluvial plains in the area between rivers. The rivers accumulate natural levees through sediment deposition over time, and deposit fine alluvium during flooding when the water over-tops the levees. Flooding along the margins of the rivers prevents the development of peat, but this progressively diminishes as further away from the river channel and freshwater swamp forest develops. This separates topogenous peats, which receive inputs of nutrients from river water, from ombrogenous peat bogs, which receive input of water only in the form of rainfall (Kent, 2019). The result is a dome-shaped area of peat between the two rivers, sometimes reaching depths upto 12 m, as noted by Anderson (1983) in Sarawak. Many peatlands which are now far inland developed along the former coastline such that some may be around 100 km inland such as the peat areas around Marudi in Sarawak. The age of the oldest inland peat areas has been estimated as 4000–5000 years (Anderson, 1983; Kent, 2019). An important feature is that the mineral soil layer below the peat may be below mean sea level.

The Peruvian highlands encompass seasonally wet grasslands and peatlands, at an average altitude of 3881 m asl and mean annual precipitation of

762 mm (Chimner and Karberg, 2008). Most areas in the Andes are marked by wet and dry seasons, where the former spans from November to April. The Pastaza-Maranon foreland basin in Northwest Peru contains extensive peatlands within a subsiding basin formed during the Cenozoic uplift of the Andes (Salvador et al., 2014). High rainfall, frequent flooding and low-lying topography have enabled significant thicknesses (upto 7.5 m) of peat to accumulate (Salvador et al., 2014; Fonkén, 2014). The correspondence between thick peat and forest may be the result of long term geomorphological stability which has allowed peat to accumulate above the maximum flood level, leading to ombrotrophic conditions, low nutrient status and vegetation succession to forest (Salvador et al., 2014; Fonkén, 2014). This explanation is supported by geological evidence that this region has experienced a lower frequency of river avulsions and increased stability since the isolation of the Rio Tigre from the Rio Pastaza c.8000 years BP (Salvador et al., 2014; Fonkén, 2014).

2.8 Large-scale trends in wetland vegetation

In any place where exposed substrate is available for plants to germinate, eventually vegetation will develop, and in wetland environments the selection of plants that become part of the wetland vegetation is mainly determined by the period within the year in which the area is inundated. Which plants can survive in the given conditions depends on the dispersal of seeds and the properties of the species that they represent (Shipley et al., 2006). A vegetation community emerges from the selection of species during the process of community assembly from the regional species pool. In this process, species are selected through three different filters (Weiher and Keddy, 1999): species dispersal (the species must be able to reach the wetland in the form of a dispersal unit, which is either a seed or a clonal fragment), environmental filters (the species must be able to cope with environmental conditions at the site, which in a wetland means the level of inundation, the redox potential, the organic matter contents and the physiochemical variables) and lastly the species interactions (competition and all kinds of other species interactions, taking into account clonal growth which often leads to a dominant matrix species emerging).

Associated with broad-scale landscape settings, six main wetland vegetation types are found throughout the tropics, namely, swamp forests, sedge (and grass) marshlands, nutrient-poor fens and bogs, mountain seepages, saline pans and sheetrock wetlands. The first two types dominate (Archibold, 1995), whereas the last four types generally occupy smaller areas or are found only in specific regions. A major distinction in tropical wetlands is, therefore, between vegetation dominated by woody elements and vegetation dominated by graminoids. This subdivision in wetland vegetation is important because in some cases, wetland vegetation has an effect again on geomorphological processes, such as that tree cover helps the floodwaters in swamp forests to slow down and thereby lead to clastic and organic sedimentation. In general, denser vegetation means that floodwaters slow down more, and therefore it stimulates deposition of sediments more.

Abrupt slope breaks found in landforms of escarpment and steep slopes often create environmental conditions suitable for the discharge of subsurface water which leads to seepage and the formation of wetlands (Montgomery and Dietrich, 1988; Stein et al., 2004). Thus it is likely that the presence of a geological substrate with stratified layers or planar surfaces and landforms with slope breaks which facilitate groundwater seepage to the surface, are the preexisting geological and geomorphological conditions for the occurrence of wetlands.

A unique kind of wetland found in most tropical areas are sheetrock wetlands from inselbergs, mostly on granite substrates with very shallow soils. Inselbergs are erosional remnants of a rock type that is harder than the surrounding landscape. In Central Africa, there are granite inselbergs present in the rainforests of Gabon and Cameroon and there are extensive areas on these inselbergs that are permanently wet as they receive continuous rainfall (Müller, 2007; Vande Weghe, 2010). Also, the summit plateaus on the large inselbergs in the Guyana shield are very much characterized by extreme nutrient poverty as well as very high rainfall combined with a relatively flat topography.

2.9 Conclusion

Knowledge of wetland origin and geomorphic processes can result in management actions that work against natural processes, leading to potentially disastrous consequences (Ellery et al., 2016). The incorporation of geomorphic knowledge of wetland origin, and understanding of wetlands from a geomorphic perspective can improve our ability to interpret and predict changes and complement the assessment of natural processes within wetlands. Correct identification of the factors giving rise to wetlands, and improved understanding of the geomorphological and sedimentological processes governing their development, is vital for the prioritization of restoration efforts and the design of sustainable management guidelines for these diverse yet fragile habitats (Grenfell et al., 2019; Tooth et al., 2002), especially in the face of global climate change.

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Chapter 3

Hydrology, geomorphology, and soils: an overview

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3.1 Introduction

3.1.1 General wetlands overview

Wetlands are unique hydrologic features which are embedded within terrestrial landscapes or straddle terrestrial-aquatic interfaces (Mitsch and Gosselink, 2015; Wasserman and Dalu, 2022, Chapter 1). Accordingly, wetland ecology, geomorphology, and physicochemical environment are strongly driven by hydrologic conditions (Jackson et al., 2014; Deemy et al., 2022, Chapter 4). Wetlands exist across a spectrum of hydrologic function from headwaters to terminal storages (Mitsch and Gosselink, 2015) and features of the same geomorphic class or ecological habitat type may exist along a gradient of hydrologic conditions (Deemy and Rasmussen, 2019).

Pronounced wet and dry season water-level fluctuations are a major defining feature of tropical wetlands (Girard, 2011; Junk, 2002), as are pronounced atmospheric hydrologic flux driven by El Niño Southern Oscillation (ENSO)-driven precipitation (Lee et al., 2020; Zhu et al., 2017), and particularly high rates of evaporation (Schwerdtfeger et al., 2014). During the wet season or after a major ENSO-driven influx of precipitation, tropical wetlands will exhibit an abundance of free surface water with evapotranspiration (ET) only being limited by energy influx. However, as tropical wetlands enter the dry season ET becomes limited by shrinking free water surface and soil water saturation (Schwerdtfeger et al., 2014).

Wetland geomorphology influences a variety of development processes and ecological functions (Cherry, 2011). Strong feedback loops between

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geomorphology and hydrology contribute to biogeochemical cycling, soils development, and ecological succession (Johnston et al., 1997). Topographical geomorphology influences how water flows over or seeps through soils (Kolka and Thompson, 2006) and contributes to spatial heterogeneity which drives biodiversity (Davidson et al., 2012; Piedade et al., 2022, Chapter 7, Brendonck et al., 2022a,b, Chapters 9 and 10; Dube et al., 2022, Chapter 11; Reichard, 2022, Chapter 12; Moraes et al., 2022, Chapter 13; Tarakini et al., 2022, Chapter 15) and biogeochemical function in wetlands (Frei et al., 2012; Deemy et al., 2022, Chapter 6; Moyo, 2022, Chapter 5; Cuthbert et al., 2022, Chapter 17). Water flow or lack thereof in wetlands in combination with hydropattern contributes to detritus and sediment accumulation (Jackson et al., 2014; Craft, 2001). The fluctuation in water flow can alter the general wetland bathymetry and drives shifts in vegetation recruitment patterns and other mechanisms that impact nutrient cycling (Johnston et al., 2001; Piedade et al., 2022, Chapter 7).

Fire, which is limited by inundation frequency and duration, is critical in maintenance and evolution of wetland geomorphology (Wade et al., 1980, Wösten et al., 2006) as well as the vegetative community (Stuber et al., 2016). Tree fall and animal bioturbation in wetlands can locally change basin morphology (Craft, 2001) in wetlands while fires associated with drought cycles can drive large magnitude changes in wetland basins (Stuber et al., 2016). Peatlands are especially prone to wide scale changes in response to fire (Wösten et al., 2006) or draining because their soils contain high percentages of organic matter that when combusted or oxidized leave little structure behind (Hoyt et al., 2020). Soil surface elevation then decreases and the hydrology of the system responds accordingly (Hooijer et al., 2010).

Wetlands develop unique mineral or organic soils due to the flooding and draining in these systems (D’Angelo and Reddy, 1999). The pulsing nature of hydrologic inputs in tropical wetlands drives soil carbon storage and methane emissions (Mitsch et al., 2010). These conditions are suitable for both aerobic and anaerobic microbial communities that reduce a variety of chemical compounds as electron acceptors during respiration (Lovley and Klug, 1986). Decomposition under these conditions is slow and organic matter accumulates faster than in aerobic upland soils (Nahlik and Fennessy, 2006). Accumulation of organic matter also contributes to water retention and creation of perching layers in wetlands (Mezbahuddin et al., 2015; Richardson et al., 2001; Collins and Kuehl, 2001).

3.1.2 Chapter scope and objectives

The objective of this chapter is to provide an overview of the hydrology and geomorphology of subtropical and tropical wetlands embedded among terrestrial landscapes. In accordance with the theme of this book we do not address riverine, estuarine, or marine wetlands. This chapter explains basic concepts in wetland hydrology, geomorphology, and soils as context typically associated with targeted examples of tropical and subtropical depressional wetlands, karst sinkhole wetlands, and peatlands. The focal categories of wetlands that are highlighted in this chapter highlight a combination of landscape positions, elevational settings, and hydrologic drivers.

3.1.3 Focal wetland types

3.1.3.1 Depressional wetlands

For the purpose of this chapter we define depressional wetlands as surface depressions embedded in uplands (see also Job and Sieben, 2022, Chapter 2). We do not include floodplain or riverine derived features such as meander scars or oxbows. Depressions can be karstic but will lack the perennial or regular/periodic groundwater connection of a karst sinkhole wetland. We define karst wetlands as those generally forming in karst collapse features directly embedded in the surface aquifer (typically in perennially or seasonally saturated zones below the majority of the vadose zone) where karst groundwater hydrology will exert a controlling influence on the wetland. Therefore, we distinguish depressional wetlands as those embedded in uplands which are not in direct contact with groundwater and not derived by riverine processes.

Episodic groundwater events may provide inflows to depressional wetlands but these features are typically only connected to surface aquifers through subsurface leakage and spillage. Typically, the confining layer below that contributes to depressional-wetlands formation will limit the regularity of groundwater inflows and outflows.

3.1.3.2 Karst sinkhole wetlands

In this chapter we specifically address karst sinkhole wetlands which we define as wetlands created by hydric conditions induced through the collapse of bedrock/substrate voids in weathered landscapes. We differentiate karst sinkhole wetlands from depressional wetlands by their direct, regular connection to groundwater, whereas depressional wetlands have occasional or episodic connections to groundwater. Essentially, we distinguish between the surface condition hydrologic drivers in depressional wetlands with the weathered bedrock/saturated zone hydrologic drivers in karst sinkhole wetlands.

3.1.3.3 Peatlands

While a wide spectrum of peatlands can be considered, we limit our focus to peatlands which are typically isolated from other surface waters even if they exist close to coastlines. Peatlands addressed in this chapter are those forming as features embedded in uplands or on elevated landscapes. In keeping with the theme of this text we have also done our best to limit our examples to peatlands which do not regularly receive substantial surface water inputs from riverine or estuarine sources.

3.2 Wetland hydrology

3.2.1 The water budget: balancing inputs with outputs

The water balance is a fundamental concept in hydrology that is useful for estimating the relative contributions of system inputs and outputs and is particularly useful for wetlands because of the important role that they provide in storing water (Fig. 3.1). Simple water budgets aggregate all inputs and outputs but can be detailed further to include specific atmospheric exchanges, surface water inputs/outputs, groundwater inputs/outputs, and anthropogenic inputs/outputs (Rasmussen et al., 2018). The water balance equation reflects the conservation of mass to account for fluctuations in water storage:

$$\Delta S = I - O \tag{3.1}$$

where ΔS is the change in storage per unit time interval, and I and O represent the total inputs and outputs, respectively, expressed as discharges.

Inputs account for all wetland inflows, including precipitation, P, groundwater, GW_i, surface water, SW_i, and anthropogenic inputs, H_i (e.g., wastewater discharges, agricultural runoff):

$$I = P + GW_i + SW_i + H_i \tag{3.2}$$

Outputs account for all wetland outflows, including evapotranspiration (ET), groundwater GW_o, surface water SW_o, and anthropogenic outputs H_o (water supply for e.g., irrigation, industrial, municipal, thermoelectric cooling):

$$O = ET + GW_o + SW_o + H_o \tag{3.3}$$

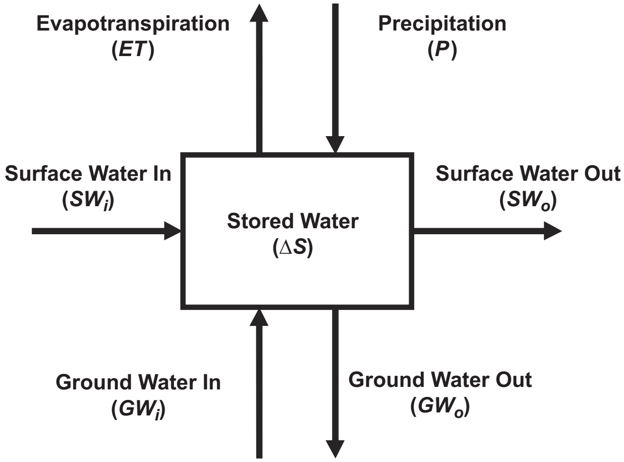

FIGURE 3.1 Box diagram demonstrating the hydrologic mass balance concept.

We can simplify these equations to yield:

$$\Delta S = (P - ET) + \Delta GW + \Delta SW + \Delta H \tag{3.4}$$

where ΔGW, ΔSW, and ΔH represent the difference between inflows and outflows for these components.

Water-budget inflows and outflows can be further specified as necessary. A common instance of this is in customizing the evapotranspiration factor when models require the separation of plant transpiration and free-water surface evaporation (Jackson, 2006). This can become necessary in wetlands with large plant surface area available for transpiration. Furthermore, plant transpiration can be detailed by species which becomes especially relevant for comparing forested wetlands dominated by different tree species.

Table 3.1 summarizes different approaches for estimating evapotranspiration. Note that each method incorporates different types of inputs. The free water evaporation equation (Dingman, 1994) can be used to determine evapotranspiration from a wetland as a function of vapor pressure:

$$E = cW(e_s - e_a) \tag{3.5}$$

where E is the evaporation, W is the wind speed 2 m above the water surface, e_s is the saturated vapor pressure, and e_a is the actual vapor pressure. This equation assumes that evaporation is not limited by the water supply.

Many empirical equations for evapotranspiration have been developed. Most provide generally accurate estimates of evapotranspiration and selection

TABLE 3.1 Summary of data requirements and notes on common evapotranspiration equations.

Method	Data requirements	Notes	Citations
Free water evaporation	Vapor pressure	Theoretical	Dingman (1994)
Thornthwaite	Mean monthly air temperature	Empirical, limited precision, underpredicts, cost effective	Thornthwaite (1948)
Penman-Monteith	Net radiation, total shortwave radiation, wetland albedo, outgoing longwave radiation, windspeed, air temperature	Empirical, fairly precise, data intensive, underpredicts	Pennman (1948), Monteith (1965)
Hammer and Kadlec	Incident shortwave radiation, air temperature, relative humidity, windspeed	Sensitive to radiation inputs, fairly precise	Scheffe (1978), Hammer and Kadlec (1983)

of a method is dependent on data available as well as precision appropriate to the investigation. Despite its simplicity, the Thornthwaite equation (Eq. 3.6) has been shown to be one of the most efficient estimating equations regarding accuracy relative to sensor cost.

$$ET = c\left(\frac{T}{I}\right)^{a} \tag{3.6}$$

where ET is the potential monthly evapotranspiration, T is the mean monthly temperature, I is the annual heat index, and a is a polynomial function of I.

If information on the inputs and outputs is insufficient to create a detailed water budget, it is possible to use starting and ending water storage to estimate the change in storage through time. This necessitates a detailed survey or estimate of wetland volume and data on the change in stage between the two time points of interest.

$$\Delta S = \Delta hA \tag{3.7}$$

where A is the surface area and Δh is the change in stage.

Broadly, wetlands can be classified by hydrologic drivers based on the dominant source of water (Table 3.2). In some systems, wetland water sources remain steady regardless of meteorological conditions such as those driven by groundwater. In other systems the dominant drivers are dynamic or highly sensitive to meteorological conditions such as those driven by seasonal precipitation or storm flows (e.g., Fig. 3.2).

TABLE 3.2 Summary of subtropical and tropical wetland inflows and outflows.

Wetland type	Primary inflows	Primary outflows
Depressional wetlands	Precipitation, episodic surface runoff	Evapotranspiration, episodic surface outflows
Karst sinkhole wetlands	Precipitation, groundwater inflow	Evapotranspiration, groundwater outflow
Hillslope fens	Precipitation, surface runoff, soil/ groundwater inflow	Evapotranspiration, surface outflow (can form stream headwaters), groundwater outflow
Elevated peatlands or hilltop peat bogs	Precipitation	Evapotranspiration, groundwater outflow, surface overflow
Peatlands	Precipitation, limited surface inputs	Evapotranspiration, limited leakage to groundwater, surface outflow (may form headwaters for streams)

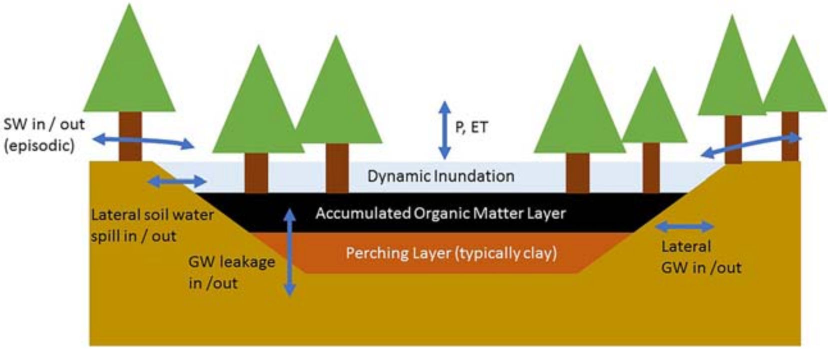

FIGURE 3.2 Depressional wetland with episodic inputs and outputs that also accounts for potential soil water exchanges, lateral groundwater flow, and leakage in and out from vertical groundwater inputs.

3.2.2 Hydropattern: hydrologic duration, timing, and magnitude

Hydropattern describes the overall hydrologic time series and integrates duration, magnitude, and timing of discharge or stage on a hydrograph (Jackson, 2006). Wetlands ecosystems are driven by not only the presence of water but also the timing, duration, frequency, and stochasticity of inundation (United States EPA, 2008). Analyzing the average or typical variation in a hydrologic time series is a complex task not easily completed by a single metric or set of metrics. This has driven the development of a variety of methods and approaches for describing the hydropattern of wetlands. Table 3.3 summarizes some of these methods, along with the typical metric for characterizing the type of system.

Hydroperiod describes the duration of surface inundation and is often incorrectly used as an interchangeable term with hydropattern (Jackson, 2006). This malapropism should be avoided when investigating wetlands because the ecological community in wetlands is driven by the frequency, timing, magnitude, *and* duration of inundation (Rasmussen et al., 2018; Jackson et al., 2014). Hydroperiod, in its correct definition, is a useful tool in understanding wetlands but should be carefully and appropriately applied to analyzing wetland inundation time series data (Jackson, 2006).

Hydropattern is a critical driver of ecological communities in wetlands because it drives the physicochemical conditions that drive the plant and animal communities. This ranges from constraints on biogeochemical cycling to acting as a filter for animal colonization.

Plant communities tend to respond to a combination in fire frequency and hydropattern (Stuber et al., 2016). In turn, feedback between hydropattern and fire can drive successional cycles in the hydrology of a wetland or wetland complex. This can be especially relevant to peatlands where drought and fire cycles can alter wetland bathymetry and change flow patterns within the system (Hooijer et al., 2010).

TABLE 3.3 Partial summary of metrics for evaluating subtropical and tropical wetlands.

Metric	Description	Metric type
Wetting/drying dates	Beginning and ending periods of wetted surface	Timing
Inundation duration	Annual mean or median of wetted surface	Duration
Stage duration curve	Curve showing the length of time at a given stage	Duration
Stage frequency	Histogram that shows the frequency distribution of events falling into given stage ranges	Frequency
Stage excursion frequency	Stage frequency histogram normalized to mean annual stages frequency	Frequency
Stage recurrence intervals	Curve that shows the annual probability of water levels reaching a given stage	Frequency
Empirical cumulative distribution function	Curve that shows the cumulative number of observations below a given threshold	Frequency
Double mass curves	Coupled analysis of cumulative observations for a pair of parameters (e.g., precipitation and runoff) to determine consistency of the relationship through time	Variation
Stage time series (hydrograph)	Graphically assess stage changes through time	Timing/ duration
Time to peak	Measures time from precipitation to the hydrograph peak	Magnitude/ response
Water-level fluctuation	Generally mean change in stage for a given time period, full suite of summary statistics can also provide instinct.	Variation
Summary statistics	Statistical summary stats (lower bound, upper bound, first & third quantiles, median, mean, min, max) of observed stages	Magnitude
Wet/dry day proportions	Provides insight variable responses to climate conditions for waters in close proximity or for interregional comparisons	Frequency/ duration

While the magnitude and timing of inundation are major drivers of plant communities, macroinvertebrate and fish communities are generally more affected by the duration of inundation (Kirkman et al., 2011). Perennially inundated wetlands often have more developed fish communities than those with less frequent inundation due to short drought return periods. Conversely, amphibian communities tend to be more diverse in wetlands with seasonal wetting and drying due to the lack of fish community (Kirkman et al., 2011). In extreme cases, wetlands can remain dry for decades prior to wetting and supporting distinct communities of animals and plants regionally typical of wetlands (Roshier and Rumbachs, 2004).

3.2.3 Wetland hydraulics: physics of flow and storage

The physics of water flow drives all aspects of ecology in aquatic ecosystems (Mitsch and Gosselink, 2015; Jackson et al., 2014). By definition, wetland hydraulics are the physics of flow and storage of water within a wetland (Jackson et al., 2014). Wetlands hydraulics are quite important to everything from biogeochemical cycling and physicochemical conditions to sedimentation patterns and vegetation colonization (Jackson et al., 2014; Craft, 2001).

Typically, wetlands are slow surface water environments with long residence times that often facilitate high levels of sediment storage (relative to inputs) and high levels of nutrient processing and even contaminant storage. Generally, larger wetlands will have longer residence times (i.e., Alaka'i Swamp, Okefenokee) and smaller wetlands will have shorter residence times (small isolated depressional wetland). These residence times determine the extent to which wetlands function as storages or sources of various materials (United States EPA, 2008). Residence time can be calculated by the following equation:

$$\tau = \frac{V}{O} \tag{3.8}$$

where τ is the mean residence time at steady state, V is the volume of surface water, and O is the outflow rate (which can be interchanged with inflow, if necessary, at steady state because $\Delta V = 0$).

Even in lentic (slow water) systems, small differences in water velocity can fundamentally alter the expected ecological community. Water velocity of inflow and throughflow determine sediment storage, nutrient processing, and carbon import and export in wetlands. If velocity is too high water will not be stored in the wetland long enough for microbes and plants to act on dissolved carbon and nutrients. Additionally, velocity is a critical determinant of sedimentation in wetlands. The Hjulström curve (Fig. 3.3) is a simplified graph used by hydrologists and geologists to determine at what flow speeds sediment of various sizes will be eroded, transported, and deposited (Hjulstrom, 1935). Notice that fine grained sediment remains in suspension even at very slow flow speeds and can only be deposited when water is near stagnant. When water is stagnant or flows are laminar, meaning that turbulence isn't sufficient to meaningfully impact sediment deposition, sediment-settling rates can be estimated using Stokes' Law (Table 3.4):

$$v = \frac{2\Delta\gamma r^2}{9\mu} \tag{3.9}$$

where v is the vertical particle settling velocity, $\Delta\gamma$ is the specific-weight difference between particles and water, r is the particle diameter, and μ is the fluid viscosity.

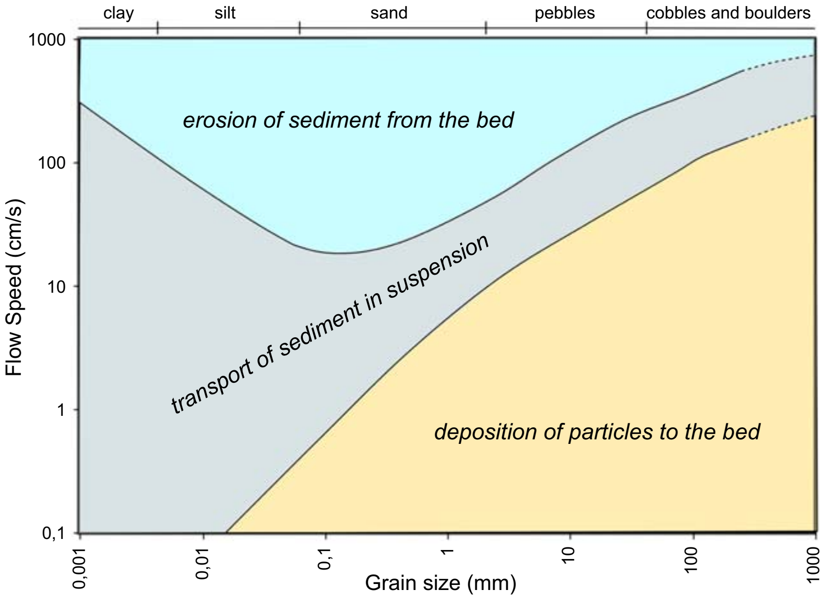

FIGURE 3.3 The Hjulström curve (Fig. 3.3) is a simplified graph used by hydrologists and geologists to determine at what flow speeds sediment of various sizes will be eroded, transported, and deposited (Hjulstrom, 1935).

TABLE 3.4 Representative settling times for sediments in a 0.5-m deep wetland.

Diameter (mm)	Texture	Settling time (s)
1	Sand	<5 s
0.1	Silt	1 day
0.0001	Clay	1 year

Velocity within the wetland is influenced by a combination of vegetation and geomorphology. Specifically, vegetation and physical features of the wetland create resistance to hydrologic flow, which is commonly referred to as roughness. Resistance to flow interacts with sediment retention, nutrient processing, and carbon balances by driving development of the ecological community through positive and negative feedback loops (shown in Fig. 3.4), which in turn influence the hydrologic roughness of the system. Roughness is a critical but often poorly defined (in natural systems) determinant of discharge

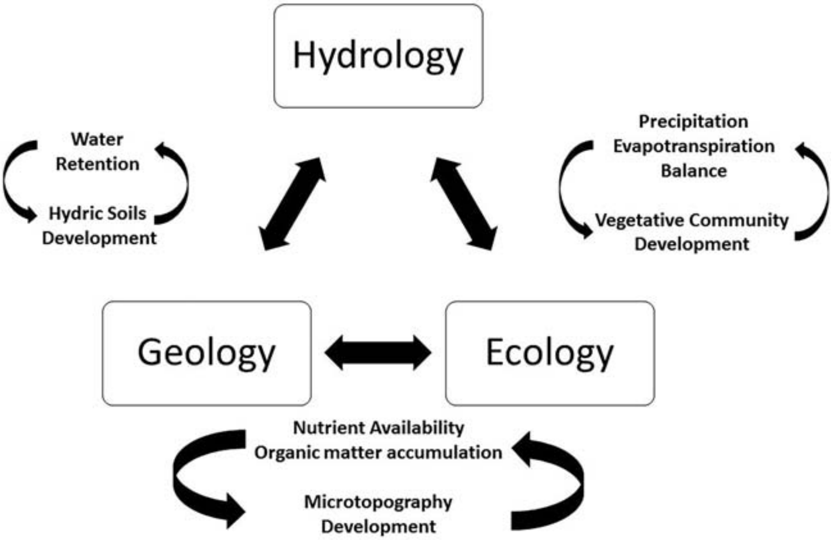

FIGURE 3.4 Hydrologically driven feedbacks within wetland systems that link geology, hydrology, and ecology.

when combined with wetted channel area (flow area), and wetland slope (energy/gravity gradient). Discharge can be calculated from these determinants using the slope-area method. The most common estimation technique is based on Manning's Equation (Manning, 1891):

$$Q = vA = \frac{A_x R^{2/3} \quad s^{\quad 0.5}}{n} \tag{3.10}$$

where Q is flow, v is velocity, A_x is the wetted cross-sectional channel area, R is the hydraulic radius, s is the channel slope, and n is the channel roughness.

One of the greatest challenges in using Manning's equation is the estimation of the roughness coefficient (n). Table 3.5 provides guiding examples for determining an appropriate channel roughness (Cowan, 1956; Chow, 1956). Calibration of channel roughness may be necessary and these values should be taken as a starting point in determining an appropriate n.

3.2.4 Hydraulic connectivity

Seemingly isolated wetlands can sometimes have hydraulic connectivity to other water bodies (Fig. 3.5). This is typically indicated when changes in stage are mirrored between the two water bodies. Coastal wetlands, river sloughs, and karst/kettle hole wetlands can exhibit this behavior because

TABLE 3.5 Examples of channel roughness coefficients (*n*) developed for use in Manning's Equation.

Channel condition	Manning coefficient, *n*
Straight, bare soil substrate	0.020
Winding stream, sparse vegetation	0.035
Rocky mountain stream	0.04–0.050
Winding stream, dense plant growth	0.042–0.052
Slow flow stream, dense plant growth	0.065–0.112
Dense herbaceous or tree growth	0.075–0.150

Source: Adapted from Mitsch, W.J., Gosselink, J.G., 2015. Wetlands, fifth ed. John Wiley & Sons, Inc.; Jarret (1985); Cowan, W.L., 1956. Estimating hydraulic roughness coefficients. Agricultural Engineering 37 (7), 473–475.; Chow, V.T., 1956. Open Channel Hydraulics. McGraw Hill, New York.

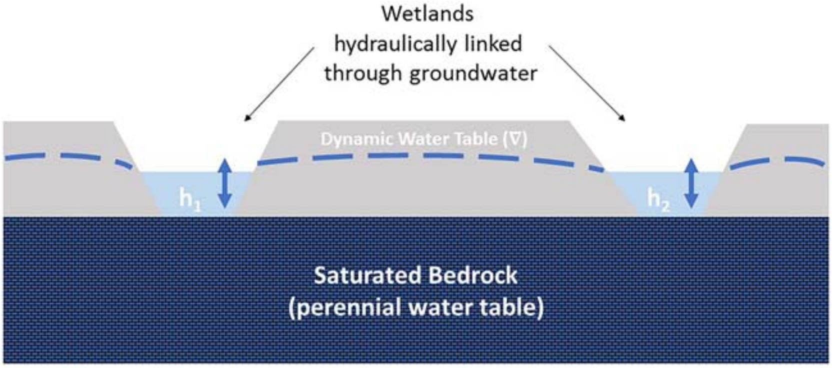

FIGURE 3.5 Wetlands hydraulically linked by groundwater; changes in the dynamic water table (precipitation, withdrawals from perennial water table, etc.) elicit similar responses in each wetland depending on heterogeneity of the surface aquifer.

they are often directly connected to groundwater and thus subject to changes in the water table.

Even where groundwater source is at atmospheric pressure, any changes in water-table height will elicit a pressure wave response in connected wetland features. This is well illustrated by the slight tidal signal exhibited in depressional wetlands on barrier islands that are connected to the freshwater lens. Tides cause small fluctuations in the height of the freshwater lens in each cycle, which are then reflected in water levels of depressions connected to groundwater.

3.3 Collection and analysis of hydrologic data

3.3.1 Collecting hydrologic data

Hydrologic data can be collected through a variety of manual and automated methods. These range from simple staff gauges read at monthly intervals through automated data loggers that measure water level at one second intervals and report values in real time via wireless network connections. Here we highlight a few common, simple, low cost methods for collecting hydrologic data.

3.3.1.1 Rain gauges

Rain gauges can take a variety of forms and range from inexpensive manually checked plastic cylinders to automated tipping bucket systems that can provide measures of intensity as well as volume (Fig. 3.6).

3.3.1.2 Measuring wetland stage

One of the cheapest and most common tools in hydrology is the staff gauge (Fig. 3.7). Staff gauges can be purchased from a variety of suppliers or made

FIGURE 3.6 Plastic rain gauge installed on a small barrier island freshwater depression. Quantification of the rainfall-stage and water-quality relationship is possible when combined with a stilling well containing pressure transducers and a specific conductance probe. *Photo credit: James B. Deemy.*

FIGURE 3.7 Staff gauge used to measure water level in a depressional subtropical forested wetland. *Photo credit: James B. Deemy.*

by hand using a wide range of materials. Staff gauges must be read manually, which means that temporal resolution of data will be necessarily limited. Generally, one measurement per day at best but weekly and monthly measurements are more common.

Another common and relatively inexpensive tool for measuring water levels are pressure transducers coupled to dataloggers. Some pressure transducers include internal dataloggers while others can be "plugged in" to customizable systems.

$$h = h_o + cP \tag{3.11}$$

where h_o is a reference stage, P is fluid pressure, and c is a calibration coefficient used to convert pressure to stage.

Stilling wells are recommended for use with pressure transducers to improve the accuracy of stage measurements that may otherwise be degraded by ripples and wind-driven waves (Figs. 3.8 and 3.9). While large waves can still induce variation, the housing reduces these disturbances. Stilling wells also have an added advantage of reducing sediment burial or fouling of the measuring device(s).

Additionally, water levels monitored using an absolute pressure sensor must be converted to gauge by using a second pressure transducer that is kept above maximum water level.

$$WL_1 = PT_1 - PT_o \tag{3.12}$$

where WL_1 is the adjusted water level at a site, PT_1 is the submerged pressure recorded by an absolute pressure sensor at the site, and PT_o is atmospheric pressure recorded at the site.

To estimate discharge, water-level measurements must be coupled with the channel cross-sectional area for lotic systems, or pond area for

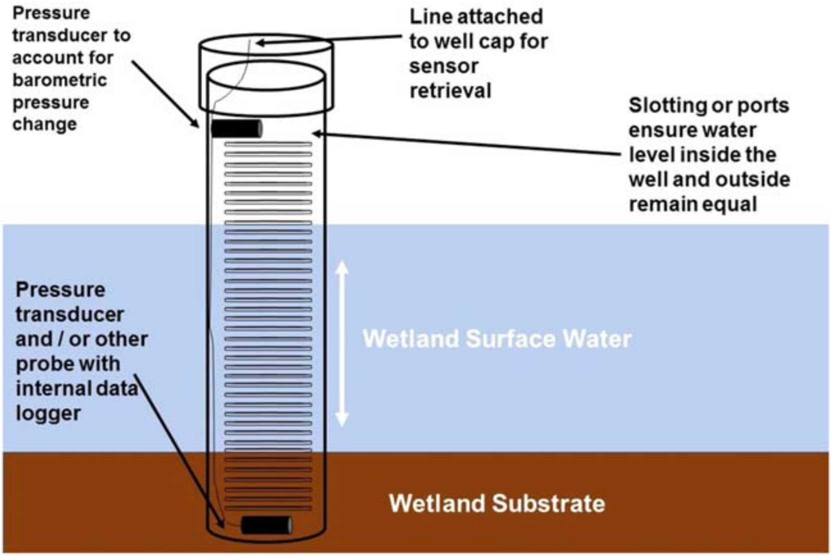

FIGURE 3.8 Schematic of a stilling well used to calm water for precision water-level measurements.

lentic systems. Channel dimensions and/or pond volume should be periodically remeasured to account for geomorphic alterations by erosion, sedimentation, vegetation, or even animals (i.e., alligator or hog wallows).

When wetland water levels often fall below the surface of the wetland, piezometers can be installed (Rasmussen et al., 2018). These shallow nonpumping wells can be used for monitoring the depth to saturation in soil substrate during frequent or seasonal dry periods.

3.3.1.3 Water quality

Additional water quality data can also assist in understanding wetland processes. The specific conductance is an indicator of the concentration of dissolved solids, in that higher salt concentrations increase the electrical conductivity of water. Precipitation inputs typically have lower conductivities than groundwater, and even surface water. Point sources of wastewater discharges often have higher conductivities due to their elevated dissolved solids concentrations.

Temperature can be used to indicate the relative sources of water inputs, in that groundwater temperatures tend to be more constant than precipitation or surface-water inflows. pH is another important indicator, especially in karst terrains where groundwater inputs with high carbonate concentrations are accompanied by higher pH. Dissolved oxygen is a key factor that affects redox reactions, so monitoring the effect of respiration and photosynthesis

FIGURE 3.9 Stilling well installed in a small, semiisolated, subtropical, freshwater, depressional wetland on St. Simons Island Georgia, United States. *Photo credit: James B. Deemy.*

provides important information about biological activity (see Dalu et al., 2022, Chapter 8). Turbidity is another useful measurement that can be used for determining the concentration of finer suspended solids (e.g., silts, clays) that are often associated with nutrients and pathogens from nonpoint sources from urban and agricultural landscapes.

Water quality data useful to hydrologic investigations can be collected with a variety of tools. These tools span a range from deployable sensors that record continuous measurements to hand held devices used to measure characteristics during sampling. Additionally, samples can be returned to laboratory settings when increased precision and accuracy are required.

3.3.2 Analysis of hydrologic data

Here we highlight a few common approaches to analysis of hydrologic data that are particularly relevant to wetland systems embedded in uplands.

3.3.2.1 Recurrence interval

Recurrence intervals are one of the most important concepts in flood analysis and are a critical consideration in connectivity. The recurrence interval is a measure of how often an event is expected to occur based on the probability of exceeding a given stage threshold (annual exceedance probability). To calculate recurrence intervals the following equation is used:

$$T_r = \frac{1}{P} \tag{3.13}$$

where T_r is the return period (years) and P is the annual exceedance probability.

3.3.2.2 Stage frequency and duration

Stage frequency is simply the number of measurements at a given water level. Stage-frequency analysis using histograms or empirical cumulative density functions provides insight into the hydrologic behavior of a system (Fig. 3.10). These tools can be used to understand both short- and long-term water-level variation in a system. Investigations of frequency distribution provide an understanding of dry-day frequency, flooding or high stage frequency, and allow comparisons of short-term behavior and long-term observations (Nilsson et al., 2013). Commonly stage frequency includes standard summary statistics (mean, median, quantiles) but inclusion of in the extreme high and low stages (1st, 5th, 10th, 90th, 95th, 99th percentiles) can also yield insight to wetland water-level variability (Rasmussen et al., 2018).

Histograms provide an excellent tool for comparing the shape and skew of stage frequency among different wetlands or among different time periods for a given wetland. The information provided by comparing the shape of stage frequencies can be used for determining if two locations differ in response to similar climate conditions, such as when comparing two wetlands or groups of wetlands dominated by differing vegetation.

Empirical cumulative density functions (ECDFs) show the cumulative number of observations that fall below a given threshold (Fig. 3.11). In the case of stage analysis this threshold is a given stage height. This tool can be used similarly to histograms in examining the shape of the cumulative distribution of stages. Additionally, a Kolmogorov-Smirnov (K-S) test can be used to statistically determine if two ECDFs have the same distribution or differing distributions (Nilsson et al., 2013).

Stage duration is simply how long a wetland remains inundated to a given depth (Rasmussen et al., 2018). This descriptive characteristic of

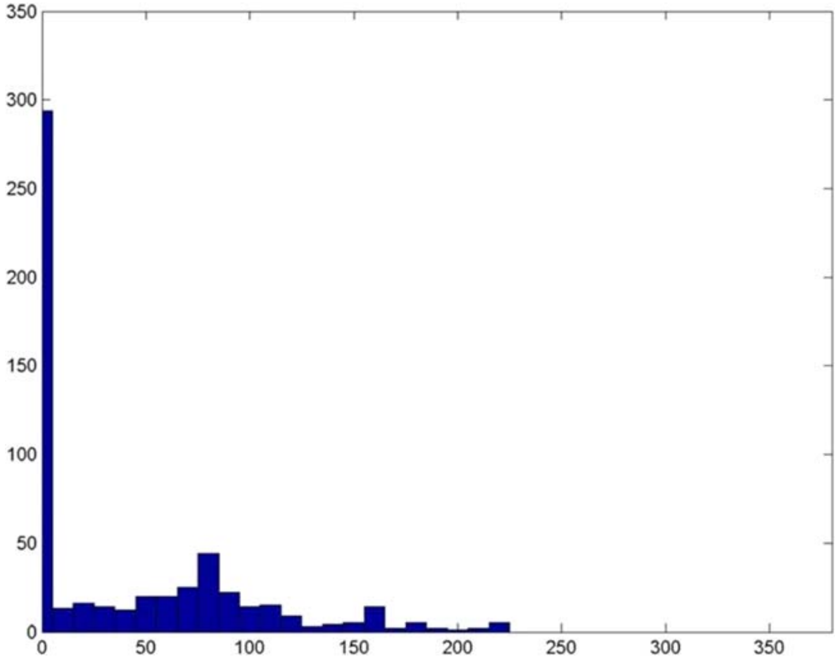

FIGURE 3.10 Histogram showing the distribution of observed stages in a depressional wetland. Note the large number of days when the water table lies below the ground surface.

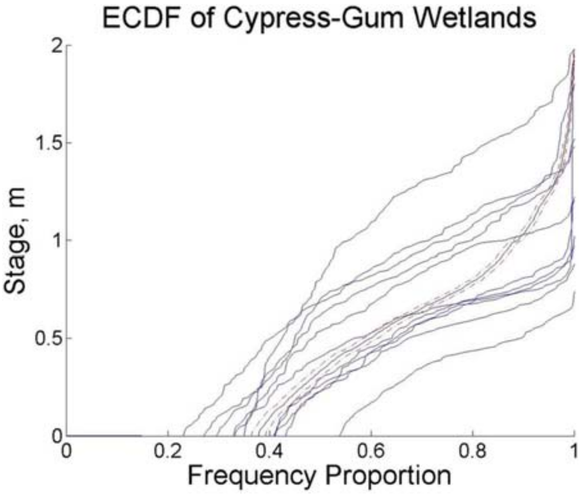

FIGURE 3.11 Empirical plot of observed stages in a group of subtropical depressional cypress-gum wetlands. Mean and 95% confidence intervals show the highly variable hydrology within the same wetland vegetation type.

hydropattern can be shown through stage duration curves as a summary of all hydrologic measures, compared through annual or decadal cycles, or even used to compare seasonal hydrologic variability. Typically, these curves show that low stages persist longer and higher stages account for smaller amounts of time.

Stage duration distributions and stage frequency distributions can be combined to create stage-duration-frequency relationships. This provides insight into the frequency and rate of change in wetland water levels. Stage-duration-frequency relationships can indicate if a wetland can be expected to change stages rapidly or more moderately (Rasmussen et al., 2018).

3.4 Wetland geomorphology

3.4.1 General determinants

Wetlands are shaped by the movements of rock, sediment, water, and organic material over a landscape. Therefore wetland geomorphology, meaning the shape of the land surface, is heavily impacted by the substrate, including characteristics of both hard rock and mobile sediment. In turn, the shape of the landscape directs the flow of water and transport of sediment and organic material, creating complex morphodynamic relationships and feedbacks (Mitsch and Gosselink, 2015; Rasmussen et al., 2018).

Wetland geomorphology is a critical driver of wetland hydrology (Jackson et al., 2014). For example, hydrologic storage is partially limited by surface area to volume ratios at both the evaporative boundary (free water surface) and the substrate boundary (Mohamed et al., 2012). Wetlands that are wide and shallow, such as those formed in low-gradient, clay-rich environments, have greater free water surface areas proportional to their volumes, resulting in relatively high evaporation rates. In contrast, wetlands that are deep and narrow, such as those formed in karst environments, have smaller free water surface areas proportional to their volumes, resulting in relatively small evaporation rates (Mitsch and Gosselink, 2015; Jackson et al., 2014). Additionally, the substrate surface available for infiltration determines loss/gains from groundwater inflows/outflows, respectively (Rasmussen et al., 2018).

Geomorphology of wetlands is the result of morphodynamic feedback between the biological community, local hydrology, and the physical landform (Kolka and Thompson, 2006). Plants act to stabilize substrates and often induce the buildup of organic matter. Where hydrologic and climate conditions are suitable, peat formation may follow (Kleinen et al., 2012). If the system experiences periodic flooding, then inorganic sediments and coarse woody debris become interbedded with accumulating organic matter (Richardson et al., 2001). All of these processes contribute to variability in erosion patterns and alterations from fire. Patterns in substrate accumulation also drive changes in hydrology, which provide further feedback to deposition and erosion within the wetland (Richardson et al., 2001).

3.4.2 Landscape position

Wetlands can form in a wide variety of settings, spanning from humid regions with abundant precipitation to arid regions with surface-water deficits (Tooth and McCarty, 2007). Still, landscape position is a major factor in wetland development because wetlands will only form where some combination of factors allow for soil saturation or surface inundation (Richardson et al., 2001). Accordingly, wetlands not associated with another water body tend to develop in places where the water table intersects the surface, often due to a perching layer, or where substrate accumulates to restrict infiltration (Rains et al., 2006). Seeps or natural springs can develop where mass wasting or gradual erosion create convex hillslopes that intersect the water table. Wetland communities may develop if the soil becomes saturated (Craft, 2001). Typically, these hillslope features are classified as fens because of their mineral-laden groundwater inflow (Mitsch and Gosselink, 2015). Saturated soil conditions contribute to the development of hydric soils and the accumulation of organic matter (Collins and Kuehl, 2001). Because wetlands forming through this mechanism are dependent on water-table elevation and groundwater discharge, they are highly sensitive to groundwater fluctuations.

Due to their low slopes, high biomass, and gradual water flow, wetlands generally receive and accumulate sediment, mainly silt and clay, that was eroded and transported from elsewhere. These smaller particles can accumulate in substrate pore space, decreasing porosity and permeability and restricting infiltration (Harris, 2001). Organic sediments may also begin to accumulate in pore space (Bridgham et al., 2001). Alternatively, parent materials may restrict infiltration if they weather in place and then illuviate downward to deeper soil layers. Once infiltration is reduced, saturation at the surface can slow decomposition of organic matter, which will then increase the water-holding capacity of the soils (Richardson et al., 2001). Ponding may ensue, thus generating a positive feedback that leads to increased organic matter accumulation. This mechanism explains why wetlands can counterintuitively occur at relatively high elevations. Hilltop and high-elevation bogs likely form from sediments that weather in place and accumulate in the soil through illuviation, establishing an ombrotrophic bog that depends on atmospheric moisture rather than a connection to groundwater (Mitsch and Gosselink, 2015; Mitsch et al., 2009).

Depressional wetlands can form through either of these mechanisms. Some depressions extend into the water table, such as those on barrier islands, and have a strong groundwater component to their water balance. Others, such as those occurring at high elevations may be entirely driven by a perching layer, such as a clay lens, that restricts vertical water movement within the substrate (Kolka and Thompson, 2006).

3.4.3 Parent material

The underlying parent material strongly influences surface landforms and surface topography often reflects underlying geologic structures. These influences can range from large regional scale topography to local scale topography. Regional scale bedrock characteristics influence the general elevation and topography of a physiographic region. At local scales, bedrock, weatherability, and local variation influence local topography and microterrains.

Local scale processes become particularly evident in regions with bedrock susceptible to weathering. For example, a karstic landscape resulting from limestone dissolution will exhibit an abundance of surface depressions and may have frequent low-magnitude changes in elevation (Tiner, 2003). These depressions are generally the result of collapsed voids in the bedrock resulting from substrate chemical dissolution in combination with changes in hydraulic support as groundwater levels rise and fall. As the karst system develops, above-ground wetlands may shrink or completely disappear as water is diverted to developing subterranean caves.

Like chemical weathering, physical weathering of bedrock can influence the location and water budget of wetlands (Ashley et al., 2002; Kvaerner and Snilsberg, 2011). Fractures in crystalline bedrock create preferential flow pathways for water through the substrate, and thus are often a critical determinant in the position of montane wetlands and fens. Montane wetlands can occur where small hillslope depressions are fed by fracture discharge or where bedrock depressions are sufficient to store enough water for prolonged soil saturation. Fens are typically sustained by groundwater discharge at the foot of hillslopes, so they are dependent on soil water discharge or localized groundwater discharge (Mitsch and Gosselink, 2015). Fens may also develop on convex slopes, as previously discussed, or where erosional features cut into soil water flow paths (Jackson et al., 2014).

In addition to the hard bedrock, sediments are also a key feature in wetland hydrology because they are closely linked to water storage capacity, retention, and leakage, as well as the development of soils (Richardson et al., 2001). Wetlands may receive sediment supply from a variety of sources, including autochthonous organic matter deposition, upland runoff, and episodic flow events. Deposition of mineral sediments from runoff and surface inflows can change hydrology of the wetland by filling depressions and/or pore spaces created by vegetation and burrowing animals within the substrate (Bodhinayake and Si, 2004), which reduces porosity and infiltration. Perching and water retention are also affected by accumulated layers of organic matter. In karst wetlands, deposition of both mineral and organic sediments is critical to soil formation if the initial landscape is incised directly into bedrock (Bautista et al., 2011).

Sediments also impact water chemistry. Fine-grained sediments easily adsorb dissolved material. Therefore the delivery and retention of silt and clay directly impact the budget of nutrients and pollutants in a wetland.

Likewise, because fine-grained materials, both organic and inorganic, are efficient filters, many wetlands contain elevated concentrations of uranium and other heavy metals (Owen and Otton, 1995). Wetland substrate characteristics are not static; they can change over time as the wetland develops or if hydrologic regimes change. For example, a drought-associated fire in a depressional wetland may result in substantial combustion of organic sediment and promote aeolian, or wind-driven, activity (Tooth and McCarty, 2007). This may shift the balance of organic- and mineral-sediment influence on substrate infiltration as well as soil chemistry and water-column chemistry after rewetting.

3.5 Wetland soils

Soil development is highly dependent on hydrologic regime because water is a driver of all major mechanisms that form soils (Fig. 3.12). Hydrologic conditions determine in which states wetland soils occur: (1) flooded (water is above soil surface), (2) under saturated (no water above soil surface), and (3) water level is below soil surface at a particular depth (Inglett et al., 2005). Water drives transportation of material within soils, can supply aggrading material or drive surface erosion, and is generally a key compound in

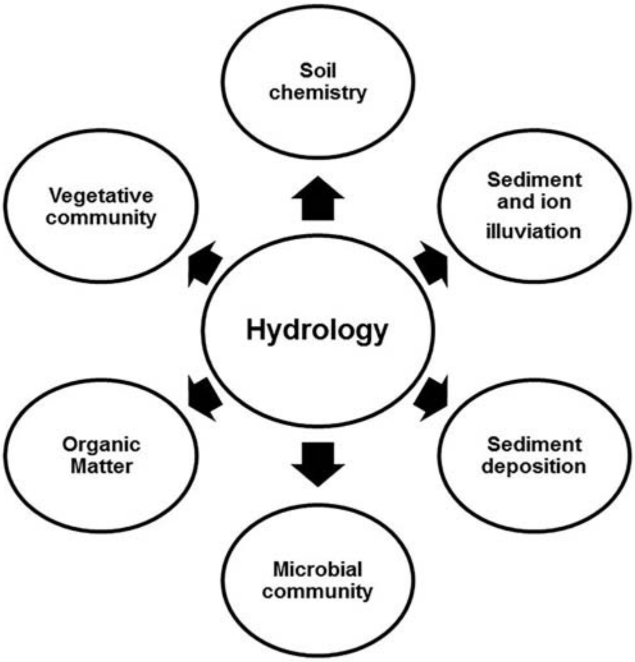

FIGURE 3.12 Conceptual figure linking soil formation and hydrology.

chemical transformations within soils (Vepraskas and Faulkner, 2001). Wetland soils are by definition hydric in nature and thus are even more strongly linked to the local hydrologic regime than other soils (Sprecher, 2001). Soil structure, texture, bulk density, pore size distribution, and porosity affect the hydraulic conductivity, amount of water stored, and accessibility to water (Jackson et al., 2014; Richardson et al., 2001).

Wetlands and thus wetland soils develop at positions within the landscape at which water accumulates (Richardson et al., 2001). These can be at the bases of slopes or where slope angles change such that hydrologic flow discharges at the substrate surface (Jackson et al., 2014). Wetlands can also occur higher on slopes where concave features intercept soil water flow lines. Perching layers can sometimes form where water accumulates due to organic matter build up or settling of clays (Kolka and Thompson, 2006). These then act as a positive feedback by restricting drainage and facilitating accumulation of organic matter and/or clays.

Where surfaces are relatively flat (floodplains, inland coastal plain environments) freshwater wetlands frequently develop in depressional features. If surrounding upland soils are conducive to runoff, generation of water may flow into these depressions through surface runoff during storm events (Deemy et al., 2019). Other upland soils may generate soil water flow downgradient that intersects the depression and drive saturated conditions over localized perching layers. Depressions may be underlain by perching layers or perching layers that develop through depositional processes (Deemy and Rasmussen, 2019). Where the water table occurs close to the surface, depressions may remain saturated or contain standing water without a perching layer.

Wetland soils develop from prolonged periods of saturation and/or develop high levels of organic matter (Fig. 3.13). Mineral soils (those soils

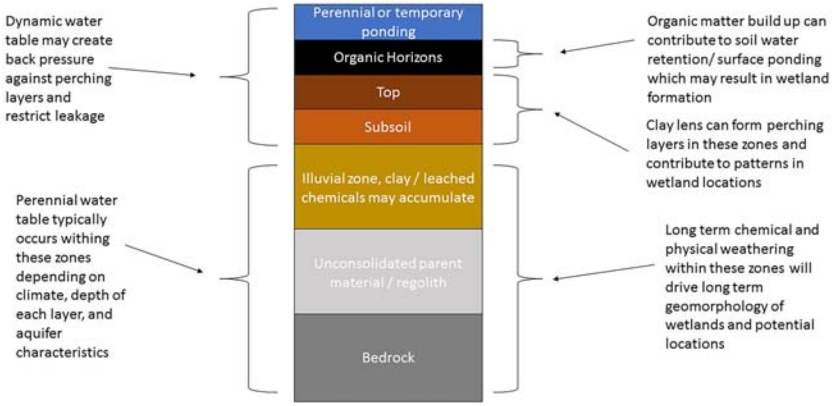

FIGURE 3.13 Idealized soil zones and their function in wetland development.

with less than ~20% organic dry mass) wetlands soils must be saturated for long periods of time to be considered wetland soils, whereas soils with more organic matter (>20%) require shorter periods of saturation to be considered wetland soils (Tables 3.6 and 3.7). Wetland soils also generally have substantial clay content that contributes to water perching mineral layers (Mitsch and Gosselink, 2015).

Soils in wetlands, particularly those with higher mineral content, typically develop layers from changing water levels (Fig. 3.14). The top layer will be an organic layer with a depth dependent on hydroperiod/hydropattern, vegetation composition/productivity, and fire frequency among other factors. The next layer will typically be a mix of mineral and organic content that experiences more frequent bioturbation and abiotic disturbances (Kolka and Thompson, 2006). After this layer there is often a gleyed layer where most soluble chemicals will have leached downward due to fluctuation in water levels. Accumulation of these chemicals where soil remains saturated except during the driest periods demarcate the next layer (Table 3.8).

TABLE 3.6 Soil horizons associated with wetland soils (Sprecher, 2001).

Horizon	Indicator	Formation mechanism	Expected material
Oi	Fibric organic matter	Slow or reduced decomposition	Peat
Oe	Hemic organic matter	Reduced decomposition rates	Peaty muck or mucky peat
Oa	Sapric organic matter	Decomposition rates inhibited	Muck
Bw	Weathered, weak B horizon	Dynamic water influence	Varies
Bt	Illuvial clay	Clay deposition by vertical water drainage	Coated sands
Bg	Substantial gleiing	Gleying produced by hydric removal of metals/ions	Gleyed sands/loams
Btg	Illuvial clay and substantial gleiing	Combined mechanisms of Bg and Bt	Gleyed coated sands
Bh	Organic accumulation	Humic material in subsoil from illuvial transport	Varies but consistently below highly leached E horizon

TABLE 3.7 Common soil orders of the tropics and subtropics (Mitsch and Gosselink, 2015).

Soil order	Major indicator	Setting/climate
Histosols	Highly organic	Perennially wet depressions, peatlands
Oxisols	High iron content	Tropical uplands/ecotones
Spodosols	Organic subsoil, Al/Fe sesquioxides	Subtropical flatwoods
Ultisols	Clay illuviation	Subtropical/tropical humid forests depressions
Vertisols	Shrink-swell clays	Clay beds in depressions

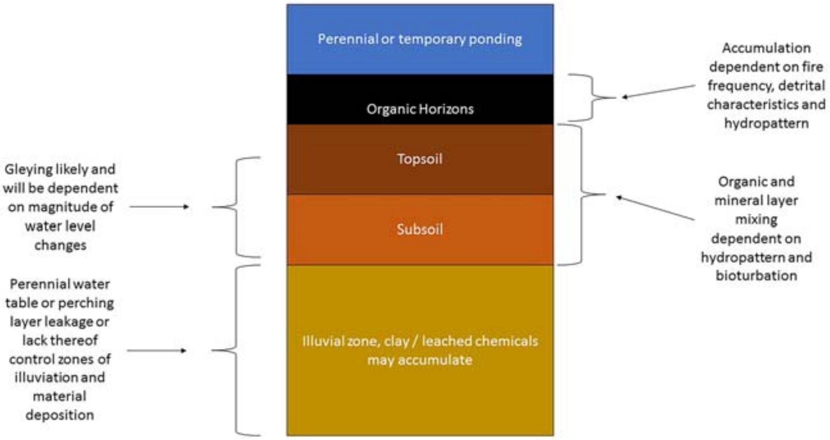

FIGURE 3.14 Schematic of soil drainage concepts in context of soils development.

Tropical wetland soil developments are heavily influenced by interactions of landscape position and precipitation patterns (wet vs dry season). In tropical wetlands that occur at landscape positions where seasonal drying is mitigated by perched water ponding or hillslope drainage, organic matter accumulation will be greater than where seasonal drying occurs (Dommain et al., 2010; Vepraskas and Faulkner, 2001). Precipitation regimes are also a critical component of organic matter development in soils. The interactions of vegetative growth and seasonal/perennial ponding will be a critical factor in the development of soil organic matter as well as the export of carbon dioxide and methane during decomposition (Sjögersten et al., 2018; Dommain et al., 2010).

TABLE 3.8 Soils drainage classes with water-level description and typical substrates.

Drainage class	Water table	General soil example	Landscape position example	Hydric features
Very poorly drained	Typically near-surface all year or prolonged periods of the growing season	Clay	Bottomlands/ stream banks	Highly frequent
Poorly drained	Periodically near-surface each year particularly so during growing season	Sandy or silty clay	Flatwoods, floodplains or toeslopes	Frequent
Somewhat poorly drained	Occurs close to the surface for substantial periods of growing season	Clay loam	Hilltops with perching layer	Common
Moderately well drained	Reaches the rooting zone for brief periods during most growing seasons	Loam	Midslope or low rise	Occasional
Well drained	Below most of the rooting zone annually but supports vegetation growth	Sandy loam	Hillslope near apex	Uncommon
Somewhat excessively drained	Well below the rooting zone excent under very wet conditions	Loamy sand	Sandy slope	Rare
Excessively drained	Well below the rooting zone except during extreme wet periods	Sand	Peak of aeolian or remnant marine dune	Exceedingly rare

Source: Soil Survey Staff, 1999. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. U.S. Department of Agriculture Handbook 436 (2nd edition). Natural Resources Conservation Service; Sprecher, S.W., 2001. Basic concepts in soil science. In: Richardson, J.L., Vepraskas, M.J. (Eds.), Wetland Soils: Genesis, Hydrology, Landscapes, and Classification. CRC Press; Watts, F.C., Carlisle, V.W., Hurt, G.W., 2001. Flatwoods and associated landforms of the South Atlantic and Gulf Coastal Lowlands. In: Richardson, J.L., Vepraskas, M.J. (Eds.). Wetland Soils: Genesis, Hydrology, Landscapes, and Classification. CRC Press.

While wetlands in many tropical regions are characterized by mineral forest soils, extensive peatlands can develop, such as those in Southeast Asia (Dommain et al., 2010). Landscape position close to or below the water table induces long-term flooding as long as seasonal recharge occurs. These conditions are similar to conditions that enable the peat accumulation in the Okefenokee forest mosaic wetland system. Additionally, organic matter deposition and hydrology interact to form these peatlands despite high decomposition rates driven by continuously warm conditions because higher temperatures allow for increased deposition relative to northern peat bogs of Europe or North America (Dommain et al., 2010; Bridgham et al., 2001).

Subtropical wetland soils development are driven by landscape position and seasonally variable combinations of precipitation and temperature. The reduced growing season and lower winter temperatures in subtropical areas contribute to reduced annual decomposition, which can lead to higher rates of organic matter accumulation in seasonally drying systems (Collins and Kuehl, 2001). In some cases, the dynamic wetting and drying of soils may lead to decomposition rates that lead to little organic matter build up (Mitsch and Gosselink, 2015). This is often the case in both tropical and subtropical wet mineral forests where organic layers are present but with minimal depth. Thus a hydrologic regime conducive to periodic wetting and in many cases prolonged wetting are critical for development of organic soils in these wetland environments (Collins and Kuehl, 2001).

3.6 Terrestrially embedded wetlands: surface depressions, karst sinkholes, and peatlands

In accordance with the theme of this text we highlight several specific types of nonmarine/riverine wetlands with a focus on subtropical and tropical examples. Depressional wetlands, karst sinkhole wetlands, and peatlands were selected because of district ecological conditions relating to hydrology and geomorphology.

3.6.1 Depressional wetlands

Depressional wetlands form in areas with lower elevation relative to the area immediately surrounding them (Mitsch and Gosselink, 2015). They are generally disconnected from surface water sources via perennial flow but may have consistent connections to dynamic groundwater inputs but generally lack perennial groundwater influence (Tiner, 2003). Depressional wetlands are thus typically driven by atmospheric hydrologic flux (precipitation and evapotranspiration). These systems generally develop because there is a confining layer minimizing infiltration of rainwater sufficient for development of hydric soils and wetland vegetative communities (Richardson et al., 2001).

Groundwater connections often take the form of leakage and depressional wetlands can have a role in local aquifer recharge if they form a focal point for surface runoff collection (Golden et al., 2016). Wetland depressions can store precipitation and surface water runoff during low recurrence surface flow events associated with storms or atypically wet periods (Cohen et al., 2016).

For this reason many isolated depressional wetlands have a mitigating effect on floods despite lack of perennial connection to other surface waters (Rajib et al., 2020; Evenson et al., 2018). The stored water can contribute to both local soil water availability and leakage to groundwater.

However, if the perching layer is sloped, fractured, or otherwise allows substantial leakage a depressional wetland may be driven by vertical subsurface flux in addition to vertical atmospheric exchange (Jackson et al., 2014). Precipitation and evapotranspiration account for the majority of exchange in most depressional wetlands but groundwater exchanges could be substantial if the water table is high enough or sufficiently dynamic (Mitsch and Gosselink, 2015). In such a case surface flows would only become substantial during periodic surface connections driven by runoff events and atypically intense precipitation and likely have less long-term influence than in wetlands generally isolated from groundwater.

Storm events and intense precipitation events may also connect normally isolated depressional wetlands through episodically flowing channels (Wilcox et al., 2011; Deemy and Rasmussen, 2017). Episodic flows are defined as relatively low frequency overland flow events or events with low recurrence intervals (Deemy et al., 2019). Connections to downstream wetlands may be observed through hydrograph similarity and similarities in water quality through end member mixing models (Fig. 3.15). Additionally, mapping episodic flow channel geomorphology can assist in understanding source waters where channels are distinct enough to identify. Where practical these approaches should be combined to increase confidence in conclusions about source waters.

Therefore water budgets for depressional wetlands are typically sensitive to precipitation and evapotranspiration measurements which can be problematic when modeling function of these wetlands within greater watersheds. Wetland watersheds and contributing areas can also be difficult to determine in smaller isolated wetland systems, which adds to the difficulty in accurately determining atmospheric hydrologic flux. The vertical nature of these systems,

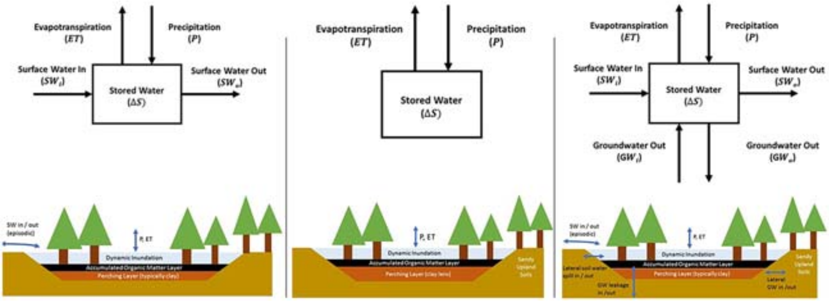

FIGURE 3.15 Water budgets for depressional wetlands associated with a range of hydrologic inflows and outflows.

especially if connected to groundwater, makes it necessary to understand the soil hydrology and the underlying geology. Another compounding factor in water budgets for these systems is determining the role, if any, of episodic flows. The low recurrence interval of these lateral surface exchanges can be difficult to model and even more difficult to evaluate within models (Deemy and Rasmussen, 2019).

3.6.1.1 Dougherty Plain, Georgia, United States

The Dougherty Plain located in southwest Georgia of the United States is an example of a subtropical region with a mantled karst topography (Deemy and Rasmussen, 2019). The karstic topography of the Dougherty Plain allows for a high density of isolated wetlands occurring in tight clusters (Martin et al., 2012), due to the dissolving of limestone near the surface and the eventual collapse of the subsurface area, forming depressional wetlands (Hendricks and Goodwin, 1952; Beck and Arden, 1983). Fig. 3.16 illustrates a commonly observed example of open canopy depressional wetlands on the Dougherty Plain. Table 3.8 provides a summary of depressional wetland environments.

The Dougherty Plain is a 670,000-ha physiographic province in Southwest Georgia in the subtropical southeastern United States (Fig. 3.17). Few headwater streams occur in this region but high density clusters of wetland depressions may account for over 12,000 total depressional wetland features (Martin et al., 2012). The vast majority of these wetlands appear to be isolated from perennial connections to other surface waters with a small subset exhibiting episodic overland flow as the result of intense or frequent storms that saturate soils sufficient for production of surface runoff (Deemy and Rasmussen, 2019).

The water budgets of depressional wetlands in this region are primarily dependent on precipitation and evapotranspiration (Fig. 3.18). However, some depressional wetlands on the Dougherty Plain receive substantial

FIGURE 3.16 Open-canopy depressional wetland after late-fall precipitation. *Photo credit James B. Deemy.*

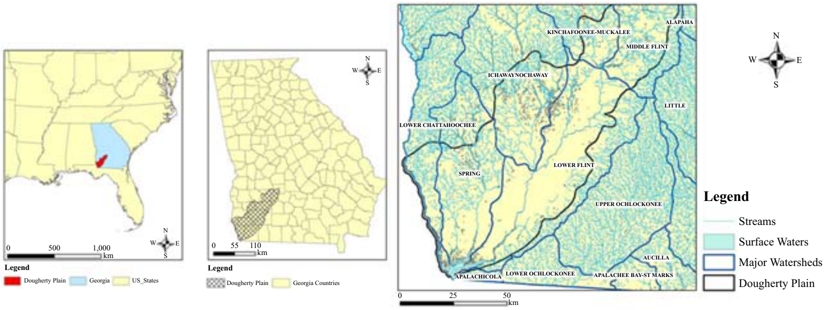

FIGURE 3.17 Dougherty Plain in the southeastern United States, characterized by a lack of streams relative to the surrounding physiographic landscapes. *Modified from Deemy, J.B., Rasmussen, T.C., 2019. Depressional wetlands and episodic flows: conceptual hydrologic model for the Dougherty Plain of Georgia. Southeastern Geology 53 (4), 232–248.*

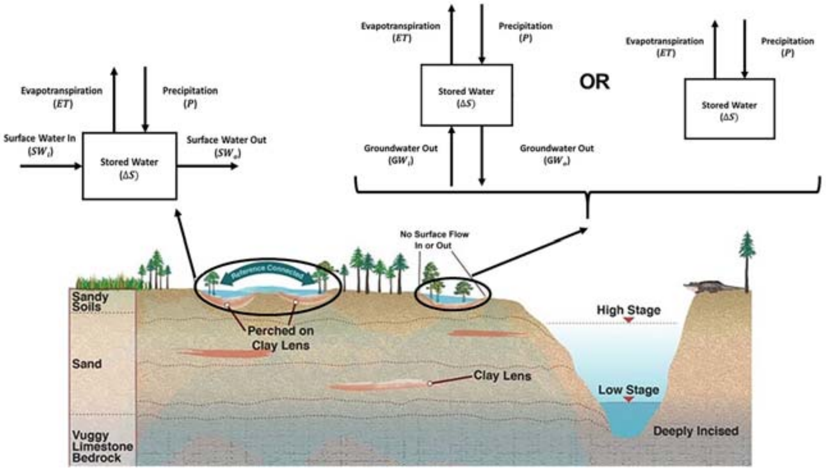

FIGURE 3.18 Conceptual model of depressional wetlands in the Dougherty Plain linking water budget diagrams with wetland setting. *Modified from Deemy, J.B., Rasmussen, T.C., 2019. Depressional wetlands and episodic flows: conceptual hydrologic model for the Dougherty Plain of Georgia. Southeastern Geology 53 (4), 232–248.*

surface inputs from episodic surface flows, extreme low recurrence riverine flood events, or periods of extreme high ground water (Hendricks and Goodwin, 1952; Deemy and Rasmussen, 2019). Wetlands at high stages are likely to spill with precipitation because they are not typically incised and relative differences between wetland elevation and uplands are generally small (1 m or less). Precipitation driven spillage can be a source groundwater recharge or may contribute wetlands functioning as temporary headwater for episodic flows (Deemy and Rasmussen, 2019).

Depressional wetlands with episodic connections typically fall into two categories. The first are wetlands that are a part of a complex containing two or more close proximity depressions but are isolated from perennial surface waters. The second are wetlands connected to storm runoff generated overland flows that terminate in nearby stream features. Wetlands with episodic connections regardless of type have similar stage distributions but differ from wetlands without episodic connections (Deemy and Rasmussen, unpublished data).

Similarities observed in the frequency of dry days also indicate that climate has a similar influence on these two wetland types (Deemy and Rasmussen, unpublished data). Differences in wetland geomorphology likely drive the differences in hydropattern because basin shape would drive differences in hydropattern, vegetation, and connectivity potential.

3.6.2 Karst wetlands

Karst wetlands are formed through chemical weathering of carbonate rich or other bedrock susceptible to chemical weathering (Tiner, 2003). Acidic rain water mixes with organic matter in soils (generally becoming more acidic) and percolates through substrate reacting with regolith and bedrock (Han and Liu, 2004). Chemical erosion of the bedrock typically begins in cracks and fractures, eventually expanding to visible voids that can become caverns (Wall et al., 2017).

Occasionally, drought or groundwater withdrawal will drain these caverns and lack of hydraulic support can cause them to collapse (Sullivan et al., 2019). A sinkhole forms when voids present in weathered bedrock collapse leaving sinkhole features or steep depressions (Tihansky, 1999). These collapses leave sinkholes that may be in direct contact with the perennial water table (Upchurch et al., 2019). Water inflow then occurs directly from the karst aquifer and can create conditions sufficient for wetland soils and vegetative communities to develop. This differentiates them from depressional wetlands which, if connected to groundwater, are connected to the dynamic water table with periodic (regular) or episodic (event based) influence and not in direct contact with the perennial aquifer. The resulting wetlands may include karst pans, compound sinks, and sinkholes (Wolfe, 1996).

Over time sediment, organic matter, and other debris begin to accumulate, which forms a substrate layer capable of supporting wetland ecosystems. Karst wetland soils generally form more slowly than other types of wetlands due to weathering of carbonate bedrock (Wang et al., 2004). In warm, moist climates such as tropical and subtropical areas, the soils found in karst wetlands are generally shallow (Wang et al., 2004), susceptible to erosion (Cao et al., 2004), and may exhibit less organic matter (Sedov et al., 2008). Wetland formation can be expedited in locations with mantled karst geology because surface soils/materials typically slump or erode into the collapse (Tihansky, 1999; Winter, 1998). If conditions are sufficiently wet then organic materials accumulate and may combine with allochthonous clays to fill pore spaces. Increased water retention can result depending on hydrologic regime and fluctuations in groundwater levels.

Typically, hydrology of karst wetlands is dependent on a combination of groundwater inputs/outputs, evapotranspiration, precipitation events, and runoff. If karst wetlands are well connected through groundwater they respond somewhat synchronously to changes in precipitation or groundwater withdrawals (Klammler et al., 2020). Groundwater inputs are typically sourced to flow through faults which intersect the wetland, such as in the Sia Ka'an wetlands on the Yucatan Peninsula, Mexico (Gondwe et al., 2010). Surface outflows from wetlands in karst terrains are not common but can occur where former sinkholes form headwaters for incised streams. However, monsoon climates can provide exceptions, such as has been observed in doline wetlands on the Korean Peninsula where atmospheric hydrologic flux is the major hydrologic driver (Lee et al., 2020).

The morphology of a karst wetland depends on depth to bedrock, magnitude of underground void systems, and local climate. Interactions of these drivers can often lead to nonregular spatial distribution in wetlands. However, in some systems, long-term biogeomorphic feedbacks control development of wetland spatial distribution and basin area (Quintero and Cohen, 2019). Increasing soil depth stabilizes depressions and competition for water among communities in separate depressions likely drive regular patterning (Dong et al., 2019). At the landscape scale this yields truncated power law distributions in wetland basin area and regular hexagonal spatial patterning (Quintero and Cohen, 2019).

3.6.3 Peatlands

Subtropical and tropical peatlands have historically received less scientific attention than high latitude peatlands (especially those in the northern hemisphere). Exceptions include, most notably the subtropical Okefenokee Swamp and peatlands of southeast Asia but proportional to their frequency and areal coverage these systems are largely understudied. Tropical peatlands account for approximately 10%–15% of global peatlands and occur across tropical areas of the east Asia mainland as well as southeast Asia, Caribbean islands, Central America, South America, and southern Africa (Hooijer, 2005).

Tropical peatlands generally take the form of freshwater rainfed forested wetlands (Melling, 2016) but herbaceous fens can also develop in some cases. Peatlands develop where organic matter production exceeds decomposition (Page et al., 2006). Peat is also distinct as a substrate because of the higher quantities of recognizable plant matter (particularly fibrous material) (Mitsch and Gosselink, 2015). Long growing seasons and high growth rates of plants in both subtropical/tropical environments contribute necessary detritus for peat formation (Table 3.9). In tropical regions heterogeneous, mixed

TABLE 3.9 Carbon accumulation in peatlands for boreal, temperate, and tropical regions.

Climate	Peat accumulation (g-C m^{-2} $year^{-1}$)	Source
Boreal	50–80	Thormann et al. (1999)
Temperate (Bog, MA, United States)	180	Hemond (1980)
Tropical (Brazillian mountain peatland)	192	Lourençato et al. (2017)

stage (slightly to partially) decomposition of woody material is often present in peat (Melling, 2016). Peatlands develop along a gradient from completely rainfed (ombrogenous) through those open to regular surface through flow and subsurface through flow (soligenous) (Mitsch and Gosselink, 2015; Bridgham et al., 2001). Depressional peatlands may also develop where the surface topography allows some groundwater flow but is typically precipitation fed (Mitsch and Gosselink, 2015).

Tropical peatlands form in locations with water tables that are close to the soil surface if not occurring above the soil. Generally this occurs where a perching layer and flat topography combine to allow water accumulation. Regional water tables can also contribute but are less common water input. However, exceptions exist depending on regional setting and underlying substrate (i.e., most are underlain by clays but some have been found to occur over sand, which would consequently change the magnitude of groundwater flux) (Cobb and Harvey, 2019). Precipitation is the main driver of variation in the water level because temperatures tend to be relatively stable in tropical peatlands and perching layers restrict variability in groundwater outflows. Additionally, peatlands tend to exhibit little change in discharge until high stage or full saturation is reached at which point outflows can become flashier (Cobb and Harvey, 2019). This is partly due to high permeability (Baird et al., 2017) and relatively uniform conductivity of peat in many tropical peatlands (Cobb and Harvey, 2019). The slightly convex or domed morphology of peatlands typically means that they have little surface inflow (Moore et al., 2011).

Seasonal precipitation patterns drive the vast majority of water-table fluctuations and ENSO-driven climate patterns can drive large magnitude events (Khan et al., 2006), which change decomposition/accumulation of peat (Zhu et al., 2017). Generally, evapotranspiration and overland flow will be responsible for the majority of water loss from tropical peatlands (Kelly et al., 2014), due to a combination of water holding capacity of peat and runoff from saturated surfaces (Baird et al., 2017; Cobb and Harvey, 2019).

Soil saturation close to the surface is critical to preventing the decomposition of peat and also provides hydrostatic support to peat structure (Mezbahuddin et al., 2015). When pores are drained as a result of anthropogenic disturbance, drought, or seasonal cycles, subsidence may occur associated with collapse of pore space that is no longer supported by hydrostatic pressure (Hooijer et al., 2012). Peatlands are particularly dependent on saturation for soil structure because water can account for up to 90% of undrained substrate (Hooijer et al., 2010). If deep layers become dewatered they will not only be prone to deeper burning fires and oxidative decomposition (Hooijer et al., 2010) but also subsidence, compaction, and consolidation which when combined can generate substantial changes to the wetland basin morphology (Hooijer et al., 2012).

Draining of tropical peatlands in southeast Asia can result in the rapid oxidation of stored organic matter which leads to carbon dioxide release in magnitudes similar to annual combined fossil fuel use and fire emissions in the region (Hoyt et al., 2020). However, when degraded sites are hydrologically restored and flooding returns tropical peatlands do show reduction in carbon mineralization which drives a reduction in subsidence of the wetland substrate (Jauhiainen et al., 2016).

3.6.3.1 Alaka'i Swamp, Hawai'i, United States

The island of Kauai, Hawai'i, began its formation during the late Tertiary period, likely during the Pleistocene epoch (MacDonald et al., 1960). At the end of its growth as an emerging basaltic shield volcano, the summit collapsed, creating a caldera that was between 16 and 19 km across. Throughout the remainder of the Pleistocene epoch, the topography of Kauai became characterized by changes in sea level, erosion, active faults, and periodic volcanism (MacDonald et al., 1960). As a result, Kauai's highest elevation is approximately 1219 m lower than it once was.

However, parts of the original Kauai volcano caldera form the base of the Alaka'i Swamp, the highest known elevation (1288–1585 m above sea level) bog in the world (MacDonald et al., 1960). This swamp is located on a summit plateau with Waimea Canyon (which is ~793 m deep to the west), Olokele Canyon to the south and Kalalau Valley to the northwest. The Alaka'i Swamp is considered an upland swamp characterized by a mosaic of montane wet forest and shallow bogs (Browning et al., 2019). The primary hydrologic inputs are fog-drip (Fig. 3.19) and precipitation which, on average, exceeds 5000 mm year^{-1} (van't Woudt and Nelson, 1963; Chimner, 2004; Browning et al., 2019) (Fig. 3.20).

The combination of primary vegetation: *Metrosideros polymorpha*, (common name: 'Ōhi'a lehua) a flowering evergreen tree that is typical of Hawaii's rainforests, high elevation and high precipitation, generate unique soils of the Alaka'i Swamp. The parent material for the Alaka'i soil series is

FIGURE 3.19 Alaka'i Swamp in Hawai'i, where fog drip is the primary hydrologic input. *Photo credit: Kimberly K. Takagi.*

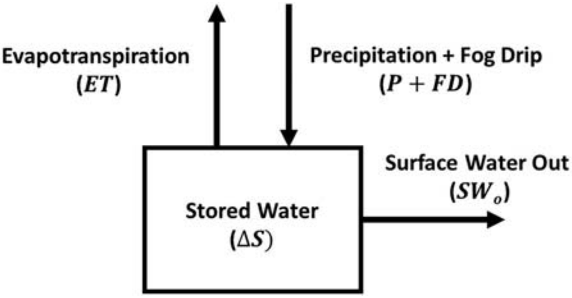

FIGURE 3.20 Hydrologic balance in the Alaka'i Swamp; Surface water outflow supply headwater inputs for Waimea River and the Makaweli-Olokele River Basins. The high elevation setting means that the swamp lacks surface water inputs and nearly no groundwater seepage occurs due to thick organic soils preventing deep seepage to groundwater.

weathered basalt, which is overlain by clay and organic material (USDA, 2020). Organic material accounts for >50% of soil composition in surface horizons (Deenik and McClellan, 2007).

Initially, the lava and pyroclastic materials that form the basis of the Alaka'i Swamp soils were readily permeable to water. However, over time secondary clays formed, an iron hard pan was produced as a result of geochemical weathering, and increased organic matter accumulation (paludification) all contributed to eventual decreased permeability and an increase in soil water content (Kitayama et al., 1997). As a result, the soil tends to have a high organic carbon content, high acidity (3.7–5.3), and low permeability (Chimner, 2004; Kitayama et al., 1997; Deenik and McClellan, 2007). Soil mineral composition is generally noncrystalline and primarily made up of illite and kaolinite with minor amounts of anatase, gibbsite, and hydrated illite (van't Woudt and Nelson, 1963).

Thus on the steeper slopes of the Alaka'i Swamp, water storage is minimal whereas on flat and gently sloping surfaces, the top soils are commonly saturated (van't Woudt and Nelson, 1963). Previous calculations conducted by van't Woudt and Nelson (1963) indicate that at saturation, the Alaka'i Swamp can store up to 2200 acre-feet of water (2.7×10^6 m^3) and release between $9.0 \times 10^5 - 1.4 \times 10^6$ m^3 of water to streamflow. A close relationship between rainfall and streamflow indicates that there is little deep seepage to the basal water table and that the Alaka'i Swamp acts as a collecting feature and headwater. The surface overflow supplies both the Waimea River and the Makaweli-Olokele River Basins (van't Woudt and Nelson, 1963).

3.7 Conclusion

In summary, wetland ecology, geomorphology, and physicochemical environment are strongly linked to hydrologic conditions. Depressional and karst wetlands, as well as peatlands in tropical and subtropical environments provide a spectrum of wetlands with which to understand the hydrologic function of nonriverine and nonestuarine wetlands. These wetlands function in a variety of water storage roles ranging from small patches of surface storage to saturated landscape level features as well as serving as sites where runoff may concentrate and recharge groundwater. Due to their saturation and slow flow velocities these sites can accumulate large quantities of carbon in their soils if inundation persists throughout the year or most of the year. Small wetlands which inundate and draw down more rapidly often serve as biogeochemical hotspots due to the broad range of conditions available to microbial communities throughout the year. Thus each of these focal wetland types provides an excellent spectrum of conditions to study hydrology and geomorphololgy of freshwater wetlands in a changing world.

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Chapter 4

Physicochemical environment

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4.1 Introduction

The physicochemistry of wetlands is determined by water (Mitsch and Gosselink, 2015), especially the timing, duration, and magnitude of inundation (hydropattern), which define the physical and chemical processes within wetlands (Nhiwatiwa and Dalu, 2017; Rasmussen et al., 2018; Richardson et al., 2001). Hydropattern is a determining factor in every aspect of wetlands, from mixing in the water column, to redox reactions in the substrate (Vepraskas and Faulkner, 2001). It is also a major element that drives both the physical and chemical conditions within the wetland from sediment settling conditions (Jackson, 2006), through nutrient assimilation rates (Mitsch et al., 2009), and redox reactions (Vepraskas and Faulkner, 2001).

Wetlands are typically lentic (slow or stagnant) water bodies that develop anoxic or hypoxic conditions (Mitsch and Gosselink, 2015; Moyo, 2022, Chapter 5). Long residence times due to low velocities allow for the settling of particles, leaching of compounds from bulk organic material (leaves, woody debris), and for development of photosynthetic communities in the water column (Collins and Kuehl, 2001; Dalu et al., 2022; Mitsch and Gosselink, 2015; Richardson et al., 2001, Chapter 8; Piedade et al., 2022, Chapter 7). Saturated soil conditions also generate environments that are biogeochemically distinct from soils in nearby oxidative uplands (Boon, 2006; Craft, 2001; Vepraskas and Faulkner, 2001).

Microbial communities facilitate both chemoautotrophic reactions and chemosynthetic respiration which give wetlands a role as chemical transformation sites (Boon, 2006; Collins and Kuehl, 2001; Vepraskas and Faulkner, 2001; Deemy et al., 2022a, Chapter 6). The results of these soil reactions can be closely linked to, or even drive changes of physicochemical conditions in the water column by altering pH, dissolved gas balances, or supplying

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reactants to aerobic biogeochemical reactions (Mitsch and Gosselink, 2015; Craft, 2001).

This chapter explains fundamental physicochemical concepts in wetlands as context for specific tropical and subtropical wetlands. Specific objectives of this chapter are to provide an overview of the physicochemical environment in subtropical and tropical wetlands and highlight threats to wetlands.

4.2 Hydrology and physicochemistry

Hydrologic conditions are the driving determinant of wetland physicochemical environments (Deemy et al., 2022; Mitsch and Gosselink, 2015, Chapter 3). Duration, frequency, and source of inundation/saturation are critical constraints to biogeochemical function (Boon, 2006; Craft, 2001) and will drive water column chemistry (Mendelssohn and Batzer, 2006), as well as soil redox reactions (Vepraskas and Faulkner, 2001). Pulsing cycles between floods and droughts drives changes in productivity (Davidson et al., 2012; Odum et al., 1995), shifts in oxidative versus anoxic soil and water column biogeochemistry (Vepraskas and Faulkner, 2001), and changes in basin geomorphology (Richardson and Brinson, 2001).

When inundated, generally low velocities allow for the photosynthetic community (benthic and floating algae, submerged and floating macrophytes) in the water column to be a source of dissolved oxygen and organic matter productivity. Photosynthesis is limited by light penetration in the water column, as well as shading from over story plants (Pedersen et al., 2013). However, where light availability is sufficient, the photosynthetic community can alleviate hypoxic or anoxic conditions (Chislock et al., 2013).

The ecological implication being the prevention of obligate anaerobe microbial communities from developing in the water column (Cabral, 2010) and potential alleviation of dissolved oxygen stress to invertebrates and fish (McCormick and Levin, 2017). In open canopy wetlands, oscillating patterns in dissolved oxygen as well as pH can be driven by diurnal patterns in photosynthesis (Mulholland et al., 2005). Closed canopy wetlands will generally experience more intense and longer periods of low dissolved oxygen due to the shading constraints on photosynthetic activity (Dodds et al., 2019).

Despite photosynthetic contributions to dissolved oxygen, even open canopy, herbaceous plant dominated wetlands tend to have low dissolved oxygen levels (Hagarthey et al., 2010), which is due to biological oxygen demand typically exceeding oxygen diffusion in the water column (Mendelssohn and Batzer, 2006). Primary productivity is high in wetland plant and algal communities which generate large quantities of labile organic matter available for decomposition, thus elevating biological oxygen demand (Wright and Reddy, 2009).

Anoxic/hypoxic conditions drive much of the unique biogeochemical reactions emblematic of wetland ecosystems (Chapman et al., 2019).

Consequently, it is this natural low oxygen environment that facilitates conditions which distinguish wetlands from other aquatic systems (Lee et al., 2017). These conditions are in fact critical requirements for the development of obligate microbial communities that drive nitrogen, sulfur, and carbon cycling in wetland redox reactions (Pezeshki and DeLaune, 2012). In wetlands with dynamic water levels or rapid cycles of flooding and drying, these redox communities can often only develop in deeper saturated soils/sediments where oxygen remains consistently depleted (Schonbrunner et al., 2012).

In wetlands with persistent water levels and slow flooding/drying cycles, thermal stratification often contributes to hypoxic or anoxic conditions (Wlosinski and Koljord, 1996). Thermal stratification is more common during summer months and can be exacerbated by open canopies that allow direct sunlight to warm the water column (Wagner and Adrian, 2011). Closed canopies may experience less thermal stratification but will also have lower rates of photosynthetic production and associated oxygenation within the water column (James et al., 2017). In tropical systems with seasonal pulses of precipitation/flooding, water table depth changes can be a critical determinant of soil respiration (Mezbahuddin et al., 2014).

Chemolithotrophic bacteria (primarily methanotrophs and nitrifying bacteria) account for substantial portions of biological oxygen demand (Bodelier and Frenzel, 1999). In some wetlands, these microbes can account for as much as 50% of the water columns bacterial community (Ross et al., 1997). Dissolved methane supplied by anaerobic methanogens in the sediment (Blodau, 2002) drives aerobic respiration of methanotrophic bacteria on the sediment surface or just above it in the water column (Miller et al., 2004). Methanotrophic activity also accounts for substantial nitrogen fixation during peatland development (Larmola et al., 2014).

Hypoxic and anoxic sediments occur during periods of inundation. The duration, timing, and extent of inundation can be very important for determining the overall character of organic substrates in wetlands (Table 4.1) (Seitaj et al., 2016). Wetlands that have longer hydroperiods will have sediments that experience anoxia more frequently, and in some wetlands, continuously (Covertino et al., 2013). Consistent saturation will generally drive lower and less complete decomposition of vegetation. In which case, sediments and soils will contain more recognizable fibrous plant matter (Hemond and Fechner, 2015). Thus these soils will be more likely to develop peaty soils rather than mucky soils. Conversely, wetlands with regular inundation and occasional drying will be more likely to develop mucky soils because decomposition will more completely decompose plant material (Jackson et al., 2014). Alternatively, wetlands with only rare inundation, frequent short periods of wetting, or incomplete soil saturation will experience anoxic conditions infrequently and thus have higher decomposition rates (McNicol and Silver, 2014). Greater decomposition will lead to more

TABLE 4.1 Organic soil substrate examples with defining characteristics and potential setting (Sprecher, 2001; Collins and Kuehl, 2001).

Organic substrate	Characteristics	Setting
Peat	Organic matter with recognizable fibric material	Bog, fen
Muck	Organic matter with no recognizable fibric material, may have slightly higher mineral sediment content	Depressional wetland, bog
Mull	Forest humus where organic matter accumulates in a well-developed A horizon	Moist flatwoods (coastal plain), humid forests
Mor	Forest humus where organic matter accumulates on the surface (Oe horizon)	Wet flatwoods (coastal plain), forested toeslopes
Moder	Transition forest humus between mor and mull	Moist/wet flatwoods (coastal plain)

mineral wetland soils with thinner organic horizons (Kolka and Thompson, 2006a, b). As a result, many tropical and subtropical wetland soils tend to have higher proportions of mineral content compared to high latitude wetlands.

4.2.1 Redox reactions and carbon cycling

Reduction and oxidation, or redox reactions, are one of the most important drivers of the wetland environment. The dynamic wetting and drying of wetlands temporally drive the varying conditions for chemical reactions in the wetland environment. These conditions ultimately determine the rate at which decomposition will occur and whether a given wetland will store or remineralize carbon (Fig. 4.1). Redox reactions are therefore also responsible for the mobilization of compounds bound in solids (e.g., minerals dissolving) and the degassing of dissolved ions to the atmosphere (Zhang and Furman, 2021).

Reactions where electrons are lost from atoms are oxidation because many of the first reactions involving this process were discovered to also involve oxygen. Reduction occurs when a compound becomes more negatively charged through the acquisition of electrons. Paired reactions in redox chemistry involve two separate "half-reactions" (McMahon and Chapelle, 2008) (Fig. 4.2).

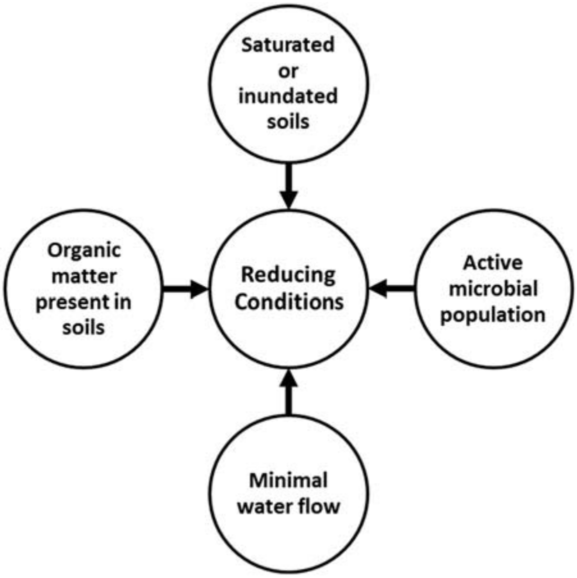

FIGURE 4.1 Conditions required for extensive reducing reactions in wetlands.

FIGURE 4.2 Idealized series of redox reactions that occur in wetland soils (Vepraskas and Faulkner, 2001).

An important element of redox chemistry is that electron acceptors and electron donors must be included. Without organic matter (electron source), microbial facilitators, or an electron acceptor molecule (elemental oxygen or sulfate), these reactions cannot take place. The lack of oxygen as an electron acceptor in saturated soils is a major mechanism behind organic matter accumulation in wetland soils. The necessary microbial facilitators and organic matter electron sources are present but must use less efficient acceptor compounds than elemental oxygen. Some examples of alternate compounds include nitrate, manganese dioxide, iron hydroxide, sulfate, and carbon dioxide. These are used in less efficient microbial respiration processes than oxygen, and therefore contribute to slower decomposition rates (Vepraskas et al., 2016).

Typical reduction reactions in wetland soils occur with compounds that contain oxygen and involve the removal of protons from solution. Water is almost always produced as a byproduct during these reactions. These reducing reactions are the mechanism by which redoximorphic features (a major hydric soils indicator) are produced (Vepraskas et al., 2006). Denitrification, manganese reduction, iron reduction, sulfate reduction, and methanogenesis (CO_2 reduction) are all common wetland soils reduction reactions (Vepraskas et al., 2016).

Oxygen reduction reactions occur in the wetland if sufficient oxygen is present, causing acidic wetland soils to increase in pH or become more basic because free protons (H^+ ions) are removed from the solution. Therefore wetland soils can become less acidic during drawdown events that allow oxygen to diffuse into soil water (Niedermeier and Robinson, 2007). Biotic activity can also introduce oxygen to soil water and facilitate oxygen reduction locally. This has an ameliorating effect on pH conditions, which can generate a positive feedback by making soil conditions more conducive to plant growth. If conditions of soil saturation or inundation persist, organic soils may develop, due to anaerobic conditions facilitating the accumulation of organic carbon (Orcutt and Nilsen, 2000).

After oxygen depletion in soil, nitrate is generally the first compound to be reduced in the presence of available hydrogen ions. Like oxygen reduction reactions, the reaction produces a gas (elemental nitrogen) and water. This reaction is of great interest when considering the water quality improvement function of wetlands. In this case, or in the case of treatment wetlands, the role of vegetation is to provide a sufficient organic substrate for microbial populations to facilitate this reaction among others (Faulwetter et al., 2009).

$$2\,NO_3^- + 10\,e^- + 12\,H^+ \rightarrow N_2 + 6\,H_2O \tag{4.1}$$

After nitrate has been depleted (or at least locally depleted), manganese oxide will be reduced. The resulting Mn^{2+} will remain in solution and can be transported with any water movement. For wetland delineation purposes, manganese oxide is a dark (black) mineral that can sometimes be easily identified but may be hard to spot in organic rich soils. When reduced, the dissolved mineral components no longer exhibit color (Aller, 1990).

$$MnO_2 + 2\,e^- + 4\,H^+ \rightarrow Mn^{2+} + 2\,H_2O \tag{4.2}$$

Iron hydroxide is the next compound to be reduced under the idealized linear progression of reactions presented here. The iron oxide/hydroxide compound will be reduced to elemental iron and water by microbial activity. The oxidized states of iron generate the classic red, yellow, and brown redoximorphic features used in delineation of wetland soils. These features most often occur along roots or former root channels in soils as well as animal burrows. Once iron oxides/hydroxides have been reduced, they lose color. The dissolved iron will remain in solution which can then be transported if flow occurs. There are a variety of iron compounds that are readily reduced in wetlands, and we provide a common example below (Bigham et al., 2002).

$$Fe(OH)_3 + e^- + 3\,H^+ \rightarrow Fe^{2+} + 3\,H_2O \tag{4.3}$$

Sulfate is reduced once iron oxides/hydroxides have been at least locally depleted. Given sufficient organic matter availability, obligate anaerobic bacteria will reduce sulfate to hydrogen sulfide gas and water. When investigating wetlands hydrogen sulfide can be detected when the soil substrate is disturbed which releases trapped bubbles of the gas (Skyring, 1987).

$$SO_4^{2-} + 8\ e^- + 10\ H^+ \rightarrow H_2S + 4\ H_2O \qquad (4.4)$$

Methanogenesis is one of the least efficient microbial respiration processes and occurs in obligate anaerobes when other compounds have been depleted. Carbon dioxide is reduced to methane and water by these microbes. Methane is an odorless and colorless gas that can build up in wetland soils. Methane, which is flammable, theoretically combusts during drought-induced fires and may factor into deep substrate burns during peatland fires (Capone and Kiene, 1988).

$$CO_2 + 8\ e^- + 8\ H^+ \rightarrow CH_4 + 2\ H_2O \qquad (4.5)$$

Lastly, in some wetlands (i.e., ombrotrophic bogs), humic acids have been shown to act both as terminal electron acceptors and potential methanogen inhibitors in the chemical remineralization of carbon in wetland soils (Keller et al., 2009; Keller and Takagi, 2013).

While the progression of the reactions here are presented in a linear and idealized manner (Fig. 4.3), this is unlikely in nature because the reactions are biologically and chemically mediated. As one compound is locally consumed by the microbial population, it will become scarce, and the population will decline. Prior to complete consumption other microbes which reduce, the next compound will begin to increase in population given adequate organic matter and anaerobic conditions (Brown et al., 2000). Disturbances such as bioturbation, hydrologic disturbance, or drought could reset succession within the microbial community and oxidize reduced metal elements

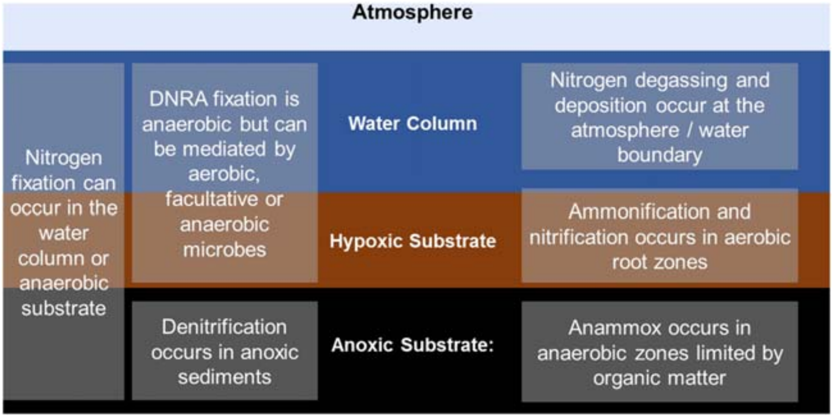

FIGURE 4.3 Vertical zonation of nitrogen reactions within a wetland as a function of oxygen influence.

present. The progression of reducing reactions can then begin again (Mosher et al., 2012).

The oxidation−reduction reaction balance in wetland soils also drive soil pH and are dependent on hydrologic fluctuations. Reducing reactions consume available protons, while the oxidation of organic matter supplies proton availability in the soil. Acidic wetland soils under reducing conditions will shift toward neutral pH but may not achieve neutral due to free protons produced during the breakdown of organic matter (Husson, 2013). Iron oxide and hydroxide species also contribute to the maintenance of acidic pH in some wetland soils under reducing conditions. Alkaline soils, however, will decrease in pH under reducing conditions through carbonic acid producing reactions resulting from organic matter decomposition (Colombo et al., 2014).

Wetland soil pH can change relatively rapidly in response to inundation with multiple pH unit changes occurring in less than three weeks. Submerged conditions that generate hypoxic or anoxic soil conditions can drive changes as large as three pH units, although most changes will be less than two pH units (Felle, 2005). Soil pH is a critical factor in nutrient availability in wetlands. For example, phosphorus availability is driven by pH. Additionally, the low pH generally observed in wetland soils can at least partially drive plant community development (Trettin et al., 2020). Depressional pitcher plant bogs in the subtropical southeastern United States are a particularly strong example with pH levels <4. As a result, phosphorus in these wetlands is often unavailable to plants because the low pH prevents plant uptake from the soil. Nitrogen reduction from nitrous oxide to nitrogen gas is also inhibited below a pH of 6 (Cameron et al., 2013).

Soils in karstic regions can develop high pH values and high calcium concentrations from the dissolution of carbonate bedrock. Karst wetland soils in tropical regions are also associated with precipitation driven leaching and biological uptake of nitrogen, phosphorus, and other nutrients, which can create limiting conditions not seen in noncarbonate-based soils (Cao et al., 2004).

4.2.2 Dissolved organic matter

Humic acid and other leached compounds from floating or benthic organic matter are responsible for dark-brown stained water in wetlands (Wright and Reddy, 2009). Wetlands with particularly high organic matter content and low flow will have the most intense staining. The reaction between organic compounds and carbon dioxide with water produces acidic water conditions in the water column of most nonmarine wetlands (Kayranli et al., 2010). Notable exceptions can occur in wetlands with mineral-laden groundwater flow or those incised directly into carbonate bedrock. Thus the balance of carbonate ions, carbon dioxide, and dissolved organic compounds in the water column ultimately drive the system's pH. This balance is also important to nutrient availability and vegetative growing conditions (Wright and Reddy, 2009).

Diel pH patterns follow similar patterns of dissolved oxygen enrichment from photosynthesis and dissolved oxygen depletion, due to aerobic respiration (Staehr et al., 2010). Photosynthesis drives a net removal of dissolved carbon dioxide from the water column which reduces available carbon dioxide to react with water and produce carbonic acid. Conversely, respiration at night drives increases in dissolved carbon dioxide and increases carbonic acid reactions in the wetland (Maher et al., 2015).

The effects of these fluctuations can drive changes in multiple unit pH changes in a wetland water column across a single day. In most wetlands, the water column will remain acidic even during large magnitude changes (1 or 2 full pH units). However, in some wetlands it may be possible for photosynthesis to drive pH across neutral into the basic range while nightly respiration will drive the reverse. In wetlands that are nearly neutral, or even slightly basic, these diurnal shifts could reach pH levels that alter daily nutrient availability in each wetland. For example, phosphorus sorption–desorption on particulates is partially controlled by pH, so any shifts in water column acidity can drive changes in phosphorus availability. Furthermore, shifts in water column nitrogen can also be associated with pH. If water within a wetland were to reach a pH of 8, ammonium will readily convert to ammonia, which can then potentially volatilize across the air–water boundary (Boon, 2006; Fig. 4.4).

In tropical karst wetlands of the Yucatan Peninsula, Mexico, flooding duration has been associated with the development of Calcisols resulting from photosynthetically driven carbonate precipitation (Solleiro-Rebolledo et al., 2011).

4.2.3 Nitrogen and phosphorus processing

Atmospheric diffusion of elemental nitrogen is the main flux of nitrogen gas into wetlands, which becomes biologically available after processing by nitrogen fixing bacteria within the water column or at the sediment surface

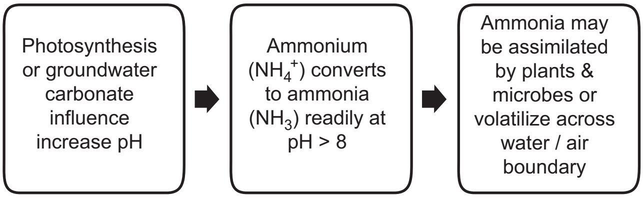

FIGURE 4.4 Process diagram for ammonia volatilization due to photosynthesis-driven pH change or the influence of carbonate-laden groundwater.

(Mitsch and Gosselink, 2015). Labile inputs of nitrogen through surface water inflows or groundwater transported nitrogen also contribute to wetland productivity (Mitsch and Gosselink, 2015; Boon, 2006). Anthropogenic activity (suburban runoff, livestock waste, ammonium nitrate fertilizer, etc.) is also a major source of labile nitrogen depending on the wetland setting. These sources of labile nitrogen are often rapidly assimilated by the wetland community and can fuel blooms of productivity (Kendall, 1998).

While nitrogen enriched water column conditions can stimulate organic matter decomposition, the rate of decomposition may not balance with increases in production (Hedges, 2002). Thus organic matter may accumulate and result in sediment accretion, which has been observed in the Florida Everglades under increased nutrient conditions (Craft and Richardson, 1993).

Nitrogen in hydric soils occurs in organic forms bound in organisms or detrital materials, inorganic species in the water column or sediment (Fig. 4.5), as well as in dissolved gaseous forms (Weigelhofer et al., 2018). Organic nitrogen can occur in labile biological materials (proteins/amino acids) or bound within more recalcitrant materials. Nitrate and ammonium ions are rapidly incorporated by the biotic community within the water column. In sediments, ammonium consumption is much slower and ammonium levels can be five times that stored in the water column. Whereas, under anoxic conditions, nitrate is rapidly depleted through reducing reactions. This leads to the production of both nitrogen and nitrous oxide gas. These gaseous compounds can form bubbles within the soil or become dissolved in the water column before ultimately degassing to the atmosphere. While some elemental nitrogen in soil may be taken up by nitrogen fixing bacteria, the bulk of nitrogen fixation is a result of atmospheric gas transport to the rooting zone by plants (Herbert, 1999).

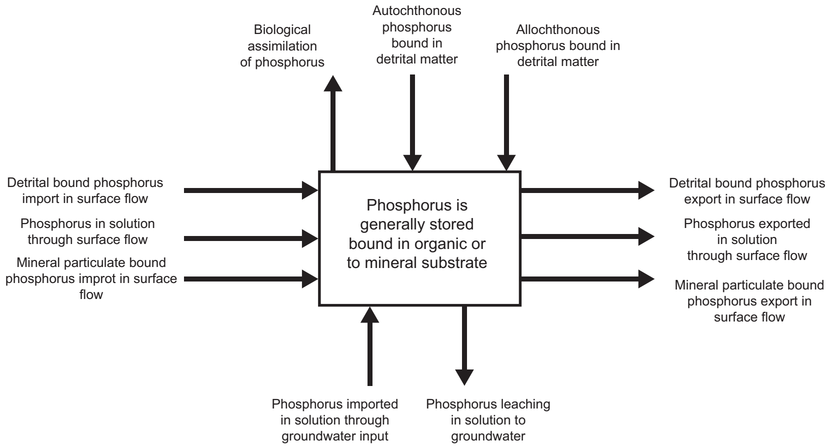

FIGURE 4.5 Conceptual diagram of phosphorus inputs and outputs in wetlands.

Nitrogen is primarily introduced to soils through nitrogen fixation in the rooting zone and to a small extent, by fixation in the water column. While water column nitrogen fixation is photosynthetically driven, nitrogen fixation in the soil can occur in the upper layers of anaerobic sediment. Some of the nitrogen gas required for nitrogen fixation in the soil may diffuse (slowly) through the water column, but the majority occurs in the rooting zone because of atmospheric gases being transported to the roots by plants. Gas leaking from the roots will supply some dissolved oxygen and nitrogen gas to microbial communities in the nearby substrate (Buresh et al., 1980).

In the root zone, oxygen availability is critical for microbial driven ammonification rates. Here, biologically available ammonium is produced from often recalcitrant organic materials. Ammonification is a mineralization process of nitrogen from organic materials which can occur anaerobically, but aerobic ammonification is much more rapid. Anaerobic ammonification results in increased levels of available ammonium because aerobic nitrification cannot occur at the site of mineralization (Liou and Madsen, 2008). Most labile, mineralizable nitrogen, will be transformed to ammonium in a matter of weeks after inundation in wetlands with periodic wetting and drying cycles. The link between ammonium production and immobilization or uptake by plants is such that they are nearly simultaneous and considered to cooccur (Smith and Jacinthe, 2014).

Nitrification is the microbial mediated chemoautotrophic process by which nitrate is produced from ammonium. The first step is for ammonium to be oxidized to nitrite, which is followed by oxidation to nitrate (Holtappels et al., 2011). Nitrification is dependent on adequate ammonium and dissolved oxygen supply, which limits its spatial extent within wetland soils both in depth and in lateral dimensions. In the absence of roots, only the first few centimeters of sediment will have enough dissolved oxygen for substantial nitrification to occur (Sopilniak et al., 2017).

This process generally occurs where subsurface flow or plant roots introduce oxygen to the soil and facilitate aerobic microbial communities. Nitrification driven depletion of ammonium in oxygenated sediment zones may also draw ammonium up from deeper sediments through diffusion and be a mechanism of nitrogen flow within wetland ecosystems (Yousaf et al., 2021).

Anammox or anaerobic ammonium oxidation is a process by which nitrite is used in the oxidation of ammonium. This process generally occurs in anoxic wetland soils where organic matter availability may limit microbial communities. Tropical temperatures generally exceed the ideal range for anammox activity (15), which may mean that anammox may not be as active in tropical wetlands as in other regions (Souza et al., 2012). Rapid nitrate assimilation in wetlands may also contribute to lower rates of anammox activity (Hou et al., 2015).

Denitrification is the process by which nitrate is reduced to nitrogen gas or nitrous oxide. This microbial mediated process is a form of anaerobic respiration used by a range of bacterial species. These bacteria use nitrate as a terminal electron acceptor during the decomposition of organic material. Immobilized nitrogen stored in plants and detrital material can return to the atmosphere through the degassing of denitrification products.

Theoretically, some nitrogen gas produced in anaerobic sediments may be taken up by nitrogen fixers in the water column and recycled through the biological community. Due to the rapid depletion or nitrate in anoxic and hypoxic soils denitrification is localized spatially within anoxic wetland sediments (Seitzinger et al., 2006).

Nitrogen is typically lost from the wetland system through denitrification and subsequent degassing and leaching to deeper substrates. Once nitrate is reduced to nitrous oxide or nitrogen gas, the bulk escapes to the atmosphere and a small portion may be fixed by microbes in the water column. Nitrate in the absence of sufficient organic matter can leach to deeper sediment layers where it is less available to the wetland community or lost to groundwater (Williams, 1985).

Very little phosphorus typically occurs in the water column because it is rapidly assimilated into the biological community. Water column microbes account for nearly all of the phosphorus uptake because plants take up nearly all or all of their phosphorus from soils. The exception would be in the case of floating aquatic vegetation which, by definition, would need to assimilate phosphorus from the water column (Reddy et al., 1999).

Diel patterns in algal production can drive precipitation of phosphorus from the water column. Algal photosynthesis drives removal of carbon dioxide, which shifts carbonate balances and increases pH. If pH levels reach 9 or 10, phosphate will adsorb to calcite. Calcium phosphate then precipitates from the water column, assuming availability of calcium ions (Chen et al., 2018).

Phosphate binds to positive cation sites (Mg or Ca) in both dolomites, $Mg(CO_3)_2$, and calcite, $CaCO_3$. This is most common in wetlands with extensive algal production and drives the formation of calcareous sediments such as the marls produced by periphyton in the Florida Everglades (Fig. 4.6). It should also be noted that plants associated with periphyton assemblages can be integral to this process (Dodds, 2003).

Clay sediments can remain in the water column for relatively long periods of time and can sequester phosphorus compounds that are in the solution. Two mechanisms most likely account for the clay sequestration of phosphorus. The first is that phosphates can bind to the positive sites on the clay particle surface. The second is that the similarity in structure between phosphates and silicates allow for phosphate substitution for silicates in the structural matrix of the particle (Yin et al., 2020).

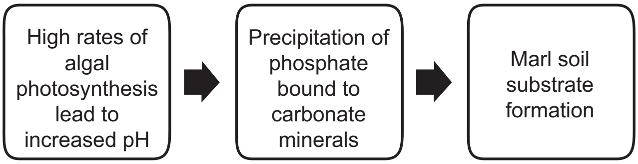

FIGURE 4.6 Conceptual diagram of marl formation driven by pH changes associated with high rates of water column photosynthesis.

Phosphorus exists in soils as orthophosphate ions, organically bound phosphate, and mineral bound phosphate. Valence stability of phosphorus in soils prevents it from being directly involved in reduction—oxidation processes, but changes in pH resulting from these reactions can be major drivers of phosphorus availability to the biological community. Additionally, organic matter decomposition can free organically bound orthophosphate species (Pezeshki and DeLaune, 2012).

Phosphorus can occur in wetlands either bound in plant material, or to sediment or dissolved in solution (Fig. 4.5). Wetlands functioning as terminal hydrologic features will store and sequester phosphorus (e.g., isolated subtropical depressional wetlands). Unlike nitrogen, there is no direct mechanism for export of phosphorus except in solution. Accordingly, phosphorus may be lost to groundwater or transported during hydrologic export, but will otherwise be sequestered in plant tissue, bound to sediments, or exist in solution (Ballantine and Tanner, 2010).

Biologically bound phosphorus can occur in accordance with a variety of biological molecules, including inositol phosphates (growth, cell differentiation, etc.), phospholipids (cell membranes), and nucleic acid (deoxyribonucleic acid, ribonucleic acid). Phosphorus can also cycle in wetlands in accordance with the growing season where growth of herbaceous plants is followed by subsequent senescence. Wetlands with long growing seasons will therefore have longer storages of biologically bound phosphorus (Kröger et al., 2007).

Depending on the wetland, phosphorus stored and bound in partially decomposed detrital plant material can make up substantial storages. Orthophosphate ions can be electrostatically bound to organic acids that are the result of detrital decomposition. These can include both humic and fulvic acids. Calcium, magnesium, aluminum, and iron cations act as binding agents between the negatively charged phosphate and acid compounds. Organic soils, which are largely composed of plant matter and partially decomposed detrital materials, can store the vast majority (greater than 90%) of phosphorus in some wetlands (Thomas, 2003).

Minerally bound phosphorus typically occurs as orthophosphates that are bound to aluminum or iron oxides/hydroxides. In mild to moderate acidic conditions (less than 7 but greater than 4), orthophosphates readily and preferentially bind to iron and aluminum oxides/hydroxides. However, mineral phosphates are rapidly freed when soil pH decreases to less than 4 (Lijklema, 1980).

Wetlands have somewhat finite capacities of phosphorus uptake because there are limited binding sites available for phosphorus, and biological activity tends to cycle phosphorus within the wetland. Inputs of mineral sediments that supply iron and aluminum ions increase the potential for sequestration (Reddy et al., 2005).

Dust deposited by eolian transport or sediments deposited by episodic flows can contribute to the availability of phosphorus binding sites when these materials are iron or aluminum rich. Therefore sedimentation from outside the wetland boundaries is a major driver of the long-term sequestration and storage of phosphorus. A variety of clays in the tropics and subtropics that are rich in iron oxides, can also contribute to soil phosphorus sequestration (Turner et al., 2006).

In summary, phosphate generally flows into the wetland, is dissolved in the water column, or bound to suspended particles. Algal species and floating aquatic plants may take up a small portion of dissolved phosphate directly from the water column. Shifts in pH may cause precipitation, chemical interaction with substrates, or adsorption to suspended particles, which can result in deposition and sometimes mineral sequestration of phosphorus in the wetland (Trettin et al., 2020).

Once precipitated or deposited to wetland soils, it may become available for wetland plants. Rooted plants assimilate most of their inorganic phosphorus from the soil substrate and after senescence plant detrital matter will contain organic phosphorus, essentially redepositing phosphorus to the wetland soils. This organic phosphorus can become stored in peat or organic material, mineralized by microbial processes, or resuspended to the water column and exported by disturbances (Reddy et al., 1999).

4.2.4 Sulfur and methane

Hypoxic and anoxic conditions within wetland sediments provide suitable environments for both sulfate reducing bacteria and methanogens. These bacteria require anaerobic conditions and cannot survive in aerobic areas of wetlands (Valentine and Reeburgh, 2008). Accumulation of hydrogen sulfide and methane can result in bubbles of these gasses pushing through sediments and degassing when breaching the surface. Sulfate reducing bacteria are responsible for the classic salt marsh scent while methanogens go largely unnoticed due to methane's lack of odor (Skyring, 1987).

Methane production in tropical wetlands is far more variable than boreal wetlands because of various climate cycles, as well as the expected annual wet–dry cycles. These period droughts can oxygenate soils and prevent methane production. In wet years and seasons, methane production tends to lag peak water levels by several months (Bloom et al., 2012). The lag is likely due to the exhaustion of other reducing reaction pathways.

Sulfur occurs in various organic forms and as inorganic sulfide species (e.g., hydrogen sulfide). Generally, more than 70% of sulfur in wetland soils is organic with the remaining percentage distributed among a combination of inorganic hydrogen sulfide, iron sulfide (pyrite), or sulfate. The bulk of these inorganic forms is typically sulfate with some or no pyrite, and gaseous hydrogen sulfide making up the remainder. While wetlands store substantial quantities of phosphorus, their outfluxes are such that they act as transformers rather than long-term sinks (Pester et al., 2012).

Under aerobic soil conditions, sulfur can be immobilized by the biotic community. For example, biologically mediated processes include the oxidation of inorganic sulfides as well as the mineralization of organic species (Kertesz and Mirleau, 2004).

Furthermore, under anoxic soil conditions, sulfate is microbially reduced to hydrogen sulfide gas. The hydrogen sulfide produced may either degas to the atmosphere, or in some cases, react with organic matter and become an organic sulfur species. These processes form the basis of the demineralization and remineralization processes that cycle sulfur species within wetlands (Heinen and Lauwers, 1995).

Iron cations produced in other redox reactions can bind to sulfate and form iron sulfides. This generally requires occasional limited aeration events. Sulfide precipitation can also drive the immobilization of zinc and copper in wetlands which can limit plant production (Neal et al., 2001).

During periodic aeration of wetland soils, sulfate can become chemically bound to cation rich clays. However, orthophosphate species can displace sulfate and due to phosphates, higher affinity for these binding sites will not be equally displaced by sulfur. It logically follows that pulsing phosphate additions from storm flows or wetting and drying cycles, could drive loss of sulfur from wetlands (Smith and Jacinthe, 2014).

When tropical wetlands become drained (anthropogenically or during natural drought cycles), they are highly prone to rapid oxidative decomposition (Hooijer et al., 2009). In many ways, tropical peatlands are more dependent on precipitation regimes for organic matter accumulation than those in more northern latitudes. Thus precipitation becomes a critical driver of the carbon balance and peat accumulation driven geomorphology of these systems (Cobb et al., 2017).

4.3 Threats to wetlands in the tropics and subtropics

Oil palm plantations are a substantial part of many countries' economies. The conversion of tropical peatlands to oil palm plantations are being driven by the rising demand for biofuels and food production (Koh et al., 2008). Approximately 90% of palm oil is used for cooking and food products, leaving 10% to industrial uses (Ramdani and Hino, 2013; Irvine et al., 2021, Chapter 19).

Regional analyses in Southeast Asia, where peat swamp forest conversions to oil—palm development is rampant and increasing, has revealed substantial greenhouse gas emissions, loss in biodiversity, increased deforestation, and large impacts on carbon across all regions (Ramdani and Hino, 2013; Koh et al., 2011). It is estimated that the conversion of these peat swamp forests to oil palm will result in net peat carbon emissions of 5.2 ± 1.1 mg ha^{-1} year^{-1}, and a net carbon loss of 155.5 ± 39.2 mg ha^{-1} year^{-1} (Koh et al., 2011).

Indonesia holds around half of the world's tropical peatlands, and a study on the Riau Province revealed that the moratorium on deforestation has largely impacted the oil—palm industry (Ramdani and Hino, 2013). To maintain the health and ecological roles of tropical and subtropical wetlands, a heavy emphasis needs to be placed on sustainable land use and restoration of already damaged wetlands.

Through conversion to agricultural uses, it is estimated that more than 50% of the land area of peatlands, depressional wetlands, riparian lakes, late littoral zones, and floodplains have been lost in North America, Europe, and Australia (Verhoeven and Setter, 2009). In addition to this, timber harvesting and related activity also plays a large role in the loss of forested freshwater wetlands (Dahl, 2011; Wasserman and Dalu, 2022, Chapter 1).

Agricultural needs are perpetuated by the need to feed Earth's growing population. This, in turn, increases the use of pesticides and fertilizers to mass produce food. Because peatlands are very fertile for agricultural development due to their high mineral content (Verhoeven and Setter, 2009), they are often the first to be converted. The increased demands for the use of pesticides and fertilizers on these wetlands has led to a massive loss of wetland productivity, ecological function, and biodiversity (Verhoeven and Setter, 2009). Reconciling the use of these pesticides and fertilizers will play an integral role in future wetland conservation efforts.

Salinization is another threat to wetland structure and ecological function (Cuthbert et al., 2019). Changes in salinity are caused by an array of activities, including freshwater flows, sea level rise, land clearance, storm surges, and most notably, irrigation. Irrigation practices alter the physicochemical properties of the soil—water environment, which cause increases in ionic concentrations and changes to the chemical equilibria. As a result, salinization typically causes a decrease in inorganic nitrogen removal and carbon storage, an increase in toxic sulfides, and an overall negative implication to the health/functioning of wetland biota (Herbert et al., 2015).

Agriculturally, salt affected soil—water environments affect plant growth by altering properties of both the soil and plant. Highly saline soils can have high osmotic pressure, which can cause an accumulation of toxic ions in plant tissue. This in turn causes the plants mineral nutrition to be negatively altered (Allison, 1964). Ultimately, poor wetland irrigation practices cause an excessive build up of salts, which results in poor soil quality, stunted growth of plants, and decreased productivity.

Anthropogenic modifications to the hydrologic cycle are causing salinization in wetlands to occur on a geographic scale at an unprecedented rate. Irrigation management practices as well as remedial efforts need to be introduced, before the physiological stress of salinization causes wetland communities and their ecological functions to shift to an irreparable change (Herbert et al., 2015).

4.4 Conclusions

Hydrology is the fundamental driver of wetland physicochemical environments and is a critical component to wetland biogeochemistry. Seasonal inundation and extended growing seasons can also drive distinct balances of organic matter production and accumulation in tropical and subtropical wetlands (Cuthbert et al., 2022, Chapter 17). Thus any alterations to the hydrology of wetlands can cause rapid changes to the biogeochemistry and ecological function of wetlands. Disturbances to large tropical peatlands are extreme examples of these fundamental changes but subtler changes through time have been observed where agricultural runoff alters the salinity of normally freshwater wetlands in the subtropics. Therefore maintaining hydrologic source integrity is as important to managing for water quantities in maintaining wetland physicochemistry.

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Chapter 5

Carbon sequestration and fluxes

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5.1 Introduction and overview

Wetlands play an important role in a myriad of ecosystems globally, including the cycling of water, carbon, and nutrients (Sharifi et al., 2013; Hong et al., 2019; Deemy et al., 2022a, Chapter 6; Cuthbert et al., 2022, Chapter 17). They provide ecosystem services including production of food, water purification, waterflow regulation, biodiversity, pollination, tourism, and recreation (Knight, 1997; Hey et al., 2012; Dalu and Chauke, 2019; Dixon et al., 2021; Deemy et al., 2022b, Chapter 3; Irvine et al., 2022, Chapter 19; Marambanyika et al., 2022, Chapter 22; Laltaika, 2022, Chapter 23; Wasserman and Dalu, 2022, Chapter 1). They are among the world's most productive and biologically diverse ecosystems, and provide essential habitat for many kinds of waterbirds, fish, amphibians, invertebrates, and plants (O'Neill and Thorp, 2014; Chandler et al., 2017; Peel et al., 2019; Tarakini et al., 2022, Chapter 14; Reichard, 2022, Chapter 12; Moraes et al., 2022, Chapter 13; Brendonck et al., 2022a,b, Chapters 9 and 10; Dube et al., 2022, Chapter 11; Piedade et al., 2021, Chapter 7; Dalu et al., 2022, Chapter 8).

The transfer of material between terrestrial and aquatic systems is a fundamental ecological process. Climate, hydrology, and geomorphology all affect the rates and quantities of material flowing into wetlands (Sharifi et al., 2013; Deemy et al., 2022a,b, Chapters 3 and 6). One material that is of interest to researchers and resource managers is carbon, which is an essential building block of all life and is of environmental significance in light of climate change. In recent decades, tropical wetlands have been receiving more attention not only because of their contribution to the global carbon budget and climate change, but also because of their potential to emit more carbon compared to their temperate counterparts. To understand how tropical wetlands contribute to global climate change, it is important to understand their capacity to store and sequester carbon, and the main factors that drive carbon fluxes in wetlands (Ribeiro et al., 2021). Specifically, tropical and

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subtropical wetlands may contribute at least 50% of total wetland methane emissions, and over 80% of the natural sources, to the atmosphere partially due to large inundations and wet-dry seasons (Meng et al., 2015).

Wetlands and their future have been discussed in detail elsewhere (Allan and Castillo, 2007; Cui et al., 2016; Fritz and Whiles, 2018). For instance, the Intergovernmental Panel on Climate Change (IPCC) has explored the issues facing wetlands using different biogeographical and socio-economic data from different continents (Fischlin et al., 2007; IPCC, 2019). Carbon cycling in wetlands, like many other ecosystems, have also received considerable global attention and much has been discussed elsewhere (Bridgham et al., 2006; Boardman et al., 2011; Abdalla et al., 2016). Only recently tropical wetlands were discussed by Dixon et al. (2021), who took a broader view of wetlands by elaborately covering the social, cultural, economic, political, and other variables that influence wetlands. As such, this chapter will emphasize tropical freshwater wetlands, anticipated impacts of climate change along with other anthropogenic stressors on various kinds of wetlands in tropical and subtropical ecosystems.

The objective of this chapter is to provide a description of carbon cycling in subtropical and tropical wetlands. The chapter discusses carbon cycling in tropical wetlands using examples from North and South America, Africa, Asia, and Australia. This chapter gives the reader an overview of carbon cycling in freshwater wetlands, including the major sources and sinks of carbon, the processes governing carbon fluxes and transformations, and some consequences of changes in those processes. Tropical wetlands are treated as not having strict geographical borders (Gopal et al., 2008) because some countries extend over different climatic zones but represent single units. To this end, tropics refer to the areas bounded by the Tropics of Cancer and Capricorn (Gopal et al., 2008).

5.2 Wetland definition

Owing to their efficacy in trapping sediments and nutrients, wetlands are commonly defined under the moniker "kidneys of the catchment" (Junk, 2002; Mitsch et al., 2010). While there is general consensus on the importance of wetlands, the term "wetland" has been in use for more than 60^+ years but there remains a lot of dubiety about what is or is not a wetland (Cowardin, 1982; Maltby, 2009). The myriad of definitions prompted the Ramsar Convention, an intergovernmental treaty on worldwide wetlands conservation to give a unifying definition of wetlands that includes all inland and coastal aquatic systems (An Introduction to the Convention on Wetlands, 2016). According to the Ramsar Convention, wetlands are areas of marsh, fen, peatland, or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish, or salt, including areas of marine water, the depth of which at low tide does not exceed 6 m. To this end, this chapter is confined to inland wetlands in the tropics while excluding lakes, reservoirs, river channels (see Wasserman and Dalu, 2022, Chapter 1). In addition caves and similar subterranean wetlands are excluded.

5.3 Wetlands in the global carbon cycle

The influx (flow into wetlands) and efflux (flow out of a wetland) of carbon in wetland systems occurs under aerobic and anaerobic conditions (Fig. 5.1). Photosynthesis (Eq. 5.1) and aerobic respiration (Eq. 5.2) occur in aerobic zones of the wetland. The overall reaction can be encapsulated as:

$$6CO_2 + 6H_2O + \text{solar energy} \rightarrow 6O_2 + C_6H_{12}O_6(\text{carbohydrates}) \tag{5.1}$$

$$C_6H_{12}O_6(\text{carbohydrates}) + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{energy} \tag{5.2}$$

A fraction of the organic carbon is oxidized by the plant for energy. Subsequently, carbon is released as carbon dioxide through the leaves and

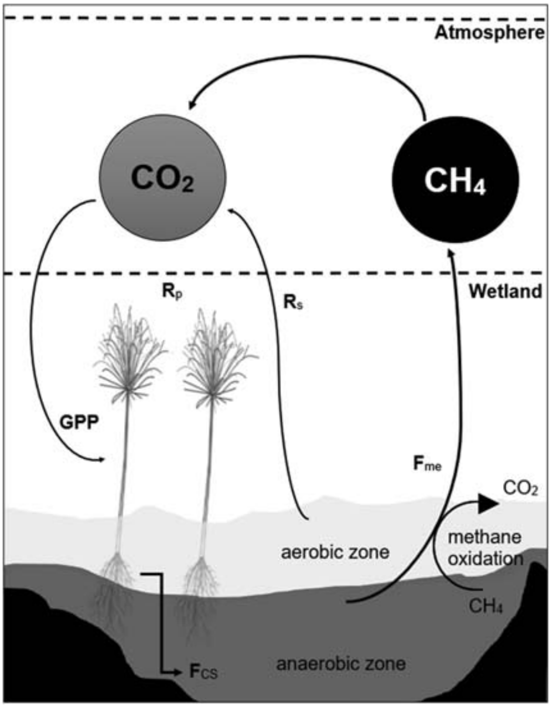

FIGURE 5.1 A simplified wetland carbon cycle. *CH_4*, Methane; *CO_2*, carbon dioxide; *GPP*, gross primary productivity; *R_p*, plant respiration; *R_s*, soil respiration; *F_{cs}*, carbon sequestration; *F_{me}*, methane emissions. See text for more detailed descriptions. *Modified from Mitsch, W.J., Bernal, B., Nahlik, A.M., et al., 2013. Wetlands, carbon, and climate change. Landscape Ecology 28, 583–597.*

roots via respiration. Carbon that is released via stomata on leaves goes back into the atmosphere while the carbon dioxide released by roots dissolves into the soil as dissolved inorganic carbon. Carbon that is not used for energy is built into the cells, tissues, and organs of the plant. This net primary production (NPP) is the basis for nearly all of the rest of life on earth. Some of this fixed carbon may be subsequently released through the roots into the soil solution as dissolved organic carbon (DOC; Fig. 5.2). Roots also release biochemicals (polysaccharides, enzymes, organic acids, sugars, and amino acids) that play a dominant role in a number of key ecosystem processes including the population dynamics of microbes, the breakdown of organic matter, and the bioaccumulation of nutrients (Li et al., 2015; Sun et al., 2019). The death and subsequent shading of leaves (or death of the roots or whole plant) releases more carbon to the sediment as DOC and particulate organic carbon (POC). Energy produced during photosynthesis also supports a myriad of organisms such as detritivore and decomposer organisms (e.g., insects, nematodes, prokaryotes, fungi). Because aerobic oxidation has a very high energy yield, aerobic organisms are very efficient at breaking down organic carbon and so, where oxygen is present, they dominate carbon metabolism. Wetlands also tend to have anoxic conditions that allow for anaerobic process to occur. These anaerobic processes are less efficient in

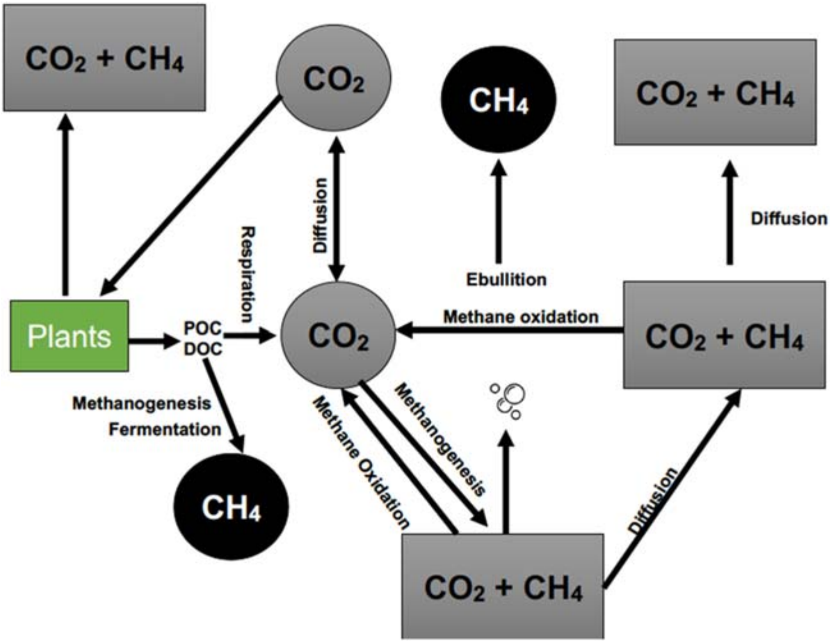

FIGURE 5.2 Major pathways include photosynthesis, respiration, fermentation, methanogenesis, and methane oxidation (anaerobic and aerobic).

transferring energy compared to aerobic processes. Two of the major anaerobic processes that occur are fermentation and methanogenesis.

5.4 Fermentation

Fermentation involves the anaerobic reduction of POC and DOC into simple compounds (e.g., lactic acid and ethanol). Fermentation in wetlands is carried out by a broad range of fungi and microorganisms. These meet their metabolic requirements by utilizing more oxidized forms of carbon in a compound to oxidize more reduced forms of carbon in the same compound. In tropical wetlands, fermentation reactions occur on broad range of conditions. For instance, fermentation can occur in highly aerobic conditions to strongly anaerobic conditions. POC can also be metabolized aerobically or anaerobically by denitrifying bacteria. Fermentation represents one of the major ways in which high-molecular-weight carbohydrates are broken down to low-molecular-weight organic compounds, usually as DOC, which are, in turn, available to other microbes.

$$C_6H_{12}O_6\text{(carbohydrates)} \rightarrow 2CH_3CH_2OCOOH \text{ (lactic acid)} \tag{5.3}$$

$$C_6H_{12}O_6\text{(carbohydrates)} \rightarrow 2CH_3CH_2OH \text{ (ethanol)} + 2CO_2 \tag{5.4}$$

5.5 Methanogenesis

Certain prokaryotes (methanogens; of the Domain Archaea) reduce CO_2 to methane using molecular hydrogen. Alternatively, prokaryotes can produce methane by using a low-molecular-weight organic compound, such as acetic acid.

$$CO_2 + 4H_2 \rightarrow CH_4\text{(methane)} + 2H_2O \tag{5.5}$$

$$CH_3COOH \text{ (acetic acid)} \rightarrow CH_4\text{(methane)} + CO_2 \tag{5.6}$$

Methanogenesis deserves special attention, because one of the by-products is methane (CH_4), an environmentally significant greenhouse gas. Methane can be released to the atmosphere when sediments are disturbed.

5.6 Methane oxidation

Methanotrophic bacteria ("methane consuming") are responsible for sequentially oxidizing methane to produce carbon dioxide. Methanotrophic bacteria use the energy released by the oxidation of methane to carbon dioxide to meet their metabolic requirements.

$$CH_4\text{(methane)} \rightarrow CH_3OH \text{ (methanol)} \rightarrow HCHO \text{ (formaldehyde)} \rightarrow CO_2 \tag{5.7}$$

Non-flooded wetlands (e.g., forests, agricultural land, grasslands) are major biological sinks of methane where methanotrophs are ubiquitous. The oxidation of methane is reliant on the availability of oxygen, as such methane oxidation occurs mainly in freshwater wetlands during dry periods, when the level of the water table descends and the soil of the wetland is exposed to air (Roy Chowdhury et al., 2014; Lee et al., 2020). Maietta et al. (2020) demonstrated that soil and methane-cycling microbial community diversity and structure are strongly related to water level changes and saturation duration. These data show that in tropical wetlands one can expect wetlands that experience inundation or saturation for part of the season will harbor a different soil microbial composition distinct from soils that are rarely saturated or inundated.

5.7 Methane emissions

Methane emissions can be considered the consequence of methanogenesis and methane oxidation. Methane emissions have a considerable range from both saltwater and freshwater wetlands as well as from domestic wetlands. Comparing and documenting the rates of methane production from disparate studies is challenging, because researchers do not always report methane production rates at the same scales. Broadly, an averaging of methane emissions from different wetland types reveals that tropical floodplains (and seasonally flooded wetlands) emit more methane than ephemeral ponds and temperate ephemeral ponds (Fig. 5.3). Methane emissions from peatlands are excluded here as they are well documented elsewhere (Abdalla et al., 2016). The quantity of methane emitted from tropical wetlands is likely significant especially considering that of the $109-180$ Tg CH_4 year^{-1} emitted by wetlands globally, $42-137$ Tg CH_4 year^{-1} of that comes from the tropics (Bartlett et al., 1988; Bergamaschi et al., 2007).

Considering methane emissions in tropical wetlands, it is evident that they follow very predictable seasonal patterns; with some exceptions. Summer rates can be highest in seasonal climates, but estimation of total methane generation requires year-long measurements, particularly in subtropical and tropical regions. The pattern also depends on the degree of flooding and the presence or absence of vegetation. Methane emissions in tropical and subtropical regions show some predictable patterns associated with changes in hydrologic conditions. Specifically, tropical wetlands in different climates will follow a general bicorn curve, where increasing water level or days of inundation (process of a dry area being permanently drowned or submerged) are associated with methane emissions (Fig. 5.4). The lower methane emissions in shallow depths may be due to better oxygen diffusion in the water column, which creates oxidation conditions at the soil–water interface. Consequently, this lowers emissions in deep water because of stratification patterns, a typical feature in tropical water bodies. For instance, Villa and Mitsch (2015) used days after inundation as a proxy

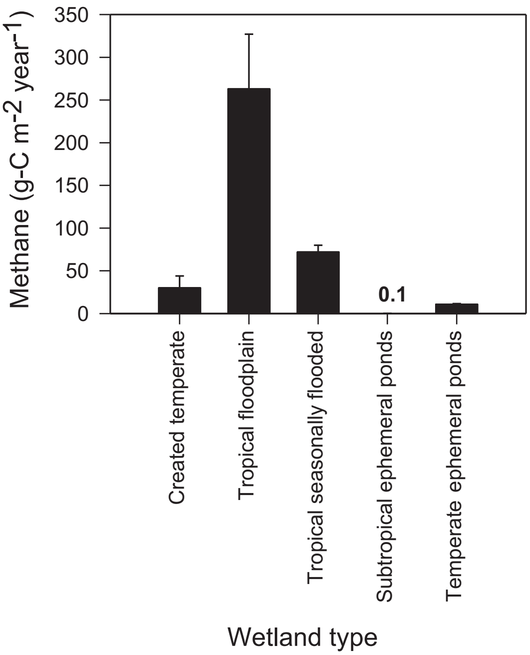

FIGURE 5.3 Comparison of methane emission rates from different wetland types. *Data extracted from Mitsch, W.J., Bernal, B., Nahlik, A.M., et al., 2013. Wetlands, carbon, and climate change. Landscape Ecology 28, 583–597; Ross, B., 2017. Assessing Hydrology, Carbon Flux, and Soil Spatial Variability Within Vernal Pool Wetlands. Open Access Master's Theses. https://doi.org/10.23860/thesis-ross-bianca-2017; Kifner, L., Calhoun A., Norton S., et al., 2018. Methane and carbon dioxide dynamics within four vernal pools in Maine, USA. Biogeochemistry. https://doi.org/10.1007/s10533-018-0467-5.*

for the summer seasonal rains, whereby they found that methane emissions were low just after inundation, increased for ~2 months of inundation, but began to decrease when flooding lasted longer than 2 months.

5.8 Ebullition

Methane, being lighter than air coupled with its partial solubility in water, can be released from anaerobic sediment or soil surface through the water column by diffusion. In circumstances where methane production is high, the methane may bubble to the surface by a process commonly called ebullition. Ebullition is common in highly productive saturated wetlands such as tropical swamps. In tropical wetlands, the CH_4 concentration in gas bubbles is related to the depth of the overlying water column (Fig. 5.3), whereby gas bubbles increase within waters of <1 m depth. In contrast, ebullition is always >50% in waters of >1 m depth (Hamilton et al., 2014). It is worth

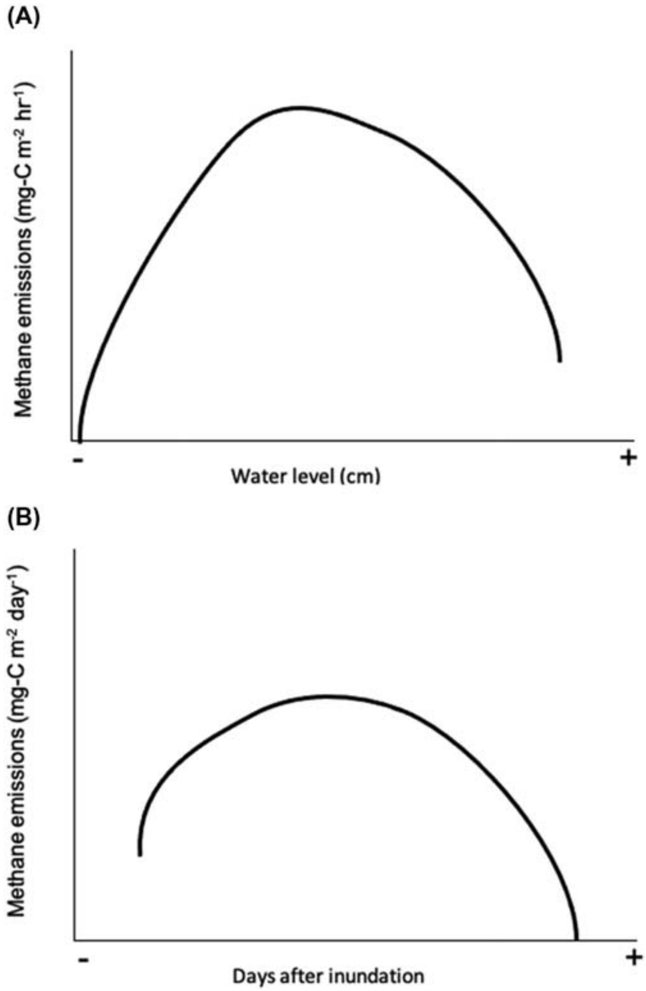

FIGURE 5.4 Schematic of relationships between hydrologic conditions and methane emissions for tropical and subtropical wetlands: (A) methane emissions versus water level (Nahlik and Mitsch, 2011); (B) methane emissions versus inundation for seasonally wet subtropical wetlands (Villa and Mitsch, 2015).

noting that stems and roots of vascular plants can also provide a direct pathway for methane to bypass the sediment and pass directly into the atmosphere. In wetlands that are dominated by vascular plants for most of the year, plant-mediated transport is usually the main way that methane is released to the surface via plant transport and diffusion.

5.9 Carbon–sulfur nexus

The sulfur cycle (see Deemy et al., 2022b, Chapter 6) is important in some wetlands for the oxidation of organic carbon (Eqs. 5.8 and 5.9) via sulfur-reducing bacteria. The oxidation of carbon by sulfur is beyond the scope of this chapter as these processes tend to occur in coastal wetlands where sulfur is ubiquitous.

$$CH_3COOH\ \text{(acetate)} + SO_4^{-2} \rightarrow 2CO_2 + H_2S + 2H_2O \tag{5.8}$$

$$2CH_3CHOHCOOH\ \text{(lactate)} + SO_4^{-2} \rightarrow 2CH_3COOH + 2CO_2 + H_2S + 2H_2O \tag{5.9}$$

5.10 Carbon gains and losses in tropical and subtropical wetlands

Wetland functions produce wetland services of economic value to individuals or to society or both (Barbier, 2019). As such, it is not surprising that researchers and environmental managers are interested in the factors that drive carbon sequestration or release of carbon into the atmosphere. One question we could ask is: "How much carbon will wetlands store over the long term and what factors may control the loss of stored carbon?"

One way to untangle this question is to start by enumerating the amount of carbon stored and accumulated into wetlands. Broadly defined, one can consider carbon accumulation as the difference between the carbon gained from primary production and physical transport into the wetland (influx) and the carbon lost through decomposition and transport mechanisms out of the wetland (efflux):

$$C_{\text{accumulation}} \approx (C_{\text{NPP}} + C_{\text{influx}}) - \left(C_{\text{decomposition}} + C_{\text{efflux}}\right) \tag{5.10}$$

The variables (NPP, influx, decomposition, efflux) will differ based on the wetland type. For instance, tropical peatlands tend to have lower rates of all four factors than their tropical nonpeatlands counterparts (Sjögersten et al., 2014). In addition, carbon influx from NPP is generally higher in tropical wetlands (193–2438 gC m^{-2} $year^{-1}$; Sjögersten et al., 2014) compared to temperate wetlands; although there is considerable variability among wetland types. A further important aspect of carbon influx to tropical wetlands is a more rapid root turnover rate (70% $year^{-1}$) than in equivalent temperate and boreal systems (55 and 45% $year^{-1}$, respectively). This observation suggests that carbon inputs from root turnover might contribute significantly to the high carbon accumulation rates in tropical wetlands, but data for root production are lacking and are thus warranted (Gill and Jackson, 2000; Chimner and Ewel, 2005).

Carbon accumulation in wetlands can be highly sensitive to environmental conditions (depicted in Fig. 5.5). For instance, a rise in temperature can increase plant productivity, potentially leading to an increase in carbon storage. Conversely, higher temperatures may increase both aerobic and anaerobic respiration, thus decreasing carbon storage. To this end, the response of

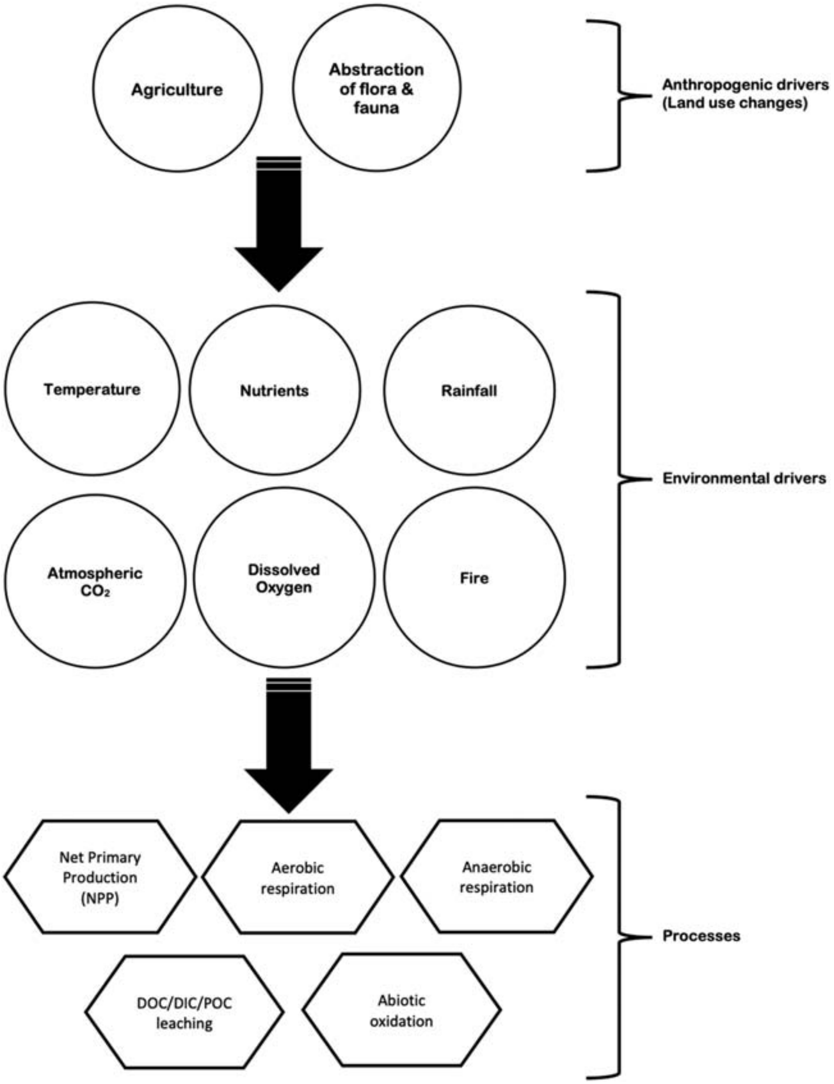

FIGURE 5.5 Major processes involved in carbon storage and release in wetlands, and major environmental drivers influencing those processes. Note that the processes are influenced by more than one (in some cases, all) of the environmental drivers.

wetlands to environmental shifts may vary greatly among disparate wetland types. More rainfall can increase methane emission in tropical peatlands (by raising the water table closer to the surface, thus reducing the zone of methane oxidation) but have no effect or even decrease methane emission in a tropic marsh (owing, e.g., to an increased flow of oxygenated water). Similarly, fire may reduce carbon storage through combustion of plant material, which takes place during the fire itself, and by secondary effects such as a change in soil pH as a result of ash. However, the removal of old plant growth and the increased availability of nutrients stimulate vegetation growth and can ultimately lead to increased carbon storage. From the aforementioned effects, it is clear that the net effect on the cycling of carbon of a change in external conditions such as temperature, fire, or precipitation can be extremely difficult to predict.

5.11 Global carbon storage in the tropics

Having discussed the factors that drive carbon stored in wetlands, one may be interested in estimating how much carbon is stored in tropical wetlands. Mathematically, this would seem like an easy feat: one simply needs to multiply the area of all wetlands by the average amounts of carbon stored in tropical wetlands. Strikingly, the data in the literature reveal that there is considerable uncertainty on the area covered by wetlands on the earth's surface. Major discrepancies still exist in the global extent and importance of floodplains and tropical wetlands, and even in how wetlands are defined by different countries. Additionally, the amount of accumulated organic matter varies widely among wetlands and regions (Fig. 5.6), particularly in peatlands where data on peatland cores are scanty, especially in Africa. As more research goes into tropical peatlands of Africa and other developing countries, we will gain a confident estimate of the average depth of wetlands. Because there is still so much uncertainty about the area covered by tropical wetlands, enumerating carbon stored in tropical wetlands is difficult. However, if we take the estimate mean carbon accumulation of all freshwater wetlands to lie somewhere between 40 and 158 gC m^{-2} $year^{-1}$ and multiply this by conservative estimated area of 3.4 million km^2 of all tropical freshwater wetlands in the world, we arrive at a range of carbon accumulation of between 136 and 537 Tg $year^{-1}$. These values, while just an estimate, are tenable considering that the current estimate for carbon accumulation globally is 830 Tg $year^{-1}$ in terrestrial systems (Mitsch et al., 2013).

5.12 Measuring carbon sequestration and fluxes in wetlands

Fluxes of carbon can be determined using different measurement approaches, that include and are not limited to techniques such as eddy covariance (Rey-Sanchez et al., 2018), remote sensing (Huete et al., 2008), aircraft

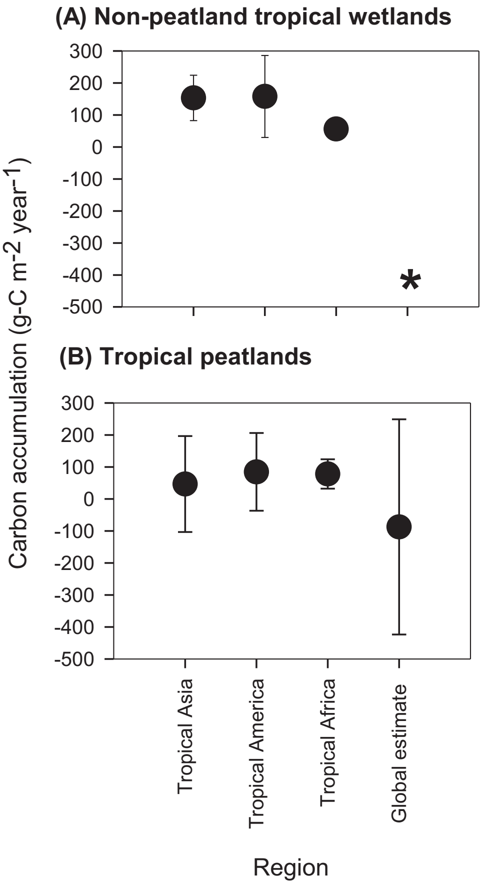

FIGURE 5.6 Carbon accumulation rates (gC m^{-2} year^{-1}) from tropical peatlands and from nontropical peatlands (for comparison) showing mean values and/or (range) if available. Positive values are carbon accumulation and negative values are carbon loss.

measurements (Smith et al., 2003), chambers (Kutzbach et al., 2007), and stable isotopes of carbon (Cui et al., 2018). It is important to be cognizant that the above-mentioned methods are different in terms of spatial and temporal scales of measurement. As such, chamber techniques and stable isotopes analyses allow researchers to study fluxes of carbon over small spatial scales. The measurements method are beyond the focus of this chapter, as these ideas area covered extensively elsewhere (Fry, 2006; Petrokofsky et al., 2012).

5.13 Wetland ecosystem modeling of carbon fluxes

Wetland ecosystem models are a potential panacea for understanding carbon fluxes at regional and global scales. Modeling is useful for deciphering the functioning of tropical wetland ecosystems, and for simulating future trajectories under different scenarios. Anthropogenic activities like wetland drainage and land-use change can be integrated in models and their impacts on fluxes of greenhouse gas concentrations can be simulated. One process-oriented model, originally developed for temperate wetlands, is the Tropical Holocene Peat Model (HPMTrop; Kurnianto et al., 2015) which has been adapted for use in the tropics appropriate for use in tropical conditions. Summarily, HPMTrop along with other similar models incorporate plant types, NPP, and water levels. Tropical climates are warm year-round, with precipitation patterns that can be partitioned into rainy and dry seasons, the models also incorporate these two precipitation patterns. In addition to models studying the accumulation of carbon in tropical wetlands, models have also been successfully utilized to address the uncertainties associated with the prediction of methane fluxes. One of the biggest uncertainties when modeling carbon fluxes is estimating the inundated area of wetlands (Meng et al., 2015). The Joint UK Land Environment Simulator (JULES) and Terrestrial Ecosystem Model (TEM) are both models that have been used to investigate the impact of surface warming, moisture availability, inundation on methane emissions (Watts et al., 2014; Jin et al., 2015). Improved data collections that include temporary ponds should see better estimates of carbon fluxes from tropical wetlands.

5.14 Carbon storage in the "anthropocene"

The major threats to wetland integrity on a global scale are direct human perturbations and climate change itself. Here the potential magnitudes of these perturbations are discussed along with their likely impacts, and some ways that carbon losses from wetlands can be mitigated by good management.

5.15 Land use changes

Humans directly affect wetlands via abstraction of water from wetlands and agriculture production. Taken together, drainage and agriculture on wetlands have reduced the global area of natural wetlands by over 54%, although estimates vary because of scarce data from Africa and the Neotropics (Davidson, 2014). Drainage for uses such as agriculture, pasture, or forestry, rapidly lowers the water table and exposes organic soils to oxidation, where they begin to decompose aerobically. This greatly increases the emission of CO_2 from the soil, decreases the emission of CH_4, and releases nutrients. The link of wetlands with the regional hydrology is also reduced and simplified when it is drained, as runoff is channelized into ditches. When wetlands are mined for peat fuel or horticulture, the organic soils are removed and burned or oxidized a short time later. The carbon in these soils is essentially all released back as CO_2 within a few years. A good example of the wetland drainage is in tropical Asia (e.g., Indonesia) where 90% of the world's palm oil is produced. Because peatlands are not very suitable for oil palm production (where the soil has poor fertility and is too wet for the trees) water in peatlands has to be logged and drained for the palm trees to be planted. Because of the draining, peatlands are a significant sources of greenhouse gas. Given that Indonesia has over 30,000 km^2 of oil palm plantations with many extensive subsistence farming they can potentially emit ~438 million tonnes of CO_2 per year (Thornton, 2017). With harvests of 2–6 tonnes of palm oil per hectare, palm oil is causing CO_2 emissions that are 10 times the magnitude of fossil fuels. Globally, palm cultivation in Indonesia is responsible for 2%–9% of worldwide emissions from tropical land use (Thornton, 2017). The drainage of wetlands exposes them to oxidation, degradation, subsidence, and vulnerability to fire.

Fire affects tropical and subtropical wetlands during the dry season. Fire results in the release of carbon stored in the wetland plants and soils back into the atmosphere. If fire frequency changes in seasonally flooded wetlands, the release of stored carbon could be much more significant than the releases that occur due to water level changes. South of the African continent (Botswana, Okavango Delta) floodplain fires are usual and have major implications on sequestered carbon. Fire in these parts of Africa occur over two dry periods that fall between the rain pulses of summer (September) and the seasonal flooding pulse (May). During the dry periods, thunderstorms are rare and most fires are induced by humans. The rationale for these human-driven fires include improvement in the quality of grazing for wildlife, tourism (increasing esthetics for tourists), improvement in hunting, and fishing (Heinl et al., 2004). Strikingly, while the aforementioned reasons may be justifiable, they do cause huge changes in carbon dynamics in wetlands.

5.16 Climate change

Another way that wetland carbon storage is impacted is via climate change. As discussed in the preceding sections, the capacity of wetlands to store or release carbon is affected by changes in environmental drivers (Fig. 5.5). Tropical wetlands may be more vulnerable than temperate wetlands because of the overexploitation of their water and biomass for the sake of economic development (Chimner and Ewel, 2005). Considering that tropical and subtropical wetlands will see a mean annual temperature increase of 2°C–4°C (IPCC, 2019), freshwater tropical wetlands are at high risk because changes in temperature will change the evapotranspiration rates, seasonal cycles of the wetland, and fire frequency (Franzluebbers et al., 2001). These changes that occur due to climate warming will potentially modify the wetland carbon accumulation rates. Climate warming is predicted to cause changes in precipitation; however, changes are expected to be variable across the world. Tropical Africa and Asia will see decreases in precipitation whereas Central

America is expected to have increases in precipitation (Fischlin et al., 2007; Hao et al., 2019). Changes in precipitation will change wetland hydroperiod, which in turn may transform some tropical wetland from being a “panacea” that sinks carbon to pandora’s box that is a source of carbon. Current biogeochemical cycles and hydroperiods in tropical wetlands can provide a depiction of the effect that climatic change (higher temperatures under wetter and/or dryer scenarios, IPCC, 2007) can have on carbon cycles of temperate freshwater wetlands. Given the large variability on tropical wetland ecosystems and their diverse biogeochemical cycles, more research is warranted to accurately estimate the current role of tropical wetlands on global carbon cycles.

The carbon balance of tropical and subtropical wetlands may be affected less by changes in the average temperature or rainfall than by an increase in variability of the climate, especially extreme weather events. A major driver is the shift in the intertropical convergence zone which in turn affects El Niño-Southern Oscillation (ENSO; Pausata et al., 2020), and subsequently affects precipitation and temperature over much of the tropics and subtropics, as well as some mid-latitude regions. ENSO events can lead to weather extremes such as drought and heavy rainfall (causing floods), and there has been an increase in the frequency, persistence, and intensity of these events over the last 30 years in most of the tropics. For instance, in Southern Africa there have been three major cyclones (Cyclone Eline, 2000; Cyclone Dineo, 2017; Cyclone Idai, 2019; Mavhura, 2020). To this end, tropical cyclones have become more stochastic and also more severe when they happen. In addition to ENSO events, a more vigorous hydrological cycle is predicted in low latitude regions as a consequence of warming ocean temperatures (increasing, e.g., hurricane strength and frequency); this could impact land masses directly, or indirectly, by altering precipitation patterns. More periods of drought and flooding would also result in a higher peak in discharge, but longer dry periods. The net effect of these perturbations is likely to be a reduction in carbon storage, although the overall impact of climate change on these areas is currently very difficult to predict. In the Amazon basin, a record drought in 2005 may be a glimpse of the type of response to climate change we will see in tropical wetlands.

There is a need to mitigate the impacts of climate change globally. The only lasting way to reduce the long-term effects of climate change on global wetlands is to reduce climate change itself. To do this, the emission of greenhouse gases from human activities must decline substantially by greatly reducing our dependency on fossil fuels, the largest challenge of our time. Even under the most optimistic scenario of emissions reductions, however, the rate of global warming is likely to double by the year 2050. The role played by wetlands in the energy balance of this warmer and more crowded world will depend largely upon the extent to which those wetlands are degraded through climate change or land use, causing release back to the atmosphere of the carbon they have stored for hundreds or thousands of years. We can counter some of this carbon loss by effective management, such as restoring drained wetlands, returning meanders and floodplains to channeled waterways, using drained peatlands for forestry instead of agriculture or horticulture, and managing rice paddies to reduce methane emission. Unfortunately, interactions and feedbacks among environmental drivers and responses means that we cannot at present predict the overall impact of climate change on wetland ecosystems. This reality makes it essential to maintain long-term wetland monitoring networks so that we may document how the global climate changes. This data can then be useful in our understanding of change to wetlands, allowing environmental managers the opportunity to add the appropriate intervention strategies.

Reducing Emissions from Deforestation and forest Degradation (REDD +) offers developing countries financial payments for reducing emissions by reducing deforestation. The REDD + initiative exists because there is a consensus that reducing deforestation and degradation and promoting reforestation in the tropics (REDD +) has substantial mitigation potential in the fight against climate change (Houghton, 2012). Tropical forests offer one of the largest opportunities to cost-effectively address near-term emissions. While climate policy uncertainties generally hamper mitigation investments, reducing deforestation could be more rapidly deployed than other mitigation strategies, which could help hedge risks of rising future climate policy costs. Forest protection strategies rely on existing technologies, entail relatively low costs, and are generally publicly acceptable given a range of noncarbon cobenefits such as the protection of biodiversity, improvements in local climatic conditions, and regulation of water supplies. The idea of using forest-based strategies as a low-cost, near-term strategy to address climate change has been around for a long time, with a typical focus on how forest strategies can help to buy time to develop lower-cost technologies to reduce fossil fuel emissions. In general, forest-based mitigation has fundamental importance and without tapping its potential at large scale, the ambitious Paris targets might already be out of reach.

5.17 Conclusions and additional considerations

Wetland ecosystems are one primary component of the global carbon cycle. Specifically, tropical and subtropical wetlands contribute at least 50% of total wetland methane emissions, and over 80% of the natural sources, to the atmosphere partially due to large, inundated areas and high temperatures. With the current global warming trends for the tropics, one can expect that tropical wetland ecosystems will experience large changes in temperature, wetting and drying cycles. Future research should continue focusing on the drivers of carbon dynamics across different wetland ecosystems. For example, a few variables that were not addressed in this chapter were soil chemistry (e.g., pH) and redox potentials, soil moisture dynamics, and vegetation types and their impacts on

CH_4 and CO_2 emissions. More field measurements of carbon budget and fluxes are required to further understand the dominant environmental variables that impact wetland carbon dynamics; this is particularly true when considering data from less studied areas of tropical Africa.

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Chapter 6

Nutrient cycling

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6.1 Introduction and overview

Wetlands can function as sinks, sources, and transformers of nutrients, organic matter, and other materials. Wetland biogeochemistry depends on interactions between hydrologically driven physicochemical conditions and biological components of the system (Mitsch and Gosselink, 2015). These functions can change over long-term successional cycles (Craft, 1996; Howard-Williams, 1985), during periodic disturbances (Craft and Casey, 2000; Rivera-Monroy et al., 2011; Deemy and Rasmussen, 2017; Deemy et al., 2020), or through the course of annual wet/dry season dynamics (Cohen et al., 2004). Trophic structure and function of a wetland can shift in accordance with these annual or decadal variations (Howard-Williams, 1985). Hydrology acts as the central mechanistic driver of wetland nutrient cycling and trophic organization in wetlands and hydropattern is closely linked to all wetland cycles and ecological functions (Mitsch and Gosselink, 2015; Cuthbert et al., 2022, Chapter 17: Wasserman and Dalu, 2022, Chapter 1: Deemy et al, 2022a, Chapter 3).

Tropical wetlands nutrient cycling and ecological functions are strongly linked to the annual wet/dry season climate as well as longer cycle climate phenomena, such as altering precipitation due to El Nino-Southern Oscillation (Childers et al., 1990; Donders et al., 2005; Deemy et al., 2022b, Chapter 4). Subtropical wetlands often experience greater seasonal variation in temperature and precipitation conditions, driving patterns in annual biogeochemistry, and community trophic dynamics. In general, the most important driver of wetland biogeochemistry is the frequency and duration of wetting and drying periods. These changes in hydrologic conditions drive microbially mediated chemical reactions transformations (Vepraskas and Faulkner, 2001). However, short and long-term eutrophic conditions can also

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have a profound impact on both nutrient cycling and ecosystem structure (Corstanje et al., 2007). Spatial patterns in soil nutrients, particularly labile phosphorus, also have a strong impact on tropical and subtropical wetland ecosystem structure (Grunwald et al., 2006).

Wetting and drying cycles drive mobilization of nutrients from organic matter (Venterink et al., 2002), pulses in aerobic/anaerobic microbial production (Boon, 2006), bioturbation, and use by micro/macro faunal communities (Craft, 2001). For wetlands with frequent wetting and drying, organic matter is quickly decomposed and degraded leading to more mineral soils with moderate pH conditions (Vepraskas and Faulkner, 2001; McLatchey and Reddy, 1998). Seasonal changes in water table depth is a critical determinant of soil substrate respiration (Mezbahuddin et al., 2014). In wetlands with well-developed organic layers due to longer periods of inundation, pH conditions in combination with anoxic sediments will drive an entirely different microbial community (Vepraskas and Faulkner, 2001; Boon 2006).

The objective of this chapter is to provide an overview of nutrient cycling and trophic dynamics in subtropical and tropical wetlands. This chapter explains basic biogeochemical and trophic dynamic concepts in wetlands as context for specific tropical and subtropical wetlands.

6.2 Biogeochemistry

Wetlands are critical to biogeochemical cycling across spatial scales from local to global (Martinez-Espinosa, 2020; Zalman et al., 2018; Bridgham et al., 2013; Bridgham et al., 2006). The role of wetlands in global biogeochemistry is greatly disproportionate to their spatial area (Martinez-Espinosa, 2020; Land et al., 2019; Evenson et al., 2018; Cheng and Basu, 2017; Marton et al., 2015; Capps et al., 2014; Bridgham et al., 2013) because these systems often experience ranges of physicochemical conditions through time (Rasmussen et al., 2016). Internal spatial heterogeneity driven by microtopographic variation in inundation also contribute to high levels of biogeochemical activity (Frei et al., 2012). The distinct interplay of biology and geology exhibited by wetlands (Jackson et al., 2014; Craft, 2001) often results in relatively high levels of biogeochemical processes relative to most other ecosystems (Cheng and Basu, 2017; Marton et al., 2015).

Wetlands are the sites of critical functions in the cycling of nitrogen, phosphorus, sulfur, and carbon (Wang et al., 2020; Dalcin Martins et al., 2017; Cobb et al., 2017; Cohen et al., 2016; Palta et al., 2014; Fenner et al., 2011; Mitsch et al., 2010, Moyo, 2022, Chapter 5). While wetlands at high latitudes are known for storing and sequestering nutrients and carbon for long periods of time (Bridgham et al., 2006), wetlands in the tropics and subtropics are more variable in their biogeochemical roles (Sjögersten et al., 2014).

Wetlands have a distinct balance of chemical transformations driven by anaerobic conditions associated with prolonged soil inundation or saturation (Mitsch and Gosselink, 2015; Craft, 2001; Vepraskas and Faulkner, 2001). Wetland soils that remain saturated or inundated for long periods of time become reducing thus enabling transformations and portions of chemical cycles distinct from those in nearby upland soils (Vepraskas and Faulkner, 2001). These chemical transformations can allow wetlands to cycle a greater portion of nutrients within the system subsidized by periodic allochthonous pulses of inputs to replenish material lost to degassing (Mitsch and Gosselink, 2015). Subtropical cypress domes and tropical peatlands function in this way and may experience several years of isolation from nonatmospheric nutrient sources prior to storm runoff or river overbanking events that deposit material (Cobb et al., 2017; Deemy and Rasmussen, 2017; Mitsch et al., 2010).

6.3 Nutrients

Nitrogen and phosphorus are typically the most limiting elements to biological production in wetland ecosystems (Valiela and Teal, 1974). Nitrogen in labile forms (i.e., ammonia, nitrate, nitrite) is generally transported to wetlands via surface runoff where it stimulates microbial and vegetation growth (Mitsch and Gosselink, 2015). Nitrogen is generally limiting in freshwater wetlands because nitrate is one of the first compounds used as a terminal electron acceptor in soil redox reactions (Mitsch and Gosselink, 2015; Vepraskas and Faulkner, 2001). Degassing of elemental nitrogen is a primary loss of nitrogen from wetlands because high rates of microbial denitrification result from saturated anoxic soil conditions (Mitsch and Gosselink, 2015; Vepraskas and Faulkner, 2001).

Nitrogen and phosphorus are often colimiting factors freshwater wetland systems (Mitsch and Gosselink, 2015; Sjögersten et al., 2011; Boon 2006; Sundareshwar et al., 2003; Craft, 2001). In freshwater, wetlands with acidic pH ranges that drive low phosphorus uptake rates (Mitsch and Gosselink, 2015; Lambers et al., 2006; Adamec, 1997) because phosphorus readily binds to aluminum, iron, and calcium at low pH (Vepraskas and Faulkner, 2001). Unique plant communities including carnivorous plants can develop in response to pH driven phosphorus limitation (Wakefield et al., 2005; Adamec, 1997). Carnivorous plants, specifically pitcher plants (*Sarracenia purpurea* L.), can also facilitate microbial communities which convert depositional atmospheric nitrogen to more labile forms enable acquisition by the plant (Wakefield et al., 2005). Increases in nutrient loading, particularly phosphorus, can drive species shifts in community composition evidenced cattails (*Typha* spp.) dominating former sawgrass (*Cladium jamaicense*) marshes in the Everglades (Surratt et al., 2012; McCormick et al., 2009; Reddy and Osborne, 2007; Reddy et al., 1993). Tropical peatland tree communities also respond to nutrient availability gradients with community composition and diversity changing in association with phosphorus availability (Troxler et al., 2013).

Micronutrients are critical elements for life but are required in very small quantities for biological function/maintenance. A variety of micronutrients have been identified as critical drivers of terrestrial ecosystems primary production including, iron (Fe), magnesium (Mg), manganese (Mn), zinc (Zn), boron (B), copper (Cu), molybdenum (Mo), and nickel (Ni) (Rengel, 2007; Wurzburger and Hendrick, 2009; Powers and Salute, 2011). Both nitrogen (fixation) and phosphorus (uptake) in tropical forests have been specifically tied to molybdenum (Wurzburger et al., 2009; Wurzburger et al., 2012). Micronutrients (Zn, K, Mg, Ni) have also been shown to be critical drivers of leaf litter decomposition (Powers and Salute, 2011) as well as limiting to vegetation production under acidic root zone conditions (Adamec, 1997).

6.4 Nitrogen cycling

Nitrogen dynamics in wetlands occur through complex interrelated processes in both the soil and water column (Mitsch and Gosselink, 2015; Vepraskas and Faulkner, 2001). These processes include atmospheric deposition, leaching from biotic sources, ammonification, nitrification, denitrification, and immobilization (Mitsch and Gosselink, 2015). Freshwater systems can be nitrogen limited and inundated soils are often limited by nitrogen availability due to various obligate anoxic biogeochemical reactions involving nitrogen (Vepraskas and Faulkner, 2001).

Nitrogen can enter wetlands through several pathways depending on the level of hydrologic exchange with groundwater and other surface waters (Winter and Rosenberry, 1998; Howard-Williams, 1985). Elemental nitrogen diffuses into the water column from the atmosphere and is taken up by nitrogen fixing bacteria in the water column or substrate (both anaerobic and aerobic zones) (Klawonn et al., 2015; Boon, 2006). Organic nitrogen, dissolved ammonia, nitrate, and nitrite can all enter wetlands through surface or groundwater transport (Jacobs et al., 2007). Animals can also generate periodic pulses of nitrogen associated with animal migrations (Olson et al., 2005; Anderson and Mitsch, 2003; Zhang et al., 2016).

Typically, nitrogen is exported from wetlands through ammonia volatilization and degassing after denitrification (Mitsch and Gosselink, 2015; Davidson, 1997). Some elemental nitrogen produced by denitrification can be recycled in the wetland by nitrogen fixing bacteria. Additionally, the relationship between organic matter and the surface of marine soil sediments have accounted for large proportions of sequestered nitrogen (Vogel et al., 2014). The association between organic matter and mineral surfaces have contributed to the identified burial rates of nitrogen in freshwater and mangrove wetlands. Respectively, Table 6.1 shows rates that range from 1320 to

TABLE 6.1 **Examples of nitrogen burial rates in tropical and subtropical wetlands.**

Location	Type	Nitrogen burial rate (mg N m^{-2} $year^{-1}$)	Reference
Taylor Slough, FL, United States	Freshwater wetlands	1320–2970	Sutula et al. (2001)
Taylor Slough, FL, United States	Mangrove wetlands	3600–7200	Sutula et al. (2001)
St. Johns River, FL, United States	Weighted range for freshwater and mangrove wetlands Freshwater wetlands	1890–4027	Sutula et al. (2001)
		6560–27000	Widney et al. (2016)

27,000 mg N m^{-2} $year^{-1}$ (Sutula et al., 2001; Widney et al., 2016; Vogel et al., 2014). Nitrogen bound in organic matter can be highly important to sequestration of nitrogen and its availability to reducing bacteria (Megonigal and Neubauer, 2019). Organically bound nitrogen can also be released and redistributed within the wetland or exported during fire events (Liao et al., 2013; Smith et al., 2001) (Fig. 6.1).

Nitrogen mineralization is coupled to decomposition rates that are a function of the microbial community and can be limited by available phosphorus. In nutrient enriched portions of the Florida Everglades, increased microbial biomass as the result of phosphorus enrichment in disturbed areas lead to greater nitrogen mineralization rates than in areas with less eutrophic conditions (Corstanje et al., 2007). Ammonium produced by mineralization processes can be taken up by plants or it can be immobilized by chemically bonding to substrates, converted to ammonia under certain pH conditions ($pH > 8$), or converted to nitrite by microbial processes (under conditions of sufficient dissolved oxygen) (Prinčič et al., 1998).

Negatively charged soil particles (particularly clays) can immobilize ammonium in the water column. This typically means that ammonium is less biologically available in soils despite being a readily available molecule in the water column. Nitrite produced by the bacteria *Nitrosomonas* sp., can be further changed to nitrate (if sufficient oxygen present) by *Nitrobacter* sp.

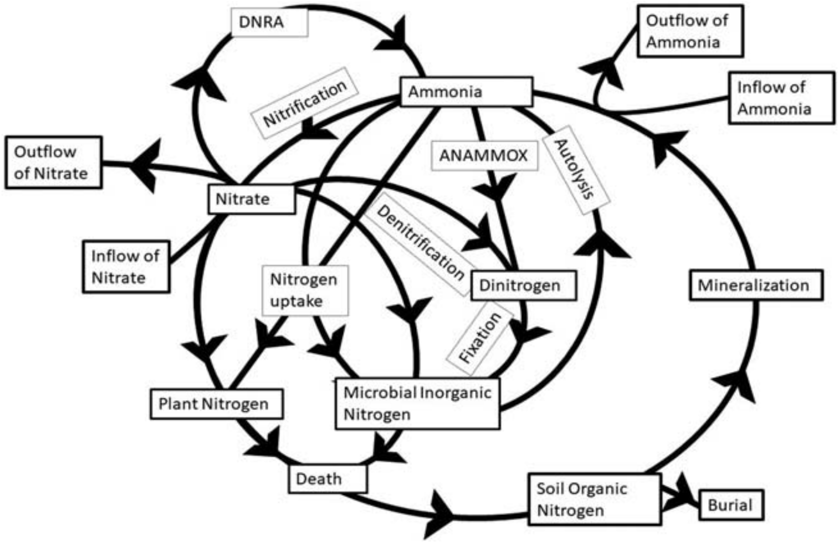

FIGURE 6.1 Conceptual model of nitrogen cycling in freshwater wetlands. Note on acronyms: dissimilatory nitrate reduction to ammonia or DNRA produces ammonia through reduction of nitrates and nitrate driven anaerobic ammonium oxidation (Anammox) is an anaerobic ammonium oxidation process. *Modified from Dørge, J., 1994. Modelling nitrogen transformations in freshwater wetlands. Estimating nitrogen retention and removal in natural wetlands in relation to their hydrology and nutrient loadings. Ecological Modelling 75, 409–420; Han, H.J., Los, F., Burger, D.F., Lu, X.X., 2016. A modelling approach to determine systematic nitrogen transformations in a tropical reservoir. Ecological Engineering 94, 37–49; Quoc Anh, D., Tantayotai, P., Cheenkachorn, K., Sriariyanun, M., 2015. Anammox process: the principle, the technological development and recent industrial applications. KMUTNB International Journal of Applied Science and Technology, 1–8.*

These reactions must take place in aerobic soil zones, areas oxygenated by roots in the rhizosphere, or potentially in the water column (Prosser, 2005).

Nitrate is a highly mobile and biologically labile molecule. This negatively charged ion is often subject to rapid assimilation by plants and microbes, which is also known as assimilatory nitrate reduction (Mitsch and Gosselink, 2015). The term assimilatory is used because the nitrate is incorporated into cellular structures. Nitrate can also be used in dissimilatory nitrous oxide reduction where nitrate is reduced by microbes, but not incorporated into the cell. Reduction to ammonia and denitrification are common sources of nitrate loss in wetlands. Nitrate is also subject to export through subsurface flow because it is highly mobile in ground or soil water flow (Vepraskas and Faulkner, 2001). Unlike positively charged phosphate ions, the negatively charged nitrate ion prevents immobilization through bonding with soil particles which tend to be negative.

Denitrification occurs under anaerobic conditions and is mediated by facultative anaerobes that use nitrate as the terminal electron acceptor during respiration

(Vepraskas and Faulkner, 2001). Nitrate is reduced to nitrous oxide and then to nitrogen gas (elemental nitrogen/dinitrogen). Denitrification may be the most significant biological source of nitrogen loss from wetland ecosystems (González-Blanco et al., 2020). Denitrification rates for a variety of wetland ecosystems are identified in Table 6.2. Reported denitrification rates range from 0.03–6.60 mg N m^{-2} h^{-1} in tropical mangroves to 1.10–20.50 mg N m^{-2} h^{-1} in floodplain and coastal wetlands (Rivera-Monroy et al., 1995; Alongi et al., 2004; Adame et al., 2019; Xue et al., 1999; Hansen et al., 1994; Tomaszek et al., 1997).

Under highly acidic conditions (peatlands), denitrification is inhibited and less of a factor (Mitsch and Gosselink, 2015). Soil temperature is also related to nitrogen loss in wetlands with more biogeochemical activity potential occurring in warmer temperatures; particularly peatlands (Hodgkins et al., 2018). Meaning that wetlands in tropics and subtropics likely sequester less nitrogen than those in northern latitudes except where inundation induces peat formation.

While both ammonia and nitrate diffuse to the saturated anaerobic soil layers in wetlands, nitrate diffusion occurs at approximately seven times the rate of ammonia diffusion. This means that nitrate loss to deeper soil layers will be a more limiting factor (generally) than ammonia diffusion.

Elemental nitrogen and nitrous oxide can both degas from wetlands to the atmosphere. Nitrogen gas predominates especially during permanently inundated conditions. Under drawdown or pulsing hydrologic conditions, wetlands will export more nitrous oxide (Hooijer et al., 2010) because reducing conditions do not persist through the full denitrification pathway (Vepraskas and Faulkner, 2001). This has implications for atmospheric composition in the face of widespread change in meteorological conditions as a result of climate change. If wetlands that are normally flooded begin to shift toward a flood pulse hydrologic regime, much of the nitrogen that is normally reduced to elemental nitrogen will be lost as nitrous oxide and increase thermal absorbance of the atmosphere.

One of the main sources of organic nitrogen in wetlands is nitrogen fixation, a microbially mediated process. This process is limited to a subset of aerobic and anaerobic bacteria as well as some cyanobacteria or blue-green algae. Nitrogen fixation activity is most active in anaerobic conditions because nitrogen fixing organisms use the enzyme nitrogenase which is inhibited by aerobic conditions (Mitsch and Gosselink, 2015). While aerobic conditions are unfavorable for nitrogenase activity, fixation can occur in aerobic zones of the wetland water column and soil profile, as well as in the rhizosphere (Šantrůčková et al., 2010). Reported annual fixation rates have ranged from as low as 30 mg N m^{-2} $year^{-1}$ in mangroves to as high as 15,000 mg N m^{-2} $year^{-1}$) in coastal salt marshes (Zuberer and Silver, 1978; Howarth et al., 1988) (Table 6.3).

This important input of nitrogen to wetlands can even occur on leaf and stem surfaces of submerged plants. Nitrogenase activity in oxygenated zones requires

TABLE 6.2 **Examples of denitrification rates in tropical and subtropical wetlands.**

Location	Type	Denitrification (mg N m^{-2} h^{-1})	Reference
Terminos Lagoon, Mexico	Tropical mangroves	0.03–0.13	Rivera-Monroy et al. (1995)
Tietê River, Brazil	Subtropical reservoir	0.22	Abe et al. (2003)
Matang Mangrove Forest Reserve, Malaysia	Tropical mangroves	0.23–6.6	Alongi et al. (2004)
Puerto Rico	Tropical small rivers	0.30–9.6	Potter et al. (2010)
Lake Naivasha, Kenya	Tropical lake	1.5–12.9	Viner (1982)
Queensland, Australia	Floodplain wetlands	1.1–9.7	Adame et al. (2019)
Champaign County, United StatesNarragansett Bay, United StatesOld Woman Creek, United States	Constructed wetlandRiparian wetlandCoastal wetland	2.0–11.80.57–1.6320.5	Xue et al. (1999)Hansen et al. (1994)Tomaszek et al. (1997)

TABLE 6.3 Examples of nitrogen fixation rates in tropical and subtropical wetlands.

Location	Type	Nitrogen fixation rate (mg N m^{-2} $year^{-1}$)	Reference
Tampa Bay, United States	Mangroves	30–2600	Zuberer and Silver (1978)
Shark R. Slough, United States	Mangroves	3000	Pelegri et al. (1997)
Everglades, United States	Cypress swamp	790–2800	Dierburg and Brezonik (1981)
	Freshwater marsh	10–600	Howarth et al. (1988)
	Peat bog	50–2100	Howarth et al. (1988)
	Cypress swamp	400–2800	Howarth et al. (1988)
	Coastal salt marsh	200–15,000	
El Eden Ecological Reserve, MexicoHID Everglades National Park, United States	Tropical wetlandSubtropical wetlands	9000200–400	Vargas and Novelo (2007)Liao and Inglett (2014)

certain cellular structures in single cell bacteria or select cells in blue-green algae colonies, which create anaerobic conditions (Vepraskas and Faulkner, 2001). Low pH can reduce activity of nitrogen fixing bacteria and in some conditions (peat bogs), activity by nitrogen fixing bacteria appears to be absent. However, in these conditions, cyanobacteria account for the majority of nitrogen fixation (Vepraskas and Faulkner, 2001; Mitsch and Gosselink, 2015).

In tropical marshes of Belize, phosphorus additions were associated with shifts from cyanobacteria mediated autotrophic nitrogen fixation to sulfur reducing bacteria mediated heterotrophic nitrogen fixation (Šantrůčková et al., 2010). Plant litter mass and quality (defined as labile N + P content) are also both associated with shifts in nitrogen fixation associated with phosphorus enriched conditions (Vepraskas and Faulkner, 2001).

Highly mobile nitrates can be transformed to the less mobile, but still biologically labile form of ammonia through a process called dissimilatory nitrate reduction to ammonia (DNRA) (Megonigal et al., 2004; Tiedje, 1988). This process is often understudied in favor of more dominant chemical pathways (e.g., denitrification) when nitrate concentrations are high but can switch to DNRA when concentrations are low (Rahman et al., 2019) (Table 6.4).

A wide variety of aerobic, anaerobic, and facultative microbes can carry out this anaerobic nitrate transformation (Megonigal et al., 2004). This anaerobic reaction is an energy producing chemical transformation that may be prevalent in deeper anoxic soil layers where infiltration or leaching transport nitrate (Tiedje, 1988). In wetlands with particularly high concentrations of organic substrate and limited nitrate, DNRA may even be a primary method of nitrate loss (Mitsch and Gosselink, 2015).

Anaerobic ammonium oxidation or Anammox contributions to nitrogen cycling in wetlands is not well quantified or understood. In anaerobic conditions, nitrite reacts with ammonium to produce water and elemental nitrogen. However, this process is likely important in wetlands limited by organic carbon substrate necessary for denitrification reactions as is the case in many small isolated subtropical wetlands (González-Blanco et al., 2020). Rapid recurrence intervals in fire frequency may also contribute to the importance of this process by limiting available organic carbon.

6.5 Phosphorus cycling

Phosphorus is possibly the most important limiting element in structuring freshwater wetland ecosystems (Morrison et al., 2016; Sutula et al., 2001) and has specifically been shown to limit productivity across peatland types (Hill et al., 2014; Sjogersten et al., 2011) as well as drive coupled patterns in microbial-macrophyte community structures (Troxler et al., 2013). Seasonal climate driven hydrologic factors, such as monsoon driven runoff in tropical wetlands of India, can also drive greater phosphorus availability or pulses in phosphorus inputs (Gogoi et al., 2019). This is in part due to phosphorus being closely associated with runoff transported sediments or particulate

TABLE 6.4 Microbial types associated with energy sources.

Microbe type	Energy source	Biosynthetic carbon source
Chemoorganotrophs	Organic compounds	Organic compounds
Chemolithotrophs	Inorganic compounds	Organic compounds
Photoautotrophs	Light	Carbon dioxide
Photoheterotrophs	Light	Organic compounds
Mixotrophs	Variable	Variable

matter (Deemy and Rasmussen, 2017) and can be responsible for sequestration in depressions (Deemy and Rasmussen, 2019).

Phosphorus affinity for particulates and it generally occurring as part of solid rather than gaseous compounds (Vepraskas and Faulkner, 2001), means that it has fundamentally different cycling processes through ecosystems than nitrogen, sulfur, or even carbon (Mitsch and Gosselink, 2015). Phosphorus can occur as part of both organic compounds and inorganic compounds in wetlands (Vepraskas and Faulkner, 2001). Mineral phosphorus species in the form of various orthophosphates are critically important biologically labile compounds that are rapidly assimilated by microbial and plant communities when available (Maitra et al., 2015; Battle and Golladay, 2007). These negatively charged ions also have a high affinity for clays, organic matter, and soluble ions (e.g., aluminum, calcium, iron, and magnesium; Maitra et al., 2015). Additionally, phosphorus chemical affinity for iron and aluminum increases with decreasing pH (Vepraskas and Faulkner, 2001). Under more basic pH conditions, orthophosphates will form complexes with calcium and magnesium. If conditions change (become less or more acidic, respectively), the phosphate will be released back into solution (Vepraskas and Faulkner, 2001) (Fig. 6.2).

Algal photosynthesis can be a critical component in determining phosphate cycling within a wetland and photosynthetic organism assemblages can

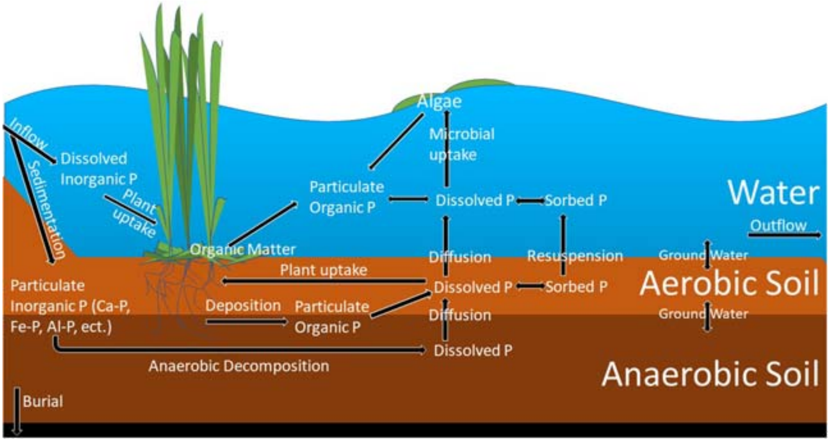

FIGURE 6.2 Conceptual model of phosphorus cycling in wetland systems (modified from Ozkan, 2008). *Modified from Currie, S., Vanzomeren, C., Berkowitz, J., 2017. Utilizing Wetlands for Phosphorus Reduction in Great Lakes Watersheds: A Review of Available Literature Examining Soil Properties and Phosphorus Removal Efficiency. U.S. Army Engineer Research and Development Center (ERDC) Environmental Laboratory, Vicksburg, MS; Hantush, M., Kalin, L., Isik, S., Yucekaya, A., 2012. Nutrient dynamics in flooded wetlands. I: model development. Journal of Hydrologic Engineering, 18, 1709–1723.*

driver differences in phosphorus availability (Gogoi et al., 2019). Periphyton, in particular, can be associated with interactions between abiotic and biotic processes that sequester carbon (Scinto and Reddy, 2003; Browder et al., 1994). If high algal photosynthetic rates drive wetland pH above 8 by removing dissolved carbon dioxide, it is possible for dissolved orthophosphates to bind with calcium, magnesium, or both and precipitate out of solution (Mitsch and Gosselink, 2015; Liptak, 2000). Unless pH ranges drop to near or below neutral (i.e., 7) at night when water column respiration drive increases in carbon dioxide, the phosphate will likely remain bound (Vepraskas and Faulkner, 2001). Sedimentary minerals that can form in this way include both calcite and dolomite (Mitsch and Gosselink, 2015; Hoch et al., 2000). Both minerals are carbonate compounds ($CaCO_3$ and $Ca(Mg)CO_3$, respectively) and often make up components of marl soils found in some subtropical wetlands and the more tropical Florida Everglades (Hoch et al., 2000; Browder et al., 1994).

Orthophosphates can readily bind to clay particles at the edge of the clay matrix where the negatively charged phosphate binds to a positively charged metal ion (Mitsch and Gosselink, 2015; Vepraskas and Faulkner, 2001). Essentially the phosphate molecule substitutes for an absent silicate molecule and sediment binding potential is finite (Vymazal, 2007). This means that available phosphorus can overwhelm available binding sites in sediments reducing a wetland's sequestration potential through time (Vymazal, 2007; Vepraskas and Faulkner, 2001).

Most phosphate is transported from uplands or among linked wetlands bound to clays or in organic matter, which means the sediment trapping characteristic of wetland plant communities also serves to generate an influx of phosphate (Mitsch and Gosselink, 2015). Greater sedimentation rates result in greater phosphate sequestration, which has been seen in cypress swamps and freshwater wetlands with rates ranging from as low as $0.43\ \mathrm{g\,P\,m^{-2}\,year^{-1}}$ to as high as $38.5\ \mathrm{g\,P\,m^{-2}\,year^{-1}}$ (Table 6.5) (White et al., 1998; Mitsch et al., 1979). Phosphate sorbed to clay (or other sediments) can become available to plants through phosphate solubilizing bacteria activity in the rhizosphere (Teng et al., 2019).

In wetland soils with anoxic conditions, reduction of iron compounds can release phosphates back to solution which make them available for the biotic community (Maitra et al., 2015). Hydrolysis reactions can also free phosphate bound to clays or metal compounds back to solution. Additionally, chemosynthetic bacteria that facilitate production of acidic compounds (various organic acids) or directly produce nitric or sulfuric acid facilitate the release of bound phosphates (Maitra et al., 2015).

Colonial nesting waterbirds can contribute significant phosphorus to wetlands, altering rates of primary and secondary production, and in some cases causing eutrophic conditions. These dynamics are reviewed in detail later in this chapter.

TABLE 6.5 Examples of phosphorus burial rates in tropical and subtropical wetlands.

Location	Type	Phosphorus burial rate ($g\ P\ m^{-2}\ year^{-1}$)	Reference
Cargill Bay, Canada	Freshwater wetland	38.5	White et al. (1998)
Frank Lake Basin 1, Canada	Freshwater wetland	24	White et al. (1998)
Frank Lake Basin 2, Canada	Freshwater wetland	0.43	White et al. (1998)
Johnson County, United States	Cypress swamp	3.48	Mitsch et al. (1979)

6.6 Sulfur cycle

Sulfur is not typically a limiting nutrient in wetlands but is used by a variety of microbes for metabolism and is a critical element for biological growth as well as maintenance (Mitsch and Gosselink, 2015). In some systems sulfate has been shown to patterns in dissolved organic matter (e.g., Everglades, Poulin et al., 2017). Generally, sulfur occurs in wetlands as elemental sulfur, sulfide, thiosulfate, and sulfate (Pester et al., 2012). Sulfur, specifically hydrogen sulfide, also contributes to the classic wetland scent immediately observable upon disturbing anoxic sediment (Hicks and Lamontagne, 2006). Sulfur content in wetlands is largely dependent on the influence of geologic substrate or marine/estuarine hydrologic contributions (Mitsch and Gosselink, 2015; Boon 2006; Howarth et al., 1988) (Fig. 6.3).

Sulfides produced by sulfate reduction reactions can cycle within wetlands because they are used in both chemoautotrophic activity (Boon 2006; Vepraskas and Faulkner, 2001) as well as photosynthetic activity (Burke et al., 1974) by select microbes (Mitsch and Gosselink, 2015). These reactions typically occur in the aerobic zones of wetlands (Bharathi, 2010). It should also be noted that nitrate can be used as the terminal electron acceptor in chemoautotrophic sulfide oxidation activity in anaerobic zones (Jost et al., 2009).

Hydrogen sulfide can also be used as a reactant in microbial photosynthetic activity. Where water is normally the electron donor in more conventional photosynthesis, hydrogen sulfide provides the electrons. Elemental sulfur is produced as a byproduct in this version of photosynthesis rather than elemental oxygen. This most commonly occurs in salt marshes or on mudflats (Minter 1982), but is certainly possible in freshwater wetlands (Burke et al., 1974). This reaction generally takes place on anaerobic sediments with available sunlight but lacking oxygenation.

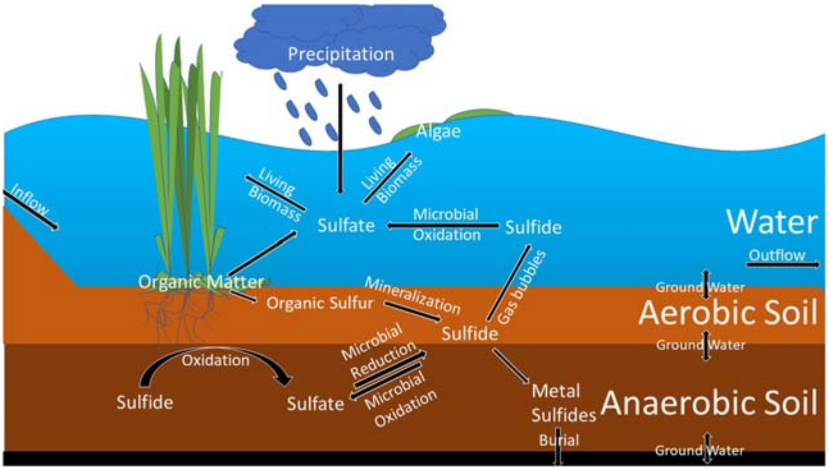

FIGURE 6.3 Conceptual model of sulfur cycling in wetland ecosystems. *Modified from Orem, W., 2007. Sulfur Contamination in the Florida Everglades: Initial Examination of Mitigation Strategies; Jørgensen, B., Findlay, A., Pellerin, A., 2019. The biogeochemical sulfur cycle of marine sediments. Frontiers in Microbiology 10, 849; Urakawa, H., Bernhard, A., 2017. Wetland management using microbial indicators. Ecological Engineering 108, 456–476.*

A variety of microbes can oxidize hydrogen sulfide to elemental sulfur and another set of species can further oxidize elemental sulfur to sulfate , which may then be reduced back to hydrogen sulfide if conditions become anoxic or if the sulfate was produced by anaerobic reactions using nitrate (Howarth et al., 1988).

Microbial activity that uses sulfate as the terminal electron acceptor in respiration is known as assimilatory sulfate reduction. This sulfur transformation is an obligate anaerobic process and generally occurs in anoxic sediment zones (Chambers and Pederson, 2006). Sulfate reduction requires an organic substrate often using those produced by fermentation reactions in submerged plant structures. Hydrogen sulfide gas is produced by these reactions and can degas to the atmosphere which represents the primary loss of sulfur from wetlands (Hicks and Lamontagne, 2006). While sulfate reduction can happen across a wide range of pH, and pH is not overly limiting to this transformation, peak reaction activity occurs at neutral pH (pH = 7).

Sulfate can also be reduced through organic reactions such as those that produce dimethyl sulfide (DMS) (Bharathi, 2010). While certainly present in wetlands, DMS producing sulfate transformations have been shown to be responsible for a much smaller outflux of sulfur than those observed in the open ocean (Fig. 6.4).

6.7 Wetland nutrient–trophic interactions

Food webs, or networks of organisms related through production and consumption, can be organized into levels by trophic status (primary producers,

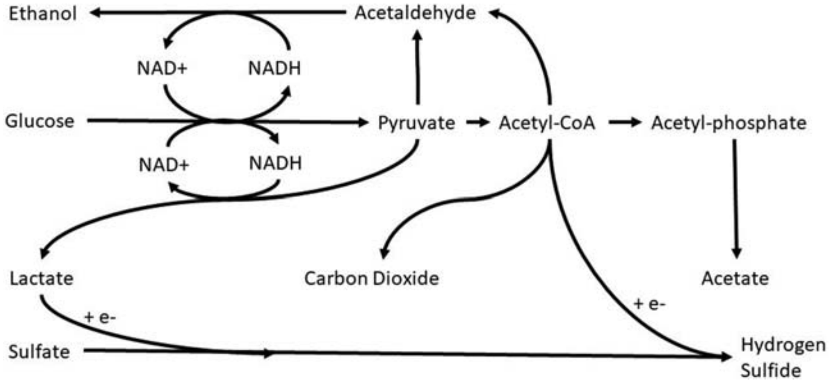

FIGURE 6.4 Conceptual model of the fermentation and the role of sulfur in wetlands. *Modified from Vepraskas M.J., Faulkner, S.P., 2001. Redox chemistry of hydric soils. In: Richardson, J.L., Vepraskas, M.J. (Eds.), Wetland Soils: Genesis, Hydrology, Landscapes, and Classification. CRC Press, pp. 85–106; Mitsch, W.J., Gosselink, J.G., 2015. Wetlands, fifth ed., John Wiley & Sons, Inc., p. 456.*

herbivores, predators, detritivores, etc.). Processes such as herbivory link trophic levels through the transformation of organic matter from one form (plants or algae) to another (animal biomass, fecal excrement, carbon dioxide). Through nutrient assimilation into plant and animal tissue, and transformation through consumptions and egestion, trophic interactions regulate biogeochemical processes. These interactions control the availability, movement, and form of nutrients in an ecosystem (Elser et al., 2000; Hessen et al., 2004; Pace et al., 1999; Wardle, 1999). Trophic interactions and biogeochemical processes are reciprocally related so that rates of primary production, herbivory, and other processes are controlled by nutrients (Elser et al., 2000; Rosemond et al., 2001), while at the same time nutrient dynamics are regulated by patterns of consumption (Pace et al., 1999; Polis and Strong, 1996; Wardle, 1999). In isolated tropical and subtropical wetlands fluxes of nutrients, abundance of plants and animals, and trophic interactions are tightly linked to seasonal wet/dry cycles and associated patterns of hydrologic connectivity and colonization (Brown et al., 2006; Pendleton et al., 2014; Pettit et al., 2017; Venarsky et al., 2020). As a result, wetlands in wet/dry climates exhibit highly dynamic nutrient budgets and food webs. The biogeochemical and trophic interactions affecting these ecosystem properties in wetlands are discussed in the sections below.

6.8 Trophic regulation of nutrient budgets

As described previously in this chapter, nutrient budgets are mass balance models of nutrient flows (inputs, outputs) and stocks (storage) through an ecosystem. Trophic interactions can affect how nutrients enter and leave an ecosystem, and the quantity of nutrients stored within living biomass, detritus, or soils. Trophic cascades, or propagating changes across trophic levels initiated by a predator, have the potential to alter nutrient storage and export. However, they are rare in tropical wetlands due to complex food webs, high biodiversity, prevalence of omnivory, and of allochthonous resources, which buffer food webs from trophic cascades (Polis and Strong, 1996; Strong, 1992). When biodiversity is high, loss of one population does not lead to a loss of ecological function (e.g., decreased herbivory) (Strong 1992, Pendleton et al., 2014), because functional redundancy across species compensates for the loss. Consumers may utilize diverse autochthonous and allochthonous resources, varying resource use seasonally (Strong 1992; Pettit et al., 2017; Venarsky et al., 2020). In dynamic wet/dry climates consumers readily shift their diet, and even their trophic level (herbivory to omnivory to carnivory), so trophic cascades are less likely (Dalu et al., 2017; Pettit et al., 2017; Schalk et al., 2017).

Migratory macrofauna and megafuana moving between environments directly affect budgets through nutrient import, export, and storage (Cuthbert et al., 2022, Chapter 17). Animal can provide a source of nutrients to an ecosystem, subsidizing isolated food webs by integrating resources from the landscape (Oliver and Schoenberg, 1989; Warfe et al., 2013). Rookeries, or colonies of nesting waterbirds, provide nutrient subsidies as guano that dramatically alter nutrient budgets and ecosystem function. Rookeries increase concentrations of nitrogen and phosphorus above reference levels, with effects lasting even after rookery abandonment (Oliver and Schoenberg, 1989; Telesford-Checkley et al., 2017). Inputs of micronutrients including sulfur, magnesium, iron, and potassium also increase from rookery presence (Telesford-Checkley et al., 2016). Consequences of guano-nutrient enrichment depend on the ecosystem nutrient status. Many tropical and subtropical wetlands are oligotrophic (Dhandapani et al., 2021; Gaiser et al., 2005; Oliver and Schoenberg, 1989; Warfe et al., 2013), and subsidized nutrients may be rapidly assimilated or immobilized (Brown et al., 2006; Irick et al., 2015; Oliver and Schoenberg, 1989). In the Okefenokee Swamp, a low-nutrient forested subtropical wetland, a rookery enhanced primary and secondary production of phytoplankton and zooplankton (Oliver and Schoenberg, 1989). On tree islands within the Everglades, a historically low-nutrient subtropical wetland complex, rookeries enrich soil-phosphorus concentrations with lasting effects on ecosystem function (Irick et al., 2015; Noe et al., 2001). By contrast, colonial waterbirds can deleteriously enrich wetland waters, causing eutrophication and low oxygen conditions (Signa et al., 2015; Telesford-Checkley et al., 2017). By integrating landscape resources, colonial waterbirds can add significant inputs of nutrients to food webs leading to positive and negative shifts in ecosystem productivity.

Fish and amphibians are also capable of regulating nutrient budgets and cycling through trophic interactions. Similar to the role of waterbirds, fish colonizing wetlands early in the wet season provide a source of nutrients through excrement derived from organic matter consumed elsewhere (Pendleton et al., 2014; Warfe et al., 2013). Seasonal dry-downs can lead to high fish mortality through desiccation and increased predation by waterbirds (Chick et al., 2008; Stevenson and Childers, 2004). Detrital fish tissue serves as a nutrient input that may fuel early wet season primary production (Stevenson and Childers, 2004). Through life-stage specific colonization of isolated pools, amphibians move significant quantities of nitrogen and phosphorus between wetland and terrestrial ecosystems (Capps et al., 2015; Cuthbert et al., 2022, Chapter 17). Fish may also contribute to nutrient export if they migrate from wetlands to adjacent waterbodies (Brazner et al., 2001; Reichard 2022, Chapter 12), though this pathway is not well studied in tropical and subtropical isolated wetlands. In addition to import and export, nutrient storage and mineralization are regulated by trophic interactions. Fish sequester phosphorus as living biomass, reducing ambient concentrations and potential nutrient export (Chick et al., 2008; Noe et al., 2001; Pendleton et al., 2014). Changes to fish abundance or grazing can therefore alter nutrient storage capacity of wetlands. In situ consumption, egestion, and excretion of autochthonous resources by fish is an important driver of nutrient mineralization (Pendleton et al., 2014). Thus trophic interactions direct the flow and storage of nutrients in isolated wetlands, and are especially important in low-nutrient systems.

6.9 Effects of nutrients on food webs

Nutrient availability is a fundamental driver of food web structure and function. Food webs in isolated tropical and subtropical wetlands exhibit seasonal patterns. As dry season conditions stress organisms and limit resources, food web complexity is reduced. During the wet season, resources grow more abundant and diverse, followed by corresponding changes in food web structure and trophic interactions (see Cuthbert et al., 2022, Chapter 17; Dalu et al., 2022, Chapter 8; Moraes et al., 2022, Chapter 13; Piedade et al., 2022, Chapter 7; Reichard 2022, Chapter 12; Tarakini et al., 2022, Chapter 14). Food web structure and trophic interactions in tropical and subtropical wetlands have developed around these characteristic low-nutrient, dynamic, and seasonal resource fluxes (Brown et al., 2006; Dalu et al., 2017; Gaiser et al., 2005; Schalk et al., 2017).

Subtropical and tropical wetland organisms are adapted to dynamic resource availability and are equipped to rapidly assimilate seasonal pulses of nutrients (Brown et al., 2006; Pettit et al., 2017; Venarsky et al., 2020; Warfe et al., 2013). Ambient nutrient concentrations remain low even during periods of high input due to rapid uptake into biomass or immobilization in the soil (Brown et al., 2006; Gaiser et al., 2005). During the wet season, macroinvertebrates and fish shift to primarily allochthonous resource use

(Pettit et al., 2017; Venarsky et al., 2020). Food web complexity increases with organism diets increasing in specialization over the wet season (Pettit et al., 2017; Schalk et al., 2017). During the dry season, food webs contract and organism diets grow more similar. Many species adopt omnivorous feeding, and develop more generalized and autochthonous resource use (Dalu et al., 2017; Pettit et al., 2017; Schalk et al., 2017).

Pulses of nutrients inputs drive biomass across trophic levels. Phosphorus enrichment completely restructures Everglades food webs (Chick et al., 2008; Gaiser et al., 2005; Noe et al., 2001). These changes are mediated by altering the structure of unique calcareous periphyton mats which only form under low-nutrient conditions, and protect algae from grazing. With even small increases in phosphorus periphyton mats are lost and plant biomass doubles (Gaiser et al., 2005). Shifting basal resources from low forage quality periphyton mats to more edible plants has cascading effects throughout the Everglades food web (Chick et al., 2008; Gaiser et al., 2005; Noe et al., 2001). Fish abundance and biomass increase and rates of plant herbivory increase (Noe et al., 2001). Phosphorus inputs elsewhere have been observed to restructure food webs, as in the Okefenokee Swamp rookery referenced earlier in this section. The abandoned rookery provided a natural experiment to test the effects of phosphorus enrichment in that system. Surveys and controlled experiments revealed the phosphorus-rich guano enhanced biomass of phytoplankton, zooplankton, and zooplanktivorous fish in a blackwater marsh (Oliver and Schoenberg, 1989). Detritivore biomass and rates of detritivory can also increase with nutrient enrichment. Phosphorus additions have been found to increase the biomass of detritivore-invertebrates (Rosemond et al., 2001). Enrichment can also lead to higher rates of detritivory if preferred basal resources by invertebrates become less available (Noe et al., 2001). In characteristically dynamic and low-nutrient isolated wetlands, food webs and associated energy transfers are tightly regulated by nutrient fluxes, and highly sensitive to minor changes.

6.10 Conclusions

Wetlands, particularly depressional ecosystems or temporary ponds, function as both biogeochemical hotspots as well as trophically distinct features embedded within the landscape. These systems provide intrinsic ecological value as well as model systems for testing and refining ecological theory. Tropical peatlands represent one of the largest and understudied global reserves of sequestered nutrients and carbon. Fauna such as birds and fish exert control over nutrient cycling and budgets through trophic interactions in subtropical and tropical wetlands. Changes to nutrient inputs through agriculture and other factors can dramatically restructure food webs, especially in historically low-nutrient systems. The seasonal wet/dry cycles in tropical and subtropical wetlands provide a foundation for unique and highly dynamic interactions between hydrology, biogeochemistry, and communities of plants and animals.

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Section 2

Biota and biotic processes

Chapter 7

Vegetation

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7.1 Introduction

In this chapter, we give an overview of the status quo of knowledge and the importance of the vegetation of tropical wetlands. Our focus lies on obligate wetland species, be it herbaceous plants, such as macrophytes and grasses, or lignified plants, such as shrubs and trees. We describe the ecology and adaptations of higher vascular plants in freshwater wetlands, but not of algae (see Dalu et al., 2022, Chapter 8 for algae). The cited species generally occur in lowland wetlands below 1000 m asl (above sea level).

According to the definition given by Gopal and Junk (2001) wetland species are "all those plants, animals and microorganisms that live in a wetland permanently or periodically, (including migrants from adjacent or distant habitats), or depend directly or indirectly on the wetland habitat or on another organism living in the wetland." We chose this broad definition because it is essential if we aim to understand how to contribute to wetland management and conservation with our overview.

Many tropical countries and regions lack detailed inventories of wetlands (Finlayson, 2012; Junk et al., 2014) and different approaches for the wetland classification have been applied which lead to uncertainties regarding the tropical wetland extension also often hindering direct comparisons (see Wasserman and Dalu, 2022, Chapter 1; Job and Seiben, 2022, Chapter 2). In several tropical

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countries classifications for specific wetlands or wetland types were developed, but unified classification systems do not yet exist. Junk et al. (2011) developed a hierarchical classification system based on climate, hydrology (see Deemy et al., 2022, Chapter 3), edaphic conditions (water, soils), and higher plants (herbs, trees) for wetland ecosystems for the Amazonian rainforest domain. The classification was extended to the Brazilian territory (Junk et al., 2014) and recently also to Colombian wetlands (Ricaurte et al., 2019), showing its adaptability to a wide range of environments in tropical regions. All wetland and habitat classifications in this chapter refer to the classification system of Brazilian wetlands (Junk et al., 2014).

Tropical freshwater wetland extension differs considerably across continents, but is generally larger than in any other climate zone on Earth. Wetland extension ranges from 20% to 30% of landscapes in tropical South America (Junk et al., 2014), where the Amazon, Orinoco, and Paraguay-Paraná River systems periodically flood areas of several hundred thousands of square kilometers, including large wetlands in both rainforest (i.e., Amazon, Orinoco) and savannah biomes (i.e., Pantanal, Llanos de Moxos, Llanos de Orinoco, and Bananal). Besides periodically flooded river floodplains, episodically and permanently flooded wetlands, such as riparian zones along low order creeks and streams, and swamps, in addition, cover huge areas (e.g., up to 1 million km^2 in the Amazon Basin, Junk et al., 2011).

Freshwater wetlands in tropical Africa are smaller than their counterparts in South America because westward mountain ranges cause orographic rainfall and reduce the transport of atmospheric humidity to easterly regions. Seasonal wetlands of the Congo River basin and Cuvette Centrale extend to an area of approximately 230,000 km^2 (Betbeder et al., 2013). Large wetland complexes are located in the African savannah biome, such as the Lake Chad Basin (mainly covered by grass and shrub savannahs, marshes) with an area of 106,000 km^2, the Nile River Basin (mainly swamps and marshes) with an extension of 92,000 km^2 (Keddy et al., 2009), and the Okavango Delta (swamps, woodlands, grasslands) with an area of 28,000 km^2 (Ramberg et al., 2006).

In Asia, the largest wetland complexes are located along the lower Mekong River basin with more than 254,000 km^2 including the river complexes of Siphandone and Stung Treng and the Tonle Sap Great Lake (Meynell, 2017). The vegetation is mainly composed of floodplain forests, peats, marshes, shrub, and grasslands, however, about 78% are man-made wetlands especially for rice agriculture (Arias et al., 2013; Meynell, 2017). Natural and constructed wetlands in India are estimated to cover an area of more than 152,600 km^2, among them natural (66,240 km^2) and constructed (39,420 km^2) inland wetlands, as well as coastal wetlands (41,400 km^2) (Gopal, 2013). Information on the extension of peatlands vary a lot in literature. While Page et al. (2011) estimate for the tropics a peatland area of about 441,000 km^2 with 56% located in SE-Asia (Indonesia and Malaysia), Gumbricht et al. (2017) estimate based on remote-sensing techniques a coverage (38°N–56°S) of more than 1.7×10^6 km^2 (soils with >30 cm of decomposed organic material with at least 50% of organic matter).

Given the large extension of freshwater wetlands across tropical continents, climate zones, and biomes habitat diversity is huge, ranging from permanent aquatic, palustrine, and terrestrial habitats, over river floodplains and freshwater tidal zones, to large aquatic-terrestrial transition zones that periodically dry out (Junk et al., 2006). The one thing they have in common is the number one affecting factor: freshwater which floods the environment and affects plant growth selecting for adapted species.

The intensity and pattern of flooding vary as much as the landscape on the continents. Many wetlands are continuous and large, others are small or in patches of different sizes (Finlayson and van der Valk, 1995; Mitra et al., 2003). Terrestrial, aquatic, and palustrine habitats are associated with major river systems or connected to smaller rivers; some merely occur in depressions which are filled by a flash flood. Large habitat diversity allows for the coexistence of amphibious species with immigrants from connected deep-water and terrestrial habitats (Junk et al., 1989, 2006). Several of these immigrant species find permanent refuge in wetlands, others use wetlands as periodic habitats.

In this chapter, we give an overview of the vegetation in tropical wetlands, the diversity of species, adaptations, physiological responses, and community compositions as related to the diversity of habitats and flooding patterns around the globe.

7.2 Environmental conditions during flooding and impacts on plants

Tropical wetlands occur in the aquatic-terrestrial transition zone (ATTZ) between the terrestrial and aquatic systems in which plant species are generally exposed to different flood regimes. In general, the ATTZ can be differentiated into two major systems. One system is characterized by a more or less stable water level and permanent flooding conditions such as swamps or peats, while the other system, which dominates in the tropics, is influenced by a flood pulse, such as floodplains, riparian forests, most interfluvial wetlands, the large savannah wetland systems and mangroves. The pulses vary in the duration, amplitude, frequency and regularity of the flood. Flood pulses are monomodal, bimodal, polymodal, of low or high amplitude, predictable or irregular. Large Amazonian rivers, the Mekong and Orinoco Rivers, for instance, present monomodal flood pulses with high amplitudes of up to 8–15 m, while the large wetlands in the savannah ecoregions have monomodal pulses with low amplitudes of a few meters. The Congo River and some Andean rivers present a bimodal flood-pulse due to the shift of the rainy season in their large catchments between the northern and southern hemispheres. Small riparian forests present polymodal and irregular flood pulses. Wetlands in tropical semiarid regions, that is, north-east Brazil, are subjected to sporadic inundations which only occur in years with high rainfall.

The floods which affect plants vary with regard to the physical and chemical differences of the inundating water (flowing and standing water, nutrient content, salinity). The duration and quality of flooding water, as well as flooded soils, are responsible for a huge variety of physical environments, which are reflected by plant diversity and species composition. The physiochemical environment requires morphological, anatomical and physiological adaptations that result in characteristic plant communities. Plant species have their optimum of occurrence according to the adaptations they develop, however, sedimentation, erosion, succession, climate change and human impacts may press the species leading to a shift in their original distribution.

7.2.1 The importance of light

Light is of fundamental importance for photosynthesis and plant growth. For the occurrence of submersed aquatic macrophytes, the necessary minimum is 1%–5% of the solar radiation at the surface, which corresponds roughly to the double of the transparency measured by the Secchi disc, a white plate of 30 cm diameter, submerged in the water until disappearance.

Transparency in white-water rivers varies between 20 and 60 cm because of fine suspended inorganic particles. In várzea lakes, these particles sink to the bottom because of reduced flow velocity and transparency increases. However, phytoplankton and colored organic substances limit transparency at about 1–2 m. The water of black-water rivers and associated floodplains is transparent but high concentrations of humic substances limit transparency also to 1–2 m. Together with flood pulse induced water level fluctuations, which also influence the light intensity at a specific place, the growth of submersed aquatic macrophytes in wetlands of both water types is limited.

Aquatic macrophytes tend to overcome this problem by life forms, which collocate their photosynthetic active organs near or above the water surface, for example, free-floating species, plants with floating leaves and emergent species. Highest transparency is observed in clear water streams, rivers, and connected wetlands, such as the Pantanal. However, trees can compete with herbaceous plants for light, because they sometimes occupy the same habitats. Amazonian river floodplains and riparian areas of streams are covered by wetland forests, which restrict the growth of aquatic macrophytes. From a total number of 387 herbaceous species, described from the Central Amazon várzea, 47 can be considered aquatic or palustric, 28 are free-floating, and 19 rooted in the ground (Junk and Piedade, 1993). In the savanna floodplain of the Pantanal, the group of aquatic or palustric plants comprises 248 species (Pott and Pott, 2000) because there is less competition with trees for light.

7.2.2 Quality of the flooding water

Around the world, the hydrochemical and physical parameters of the flooding water vary considerably, influencing plant growth and species composition (Junk et al., 2006). Conductivity and salt contents of the flooding water and soils are reflected by the presence of specific vegetation types and species. Lake borders in periodically dry environments are colonized by species-poor open halophytic communities, whereas river borders in high precipitation environments are fringed by trees and closed forests. This way, the precipitation periodicity plays a role for plant distribution. Conductivity in floodplain lakes is lower in the rainy season because of dilution by rainwater, and higher at low water levels because of decomposing organic material, concentration by evaporation, and liberation of ions from the sediment.

Most importantly, current waters can carry and deposit bed and suspension load of sediment, which, depending on the geology of the catchment areas create a range of richness in nutrients. As rivers flow from high to low altitudes, alluvial sediments may originate from mountainous areas distantly located from depositional areas and floodplains, and more fertile alluvial substrates in relation to the parent geological material of surrounding uplands makes river floodplains often “azonal” ecosystems of contrasting nutrient fertility. Depending on the content and quality of suspension material, floodplains might be classified as mesotrophic and eutrophic (higher fertility), or oligotrophic (lower fertility). These conditions might also be highly variable even within one large connected wetland system, as it is the case in the Pantanal, in Brazil, where electrical conductivity of tributary waters may vary from 40 to 80 $\mu S\ cm^{-1}$. Nutrient contents of wetland soils are decisive for the selection of functional traits of the colonizing plant communities, and both species composition and primary productivity of wetlands may differ significantly between fertile and infertile systems. This is exemplified in the Amazon river system, where oligotrophic black-water rivers draining the Guyana and Brazilian Shields N and S of the Amazon basin harbor species-poor and low productive floodplains (igapó), while eutrophic white-water rivers draining the Andes harbor an exceptionally species-rich floodplain (várzea), which belongs to one of the most species-rich (Wittmann et al., 2006) and productive (Schöngart et al., 2010) ecosystems on earth.

7.2.3 The role of oxygen

The aquatic habitat imposes strong pressures on plant survival (Thomaz et al., 2008). An excess of water is generally considered to be deleterious to plant health and growth (Schueler and Holland, 2000), and total submergence quickly kills most species. Although plants have evolved a huge variety of adaptations to cope with the constrains of the aquatic environment, there is a fundamental difference whether the plants are fully submerged or merely waterlogged so that aboveground organs still can have gas exchange with the atmosphere. Complete submergence is a very different constraint from waterlogging of the soil and root system or even partial submergence, where much of the shoot remains above the water level (Colmer and Pedersen, 2008). Completely submerged plants have no direct contact with atmospheric oxygen, but if light is available, they produce the necessary oxygen by photosynthesis. For emergent herbaceous and woody plants oxygen supply to the rhizosphere is essential for survival and growth.

As soon as water covers the soil, partial oxygen deficiency (hypoxia) arises in the rhizosphere (Kozlowski, 1984). Oxygen-consuming decomposition and fast sedimentation rates further decrease oxygen supply to the roots and may lead to a complete absence of oxygen (anoxia) in the rhizosphere. Wherever water currents get high, as, for instance, in tropical mountain streams, oxygenation is guaranteed. However, in most tropical floodplains only modest input of oxygen is available or stirred into the water body by wind and currents to allow photosynthesis. Oxygen concentrations at depths below 300 mm are typically about 1 mg L^{-1} due to depletions by decomposition of biomass. Clearly, very little oxygen is available from the floodwater itself to support plant respiration. Extremely low oxygen concentrations were recorded at Lago Camaleão (Furch and Junk, 1997) in the central Brazilian Amazon, where anoxia and the presence of H_2S were observed periodically at a depth of 1–2 m. Recorded concentrations of dissolved oxygen in the floodwater of this lake depend on the season and time of day, ranging from 0.5 to 6.0 mg L^{-1}. In extreme cases, up to 1 mg L^{-1} of H_2S have been measured at depths of 0.5 m between June and September, the months when water levels are highest. Water at 10°C contains 11.26 g m^{-3} of oxygen when in full equilibrium with air but only 7.36 g m^{-3} at 30°C, and 1 atm pressure (http://openlearn.open.ac.uk/mod/resource/view.php?id = 185880). With average temperatures of 27°C–29°C, tropical floodwaters carry less oxygen compared to colder waters, which in addition increases the rapid rates of oxygen-depleting respiration.

7.3 Major groups of plants in tropical freshwater wetlands

7.3.1 Herbaceous plants and their adaptations

Aquatic macrophytes *sensu* Chambers et al. (2008), comprises a group of plants with a huge variety of habits and forms (i.e., immersed, submerged floating, with floating leaves), and periods of growth. For example, within the same family (Araceae), the biggest species *Montrichardia linifera* can reach 6 m in height while the smallest species of the genus *Wolffiella* does not exceed 2 mm in length. In Amazonian wetlands, where flood pulses are high (Junk et al., 1989), many herbaceous species have short life cycles and occur only during the low water levels (terrestrial phase) or during the flood period (aquatic phase). Their diaspores are well adapted to survive the subsequent inundation or drought. Therefore these seemingly terrestrial plants are included in the group of aquatic herbaceous plants (Piedade et al., 2019). The highly diverse growth forms are closely associated to differences in resource capture, allocation, stress tolerance and survival strategies. That way plants can ensure rapid population recovery from disturbance and successful colonization of highly dynamic environments (Piedade et al., 2019).

The plants that have returned completely to the aquatic environment (Sculthorpe, 1985) are the submerged macrophytes, those facing the biggest problems for a life in water, such as low diffusion of CO_2 in the water, anoxic sediments and low light penetration. Aquatic plants have developed several adaptations to deal with these pressures (Thomaz et al., 2008). Many submersed species reduce the thickness of their leaves and increase their pigment content by superficial epidermal cells containing chloroplasts (Sculthorpe, 1985). Other adaptations are rather efficient photosynthesis in low light supply, reduced respiration rates, and the positioning of their photosynthetic tissues close to the water surface (Chambers et al., 2008).

Some submerged species of aquatic macrophytes (i.e., *Najas* and *Ceratophyllum*) have completed their return to the aquatic environment, reproducing underwater by means of hydrophilic pollination (Thomaz et al., 2008). However, almost all submerged species still place flowers above the water surface and are pollinated mainly by insects (Cook, 1985). For example, *Utricularia foliosa* may reach up to 10 cm above the water surface to expose flowers, while *Vallisneria* spp. produces peduncles of more than 1 m in size to raise the female flowers into the air (Thomaz et al., 2008).

7.3.2 Woody plants and flooding

Trees are terrestrial organisms (see Job and Sieben, 2022, Chapter 2). Under nonflooded and aerobic conditions, the roots are adequately ventilated with oxygen and have anaerobic metabolism to absorb water and nutrients. Therefore the terrestrial phase is the main vegetation period for woody species. In floodplains of semiarid areas, such as the Pantanal, the short flood period is the growth period, and the dry period is the stress.

In wetlands, the trees have to cope with flooding of the rhizosphere. Trees often respond with leaf shedding, reduced production of new leaves, and a reduction of photosynthetic assimilation. If there is a dormant period, it usually occurs during high water. Complete submergence occurs regularly at the seedling or sapling stage for many species that colonize low-lying positions in the flooding gradient (Parolin, 2009).

Despite a lack of both oxygen and light imposed by submergence, many seedlings survive. In Amazonian tree species, underwater growth of seedlings has been observed in the field and under experimental conditions (Waldhoff et al., 1998).

7.3.2.1 Flooding impacts

When flooded, the oxygenated soil pores are filled with water. There is a lack or depletion of oxygen because oxygen diffusion in water is reduced by 10^4 times compared to the atmosphere. The remaining oxygen is consumed by microorganisms and the roots itself (Jackson and Colmer, 2005). This reduces the redox potential of the soil and enhances the production of phytotoxic compounds such as sulfide, soluble MN^{2+} and Fe^{2+} compounds which are released through microbial transformation of mineral and organic substances (Gambrell and Patrick, 1978; Crawford, 1992; Kozlowski, 1997).

The hypoxic and anoxic conditions in the root area primarily affect the mitochondrial respiration and thus the generation of energy via the ATP synthesis, as well as the transport of assimilates to the roots. In many tree species, a reduction in the stomatal conductivity and the photosynthesis rate occurs. This leads to a reduction in the radial water transport through proteins (aquaporins), which produce channels in the cell membrane to facilitate the entrance of water and some other molecules into the cell. An internal water deficit in the leaves, a decrease in the chlorophyll content, senescence and often shedding are the consequence. Due to the impairment of water uptake, also nutrient absorption is limited, with consequences, for example, for the nitrogen metabolism (Visser et al., 2003; Bailey-Serres and Voesenek, 2008).

7.3.2.2 Adaptations to flooding

Tree species have developed various morpho-anatomical and physiological adaptations and combinations thereof in order to adapt to anaerobic conditions (Kozlowski, 1984; Crawford, 1992; Armstrong et al., 1994). Adaptations to flooding, be it waterlogging or submergence, are manifold and comprise roots, stems and shoots for anatomical, morphological or physiological responses. Especially in Central Amazonia, phenological responses (e.g., Wittmann and Parolin, 1999; Parolin et al., 2002), reductions of the photosynthetic activity during the aquatic phase (Parolin, 2001; Fernandez et al., 1999; Waldhoff et al., 1998) and thus periodic reductions of wood growth leading to annual tree rings (Worbes et al., 1992; Worbes, 1997) are well documented, as well as anaerobic metabolism (Fernandes-Corrêa and Furch, 1992; Schlüter et al., 1993), and the formation of hypertrophied lenticels, adventitious roots, aerenchyma and other adaptations (Wittmann and Parolin, 2005).

Often, a period of rest or reduced metabolic activity protects the trees from the injuries imposed by flooding. However, dormancy usually does not last for the whole aquatic period. Mostly, the plants are adapted in a way that they maintain a part of their physiological activities running throughout the year. Some trees even grow vigorously during the aquatic period. The regularity of flooding enhanced the evolution of specific structural, physiological, and phenological traits. Combinations of adaptations regarding seed germination, seedling development, and traits of roots, shoots and leaves result in a variety of responses to flooding which lead to specific species distributions and zonations (Fig. 7.1) along the flooding gradients (Parolin et al., 2004).

7.3.2.2.1 Roots, shoots, and leaves

Root activity is restricted by total submergence (Worbes, 1997). Adventitious roots, lenticels, or stem hypertrophy are typical adaptations to flooding but not always produced because of the constant changes in water levels which are typical for floodplains (Parolin et al., 2004). The potential capacity to form these adaptations was shown for species of the Amazon floodplains in flooding experiments under controlled conditions. Many roots are characterized by the formation of suberized and lignified barriers in the exodermis that regulate radial transport of solutes and gases. The radial loss of oxygen can be effectively restricted by the formation of suberized barriers or lignification of exodermal cell wall. Suberin polymers are formed by many species as pathogen defense or to act as a mechanical barrier (De Simone et al., 2003).

In shoots of wetland species, aeration is the main challenge. Its functioning is guaranteed by morphological and anatomical stress-avoiding systems such as aerenchyma. This tissue forms interconnected channels from leaf to root tip and thus facilitates gas transfer through the shoot to the root system by lowering the resistance that hampers gas diffusion and mass flow within organs (Coutts and Armstrong, 1976). However, gas transport via aerenchyma and pressure ventilation often only plays a minor role in sustaining submerged tree species

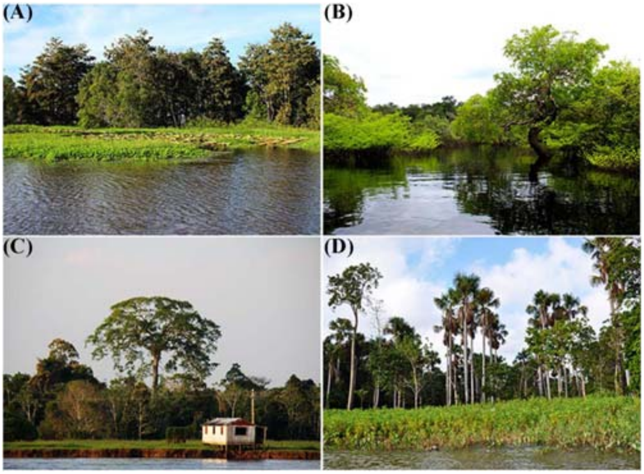

FIGURE 7.1 Floodplain forests. (A) Flooded forest in the fertile Amazon River; (B) Low productivity floodplain forest in a river of poor water and soil in the Jaú National Park; (C) *Ceiba pentandra* a species of occurrence in the Amazon and Africa; (C) *Mauritia flexuosa* an important species of palm widely distributed in tropical America. *Pictures adapted from archive of MAUA group. All pictures are from the Central Amazon, Brazil.*

(Bailey-Serres and Voesenek, 2008; Graffmann et al., 2008). Adaptations at the root and leaf level appear to be more significant in many tropical species.

Most tree species shed leaves after a while when they become submerged. Some Amazonian tree species, however, maintain their leaves for several months underwater, even in complete darkness. With submergence, the photosynthetic system becomes dormant (Waldhoff et al., 2002). This is indicated by very low photosystem II (PSII) chlorophyll fluorescence which can be measured on living plants in the field. After emergence, the photosynthetic system of these leaves becomes active again.

Deciduous or evergreen, and regardless of whether they are shed or kept underwater, many leaves of floodplain species exhibit xeromorphic traits (Waldhoff et al., 1998). Typical xeromorphic characteristics are large epidermal cells, thick outer epidermal walls, thick cuticle, compact spongy parenchyma with few small intercellular spaces, sunken stomata and transcurrent vascular bundles. These are all adaptations against heat and water loss which are typical for tropical trees in upland forests (Kubitzki, 1989; Wittmann et al., 2006). The presence of these anatomic characteristics may have helped trees to cope with the complicated hydric situation during flooding, where the roots decrease their functioning and water supply to the leaves is reduced.

7.3.2.2.2 Phenological adaptations and dispersal

Many floodplain trees synchronize fruit production with the period of highest water levels of the rivers. Hydrochory, seed dispersal by water, is especially common in species which colonize low-lying areas that are flooded for longer periods (Gottsberger, 1978; Goulding, 1980, 1983; Oliveira-Wittmann et al., 2006). After dropping into the water, the diaspores are subjected to varying periods of buoyancy and/or submergence. In Amazonian floodplains, they may float for at least two months (Kubitzki, 1985). Seed buoyancy and/or submergence increase the distance covered by the river current and increase the probability of seed predation by fish and other aquatic dispersers (Goulding, 1983; Ziburski, 1991). Therefore many tree species evolved adaptations which enhance floatation of their diaspores. Germination in buoyant and submerged seeds varies distinctly between species and genotypes of trees (Morinaga, 1926; Kozlowski, 2002). In Amazonia, the germination of seeds underwater or during floatation has been shown for several species (Oliveira-Wittmann et al., 2010; Melo et al., 2015), but seedling establishment occurs only on dry ground. Once they have been established, seedlings are extremely flooding tolerant (Lobo and Joly, 1996; Parolin and Junk, 2002).

7.3.2.3 Flooding tolerance and its consequences

Specific adaptation mechanisms and combinations among them result in different tolerances for flooding (Joly and Crawford, 1982; Schlüter and

Crawford, 2001). In the case of flood-tolerant tree species, inundations are usually not a stress factor unless they deviate from the range of normal conditions, for example, through extreme hydro-climatic events caused by land use and/or climate changes (Vartapetian and Jackson, 1997).

Despite the stresses imposed by flooding, numerous woody species thrive in the floodplains around the globe. Many grow to large trees, often with commercial value, and show extreme submergence tolerance. In central Amazonia, trees are able to overcome several weeks or months of waterlogging and submergence. Although some of the mechanisms allowing these species to be so tolerant to submergence are known (Piedade et al., 2010), the large majority of them still remain obscure.

7.4 Plant species richness

Despite a large number of species, the number of endemic species in wetlands is generally low. Most large wetlands are of relatively young age that did not allow for specific wetland speciation. The number of endemic species increases when the wetlands include ancient, rather stable habitats (Junk et al., 2006). The low number of endemic species can in part be explained also by the fact that most wetlands are connected with large rivers that serve as migratory routes or for passive transport of aquatic and in part also terrestrial organisms between the entire catchment area and the wetlands (Junk et al., 2006). It hinders the genetic isolation of wetland populations. Water level fluctuations and habitat dynamics favor mobility of the species inside the wetlands and hinder speciation by permanent gene flow between subpopulations.

7.4.1 Aquatic macrophytes

Aquatic herbaceous plants play a specific and important role in floodplains because of their relatively short life cycles and high reproduction rates, quickly colonizing a wide range of habitats in many types of wetlands in the tropics. Generally, aquatic herbaceous plants develop assemblies composed of multiple species of different life forms (Fig. 7.2). The density of herbaceous species in tropical wetlands is directly influenced by the physical and chemical properties of waters and soils.

With decreasing nutrient levels the quantity of floating plants and herbaceous shoreline vegetation is reduced, and in extremely nutrient-poor and acid rivers aquatic macrophytes may only be represented by small patchy stands of few species (Junk and Howard-Williams, 1984). However, in rather stable hydrological conditions, wetland species accumulate organic material and nutrients and can develop large monospecific stands, such as *Cyperus papyrus* in African wetlands and *Phragmites* spp. in subtropical regions of

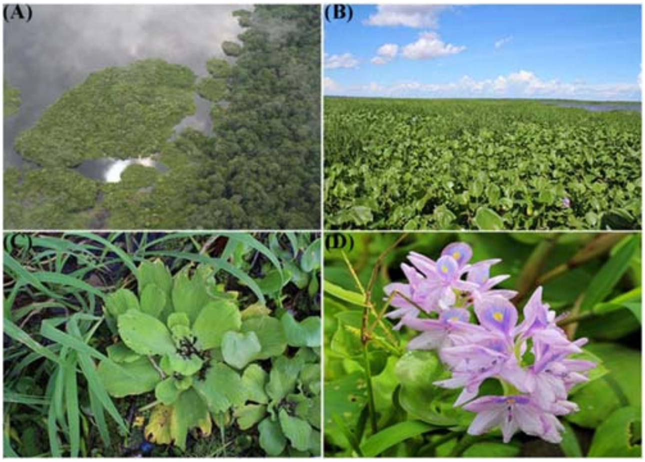

FIGURE 7.2 Aquatic herbaceous plants. (A) Assembly of several aquatic species forming a floating island colonized later by trees (matupá); (B) Extensive field of aquatic macrophytes on the Amazon River; (C) *Pistia stratiotes*; (D) *Eichhornia crassipes*, both species widely distributed in the tropics with potential for weeds. *Pictures adapted from (A) F. Wittmann, Amanã Sustainable Development Reserve; (B—D) archive of MAUA group. All pictures are from the Central Amazon, Brazil.*

Brazil. Monospecific stands of *C. papyrus* may accumulate an annual aerial production of 52 t ha^{-1} y^{-1} in Lake Naivasha, Kenya (Muthuri et al., 1989).

River floodplains that receive nutrient-rich water and sediments from the catchment area, such as the white-water rivers in the Amazon and in the Mekong basin, can support high productivity in their herbaceous communities, which often exceeds that of adjacent forests (Piedade et al., 2001). Large, monospecific stands of *Echinochloa polystachya* growing in the Brazilian Amazon white-water rivers may achieve an annual primary production of 100 t ha^{-1} y^{-1} (Piedade et al., 1991). In contrast, rivers draining areas of old and nutrient-poor sediments such as black and clear water rivers in the Amazon have small stands of aquatic macrophytes with a productivity lower than 10 t ha^{-1}.

The global diversity of vascular macrophytes, considering only species strictly fitting the definition of macrophytes proposed by Chambers et al. (2008), reports 3457 species within 456 genera, and 93 families. Out of these, 6 species (0.17% of the total) are clubmosses and horsetails; 209 species (6.05%) are ferns and fern-allies; 1520 species (43.97%) are dicotyledons and 1722 (49.81%) are monocotyledons (Murphy et al., 2019). Certainly, these numbers are conservative. If herbaceous plants with reduced adaptations to flooding are included, especially those occupying the terrestrial phase in many tropical floodplains, numbers should be much higher (Piedade et al., 2019).

Comparing different bioregions in the world, the richness of genera and species is highest in tropical regions, even with a relative lack of collection data and taxonomic studies in the tropics compared to temperate and boreal regions. Therefore it is expected that further species will be recorded and this difference will increase as studies in the tropics expand (Chambers et al., 2008). Some families stand out in the tropical region because of their high number of species with >100 macrophyte species. In the Neotropics, this is the case in Cyperaceae, Poaceae, Podostemaceae, Plantaginaceae, Eriocaulaceae, Lentibulariaceae, Isoetaceae, and Alismataceae, while in the Afrotropics Hydrocharitaceae and Lythraceae are the most species-rich families (Murphy et al., 2019).

Many species of herbaceous aquatic plants have broad world distributional ranges (Cook, 1985), which is traditionally explained by long-distance dispersal through migratory birds and, more recently, through human activities (Hutchinson, 1975). However, the study of Murphy et al. (2019) indicated that only 1.2% of all known macrophyte species show broad worldwide distribution, while approximately 80% are restricted to specific bioregions or wetlands. Aquatic plant endemism seems also to be higher in tropical than in other bioregions of the world. The most important families with elevated numbers of endemic species are: Podostemaceae (168 species: 25.5% of single-grid cell species); Araceae (65 species: 9.8%); Isoetaceae (55 species: 8.4%); Cyperaceae (46 species: 7.0%); and Eriocaulaceae (35 species: 5.3%), with a clear prevalence of higher numbers in tropical regions (Murphy et al., 2019).

7.4.2 Woody plants

Terrestrial ecosystems show a clear increase in woody plant species diversity from high latitudes to the equator with a decline in arid regions (Junk et al., 2006). This trend can also be observed in large wetlands that harbor terrestrial and flood-tolerant species. By far the highest number of flood-tolerant tree species is found near the Equator in the Amazon River floodplains. Very likely, high species numbers in Amazonian wetlands are because of climatic stability and the continuous presence of wetlands of variable sizes in the Amazonian landscape over evolutionary time scales (Wittmann et al., 2013). Wherever past climate changes led to the repeated drying out of wetlands, or their change to marine ecosystems through marine transgressions, the development of specific adaptations to freshwater inundations was set back, which hindered the development of endemic species and reduced species diversity. This is exemplified in the Pantanal, which, despite its considerable size and comparable flood amplitudes and durations lacks endemic tree species (Junk et al., 2006). Flood-tolerant endemic tree species are also unknown for Neotropical savannahs in general (Montes and José, 1995; Veneklaas et al., 2005) and throughout the Paleotropical region, with the exception of Bornean peat swamps (i.e., Posa et al., 2011). However, little information on floodplain tree species distribution is available for the African Cuvette

Centrale of the Congo River basin, another flood-pulsing system that is densely forested (Betbeder et al., 2013).

7.5 Use of wetland vegetation

Plants growing in wetlands are key components of the aquatic ecosystems (Piedade and Junk, 2000). Therefore macrophytes can also be used as tools to manipulate wetlands. For instance, fish densities can be increased and water purification provided if specific species of aquatic plants are introduced, especially in highly disturbed water bodies. The wetland vegetation plays a major role by increasing the habitat complexity of waterscapes at different scales. Plants change the spatial structure and quality of wetlands. Habitat complexity, water and sediment physicochemistry, as well as nutrient cycling, are closely related to the presence of plants and the ecosystem services they provide (Thomaz et al., 2008). Increasing habitat heterogeneity has direct and positive impacts on the aquatic biota. For example, food availability and habitat are provided for aquatic invertebrates, mammals, birds, amphibians, reptiles and fish (see Cuthbert et al., 2022, Chapter 17; Brendonck et al. (2022a,b), Chapters 9 and 10; Dube et al., 2022, Chapter 11; Reichard, 2022, Chapter 12; Moraes et al., 2022, Chapter 13; Tarakini et al., 2022, Chapter 14).

The use of floodplain plants by humans, and mainly the aquatic macrophytes, is widespread in many parts of the world (Thomaz et al., 2008). Be it the cultivation for ornamental purposes, or eutrophication and pollution control by floating macrophytes, there is a great potential in the use of wetland species. Macrophytes are employed to diminish the undesirable concentration of nutrients, heavy metals and pathogen bacteria in the sewage. They also help in the substantial reduction of costs for constructed wastewater treatment stations and the ecological and sanitary damage of sewage discharge to aquatic ecosystems. They can also be used as biofilters for the treatment of effluents resulting from fish and shrimp farming.

Tropical wetlands along the river banks are usually high-energy dynamic environments. Erosion and deposition of sediments may dominate in the initial processes of succession along shores and river margins, often directly exposing plants to a variety of stressful conditions. Some species, however, may act at local scales as engineering plants (Hastings et al., 2007), strongly influencing the environment by attenuating the current of water, holding and establishing suspended sediments and accelerating the deposition process (Gurnell, 2014; Heuner et al., 2015). This role is vital in the formation of niches that in turn increase ecosystem services and facilitate environmental conditions for later successional stages. For instance, in temperate zones sprouting riparian trees (i.e., *Populus nigra* and *Salix* spp.) may act as physical ecosystem engineers in the critical zone of vegetation—fluvial processes by trapping fine sediments and forming pioneer island subsequently colonized by other plants (Gurnell et al., 2016). In the dynamic Brazilian Amazon River banks the grasses *E. polystachya* and *Paspalum fasciculatum* play this role (Worbes et al., 1992). However, changes in land use, such as river damming and channel rectification can remove the vital hydrogeomorphic ecosystem processes in order that the engineer species get regionally extinct. In tropical regions, the introduction of exotic pastures in addition often disrupt the successional processes in river floodplains causing erosion and biodiversity loss (Piedade et al., 2020).

7.6 Conservation status of the large tropical wetland complexes

Many of the world's wetlands have historically been occupied and intensively used by humans due to their high productivity, fertile soils, and importance for water provision (Reis et al., 2017; Irvine et al., 2021, Chapter 19; Marambanyika et al., 2022, Chapter 22). Therefore all wetlands are subjected to an increasing degree of human pressure besides the effects of climatic changes. Increasing droughts and heavy floods, as well as desertification, are common threats linked to global climatic changes that will affect wetlands to different degrees. Considerable changes in wetland area are expected due to rising sea levels and changes in amount, seasonality, and distribution of precipitation patterns in most parts of the World, as predicted by the Intergovernmental Panel on Climate Change (IPCC, 2018). The reported long-term loss of natural wetlands averages between 54% and 57%, reaching up to 90% in some regions of the world (Junk et al., 2013). Many wetlands are partly protected by national and international conventions, like Ramsar Convention, but others are still overexploited or not protected at all. Strong, and often transnational efforts are required to increase wetland conservation and to promote the sustainable use of wetland resources. The Ramsar Convention on Wetlands (http://www.ramsar.org), the most important international initiative for wetland protection, is a treaty adopted in 1971 with the objective of recognizing the importance of wetlands and promoting their conservation. There are 84 Ramsar Sites covering 36,136,249 ha in tropics including some of the biggest sites as Rio Negro in Brazil (120,000 km^2), and Ngiri-Tumba-Maindombe in the Democratic Republic of Congo (60,000 km^2) (Ramsar, 2020).

In some wetlands the number of exotic species is low but the impact on native species can be high as soon as they are introduced. High habitat diversity in addition to a pronounced natural disturbance regime of extreme water level changes seem to difficult invasion of exotics, however, they in fact make many wetlands vulnerable to different levels of invasion by exotic species (Junk et al., 2006; see Pegg et al., 2022, Chapter 16). Around the world, Neotropical macrophytes such as *Eichhornia crassipes* literally overruns the native vegetation by forming immense monospecific floating stands (Prasad et al., 2002), particularly when introduced in areas were regulatory effect of the flood pulse is missing or attenuated. A good example is the massive invasion of Lake Victoria by *E. crassipes* in the 1990s, negatively affecting the fisheries in Uganda, Kenya, and Tanzania, and also disrupting the generation of hydropower in Uganda (Chambers et al., 2008). In fact, a number of aquatic plants may become aquatic weeds since they can easily reach several regions around the world accidentally or not (Piedade and Junk, 2000).

All wetland systems around the globe are more or less heavily impacted by human presence. People need water for living, for agriculture, transportation, and new towns and cities have been founded on river banks since the times of the garden Eden cited in the Bible where the rivers Euphrates and Tigris are mentioned in the Book of Genesis: “A river flowed out of Eden to water the garden.” The first writing, cuneiform signs on clay tablets, was developed in Mesopotamia around the 4th millennium BCE. Even today, life without natural water resources is not possible, despite all technologies we have developed so far. Thus humans have colonized wetlands for millennia and have mostly treated them wisely because they depended on their sustainable management (Gopal, 2009). Today, however, exploitation of native vegetation, agriculture, timber extraction, aggressive forms of conventional agriculture and drainages, mining and paddy rice cultivation are creating water supply and quality problems which affects vegetation and human population.

The transformation of natural vegetation into cropland monocultures and urban areas is an increasingly recognized threat to many wetlands around the tropics, and is of particular interest because wetlands affected by these activities lose their natural capacity to provide important ecosystem services. Since many big cities do not have efficient wastewater treatment, industrial and domestic water pollution by liquids and solids is a common phenomenon in and near urban areas. Most large-river floodplains fall periodically dry for several months and are therefore often still considered as terrestrial ecosystems for agro-industrial use, thereby leading to wetland habitat destruction or degradation down to the stream’s edge (Wittmann et al., 2015).

Many major rivers and their biota are threatened by channel rectification and the construction of dams and reservoirs. Dams are expected to have strong impacts on the existing plant communities. The construction of hydroelectric dams causes flooding of extensive areas due to the formation of lakes and, consequently, brings about modifications of the hydrologic cycles of the rivers which provoke huge losses of forested areas (Cunha and Ferreira, 2012). The artificial alterations of the hydrologic cycle and the loss of predictability of the flooded period caused by the dams are expected to heavily influence growth, survival, and species composition of wetlands and forests. This can have a major negative impact on their functions and conservation (Ferreira et al., 2010).

Political decision concerning the measures for environmental compensations of the hydroelectric enterprises must be specific to each one of the hydrographic basins. The principle of complementarity praises that in the process of the choice of areas for the creation of new units of conservation, it is better to choose areas which complement the attributes which they intend to preserve (species, habitats, and landscapes) and not to duplicate unnecessary attributes (Anacleto et al., 2005). As one of the largest global nature conservation conventions, the Ramsar Convention plays an outstanding role in limiting, mitigating, and reversing wetland loss and degradation. This is exemplified in continuously increasing wetland inventories, classification schemes, Ramsar site designations, regional, and transnational cooperation and conservation efforts (Wittmann et al., 2015).

7.7 Conclusions

Wetlands provide multiple services for the environment and human populations. The main function is to store water during periods of excess water supply and release it during periods of water shortage. Furthermore, some of them store organic material and counteract global climate change. In addition, large populations of endangered or rare species of plants and animals in all wetlands contribute to the great value of these areas for biodiversity protection.

However, there is a very strong pressure on wetlands to drain them for conversion into arable land or infrastructure purposes. Considering the predictions of the Panel of Global Climate, with respect to water availability, a wise policy requires the protection of the existing wetlands and the rehabilitation of the area, that are not completely lost (Junk et al., 2006). Unfortunately, data availability about many basic processes in wetlands is still insufficient. Numbers of species in different wetlands are often incomplete and make comparative studies very difficult (Junk et al., 2006). This is a lack to be filled. Most are known about higher plants, but information about other groups such as phytoplankton or algae is small, despite their huge importance in the food chains.

Closer cooperation between scientists working in different wetlands and joint research projects are important for information exchange, adjustment of sampling methods, and the comparison of results.

Most wetlands are the home of human populations which sustainably used their resources during centuries (see also Laltaika, 2022, Chapter 23). However, human pressure is increasing worldwide. This causes water abstraction, changes in the hydrological cycle, land reclamation, pollution, overharvesting of natural resources, and poaching as summarized in Fig. 7.3.

Therefore change imposed by the building of dams and changing the natural hydrological pattern will profoundly affect the ecological conditions in wetlands. This affects species distribution, structures, productivity, biodiversity, food chains (Junk et al., 2006), and even carbon balance owing to massive mortality of flood-adapted tree species, as occurring in the Brazilian Amazon (Schöngart et al., 2021).

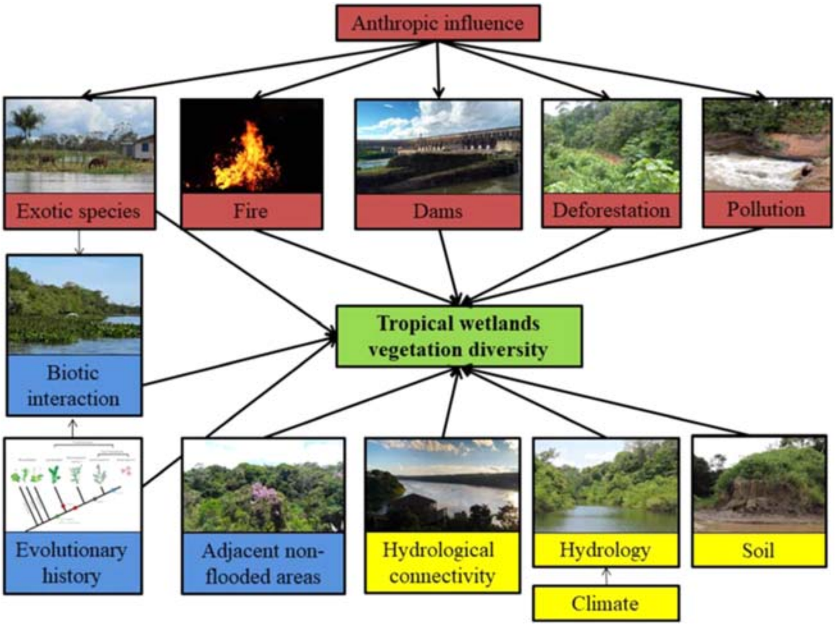

FIGURE 7.3 Major factors influencing tropical wetlands vegetation diversity and ecosystems integrity.

Most studied wetlands today are partly protected by national laws and international agreements, but administrative weakness and lack of funding threaten these areas in most tropical countries. Strong financial and moral support of large international environmental organizations will be required to endorse national activities in efficient wetland protection.

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Chapter 8

Phytoplankton dynamics

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8.1 Introduction

Wetlands provide a wide array of essential ecological services (Srichandan et al., 2015; Lin et al., 2019; Wasserman and Dalu, 2022, Chapter 1). Freshwater wetlands are diverse in nature, with large wetland types having received much attention. Many tropical wetlands, however, constitute often small, understudied habitat types scattered across various landscape, harboring communities and meta-communities of aquatic fauna (see Gálvez et al., 2021, Chapter 18). These patchy environments can also act as evolutionary hotspots and provide natural laboratories to assess evolutionary, trophic, and other important ecological processes (Srichandan et al., 2015; Dalu et al., 2017b; An et al., 2019; Wasserman et al., 2018). The endemic ecological specialist species, restricted habitat size, and anthropogenic threats to small wetland ecosystems merit more intensive research focus as these systems may harbor unique taxa (Greenway, 2010; Chia et al., 2011). Primary productivity in these systems is driven by a combination of aquatic and semi-aquatic photosynthetically active groups (Bernard and Gorham, 1978). Wetlands are typically dominated by free-floating and rooted macrophytes which form a major component of carbon fixation. While macrophytes are extremely important primary producers in tropical wetlands, phytoplankton is also a major contributor and a crucial component for secondary aquatic productivity (Behrenfeld and Falkowski, 1997). Atmospheric, hydrological, geological, and biological dynamics all affect wetland phytoplankton productivity and communities, similar to other aquatic environments (Wetzel, 2001; Robertson et al., 2001).

However, unlike in marine and other freshwater ecosystems (i.e., rivers, lakes, reservoirs) where the ecology of phytoplankton communities are relatively well studied, systematic insights on phytoplankton community

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assemblages, functional qualities, and seasonal changes associated with environmental variables are largely lacking for many tropical wetland types. While there have been far more studies conducted on wetlands in temperate than in tropical and subtropical regions, recent studies have suggested that primary production rates are typically higher within the tropical regions than comparable temperate systems (Fig. 8.1; Davies et al., 2008). Relevant literature from the tropics has, however, increased with some work indicating that tropical aquatic ecosystems present distinct ecological patterns compared to other systems (Sarma et al., 2005; They et al., 2014; Iglesias et al., 2017; Clarke et al., 2017). This chapter provides an introductory overview of phytoplankton ecology in tropical wetlands, with an emphasis on small understudied wetland types. Further, given the importance of cyanobacterial blooms in both human and animal health, the chapter also gives an overview of cyanobacterial blooms and their toxins.

8.1.1 What is phytoplankton?

The term plankton was first coined by Victor Hensen in 1887 to include all organic matter particles which can float freely and involuntarily in open water, independent of shores and bottom, and excluded large vertebrates of

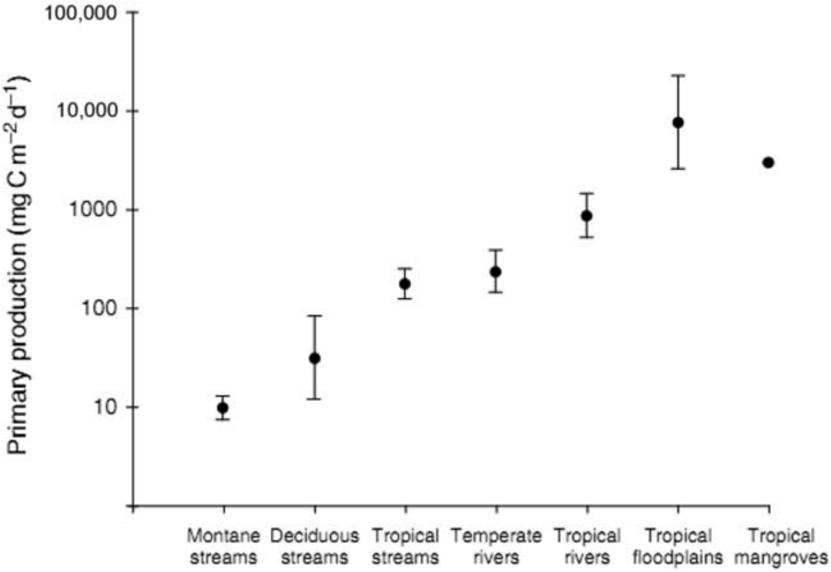


FIGURE 8.1 Primary production (mg C m^{-2} d^{-1}) rates for various ecosystems, outlining the relatively high levels of primary production in tropical aquatic environments. Reproduced with permission from *Davies Jr., P.M., Bunn Jr., S.E., Hamilton Jr., S.K., 2008. Primary production in tropical streams and rivers. In: Dudgeon, D. (Ed.), Tropical Stream Ecology. Academic Press, London.*

the open water which had the ability to swim (Reynolds, 1984). However, Hensen's definition included nonliving particles. Richard Kolkwitz in 1912 adopted the now commonly used definition which highlights that plankton are small and microscopic components found in all aquatic habitats (i.e., littoral, benthic, pelagic) and are mostly living organisms thereby excluding the nonliving components. Thus plankton were rudimentally divided into two groups, that is, plants (phytoplankton) and animals (zooplankton). Phytoplankton is generally considered the autotrophic (partial or complete) component of plankton. Autotrophy refers to the ability to synthesize food from inorganic substances using chemical or light energy (Quayle and Ferenci, 1978). Phytoplankton, typically employing light energy production through photosynthetic processes, includes several single-celled representative groups of algae and bacteria as well as infective stages of certain actinomycetes and fungi. Phytoplankton help purify waters by taking up nutrients and pollutants (regulating service) (Biggs and Kilroy, 2000). They also transform nutrients from inorganic to organic forms, such as Cyanophyta which converts atmospheric nitrogen (N_2) into ammonium (NH_3^+) (Lee et al., 2013). The various phytoplankton groups are well described in John et al. (2002) and include 15 common phyla: Bacillariophyta (diatoms), Chlorophyta (green algae), Chrysophyta (golden algae), Cryptophyta (cyptomonads), Cyanophyta (cyanobacteria), Euglenophyta (euglenoids), Eustigmatophyta, Glaucophyta, Haptophyta (Prymnesiophyta), Phaeophyta (brown algae), Prasinophyta, Pyrrophyta (dinoflagellates), Raphidophyta, Rhodophyta (red algae), and Xanthophyta (yellow-green algae), with the Chlorophyta and Bacillariophyta being the most diverse groups.

Certain phytoplankton can move independently, by means of flagella, or through various mechanisms that alter their buoyancy (Reynolds, 1984). They occur in benthic and pelagic environments, with their vertical distribution generally limited by light availability. While typically single-celled, some phytoplankton is capable of forming colonies and filaments. These seemingly inconspicuous primary producers are prevalent across marine and freshwater ecosystems, and form the base of aquatic food webs, on which almost all aquatic fauna directly or indirectly rely. In addition, as part of the photosynthetic process of converting light into energy, oxygen is released into the environment. It is thought that phytoplankton is responsible for more oxygen production than tropical rainforests such as the Amazon, which are often misleadingly referred to as the "lungs" of planet earth (Chavez et al., 2010). Given their basal role in aquatic food production and their importance in atmospheric processes, phytoplankton are among the most important and relevant groups, although their role is often overlooked by the general public (Fig. 8.2).

The cosmopolitan nature of phytoplankton has been highlighted in many scientific articles, books and reports. The Baas-Becking (1934) hypothesis which states that "everything is everywhere, but the environment selects" has dominated the view on phytoplankton distribution for over a century,

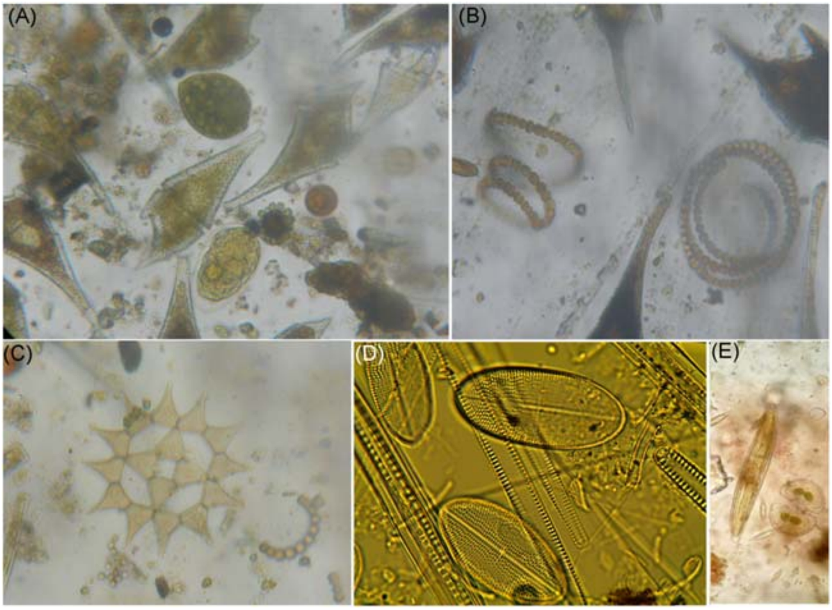


FIGURE 8.2 Various plankton taxa: (A) dinoflagellates (e.g., *Ceratium* sp.), cyanobacteria, and diatoms; (B) *Anabaena* sp. (cyanobacteria) and *Ceratium* sp. (dinoflagellate); (C) *Pediastrum* sp. (chlorophyte) and *Fragilaria* sp. (diatom); (D) diatoms, *Fragilaria* sp., and *Cocconeis* sp.; and (E) *Gyrosigma* sp. (diatom) and desmid from a water sample collected in a tropical African wetland. *Pictures by Tatenda Dalu.*

and has greatly contributed to the predominant notion that phytoplankton are cosmopolitan (Reynolds et al., 2002; Padisák et al., 2016; Mangadze et al., 2019). Thus it is true in a sense that they occur in almost each and every sufficiently irradiated aquatic habitat present on earth (Padisák et al., 2016). However, with increasing research knowledge on occurrence and distribution of phytoplankton species across different habitats and geographic regions, previously unrecorded taxa, reports on invasive species, phylogenetic assessment, and tracing of secondary metabolites (i.e., cyanotoxins) seem to contradict the Baas-Becking hypothesis (Incagnone et al., 2015; Padisák et al., 2016). Thus this suggests that all phytoplankton are neither cosmopolitan, nor ubiquitous (Padisák et al., 2016).

8.1.2 Phytoplankton reproduction and dispersal

A typical phytoplankton life cycle includes growth, reproduction, and death, but the life cycle of certain taxa can include a dormancy period (Reynolds, 1984). The golden algae, for example, can produce cysts and/or spores which can remain dormant for several months to years depending on prevailing conditions, and some diatoms and dinoflagellates form cysts during harsh periods such as wetland drying out (Timoney et al., 1997). Phytoplankton life cycles vary among the different species, and some species can produce small motile cells that keep growing and multiplying until nutrient levels decrease before forming colonies surrounded by sticky mucous coats containing nutrients that allow for continued growth and reproduction (Brand et al., 1981; Rojo, 2020).

Phytoplankton have efficient asexual and sexual reproductive strategies, and when growing conditions are suitable, they reproduce and grow quickly through various asexual reproduction means. For example, (1) fast-growing dinoflagellates divide through binary fission forming identical cells that will divide repetitively; (2) *Spirogyra* spp. (and other phytoplankton filament-forming groups) cells attach end to end, forming long filamentous chains which divide forming new filaments through simple mitosis and fragmentation (Fritsch and Rich, 1907); and (3) green algae and cyanobacteria may produce spores that continue dividing inside the parent cell, with mature endospores forming identical offspring. Sexual reproduction involves producing offspring with a unique genetic makeup and this genetic diversity enables the phytoplankton species to adapt to adverse environmental conditions. For example, (1) diatoms produce and release diploid male (spermatogonia) and female (oogonia) gametes which mate to form a zygote (auxospore) that can enter dormancy and only grow into diatoms under suitable conditions, and (2) *Volvox* spp. monecious colonies (and other green algae) produce both male and female gametes, while the diecious colonies produce either eggs or sperm (Nozaki, 1988). Thus in female *Volvox* spp. colonies, individual cells can grow to become oogametes which can enter a resting diploid zygote stage after syngamy.

Phytoplankton growth varies seasonally, and is regulated by temperature and nutrient availability (Reynolds, 1984). In many aquatic systems, winter mixing of the water column initiates spring/summer blooms by bringing nutrients from the bottom waters to the surface layers (Vincent, 1983; Vellidis et al., 2003). In shallow water wetland systems, however, nutrient availability is often less stratified than in deeper water bodies, with implications for its seasonal availability and uptake (Vellidis et al., 2003). In tropical regions, seasonal temperature effects are less prevalent than at higher latitudes, and as such, aquatic primary productivity is driven by other environmental factors, such as rainfall dynamics (Padisák et al., 2016). In both tropical and subtropical regions, seasonal rainfall is the primary driver of the freshwater wetland footprint. Many permanent wetland systems swell in size following the rains, converting adjacent terrestrial environments into wetlands. Many smaller systems are seasonal, temporary, or even ephemeral wetland environments, only becoming inundated following large rainfall events or replenishment of the water table. Further, systems of the region are often warm and characterized by large surface-area to volume ratios, with implications for evaporation rates. These factors drive variation in water volume and depth, as well as allochthonous nutrient availability, with implications for biota in freshwater wetlands of the region. Since phytoplankton vegetative forms only exist in inundated aquatic ecosystems, most phytoplankton in wetland systems have developed mechanisms (i.e., reproductive strategies and physiognomic characteristics) that make them well adapted to the variable conditions (Padial et al., 2014). Certain phytoplankton groups have specialized forms (i.e., spores, cysts, akinetes) that are resistant to the harsh terrestrial conditions (Padisák et al., 2016). For example, the cyanobacterial genus *Chroococcidiopsis* have adapted to desiccation by switching their metabolism on and off in response to environmental changes, making use of short periods of liquid water availability. Furthermore, they accumulate trehalose and sucrose in response to water stress which act as phospholipid bilayers and proteins stabilizer and then recover and resume photosynthesis when conditions are favorable (Potts, 1994; Caiola et al., 1996; Williams et al., 2014). Certain phytoplankton can survive in these habitats by not responding to rainfall during the dry season as extracellular polysaccharides regulate moisture penetration and thus protect cyanobacteria from premature "resurrection" (Williams et al., 2014).

To move from one water body to another, phytoplankton propagules have to travel over the terrestrial environment exposed to desiccation risk. Thus the phytoplankton dispersal requires some dispersal agent (i.e., air, animals, humans, water), with species transport tolerances for travel distances and conditions varying. Several phytoplankton taxa produce mucilage, and have cell walls that can act as defences, allowing for short-distance dispersal (see Genitsaris et al., 2011; Incagnone et al., 2015). Some phytoplankton (i.e., chlorophytes, cyanobacteria, cryptophytes, diatoms, euglenophytes) have cryptic dispersal methods such as the vegetative cells which are dispersed from water by bubble-burst processes for short distances generated by wind action on water surfaces (Hamilton and Lenton, 1998; Vanormelingen et al., 2008; Padisák et al., 2016). While specialized forms are common in many taxa in tropical wetland systems, most phytoplankton groups do not show such adaptation (Padisák et al., 2016). So, given the hydrologically dynamic nature of tropical, and in particular subtropical wetlands, the role of specialist life-history strategies in driving phytoplankton community assemblages and phenologies is likely much more important than in larger aquatic ecosystems.

8.2 Distribution patterns

There are no known key phytoplankton taxa that occur exclusively in tropical wetlands, although some taxa may occur in high abundances or specific forms within these systems as discussed below. Due to their long evolutionary history, cyanobacteria dominate and have adapted to all freshwater environments. *Chroococcus*, *Aphanocapsa*, *Microcystis*, *Merismopedia*, and *Synechocystis* are some of the most dominant wetland species (Muzaffar and Ahmed, 2007a,b; Anusa et al., 2012). The ability of cyanobacteria to outcompete other freshwater phytoplankton has been attributed to several factors such as (1) optimum growth at high temperatures; (2) low light, high pH:CO_2 concentrations, and nitrogen: phosphorus ratio tolerances; (3) depth regulation by buoyancy; (4) zooplankton grazing resistance; and (5) aerobic bacteria symbiotic relationships (Bellinger and Sigee, 2015). Another key advantage associated with cyanobacteria is the ability of some species to fix atmospheric N_2 in nitrogen-limited environments.

Bacillariophyta (diatoms) are a distinct group of algae with a typically thick silica cell wall. They occur mostly as nonflagellated single cells, simple colonies, or chains of cells with a very wide distribution in the planktonic and benthic freshwater environments. Diatoms have a ubiquitous freshwater distribution occurring as benthic, planktonic, epiphytic, and epizoic organisms with *Achnanthidium*, *Amphora*, *Gomphonema*, *Eunotia*, *Encyonema*, and *Nitzschia* dominating (Nhiwatiwa et al., 2019). They have distinct ecological preferences such as fast growth rates, sensitivity to environmental change and/or disturbances such as eutrophication, acidification, land use, and pollution, and short generation times, making them useful biological indicators (Mangadze et al., 2019).

Chlorophyta (green algae) are mostly microscopic unicellular organisms capable of forming large colonies and filaments. Among others, the flagellate *Haematococcus* is dominant in many small wetland systems and normally colors these systems bright red if present. Small unicellular phytoplankton, *Chlorella*, *Selanastrum*, *Chlamydomonas*, *Monoraphidium*, *Spirogyra*, *Mougeotia*, and Desmids (e.g., *Cosmarium*, *Closterium*, *Staurastrum*) can also dominate wetland green algae communities (Silva, 2007; Anusa et al., 2012; Dunck et al., 2013; Bellinger and Sigee, 2015).

Euglenoids are generally found in environments where there is an abundance of decaying organic matter in line with their autotrophic and heterotrophic nature. Some *Euglena*, *Trachelomonas*, and *Phacus* have the ability to grow in very low pH waters and are typically found in metal-contaminated wetland ponds (Silva, 2007). Xanthophyta are nonmotile, single-celled, or colonial algae with a distinctive pigmentation that gives cells a yellow or green appearance. Xanthophyta are rather limited in their exploitation of aquatic habitats, tending to occur on damp mud at the edge of wetland ponds. Where planktonic Xanthophyta occur, they tend to occur in small ditches and ponds. *Characiopsis*, *Tribonema*, *Chlamydomyxa*, and *Botrydiopsis* are some of the common wetland taxa (Silva, 2007; Dunck et al., 2013; Bellinger and Sigee, 2015).

Dinoflagellates are mostly biflagellate unicellular algae, with a few being without flagella. Dinoflagellates are meroplanktonic algae and can be present in wetlands, with *Ceratium*, *Peridinium*, and *Peridiniopsis* being common taxa. Dinoflagellates can survive in sediments as resistant cysts. Cryptophyta are generally small- to medium-sized unicellular taxa forming a small component in terms of taxa, abundance, and biomass of water bodies. Chrysophyta exhibit considerable diversity in their organizational structure, ranging from unicellular (e.g., *Synura*) to spherical and branching colonial types (e.g., *Dinobryon*). They are potentially useful as environmental indicator species (e.g., *Chromulina*, *Dinobryon*, *Lagynium*, *Synura*, *Mallomonas*) in temporary wetland systems and in paleoecology (Dunck et al., 2013; Bellinger and Sigee, 2015). Rhodophyta are predominantly marine taxa with about 3% being found in true freshwater habitats such as *Batrachospermum*, *Lemanea*, and *Hildenbandia*. Similarly, Phaeophyta are also mostly marine with about 1% being freshwater species and mostly benthic in nature. Freshwater brown algae include taxa such as *Pleurocladia* and *Heribaudiella* and can be considered the least diverse of all freshwater phytoplankton. Rhodophyta and Phaeophyta have been poorly studied in freshwater habitats, and hence their ecological characteristics are poorly known (Bellinger and Sigee, 2015).

Within Africa and Australia, there are relatively few and often limited published studies on phytoplankton community assemblages from tropical wetlands (e.g., Anusa et al., 2012; Riato et al., 2014; Mowe et al., 2015; McGregor and Sendall, 2017a,b; McGregor, 2018 and references therein). The initial comprehensive study of wetlands in southern Africa was conducted in the Highveld area by Hutchinson et al. (1932) who carried out an ecological survey of a variety of temporary and permanent wetland pans. In the southern African subtropical highveld region (as defined by Kottek et al., 2006), temporary wetland pans were found to be dominated by diatom taxa that are slightly acidic to circumneutral, dystrophic, and nutrient-poor water species (e.g., *Nitzschia acidoclinata*, *Gomphonema gracile*, and *Eunotia bilunaris*; Riato et al., 2014). Other diverse aerophilic taxa assemblages such as *Luticola mutica*, *Hantzschia amphioxys*, *Pinnularia borealis*, and *Pinnularia subcapitata* were also observed, with studies by Lowe and Collins (1973) suggesting that the taxa can grow in, or endure drought-prone, low-moisture environments. *Gomphonema parvulum* and *Nitzschia palea*, eutrophic indicator taxa, were prevalent in some Highveld wetland pans due to high nutrient and organic matter inputs as a result of agricultural practices (Riato et al., 2014).

Although wetland biota constitute a significant portion of biodiversity in both tropical Asia and America, studies of phytoplankton assemblages of wetland ecosystems are also limited in these regions (e.g., Gopal and Chauhan, 2001; de Graaf and Marttin, 2003; Kumar and Oommen, 2011). It has, however, been observed that the distribution of phytoplankton in tropical Asian and American wetlands is dependent on water quality and seasonality (Kumar and Oommen, 2011). For instance, Kumar and Oommen (2011) observed that the postmonsoon months were dominated by the Chlorophytes, whereas Bacillariophytes (*Achnanthes*, *Cyclotella*, *Cymbella*, *Fragillaria*, *Navicula*, *Mastogloia*, *Gomphonema*, and *Nitzschia*) dominated the winter months of the wetland phytoplankton community in Kanewal, India. This was easily explained by the high DO and low nutrient condition of waters in winter. Other studies in India have also recorded these and other genera belonging to Cyanophyceae, Euglenophyceae, Dinophyceae, and Chrysophyceae (Brraich and Kaur, 2015; Muzaffar and Ahmed, 2007a,b; Kumar and Oommen, 2011). In the study by Muzaffar and Ahmed (2007a,b), Cyanophyceae dominated throughout the study period, but particularly in the high water period. Subsequently, as the water levels started to subside, the Cyanophyceae declined.

8.3 Important community drivers

Phytoplankton assemblages are structured by physicochemical and biological variables within aquatic ecosystems. These variables influence rates of primary productivity and adaptive strategies of phytoplankton to cope with water movements and nutrient availability. Literature suggests that several environmental factors, together with site-specific factors, strongly correlate with variations in phytoplankton community composition in most tropical wetlands. Environmental changes in aquatic ecosystems affect phytoplankton biomass and diversity (Geethu and Balamurali, 2018). Traditionally, studies on the phytoplankton abundance, diversity, dominance, and seasonality of wetlands have emphasized the role of local environmental factors such as hydroperiod (i.e., flooding cycles), area, nutrients (nitrogen, phosphorus), altitude, and ionic composition (i.e., pH, conductivity, hardness, calcium) of water in regulating the community structure (Deemy et al., 2022a, Chapter 4; Cuthbert et al., 2022, Chapter 17). In other parts of the world, studies have highlighted that hydroperiod and nutrient concentration loads are important in phytoplankton community structuring (Wetzel, 2001; Incagnone et al., 2015; Nhiwatiwa et al., 2017, 2019; Dalu et al., 2020). Phytoplankton communities in wetland environments have been highlighted to change according to geographical and spatial factors, latitude and altitude, water availability, and distance from ocean buffering climates (Hubbell, 2001). Wetland depth and area can be important predictors of phytoplankton community structure and nutrient concentrations in wetland habitats. Large wetlands have been shown to have more diverse phytoplankton communities when compared with small wetlands, with the controlling effect not being only the area, but habitat diversity as microhabitat types generally increase with area (see Box 8.1; Browne, 1981; Anusa et al., 2012). Overall, this emphasizes that resource components might exert a strong selection pressure on wetland phytoplankton communities, with high potential for these phytoplankton communities to respond to changes in nutrient and habitat resources.

The level of availability of water has been identified as a factor driving phytoplankton diversity in wetlands. In wetlands in Nigeria, Chia et al. (2011) demonstrated that phytoplankton diversity is high during the dry months (i.e., low water level) when water levels are reduced and nutrients

BOX 8.1 Influence of pool size and hydroperiod on physicochemical water properties and phytoplankton diversity in temporary rock pools in Zimbabwe (Anusa et al., 2012).

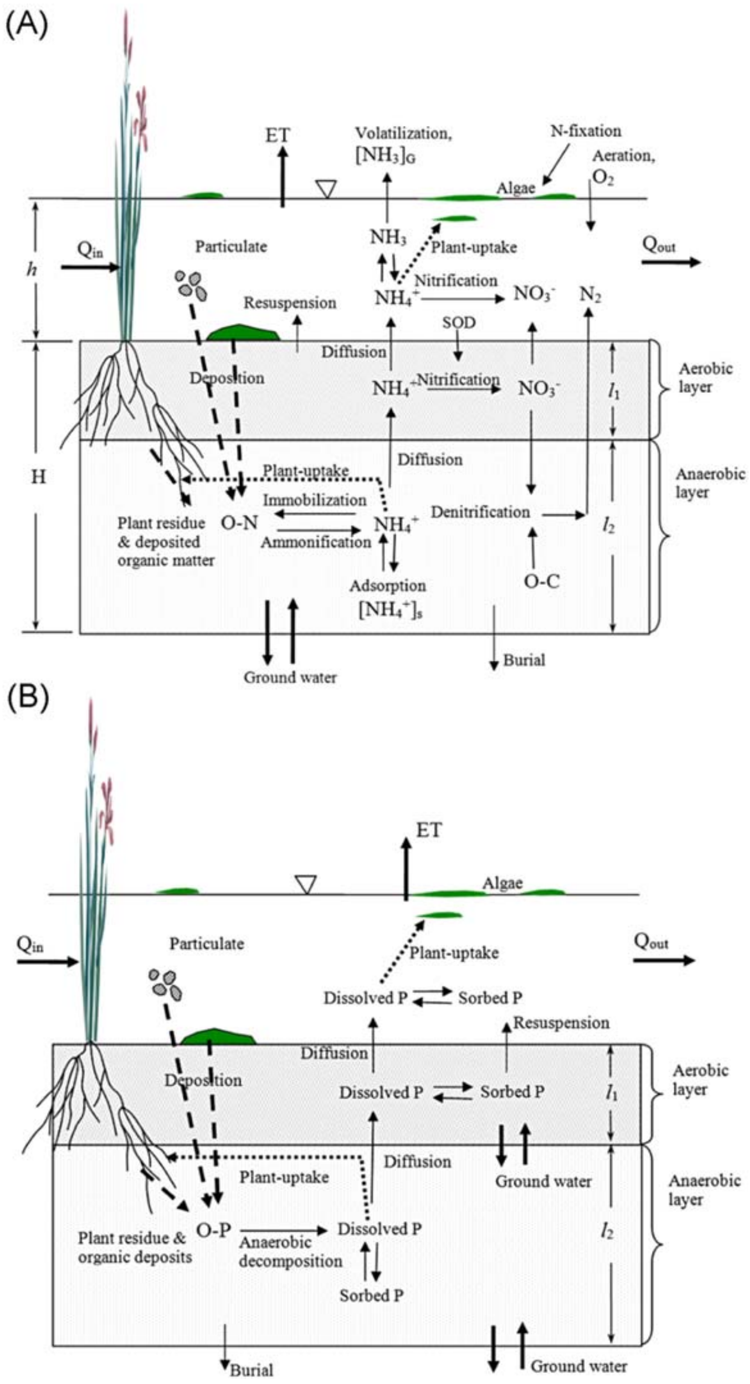
The water temperature in the temporary rock pools ranged between 20°C and 35°C, with low conductivity immediately after filling fluctuating between 6 and 50 $\mu S\ cm^{-1}$. The rock pool pH ranged from 6 (acidic) to 10 (alkaline). Rock pool systems were classified as oligotrophic open to significant nutrient inputs and outputs. The high nutrient (nitrogen and phosphorus) concentration loads in large deep pools compared to small shallow pools was observed, with these nutrient concentrations varying throughout the hydroperiod cycle, and was dependent on rock pool size which also had an effect on phytoplankton biomass in large pools. Using depth as a proxy for disturbance, phytoplankton species composition was influenced by inundation (i.e., hydroperiod) duration. Green algae (i.e., *Spirogyra rhizobrachiales*, *Tabellaria flocculosa*, *Ulothrix zonata*) and cyanobacteria (i.e., *Microcystis aeruginosa*, *Synechocystis aquatilis*) occurred abundantly in small rock pools. The initial phytoplankton community composition was dominated by short-residence green algae (*S. rhizobrachiales*, *T. flocculosa*, *U. zonata*), which were later replaced by cyanobacteria (*M. aeruginosa*, *S. aquatilis*) in large rock pools which were also driven by high nutrient concentration loads. The persistence of the cyanobacteria in large rock pools was mainly due to the long hydroperiod and stable environmental condition, compared to the small rock pools. The number of species present in pools tended to increase as pool area increased. Phytoplankton composition in long- and short-lived rock pools followed a similar trend of 70 and 105 days after filling.

Image 1 An example of temporary rock pool wetland habitat. *Photo by Tatenda Dalu.*

loads concentrated through evaporation and other factors such as excessive agricultural activities. A low diatom diversity and abundance during the summer wet months could be attributed to high dilution levels, which results in reduced nutrient concentrations available for diatoms in the small wetlands, or even reduced encounter rates. Recently, more emphasis has been placed on regional processes in studies directly addressing the spatial configuration of ponds (Nhiwatiwa et al., 2019), and in studies examining the roles of connectivity and dispersal capacity of phytoplankton *per se*, with spatial phytoplankton community patterns across wetlands having been largely ignored (Vanormelingen et al., 2008). Wetland water connectivity has been highlighted as not having a significant influence on phytoplankton community composition or diversity, although some evidence suggests occurrence of mass effects at the scale of neighboring wetland ponds (Vanormelingen et al., 2008; Nhiwatiwa et al., 2019). For example, phytoplankton cells are more easily dispersed among isolated wetland systems via air and animal vectors due to their smaller size (Kristiansen, 1996). da Silva et al. (2020) highlighted that wetland pond isolation did not influence the phytoplankton species composition, although a high stochastic distribution was observed. An interaction among local structuring (i.e., light limitation, water depth, wetland size) and spatial (dispersal) variables appears to best explain phytoplankton distribution and community structure in freshwater wetlands.

8.3.1 Nutrients

Nutrient availability and stoichiometry are key determinants of aquatic primary production (Deemy et al., 2022b, Chapter 6). Productivity in wetlands ecosystems is particularly limited by nitrogen and phosphorus (Sterner, 2008). For instance, phytoplankton changes seasonally due to phosphorus and nitrogen limitation in central Amazon floodplain wetlands depending on the suspended inorganic material concentrations that carry readily available phosphorus (Davies et al., 2008). In general, phytoplankton is phosphorus-limited in temperate wetlands and nitrogen-limited in tropical regions (Vitousek and Howarth, 1991; Poxleitner et al., 2016). Despite the abundance of nitrogen in the atmosphere, its relative inertness restricts photoautotrophic exploitation to nitrogen compounds. Therefore the principal forms of nitrogen that photoautotrophs can use are the ions nitrate, nitrite, and ammonium (Reynolds, 2006). Furthermore, nitrogen is readily lost through leaching or volatilization and denitrification to the atmosphere (Vitousek and Howarth, 1991). In tropical regions, there is increased denitrification (due to higher temperatures compared to the temperate regions) that further raises nitrogen losses (They et al., 2014). Consequently, phytoplankton species in the tropics are conditioned by physiological and morphological adaptations under nitrogen deficiency. This therefore favors dominance by nitrogen-fixing phytoplankton, for example, the cyanobacterial group Nostocales (Vitousek and Howarth, 1991; They et al., 2014). Fig. 8.3 depicts a conceptual biogeochemical pathway model for mineralization of wetland organic matter to ammonium and phosphate, and subsequent transport, retention, uptake, and removal (i.e., denitrification, volatilization, burial) across the


(A)
ET
Volatilization,
$[NH_3]_G$
N-fixation
Aeration,
O_2
Algae
Q_{in}
h
Particulate
NH_3
Plant-uptake
Q_{out}
Nitrification
NH_4^+
NO_3^-
N_2
Resuspension
SOD
Diffusion
Deposition
NH_4^+
Nitrification
NO_3^-
l_1
Aerobic layer
H
Diffusion
Plant-uptake
Anaerobic layer
Immobilization
Denitrification
Plant residue & deposited organic matter
O-N
NH_4^+
l_2
Ammonification
Adsorption
$[NH_4^+]_s$
O-C
Ground water
Burial
(B)
ET
Algae
Q_{in}
Particulate
Plant-uptake
Q_{out}
Dissolved P
Sorbed P
Resuspension
Diffusion
Deposition
Dissolved P
Sorbed P
l_1
Aerobic layer
Diffusion
Plant-uptake
Ground water
Anaerobic layer
O-P
Dissolved P
l_2
Plant residue & organic deposits
Anaerobic decomposition
Sorbed P
Burial
Ground water

water column (pelagic), wetland soil layer, and plant biomass according to Hantush et al. (2013).

A study by Dalu et al. (2020) in a tropical South African wetland observed that when nutrient concentrations were low, especially during summer, phytoplankton was dominated by small-sized, pico- and nanophytoplankton, whereas the large-sized cell fractions increased as nutrients increased in winter. These contrasting phytoplankton community structures also relate to different ecosystem functioning modes. Under nutrient limitation, an ecosystem will maximize nutrient recycling, while new primary production based on inputs from allochthonous sources generally supports highly productive ecosystems resulting in dominance of numerous large-celled phytoplankton, that is, microphytoplankton (Cózar et al., 2018). Another important means of overcoming nutrient limitation is mixotrophy. Mixotrophy, a strategy adopted by several, phylogenetically distinct, phytoplankton groups across different aquatic ecosystems, involves a combination of photosynthesis and direct access to organic carbon sources through mainly osmotrophy or phagotrophy (Nhiwatiwa et al., 2019).

8.3.2 Water temperature

Temperature has been identified as a major selective factor restricting phytoplankton species occurrence within and across tropical latitudinal bands (Padisák et al., 2016), through both direct physiological effects and indirect effects through changes in hydrological and physicochemical processes (Murulidharand and Murthy, 2015). Several studies have demonstrated the critical role of water temperature as an environmental driver of phytoplankton succession in the tropics. Gogoi et al. (2019) observed a positive correlation between temperature and phytoplankton abundance in Indian wetlands. Euglenophyceae, Xanthophyceae, and Mediophyceae were positively correlated with the water temperature (Gogoi et al., 2019). Similarly, in Argentina, elevated dominance of Cyanobacteria (particularly *Synechocystis salina*) was associated with the highest temperatures recorded (Cony et al., 2017). Murulidharand and Murthy (2015) reported that long duration of photoperiod coupled with high temperatures favored growth in different phytoplankton groups. Temperature plays an important role in controlling the

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FIGURE 8.3 (A) Nitrogen and (B) phosphate processes in wetlands across the water column, aerobic, and reduced lower soil layers. *Abbreviations*: *C*, carbon; *ET*, evapotranspiration; *h*, water column; *H*, sediment; *N*, nitrogen; NH_3, ammonia; NH_4^+, ammonium; N_2, nitrogen; NO_3^-, nitrate; *O*, oxygen; *P*, phosphate; *Q*, flow/discharge rate; *SOD*, root biomass and tillering zone. *Detailed model explanation is provided in Hantush, M.M., Kalin, L., Isik, S., Yucekaya, A., 2013. Nutrient dynamics in flooded wetlands. I: model development. Journal of Hydrologic Engineering 18, 1709–1723 (Reproduced with permission from American Society of Civil Engineers,* Journal of Hydrologic Engineering*).*

species richness, abundance, diversity, and productivity of phytoplankton in tropical wetlands (Laskar and Gupta, 2009).

Temperature also regulates biogeochemical activities in the wetland environment. For instance, oxygen solubility in water increases with reduction in temperature (Nagar, 2011). Murulidharand and Murthy (2015) reported that dissolved oxygen was negatively correlated with phytoplankton in Teetha Wetland (India) as temperatures increased. An increase in temperature also enhances the rate of decomposition and evaporation. Subsequently, there is an increase in nutrient concentration which increases the phytoplankton density (Brraich and Kaur, 2015).

8.3.3 Light

Given that light is the source of energy in photosynthetically active autotrophs, the amount and depth of light penetration through the water column is central for primary productivity levels. Low phytoplankton productivity can be a result of low light penetration. Globally, turbidity is a fundamental determinant of phytoplankton growth. Turbidity is a measure of light scatter as a result of particles in the water that hinder light penetration through the water column and availability for phytoplankton. Therefore without vertical mixing of the water column, there are limits upon the phytoplankton cell concentration that can be supported by the light energy available. Many tropical freshwater wetlands, however, are shallow and, as such, depth-associated light limitation is less of a hindrance for primary production than in larger water bodies. Indeed, given the shallow nature of many systems of the region, much of the phytoplankton community is composed of taxa that are often associated with the benthic environment, but also occur in the water column, given high levels of bentho—pelagic coupling (Threlkeld, 1994; Zapperi et al., 2016). In addition, the high angle of the sun and solar intensity results in greater inputs of light into the water column in the tropics compared to temperate regions. As a result of these light effects, in combination with temperature effects, rates of primary production are characteristically higher in tropical (lower latitude) aquatic ecosystems.

8.3.4 Hydrological effect

Given that phytoplankton populations live in suspension, they are largely dependent on the movement of water masses. It has been observed that the relationship between phytoplankton and physicochemical and biological variables is strongly controlled by the hydrological regime in the tropical regions (Martinet et al., 2014). The hydrology (due to flood pulse) induces changes in phytoplankton communities responding to nutrient concentration (due to receding waters) and dilution (flooding) (see Box 8.2; also see Deemy et al., 2022c, Chapter 4). In floodplain wetlands, phytoplankton communities are

BOX 8.2 Effects of flooding cycle on the phytoplankton community diversity in a Ramsar wetland in Bangladesh (Muzaffar and Ahmed, 2007a,b).

Freshwater wetlands in tropical Asia are strongly influenced by monsoons, and the annual flood cycle has measurable impact on the abiotic and biotic variables. The north-eastern Bangladesh Haor Basin is particularly rich in seasonal floodplain wetlands that support a wide diversity of fauna and flora. Water levels gradually rise from June to August, before receding in September. Over the course of the flood cycle, 107 phytoplankton taxa representing five classes were recorded in the system. Ammonia-N, pH, dissolved oxygen, hardness, and chloride were found to be important in structuring phytoplankton communities. Cyanophyta accounted for more than 97% of all taxa recorded. *Microcystis* dominated and were particularly high during the early high water period phase in June, before gradual declining to low abundances in December. Cyanophyta genera such as *Anabaena*, *Aphanocapsa*, *Chroococcus*, *Coelosphaerium*, *Gloeocapsa*, and *Lyngbia* were also abundant but showed varied trends. *Lyngbia* declined to low densities in December, whereas *Anabaena*, *Aphanocapsa*, and *Coelosphaerium* increased significantly, causing the overall shifts in phytoplankton communities. *Melosira* was also a dominant taxon, reaching bloom proportions early on during the high water period. Other abundance of the Cyanophyta to increase in December cycling phase and nutrient availability seemed to be important in controlling phytoplankton dynamics.

mainly associated with water level fluctuations, hydrological connectivity, and habitat diversity (Muzaffar and Ahmed, 2007a,b; Laskar et al., 2013). The influence of habitat heterogeneity on phytoplankton communities has been reported previously for tropical Brazilian floodplain wetlands, where the degree of connectivity with the mainstem river was seen to influence phytoplankton abundances and diversities, with the most distant and disconnected systems having the highest abundances and diversities (García de Emiliani, 1990). Additionally, recent studies highlight the importance of habitat fragmentation during low water periods in promoting phytoplankton diversity, because it acts as a key regulator of the occurrence of different phytoplankton functional groups within wetland systems (Devercelli, 2006; Laskar and Gupta, 2009). As in other plankton communities, phytoplankton abundance and diversity in floodplain wetlands is mostly driven by flood pulse-induced forces, interacting with climate and biotic processes such as competition. Thus in addition to the alpha diversity (site species richness), more studies are required to assess the phytoplankton gamma diversity (total species pool) and beta diversity (species turnover between and within systems), which have been rarely evaluated in floodplain and other tropical wetland types.

8.3.5 Macrophytes

Aquatic macrophytes are important elements in structuring freshwater ecosystems and are frequently used as indicators of their ecological quality (Søndergaard et al., 2010; Piedade et al., 2022, Chapter 7). There is increasing concern about the effects of free-floating macrophytes on aquatic biota given their increase through invasions, and potential shifts in their geographical range due to eutrophication and increasing winter temperatures (de Tezanos Pinto and O’Farrell, 2014). Many free-floating macrophytes are native to South America and their sensitivity to low air temperature and freezing is reflected in their predominantly tropical distribution (O’Farrell et al., 2009). Increases in free-floating macrophytes can lead to changes in chemical and physical conditions of the water, generating mosaics of environmental conditions in small water bodies (They et al., 2014). These changes have consequences for the entire food web, but their impact is easily observed on phytoplankton biomass.

Free-floating macrophytes are known to attenuate incoming light (through shading), immobilize nutrients in their biomass, enhance suspended solids sedimentation, and release allelopathic substances (de Tezanos Pinto and O’Farrell, 2014). In Argentina, O’Farrell et al. (2009) observed that the persistence of a floating macrophyte cover caused a stressful phytoplankton environment, due to the low light penetration and intensity that impaired photosynthesis and growth. The low light availability causes a shift in the algal community to mixotrophic species (species that the use autotrophy and heterotrophy) with low light requirements (de Tezanos Pinto and O’Farrell, 2014).

8.4 Tropical cyanobacterial blooms

Cyanobacterial blooms pose a health issue in freshwater systems (Paerl et al., 2020) principally because some species are able to produce toxins which are dangerous to humans and animals (Box 8.3). Although freshwater cyanobacterial blooms are a worldwide occurrence, there are variations in the typical cyanobacteria species and toxins found within the temperate and tropical regions. *Microcystis* is the most prevalent cyanobacteria bloom-causing genus in Africa, Asia, and America, followed by *Cylindrospermopsis* (Fig. 8.4A) and four toxins have been detected across Africa, Asia, Australia, and America (Fig. 8.4B; Mowe et al., 2015).

Cyanobacteria toxin poisonings are the main cause of concern over harmful algal blooms (HABs) (Carmichael et al., 2001). Among the worst reported incidents of human poisoning attributed to cyanotoxins for tropical America were from Brazil in 1988 in which 2000 gastroenteritis cases were recorded and 88 of these resulted in death (Carmichael et al., 2001). Following these incidents, there has been a lot of research on toxins in South

BOX 8.3 Cyanotoxins which are specifically harmful to people.

There are currently two kinds of cyanotoxins which are specifically known to be harmful to people: hepatotoxins (cyclic peptides) and neurotoxins (alkaloids). The cyclic peptides represent the greatest concern to human health due to their potential risk of long-term exposure to relatively low toxin concentrations in drinking water supplies. Cyclic peptides, microcystins and nodularins, cause liver poisoning in animals, particularly mammals, and can even cause death due to liver hemorrhage and failure. The cyclic peptides may also promote liver growth and tumors following chronic low-dose exposure. The alkaloid neurotoxins (i.e., anatoxins, asaxitoxins/paralytic shellfish poisoning toxins) have been shown to have only acute effects in mammals. However, some of the alkaloid toxins are known to accumulate to high concentrations in freshwater and marine animals. They therefore pose a risk in many areas of the world where local populations consume aquatic animals from contaminated water bodies with toxic cyanobacteria.

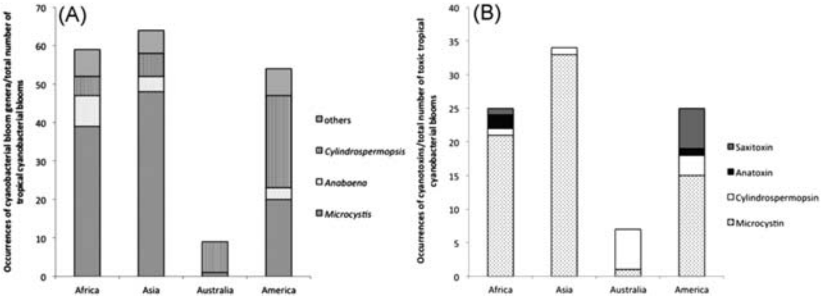

FIGURE 8.4 Proportion of tropical (A) cyanobacteria genera and (B) cyanobacterial toxins found within the different regions. *Mowe, M.A., Mitrovic, S.M., Lim, R.P., Furey, A., Yeo, D.C., 2015. Tropical cyanobacterial blooms: a review of prevalence, problem taxa, toxins and influencing environmental factors. Journal of Limnology 74, 205–224 and reproduced with permission from PAGEPress Srl.*

American wetlands aiming to document cyanobacterial blooms and progenitor species (Mowe et al., 2015).

While cyanobacterial blooms have been characteristic of eutrophic systems, there have been increasing reports of their recent occurrence in wetlands ranging from oligotrophic to eutrophic trophic states (Cottingham et al., 2015; Carey et al., 2008; Carey et al., 2014). Of concern, recent studies have observed that cyanobacterial blooms can actually induce eutrophication in water bodies by altering the nitrogen and phosphorus cycles (Cottingham et al., 2015; Carey et al., 2014). Through nitrogen fixation, cyanobacteria transforms dissolved nitrogen into biologically active forms making nitrogen that would have been inaccessible to other phytoplankton available. Further to this, many cyanobacteria taxa produce extracellular polyphosphatase enzymes which enable them to access phosphorus stored in sediments (Cottingham et al., 2015). They also have the capacity for uptake and storage of phosphorus in excess of immediate demand. This phosphorus is subsequently released into the water column through zooplankton grazing, senescence, or leakage stimulating growth of phytoplankton and starting a cycle of eutrophication (Carey et al., 2014). These observations are critical in the wake of climate change where temperatures are likely to become more favorable for cyanobacterial dominance (Kosten et al., 2012; Paerl and Otten, 2013). A more recent example of how cyanobacteria may be increasingly emerging as problem associated with climate change is that of the mass elephant mortality events that occurred in Botswana between March and June 2020 (Azeem et al., 2020). Reports suggest that "sending test samples to specialized laboratories…the deaths were caused by neurotoxins …from a species of cyanobacteria" (York, 2020). Although at the time of the writing of this chapter, specific details were yet to be published, this unprecedented event suggests that shifting environmental conditions may be having implications for phytoplankton communities in wetlands used by elephants and other wildlife as watering points.

Many techniques have been proposed, employed, and evaluated for managing cyanobacterial HABS in different wetland systems. These approaches are varied, ranging from physical, chemical to biological. Physical manipulations include activities such as rechanneling water through affected systems to promote flushing; removal of buoyant surface blooms by skimming; deployment of surface mixers/fountains and ultrasonic emission devices aimed at disrupting blooms; withdrawal of bottom waters; and dredging or excavation (Paerl et al., 2016). The success of these physical approaches has been mainly reported in relatively small ecosystems (Paerl and Otten, 2013). For instance, dredging works in shallow wetlands where sediment-derived nutrients are possibly the most important source of nutrients to the water body (Burford et al., 2019). Chemical techniques, on the other hand, encompass precipitation and immobilization of phosphorus in bottom sediments (coagulation and flocculation) and application of algaecides (e.g., copper sulfate, tetra-chlorobenzoquionone, sodium penta-chlorophenate, potassium permanganate, chlorine) (Sharma et al., 2011). Biological means of bloom control include biomanipulation of the aquatic food web to increase grazing pressure on cyanobacteria; use of aquatic plants (which compete with cyanobacterial HABS and shade the water body inhibiting bloom formation); and use of floating treatment wetlands and riparian vegetation (which filter and trap nutrients) (Paerl et al., 2016; Burford et al., 2019). However, it is important to emphasize here that most of these techniques (physical, chemical, and biological) provide short-term solutions and do not compensate for excessive nutrient loading—the root cause of cyanobacterial HABS expansion and persistence. Therefore all these approaches do not substitute and must be coupled with comprehensive nutrient input reductions in the watershed.

8.5 Phytoplankton use in water quality assessments

The ability of phytoplankton to incorporate environmental changes within a short period of time makes them ideal for biomonitoring and have been widely used as such (Geethu and Balamurali, 2018; Greenfield, 2022, Chapter 20). Inadequate and limited reference information, which is useful as a means of establishing aquatic community expectations following restoration initiatives, is a major hindrance to development of tropical region wetland health indices (Riato et al., 2017a,b, 2018; Mangadze et al., 2019). Despite the general recognition of phytoplankton as a valuable biological indicator tool in wetland assessments (Gaiser and Rühland, 2010), research on phytoplankton used to assess the biological condition of tropical wetlands is limited (Rountree et al., 2013; Riato et al., 2017a). However, the usefulness of phytoplankton, particularly diatoms, as a wetland biological assessment tool has been demonstrated in temperate and arid regional studies (e.g., John, 1993; Gaiser et al., 2004; Tibby et al., 2007). Thus recent studies (e.g., Gaiser et al., 2004; Owen et al., 2004; Tibby et al., 2007; Riato et al., 2017a, 2018) have demonstrated the effectiveness of diatoms as biological indicators of changing tropical freshwater wetland environmental conditions. Therefore monitoring of diatom community assemblages may present an important alternative in wetland assessments within the tropical regions, where the use of other biological indicator types such as fish, macroinvertebrates, and macrophytes have proven to be less effective.

Until recently, no diatom multimetric indices developed for tropical freshwater wetlands had accounted for natural variation effects on the obtained index values, where natural variability of environmental factors among sites (i.e., variables least affected by anthropogenic disturbances) could reduce diatom index accuracy (Cao et al., 2007; Hawkins et al., 2010). This was found to be particularly important for wetland habitats which are characteristically highly variable systems, even within and across wetland types, which can vary considerably over small spatial scales (Riato et al., 2017a). Thus most diatom-based multimetric indices used to assess freshwater wetland condition have mostly been developed to quantify salinity, nutrient loading, and pH changes (e.g., Lane and Brown, 2007; Miller et al., 2016; Riato et al., 2017a), but no tropical wetland condition diatom index had been developed to quantify mining impacts such as acid mine drainage (AMD). Riato et al. (2018) developed a diatom-based multimetric index for subtropical Highveld wetlands sensitive to coal mining impairment by assessing AMD impacts, and this metric was found to be suitable for optimizing wetland conservation across the region in the context of environmental management, protection, and rehabilitation, but could also be transferable to other regions, although this might require further testing (see Box 8.4). However, caution should be taken when extending diatom-based bioassessments to frequently inundated floodplain wetlands as diatom community

BOX 8.4 Diatom-based wetland multimetric index for acid mine drainage (Riato et al., 2018).

Acid mine drainage (AMD) causes severe chemical and biological degradation of aquatic habitats, specifically tropical depressional wetlands, as mines use these systems for AMD storage. Diatom-based multimetric indices (MMIs) to assess wetland condition have mostly been developed to assess agricultural and urban land-use impacts. Previous approaches to wetland diatom-based MMI development have not accounted for natural variability. Thus natural variability among wetlands may influence diatom MMIs accuracy. Epiphytic diatom MMIs sensitive to AMD were developed for a variety of Highveld depressional wetland types to account for natural variation within the metrics. For this, Riato et al. (2018) classified wetland types based on diatom typologies assigned to four categories (diversity, functional group, similarity to reference sites, taxonomic composition). Four final metrics were selected from a pool of 154 candidate metrics to develop the MMIs based on precision, responsiveness, sensitivity, and relevancy, and their broad range, high separation power, and low correlation among metrics (Table 8.1). Thus final metrics were selected from three categories: functional groups, similarity to reference sites, and taxonomic composition, which represent different aspects of diatom assemblage structure and function. The MMI performances were evaluated according to their precision in distinguishing reference sites, responsiveness to discriminate reference and disturbed sites, sensitivity to human disturbances, and relevancy to AMD-related stressors. Each MMI showed excellent discriminatory power, whether or not it accounted for natural variation. However, accounting for variation by grouping sites based on diatom typologies improved overall performance of MMIs.

assemblages may reflect the influence of both the wetland condition and floodwaters (Weilhoefer et al., 2008).

Landscape-scale models can become important tools in wetlands because diatom community assemblage patterns are constant across wetland types. Therefore spatially explicit visualizations of these diatoms models are useful for evaluating the performance of diatom-based inferences over large wetland areas around the world with high hydrologic connectivity. Since hydrology has been identified as an important driver of ecosystem change, hydrologic alterations due to restoration efforts could significantly modify phytoplankton responses. In freshwater wetlands, phytoplankton (i.e., diatoms) is an important component of mat-forming calcareous periphyton (i.e., biofilms attached on rock surfaces) assemblages that contribute to the structural organization and function of the entire periphyton matrix (Lee et al., 2013). Thus specific diatom community assemblages inhabiting periphyton mats can be used to infer past and present conditions and inform environmental management decisions based on how community assemblages are changing or have changed. Therefore there is a need for sound ecologically

TABLE 8.1 Final metric variables used for developing composite metrics within each metric category.

Category/final metric	MMI-1	MMI-2	MMI-3	MMI-4	Response
Similarity to reference sites					
%Reference taxa	x	x	x	x	−
%Tolerant taxa	x	x	x	x	+
%Similarity to reference sites	x	x	x		−
%Reference taxa found in reference sites that occurred in impaired sites			x	x	−
%Reference individuals found in reference sites that occurred in impaired sites	x				−
No. of distinct reference taxa		x	x	x	−
Functional group					
Mobile % taxa	x				−
Adnate % Lisa			x		−
Pad (attached to substrate) % taxa	x		x		+
Noncolonial			x		−
Ribbon % taxa			x		+
Ribbon % individuals	x				+
High profile guild. % taxa			x		+
Taxonomic composition					
%Encyonopsis taxa			x		+
%Cocconeis taxa			x		+
%Craticula taxa			x		−
%Ctenophora taxa	x		x		+
%Comphone taxa			x	x	v
%Nittschia individuals k				x	−

Abbreviations: *x*, metrics selected for each multimetric index best discriminated between references and disturbed sites; + *or* − , increase or decrease to disturbance direction of metric response to disturbance; *v*, a variable response.
Source: Adapted from Riato, L., Leira, M., Della Bella, V., Oberholster, P.J., 2018. Development of a diatom-based multimetric index for acid mine drainage impacted depressional wetlands. Science of the Total Environment 612, 214−222.

based tropical wetland assessments that require an understanding of how community assemblages respond to ecosystem parameters to make interpretations about past and present conditions, develop future targets, and aid in important wetland assessments (Lee et al., 2013; Riato et al., 2017a, 2018). Thus wetland environmental management programs should incorporate the obtained information from assessments to infer landscape-scale biological responses to hydrologic and community changes and to inform tropical wetland restoration targets, especially where hydroperiod regimes no longer follow natural spatiotemporal patterns. Diatom composition seems to follow a predictable relationship with two important habitat wetland characteristics, that is, hydroperiod and periphyton biovolume. Thus phytoplankton autecological information in tropical wetlands should be further utilized to investigate the poorly described flora distribution patterns (La Hée and Gaiser, 2012). Thus the potential of molecular approach to phytoplankton biomonitoring has developed over the past decades (see de Bruin et al., 2003; Keck et al., 2017) and this has lessened the dependency of qualified taxonomical expertise, which is often a stumbling block in biomonitoring efforts.

8.6 Future direction

In terms of phytoplankton tolerances, ecophysiology, and ecological preferences, much work still needs to be carried out (Dalu and Froneman, 2016). Accruing more data on autecology and taxonomy of a large number of biological indicators (i.e., phytoplankton species) will improve diatom-based biological indices, making them more powerful tools for monitoring wetland health. In particular, more information is needed on taxa that dominate in tropical systems. The array of inland wetland types in the tropics (see Wasserman and Dalu, 2022, Chapter 1; Job et al., 2022, Chapter 2 for details) also needs to be considered as many studies do not identify and outline wetland type, making comparisons across system types difficult. But perhaps the most important point of consideration for driving the field forward is the lack of human capacity in tropical regions. Most tropical regions overlay developing countries with limited capacity to train phytoplankton specialists. As a result, studies in tropical countries are often conducted by investigators from the developed world, employing a "parachute science" approach (de Vos 2020), whereby local training and collaboration is not prioritized. Given that most of the developed world lies in temperate regions, it is not surprising that temperature system paradigms pervade in tropical system investigations.

While the lack of human capacity and baseline phytoplankton information on community composition, structuring, and ecological requirements represent significant challenges, phytoplankton biomonitoring potentially holds much promise for understanding wetland ecological functioning and informing management of these unique aquatic ecosystems in the tropical regions. Therefore there is a compelling need for wetland phytoplankton systematics research to be undertaken within multiinterdisciplinary research projects, rather than focusing on species taxonomic identification, as such an approach will help in addressing the current challenging ecological problems. Thus further studies are urgently required to assess seasonal and yearly phytoplankton variation in wetland systems that experience extensive flooding.

Low-profile phytoplankton guilds dominated by pioneer life-forms have been shown to have a strong relationship with high disturbance levels such as increasing sodium (Na^+), alkalinity, and a decrease in depth (Riato et al., 2017b). Similarly, it has been observed that the phytoplanktonic guild and tube-living, rosette, and adnate life-forms dominate at high disturbance levels whereas the high-profile diatoms display an opposite trend (Riato et al., 2017b). Thus the strong ecological responses of phytoplankton life-forms and guilds to changing environmental conditions suggest that with further research, wetland phytoplankton functional groups may be used in wetland biological assessments and monitoring, where wetland phytoplankton species taxonomy are poorly described and studied. The use of phytoplankton functional groups may also be beneficial where budgets are limited, because a reliable wetland ecological status is still required, and the use of functional groups rather than species is a time- and cost-effective approach. Thus although most tropical wetlands have received inadequate and limited attention to date, advancements made by assessment, monitoring, and restoration efforts can guide newly developing wetland protection programs. Field and laboratory studies must be carried out to test for allelochemicals presence from macrophytes in water and how they impact on phytoplankton community structuring (Chia et al., 2011). The identification of specific macrophyte allelochemicals will provide an estimation of the amount of allelochemicals leached that could potentially impact on the phytoplankton community, and an understanding of the chemical transformations and mechanism of action of these allelochemicals in situ within the water column have on community structuring. More studies focusing on benthic phytoplankton production of extracellular polymeric substances as a sediment stabilization and substrate for microbial communities (see Dalu et al., 2020) are also lacking in tropical freshwater wetland literature, as well as research of potentially toxic and alien invasive phytoplankton species.

With limited studies providing a checklist of phytoplankton across the varied wetland types across tropical regions, there is a need for more studies that will contribute to a better knowledge of the phytoplankton community structuring, richness, and composition for management purposes. This is particularly vital in tropical regions where wetlands are under serious threat from environmental modifications and land-cover conversion due to anthropogenic activities (Dalu et al., 2017a). Future research is also required to identify phytoplankton indicators as well as species-specific responses to human impacts (e.g., agriculture, mining, tourism, urbanization) on freshwater wetlands as it will go a long way in providing guidance on the management of aquatic ecosystems used for multiple socio-economic purposes. This is particularly relevant for phytoplankton species that can cause direct harm to humans and animals, such as those species that produce toxins, or are implicated in eutrophication events. In addition, there is much scope for bioprospecting from species that produce secondary metabolites such as toxins as such compounds can have biomedical applications.

It is important to note that failure to recognize, understand, and manage temporary and ephemeral wetlands can lead to serious aquatic ecosystem degradation accompanied by negative impacts to the societies that depend upon them (Dalu et al., 2017a). Thus the legal status of temporary and ephemeral wetlands in comparison to permanent wetlands is different and the extent to which they are incorporated into policy, management, and regulatory decisions vary widely across the tropical region countries depending on how these systems are defined by the authorities, as well as what kinds of protection are given to some extent size of the temporary and ephemeral wetlands. For policies to be consistent across the region with current science, naturally, temporary wetland systems should be legally defined as part of the larger permanent wetland systems, and to implement these policies, we need improved mapping of all wetland systems in general (Acuña et al., 2014; Irvine et al., 2022, Chapter 21). In conclusion, it is important to maximize ecological resilience, maintain biodiversity, and ecosystem services for future generations within these wetland systems.

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Chapter 9

Zooplankton

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9.1 General introduction

Despite the key ecological role of zooplankton in lentic freshwater ecosystems, current knowledge on their systematics, species richness, and distribution is limited, especially in (sub)tropical biogeographical regions (further mostly indicated as "the tropics" here). Because of their important function in a wide range of both temporary and permanent aquatic ecosystems, ample ecological information is available on selected groups (see Wasserman and Dalu, 2022, Chapter 1). Furthermore, some species (e.g., *Daphnia magna*) became important models in ecological and evolutionary research. Increasing ecological knowledge, however, contrasts with the lack of taxonomic and biogeographical studies, due to which current insights on species richness and distribution are incomplete. This largely obstructs accurate large scale (biogeographical) comparisons. Every exploration in poorly studied regions almost always reveals new zooplankton taxa. This is particularly true for the tropics where taxonomy is a scarce skill, especially of microscopic organisms like zooplankton that often require rather expensive optical and molecular techniques for species identification.

Besides the typical zooplankton groups like the rotifers and the cladoceran and copepods crustaceans, we also include ostracods in this chapter. Although adult ostracods are mainly benthic, they are also caught in plankton samples, together with their early developmental stages. As ostracod communities play

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an important role in wetland systems and can be very species rich, they deserve a prominent position in a book on tropical wetlands. Sometimes large branchiopod crustaceans are also considered as zooplankton. However, as the Notostraca and Diplostraca orders are mainly benthic, while the Anostraca are rather good swimmers, they are treated in a separate chapter in this book (Brendonck et al., 2022a, Chapter 10).

With this chapter we aim to review and integrate current knowledge on species richness and distribution patterns of tropical zooplankton. This will be complemented with general information on ecology and life history strategies of each group. Where possible, we compare patterns of species richness and distribution between permanent and temporary wetlands. In line with the focus of this book, we here focus on the Afrotropical, Australasian, Neotropical, and Oriental biogeographical regions. Due to size constraints, this review is necessarily limited and incomplete. However, to the best of our knowledge, this is the first large scale integrative effort combining information from all zooplankton groups.

9.2 Cladocerans

9.2.1 Introduction

Cladocerans, also known as water fleas, belong to the Class Branchiopoda, Subphylum Crustacea. The majority are small-sized (0.2−7 mm; some exceptionally larger), primarily freshwater-dwelling organisms, characterized by biramous antennae, four to six limb pairs, and a bivalved carapace not covering the head (Fig. 9.1). These animals thrive in pelagic, littoral, and benthic biotopes, where they occupy key trophic roles as secondary producers, predominantly in lentic waters (Dumont and Negrea, 2002). Members of the Anomopoda, the most speciose cladoceran order, in particular chydorids, daphniids, and moinids often dominate the microcrustacean communities in a wide range of (sub)tropical wetland types. Representatives of the latter families are also particularly well-adapted to temporary waters in the (sub) tropics where they may survive prolonged periods of drought through the production of dormant embryos encased in ephippia.

9.2.2 Systematics and general species richness

Cladocerans are grouped into four extant orders, which are systematically well-defined and widely accepted (Fryer, 1987; Kotov, 2013); while several orders are now extinct (Van Damme and Kotov, 2016). The two suspension- and deposit-feeding orders, Anomopoda and Ctenopoda, are the most speciose in tropical wetlands (Chiambeng and Dumont, 2005), while the other (mainly pelagic predatory) orders are virtually absent from these environments.

General cladoceran species richness remains insufficiently known because estimates strongly depend on regional taxonomical efforts. There is especially a general shortage of field data as well as experimental work regarding

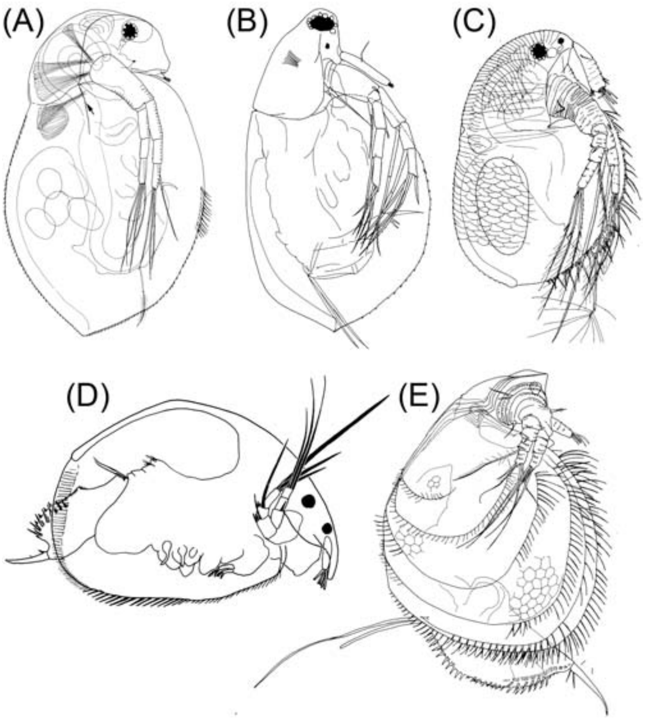

FIGURE 9.1 Selected cladocera from tropical and subtropical wetlands. (A) *Daphnia paggii* (Daphniidae), a high altitude endemic from a sub- to hyposaline temporary lagoon in the Chilean Andes (Kotov et al., 2010). (B) *Moinodaphnia maclaeyi* (Moinidae), a common pantropical species (after Kotov et al., 2012). (C) *Macrothrix spinosa* (Macrothricidae) from the Pantanal floodplains in Brazil (Hollwedel et al., 2003). (D) *Anthalona acuta* (Chydoridae), a Neotropical endemic from temporary interdunal pools in the Lencois Maranhenses, Brazil; Chydoridae are the most speciose group in most (sub)tropical wetlands (Van Damme et al., 2011). (E) *Ilyocryptus africanus* (Ilyocryptidae) from temporary rockpools, endemic to Cape Point, Republic of South Africa; one of only two species of the family ever found in temporary rockpools (Kotov and Štifter, 2005). *Drawings by AA. Kotov (A−C, E) and K. Van Damme (D), reproduced with permission from the copyright holder; not to scale (for scale bars, see original publications).*

cladocerans in the tropics (Sarma et al., 2005). This is particularly true for the many taxa residing in shallow macrophyte- and/or detritus-rich lentic habitats that are beyond the scope of most studies that generally focus on the pelagic of deep lakes. Study of zooplankton from such small water bodies requires in-depth systematic knowledge and separate sampling efforts and techniques.

Forró et al. (2008) estimated a global richness of c.620 valid cladoceran species, yet suggested that the realistic number is likely much higher. Since then, a substantial number of new cladoceran genera and species have been described and/or revised (Kotov, 2013; Kotov et al., 2013); the majority from tropical regions.

Up to 50% of cladoceran species are thought to occur exclusively in the (sub)tropics, predominantly in lentic wetlands (Dumont, 1994) with a general and strong increase in diversity around the equator (Forró et al. 2008). From aquatic habitats in tropical rainforests (from flooded forest patches to temporary puddles in tree holes), currently at least 196 cladoceran species are known worldwide (Chiambeng and Dumont, 2005), which is nearly a third of the estimated global diversity. Based on Forró et al. (2008), each of the (sub)tropical regions hosts about half (or a little more) of all cladoceran genera and between a sixth to a quarter of the global species richness, with the Australasian and Neotropical regions having a relatively higher richness and number of endemics (Table 9.1). However, regional diversity estimates are not entirely comparable because they are biased by research intensity. For example, the relatively low diversity in the Afrotropics (Table 9.1) may be partly a natural phenomenon due to historical extinctions (Chiambeng and Dumont, 2005), but lack of taxonomists and limited intensive surveys in the region also play a significant role (Van Damme et al., 2013a; Bird et al., 2019). Similar impediments have been noted for the Oriental region (Korovchinsky, 2013), where nevertheless rainforest areas stand out with the highest richness in the world, matching the Neotropics (Chiambeng and Dumont, 2005).

9.2.3 Comparison between wetland types and tropical biogeographical regions

In Table 9.1, numbers of cladoceran genera and species for the considered biogeographical regions are presented, while Table 9.2 summarizes species richness from selected areas and wetland types. Studies on cladoceran zooplankton have been carried out in all tropical regions and in permanent as well as temporary wetland types. An in-depth comparison of species richness in different types of tropical wetlands is limited. This is due to differences in the level of taxonomical research (regional as well as related to the type of habitat), level of habitat description, and sampling approach. Often, wetland types and habitat characteristics are not defined in sufficient detail in cladoceran studies. Studies that cover a wide range of temporary and permanent tropical wetland habitats usually yield a high richness; often with more than half of the known total cladoceran diversity in a region. For example, there are at least 120 cladoceran species known from the Pantanal, counted from 50 permanent and temporary wetland habitats (Brazil; da Silva Brito et al., 2020), which covers 65% of the Neotropical species (known in 2008; Table 9.1). In tropical Africa and India, cladoceran populations have been studied in river pools (Nhiwatiwa et al., 2009), rock pools (Padhye and Victor, 2015), temporary and floodplain pans (Simões et al., 2011; Riato et al., 2014; Nhiwatiwa et al., 2017), and floodplain wetlands (Lindholm et al., 2009; Gogoi et al., 2018; Dube et al., 2017). However, although highly informative, few studies pay attention to a specific wetland type and include a proper (taxonomically accurate) species list (Table 9.2).

TABLE 9.1 Number of cladoceran genera and species (with endemics between brackets) in the Afrotropical, Australasian, Oriental, and Neotropical regions; numbers from Forró et al. (2008), with the addition of the subtropical Australian Gondwanotrichidae.

	Afrotropical		Australasian		Oriental		Neotropical		Global	
	Genera	Species	Genera	Species	Genera	Species	Genera	Species	Genera	Species
Anomopoda	42(1)	125(24)	48(11)	149(78)	36(1)	89(20)	44(3)	170(89)	76	537
Bosminidae	2(0)	3(0)	2(0)	3(0)	2(0)	4(1)	2(0)	7(3)	2	14
Chydoridae	26(1)	66(17)	33(10)	85(47)	22(1)	48(11)	27(1)	89(51)	49	269
Daphniidae	5(0)	25(1)	4(0)	26(13)	4(0)	17(1)	4(0)	32(13)	5	121
Eurycercidae	1(0)	1(0)	0	0	1(0)	1(0)	1(0)	2(1)	1	8
Gondwanotrichidae	0	0	1(1)	1(1)	0	0	0	0	1	1
Ilyocryptidae	1(0)	8(3)	1(0)	5(3)	1(0)	5(3)	1(0)	9(4)	1	28
Macrothricidae	5(0)	12(2)	4(0)	20(9)	4(0)	12(4)	7(2)	21(12)	11	60
Moinidae	2(0)	10(1)	2(0)	7(3)	2(0)	3(0)	2(0)	10(5)	2	29
Neothricidae	0	0	1(1)	3(3)	0	0	0	0	1	3
Ctenopoda	4(0)	9(0)	4(0)	9(5)	6(0)	15(4)	6(0)	16(9)	8	50
Holopediidae	0	0	0	0	0	0	1(0)	1(1)	1	3

(*Continued*)

TABLE 9.1 (Continued)

	Afrotropical		Australasian		Oriental		Neotropical		Global	
	Genera	**Species**	**Genera**	**Species**	**Genera**	**Species**	**Genera**	**Species**	**Genera**	**Species**
Sididae	4(0)	9(0)	4(0)	9(5)	6(0)	15(4)	5(0)	15(8)	7	47
Haplopoda	0	0	0	0	1(0)	1(0)	0	0	1	1
Leptodoridae	0	0	0	0	1(0)	1(0)	0	0	1	1
Onychopoda	0	0	0	0	0	1(0)	0	0	10	32
Polyphemidae	0	0	0	0	1(0)	1(0)	0	0	1	2
Total	***46(1)***	***134(24)***	***52(11)***	***158(83)***	***43(1)***	***106(24)***	***50(3)***	***186(98)***	***95***	***620***

Only families from tropical wetlands are listed. Estimates are outdated and strongly tied to research intensity per region. A substantial number of new species and genera were described in recent years (Kotov et al., 2013). To put richness of genera and species of the considered biogeographical regions in perspective to those at the global scale, an extra column was added.

TABLE 9.2 Selected studies on cladoceran diversity and/or ecology in temporary and permanent (sub)tropical wetland types across tropical biogeographical regions.

Region	Area	Wetland type(s)	#spp.	Most speciose group	Remarks	References
Afrotropical	Rwenzori Mountains, Uganda	Temporary pools, permanent swamps, and lakes	11	Chydoridae	29 Water bodies, high altitude; new species	Van Damme and Eggermont (2011)
	Okavango Delta, Botswana	Temporary and permanent habitats (lakes, swamps, floodplains, rain ponds, river)	45	Chydoridae	Highest cladoceran diversity in floodplains (42 spp.) and in swamps (19 spp.), lowest in temporary rain ponds (7 spp.)	Lindholm et al. (2009)
	SE Botswana	Temporary rockpools (on granite)	1	Chydoridae	18 Pools, 1 spp. (undescribed new taxon)	Jocqué et al. (2006)
	Cameroon	Temporary and permanent habitats (rock pools, ponds, flooded rainforest, lakes)	61	Chydoridae	700 + samples	Chiambeng and Dumont (2005)
Australasia	SW Australia	Temporary rockpools	13	Chydoridae	94 Pools, intensively sampled	Jocqué et al. (2007)
	Western Australia	Temporary rockpools (gnammas)	14	Chydoridae	36 Pools on granite	Bayly (1997)

(*Continued*)

TABLE 9.2 (Continued)

Region	Area	Wetland type(s)	#spp.	Most speciose group	Remarks	References
Neotropical	Pantanal, Mato Grosso, Brazil	Temporary and permanent habitats (floodplains, lakes)	120	Chydoridae	50 Localities; general study with different wetland types	da Silva Brito et al. (2020)
	Cochabamba, Bolivia	Temporary (peat-) pools (bofedales)	21	Chydoridae	61 Pools at high altitude; 3–16 spp. per pool; new species	Coronel et al. (2007)
	Andes, Chile	Permanent lakes and temporary saline lagoon	19	Chydoridae	6 Localities at high altitude; new species and new genus	Kotov et al. (2010)
	Pernambuco, Brazil	Temporary pond	22	Chydoridae	1 Pond sampled throughout different periods	Diniz et al. (2013)
	Federal District and Góias, Brazil	Temporary shallow wetlands (moist grasslands, earth mounds, shallow ponds)	33	Chydoridae	9 Localities; groundwater-fed waters in Cerrado biome	Sousa et al. (2013)
	Lencois Maranhenses, Maranhao, Brazil	Temporary pools on sand (interdunal; groundwater fed)	34	Chydoridae	5 Localities; 9–17 spp. per pool; Sars' method	Van Damme and Dumont (2010)

Oriental	Western Ghats, India	Temporary rockpools	22	Chydoridae	12 Localities	Padhye and Victor (2015)
	Southern Thailand	Permanent swamps	73	Chydoridae	22 Localities; up to 45 spp. per locality	Van Damme et al. (2013b)
	Thale Noi Wetland, Southern Thailand	Permanent shallow wetland	40	Chydoridae	1 Wetland, sampled using activity traps	Choedchim et al. (2017)

In the Oriental region, up to 85% of the total known cladoceran fauna from Thailand (of which over 60% chydorids) and nearly 70% of the species richness in the region was specifically retrieved from shallow permanent swamps in Southern Thailand (Table 9.1) (Van Damme et al., 2013b). In addition, the focus on swamp habitats led to the discovery of several new species (*Leydigiopsis pulchra*, *Karualona serrulata*, *Notoalona pseudomacronyx*) and the identification of very specific tropical paludal communities with similar species in other continents (Van Damme et al., 2013b; Van Damme and Sinev, 2013). Similar studies were done in each region and for different wetland types, in particular in the increasingly studied Neotropics (Table 9.2). These studies underline that close examination of cladocerans in tropical wetlands is highly valuable, as these habitats continue to harbor a hidden diversity. In the Afrotropics, Lindholm et al. (2009) compared species richness in permanent and temporary habitats in the Okavango Delta, recording a relatively high richness in permanent floodplains (42 spp.), followed by swamps (19 spp.) and lowest values in temporary ponds (7 spp.). The generally lower recorded diversity in tropical temporary ponds and pools in comparison to permanent swamps and floodplains could to some extent depend on the characteristics of the habitat but also on the type and duration of sampling. In the Neotropics, Diniz et al. (2013) monitored a shallow temporary pond in Brazil over several months and counted up to 22 cladoceran species. In contrast, individual tropical temporary pools sampled over shorter periods usually yield lower species numbers (Table 9.2). In a study across 94 temporary rock pools in SW Australia Jocqué et al. (2007) collected 13 species, while only one species was collected from 18 temporary rock pools in SE Botswana (Jocqué et al., 2006). When properly sampled, (sub)tropical shallow temporary pools usually house between 0 and 17 species with on average about 6 species, of which the majority are expected to be chydorids ().

Cladoceran communities in lentic (sub)tropical freshwater environments are very similar across the regions at family level, both in temporary and in permanent waters. In each region and in a wide range of (sub)tropical wetlands, communities are dominated by small-bodied and phytophilous/epibenthic Chydoridae (Table 9.2), followed by Daphniidae, Macrothricidae, Sididae, and Bosminidae. At genus-level, *Alona* (*sensu lato*; separated into different genera), *Chydorus*, *Macrothrix*, and *Diaphanosoma* often constitute the most diverse taxa (e.g., rainforests of the world; Chiambeng and Dumont, 2005). The Chydoridae alone easily constitute 60%–70% of the overall richness in both ephemeral (e.g., rockpools in Australia; Bayly, 1997) and permanent (e.g., swamps in Thailand; Van Damme et al., 2013b) tropical waters, a trend which is similar across regions. Moinidae may be locally abundant in temporary and permanent waters, but they are generally represented by only one or two species per locality. Tropical cladoceran communities are usually characterized by a paucity of *Daphnia* species in the lowlands, partially replaced by other filter feeding daphniids (*Ceriodaphnia*, *Simocephalus*, *Scapholeberis*), sidids

(*Latonopsis*, *Pseudosida*, *Diaphanosoma*), moinids (*Moina*, *Moinodaphnia*), and to some extent by bosminids (*Bosmina*). The lower diversity of *Daphnia* is potentially due to the higher predation pressure in the tropics compared to temperate zones (Dumont, 1994), or may result from extinctions (Popova and Kotov, 2013). In contrast, *Daphnia* is sometimes well represented and even abundant in high altitude temporary and permanent tropical wetlands (Van Damme and Eggermont, 2011; Kotov et al., 2010). Suspension-feeding cladocerans thrive in relatively more open biotopes in comparison to chydorids, although shallow (few centimeters) temporary environments can sometimes harbor large populations.

Despite the relatively lower diversity in ephemeral compared to permanent wetlands, they often include peculiar taxa, such as the shallow ephemeral rockpool "specialists," represented by the genus *Dumontiellus* or *Ilyocryptus africanus* (Fig. 9.1), endemic to Southern Africa (Kotov and Štifter, 2005; Van Damme et al., 2013a); *Coronatella anemae* dominating short-lived pools in arid zones in Northern Africa and Arabia (Van Damme and Dumont, 2008); or *Daphnia jollyi* inhabiting rockpools in Western Australia (Bayly, 1997). Also medium- to high-altitude tropical temporary and permanent waters may harbor peculiar often local endemic species, such as the *Sphagnum*-specialist *Alona sphagnophila* from permanent swamps in the Rwenzori Mountains of Uganda (Van Damme and Eggermont, 2011), the eye-less endemic genus *Spinalona anophtalma* found in a temporary lagoon in Mexico (Ciros-Pérez and Elias-Gutiérrez, 1997), or *Alona boliviana* in temporary pools in the Bolivian Cordillera (Coronel et al., 2007; Sinev and Coronel, 2006). In addition, a surprising number of endemic species such as *Daphnia paggii* (Fig. 9.1) and even an endemic genus (*Geoffreya*), were found in temporary as well as permanent endorheic saline water bodies high in the Chilean Andes (Kotov et al., 2010). With some exceptions, lotic habitats are generally unfavored by cladocerans (Dumont and Negrea, 2002). In tropical floodplains, populations of riverine species may sporadically occur, such as *Nicsmirnovius* (hyporheic) and *Bosminopsis* (rheic), although these species are not typical for lentic environments.

9.2.4 Ecology

Cladocerans in general perform a crucial role in wetland ecosystems by linking primary producers (algae, bacteria) to higher levels of the food web (fish, amphibians, aquatic insects). Functional trait analysis has furthermore revealed that (sub)tropical taxa display some traits that allow survival under conditions with variable food availability as well as predation pressure (Oriental region; Rizo et al., 2017). As one of the most abundant herbivorous zooplankton groups in tropical waters, small-bodied cladocerans may influence the lower trophic levels (microbial loop, phytoplankton), thereby affecting size structure (Pagano, 2008), biomass, and community composition of phytoplankton, as also confirmed in mesocosm experiments (Silveira et al., 2010). Through their keystone role in tropical aquatic food webs, cladocerans directly or indirectly support ecosystem services such as provisioning (e.g., freshwater fish for human consumption), and regulating services (e.g., clearing water through top-down control of algae and bacteria).

In tropical temporary and therefore usually fishless systems, hydroperiod, macrophytes, and depth play important roles in structuring cladoceran communities (Eitam et al., 2004; Sousa et al., 2013; Eskinazi-Sant'Anna et al., 2020), while in permanent wetlands macrophytes, pH, conductivity, and depth were found to variably determine cladoceran communities (Rossa et al., 2001; Lima et al., 2003; Lansac-Tôha et al., 2009; Van Damme and Eggermont, 2011; Choedchim et al., 2017). In contrast to the biotic environment, the relative importance of abiotic variables to explain cladoceran community composition is poorly studied for tropical temporary shallow wetlands. Some of these variables govern cladoceran communities in a similar way in both temporary and permanent waters. The presence of macrophytes, for example, often results in temporary pond communities that are similar to littoral communities of nearby permanent lakes (e.g., Brazil; Sousa et al., 2013). The presence of macrophytes becomes especially important in shallow wetlands lacking top predators (Scheffer et al., 2006; Thomaz and Cunha, 2010). Overall, the presence of macrophytes and a well-developed detritus layer create ecological niches (van der Valk, 2006) and support typical deposit-feeding phytophagous cladoceran groups in both ephemeral and permanent tropical wetlands (mainly chydorids and macrothricids).

9.2.5 Life history

Cladocerans generally alternate asexual with sexual reproduction, producing predominantly populations of female clones, only forming males and sexual females under cues related to stress (Dumont and Negrea, 2002). All cladoceran taxa living in (sub)tropical wetlands (Anomopoda and Ctenopoda) have the ability to sexually produce dormant embryos. Anomopoda hereby generate a thick-walled chitinous envelope called the *ephippium*, which encloses and protects the dormant embryo(s) and which may act as a propagule for dispersal. Deposited in situ, ephippia may contribute to dormant drought-resistant cladoceran "egg banks" in temporary as well as in permanent waters (Brendonck and De Meester, 2003; Santangelo et al., 2015). The production of sexual stages in anomopods can be initiated by food limitation and crowding (Azuraidi et al., 2013). These cues also prevail during the drying phase of (sub)tropical temporary pools and therefore initiate sexual reproduction of propagules that provide a temporal escape from adverse conditions (Stenert et al., 2017). For permanent (sub)tropical wetland systems, the abiotic triggers initiating ephippium production and hatching from the egg bank are well understood and are thought to be initiated by similar cues in tropical as well as in temperate regions (mainly photoperiod and temperature). Studies on hatching strategies in tropical populations are, however, inhibiting generalizations.

Some tropical daphniids that are very common in both temporary and permanent waters were shown to be highly productive at high temperatures and with abundant food. Tropical populations of *Scapholeberis* and *Simocephalus*, for example, produced no less than 240–250 parthenogenetic eggs during their lifetime (of 20–40 days, respectively) at 28°C–30°C (Murugan and Sivaramakrishnan, 1976). At such elevated temperatures and abundant food conditions, life history traits of tropical cladocerans differ from temperate taxa, with usually a longer and more productive lifespan (Sarma et al., 2005; Han et al., 2011).

9.2.6 Feeding biology

Feeding biology of cladocerans in the tropics has been insufficiently studied (Pagano, 2008). Cladocerans are primarily suspension or deposit feeders. A few taxa are specialized predators, but these are virtually absent from tropical wetlands. Suspension-feeding representatives of the Anomopoda and Ctenopoda feed primarily on algae, while members of the most specious tropical family Chydoridae mainly process periphyton and detritus (Dumont and Negrea, 2002).

9.2.7 Threats and conservation

No studies related to cladoceran-specific conservation efforts in the tropics have been carried out, despite the vulnerability of tropical wetlands. In particular, land use change and pollution caused by development form direct pressures on the often peculiar cladoceran biodiversity in ephemeral as well as in permanent habitats. Cladoceran communities are sensitive to eutrophication, chemical pollution, and pH and may therefore have potential as bioindicators for assessing trophic state and human impact (e.g., Neotropical lowlands; Pérez et al., 2013). However, more ecological work is needed to confirm the bioindicator value of cladoceran species from tropical wetlands.

Many currently threatened but unstudied habitats potentially still house new and peculiar cladoceran taxa. This concern is especially illustrated by dystrophic habitats and temporary lagoons in SE Asia, where local sites with high cladoceran diversity have disappeared in recent years (Van Damme et al., 2013b; Van Damme and Maiphae, 2013). Habitat-specific taxa in the Oriental region, such as the endemic genus *Salinalona*, only known from temporary brackish lagoons, or the rare paludal endemics such as *L. pulchra*, are therefore under direct threat. Several rare species in the tropics occur nearly exclusively in protected areas, such as the peculiar chydorids *Ephemeroporus quasimodo* and *Celsinotum candango* inhabiting pristine shallow waters in the Brazilian Cerrado (Elmoor-Loureiro, 2014). Among the few cladocerans on the IUCN Red List, the West Australian endemic *D. jollyi* has been assessed as vulnerable (Benzie, 1996), herewith emphasizing the conservation value of ephemeral rock pool environments where this species occurs.

Limited experimental studies on some widespread thermophilous species complexes revealed that some may be tropical alternatives to *Daphnia* for applications in aquaculture and/or ecotoxicology, such as *Diaphanosoma* sp., *Moina micrura*, and the *Ceriodaphnia cornuta*-complex (Pagano, 2008; Martinez-Jeronimo and Ventura-Lopez, 2011; Sipaúba-Tavares et al., 2014).

Although cladocerans are not usually considered as a charismatic group for conservation, they do serve as a primary food item for invertebrate and vertebrate predators that are generally more appealing for conservation efforts such as dragonflies, amphibians, and fish (Eitam et al., 2004). Conservation measures for cladocerans in (sub)tropical wetland types should therefore be integrated with the conservation of other groups of concern (Eitam et al., 2004; Jocqué et al., 2007).

9.3 Ostracods

9.3.1 Introduction

Ostracods, also known as mussel (Martens et al., 2008) or seed shrimp (Brendonck et al., 2016), are a class of microscopic bivalved crustaceans part of the subphylum Crustacea (Smith and Delorme, 2010). Ostracods are found mostly in aquatic (marine and nonmarine) environments although some (semi) terrestrial representatives also exist (Martens et al., 2008; Smith and Delorme, 2010). This section will focus on free-living ostracods present in nonmarine inland tropical and subtropical (both permanent and temporary) wetland ecosystems.

9.3.2 Systematics and general species richness

Class Ostracoda is subdivided into the two subclasses Myodocopa and Podocopa (Martens and Horne, 2009). Myodocopa consists of exclusively marine representatives (Martens and Horne, 2009) and will not be dealt with further here. Podocopa originated between 450 and 360 million years ago and consists of three superfamilies (Cytheroidea, Darwinuloidea, and Cypridoidea) (Martens et al., 2008) with both marine and nonmarine representatives. Of these, only Darwinuloidea are fully nonmarine and consist of 1 extant family (Darwinulidae) and 35 extant species. Cypridoidea and Cytheroidea include both marine and nonmarine representatives with the former being the most species rich (4 families and 1760 species) while the latter has the highest family diversity (11 families and 531 species) (Martens et al., 2008; Meisch et al., 2019). Cyprididae and Candonidae are the two largest known families of Ostracoda with a total of 1681 described species of which Candonidae represent 40.2% (Martens et al., 2008; Meisch et al., 2019).

The first nonmarine ostracods were named and described in 1776 (Müller, 1776) and since then approximately 2330 subjective species of extant nonmarine Ostracoda have been described worldwide (Meisch et al., 2019). The most recent checklist by Meisch et al. (2019) reported that of the eight biogeographical regions (Antarctic, Afrotropical, Australasian, Nearctic, Neotropical, Oriental, Palearctic, and Pacific Oceanic Island), the highest species richness is in the Palearctic region (799 species) and the lowest in the Antarctic (3 species). With the exception of Notodromadidae, most ostracod families are found in all biogeographical regions and are thus considered cosmopolitan. In contrast, at species level approximately 90% of all known nonmarine Ostracoda are endemic, with only 10% having intercontinental distributions (Martens et al., 2008). Approximately 20%–25% of the world's nonmarine ostracods are found in the ancient lakes of which Lake Baikal (Russia) and Tanganyika (East Africa) have the richest diversity and highest endemicity of species (Martens, 1994; Martens et al., 2008).

9.3.3 Distribution in tropical biogeographical regions

If the 17 extant families of nonmarine ostracods, Cyprididae is by far the most common family found in the tropical regions (i.e., Afrotropical, Australasia, Neotropic, and Oriental) (Meisch et al., 2019). Entocytheridae consists solely of parasitic and commensal species (Martens and Savatenalinton, 2011) and will not be dealt with further here. The number of known species in the tropics is considered grossly underestimated as far less research has been published in these regions compared to areas such as the Palearctic (Cohuo et al., 2017; Martens et al., 2008). While endemicity is high at species level, the Neotropic and Oriental regions have the lowest number of endemic genera (Martens et al., 2008). Seasonal and intermittent wetlands or pools that are abundant habitats in many of the tropical regions, often have a rich biodiversity of aquatic biota but remain neglected in research and are thus potential hotspots for ostracod diversity (see Halse and McRae, 2004; Martens et al., 2012; Halse and Martens, 2019) (Table 9.3).

The Afrotropics have the greatest species diversity of nonmarine tropical ostracods with approximately 450 described species of which 382 are endemic to the continent (Martens et al., 2008; Meisch et al., 2019). This may, however, be an underestimation as approximately 50% of the species known to occur in the Afrotropical region were described before 1940, and the taxonomic status has not truly been reviewed since (Martens 1984; Baltanás and Danielopol, 2013). Genetic endemicity of ostracods is particularly high in East African ancient lakes with Southwest African temporary pools following close behind (Martens, 1998). The best known ostracod

TABLE 9.3 Total number of species and their level of endemicity of extant nonmarine Ostracoda in tropical biogeographical regions.

	Neotropical		Afrotropical		Oriental		Australasian		Global
	Species	Endemic	Species	Endemic	Species	Endemic	Species	Endemic	Species
Cypridoidea									**1760**
[a]Cyprididae	171	139	321	296	154	132	109	102	1006
[a]Candonidae	42	38	53	53	17	14	38	38	675
Ilyocyprididae	2	0	1	1	8	4	3	2	41
Notodromadidae	3	3	12	10	15	12	5	4	38
Cytheroidea									**531**
Limnocytheridae	25	23	45	44	1	1	14	14	163
[b]Cytherideidae	10	8	19	18	0	0	3	2	95
[b]Leptocytheridae	0	0	0	0	0	0	1	1	23
[b]Cytheridae	13	13	0	0	0	0	0	0	15
[b]Loxoconchidae	0	0	0	0	0	0	0	0	10
[b]Xestoleberididae	2	1	0	0	0	0	0	0	5
[b]Cytheruridae	14	14	0	0	0	0	0	0	4
[b]Hemicytheridae	0	0	0	0	0	0	0	0	2
Kliellidae	0	0	0	0	0	0	0	0	2

Darwinuloidea									**35**
Darwinulidae	12	7	9	6	4	2	9	6	35
Terrestricytheroidea									**4**
[a]Terrestricytheridae	0	0	0	0	0	0	0	0	4
Total	***333***	***250***	***453***	***382***	***271***	***175***	***328***	***293***	***2330***

Number of species per region is adapted from Martens et al., 2008, with exclusion of Entocytheridae. Total number of species (global and per region) is adapted from Meisch et al. (2019) and includes Entocytheridae.

[a] *Indicates families including limno-terrestrial species.*

[b] *Indicates families consisting predominantly of marine genera with few nonmarine representatives.*

fauna from wetlands in the African region are from the Western Cape province in South Africa. This is largely due to the work by Sars (1924) who described 40 new species and 10 new genera along with the redescription of 30 species (Martens 2001). In southern Africa, the highest level of endemism is found in temporary wetland habitats, most likely due to the lack of many cosmopolitan species and large predators (Bird et al., 2019; Martens, 1994; Martens et al., 2008).

At present, 328 nonmarine ostracod species have been recorded in Australasia (encompassing Australia, New Zealand, New Guinea, and Melanesian islands) of which 293 are endemic (Meisch et al., 2019). The number of described species for this region has increased significantly with the addition of 180 species in the last half-century. This may still be an underestimation as most of these species were found in the Pilbara region, representing 6.5% of Australia (Karanovic, 2007; Martens and Savatenalinton, 2011; Baltanás and Danielopol, 2013), while much less research has occurred in the rest of Australasia. The athalassic saline aquatic habitats of Australia, including many lakes and wetlands, possess a remarkably high diversity of nonmarine Ostracoda as approximately 37 species have been described in these ecosystems (De Deckker, 1983), several of which are able to tolerate constantly changing salinity and thus well adapted to life in both fresh and saline ecosystems (Campbell, 1995; Martens et al., 2008). Australia is also one of the few locations outside of Africa where "giant" ostracods (>3 mm) occur, with two of the four genera (*Australocypris* sp. and *Mytilocypris* sp.) represented exclusively in wetlands with increased salt concentrations (De Deckker, 1983; Halse and McRae, 2004).

The Neotropics (including the Caribbean, Central, and South America) have approximately 333 recorded species of nonmarine Ostracoda of which 250 are considered endemic (Meisch et al., 2019). The lower species diversity in the Neotropics is primarily a result of fewer speciation-prone ecosystems such as the ancient lakes in Africa (Martens and Behen, 1994). Martens and Behen (1994) reported 260 ostracod species in South America alone of which 96 were from Brazil (Martens, 1998; Higuti et al., 2010) although this has increased to 108 species in recent years (Higuti et al., 2009; Higuti et al., 2010). Approximately 42% of the described species in this region are found in the Neotropic-Caribbean, a geographic region with high habitat heterogeneity including lakes, lagoons, sinkholes, temporary ponds, and wetlands (Cohuo et al., 2017). Further investigation in the region may yield an even greater diversity of ostracods as research is still fairly limited (Karanovic and Datry, 2009).

With approximately 271 species, the Oriental region (including India, Southeast Asia, and southern China) has the lowest number of described nonmarine Ostracoda species of the tropics (Meisch et al., 2019). Of these, 175 species are endemic, with Notodromadidae as the most diverse (nonmarine) family in this region (Martens et al., 2008). The majority of species described for this region arises from research in the 1960s to 1980s, predominantly from India and Southeast Asia. Hence most areas are still severely underrepresented (Karuthapandi et al., 2014; Savatenalinton and Suttajit, 2016). In the past decade, intensive sampling of various ecosystems in Thailand (including pools, lakes, swamps, reservoirs, springs, canals, rivers, rice-fields, and waterfalls) added a number of new species and genera to the list of nonmarine Ostracoda from the Oriental region (see Savatenalinton et al., 2008; Savatenalinton et al., 2008, 2009a, 2009b, 2010, 2013; Savatenalinton, 2014, 2015). Of the five genera considered endemic to the Orient, namely *Batucypretta*, *Indiacypris*, *Indocandona*, *Astenocypris*, and *Pseudocypretta*, the latter two were part of the abovementioned research effort. This is indicative of the need of comprehensive research in this understudied region as many species may still be undiscovered (Savatenalinton and Suttajit, 2016).

9.3.4 Ecology

Whether saline or fresh, ostracods are found in most aquatic habitats ranging from small temporary or permanent pools to larger lakes, streams, and oceans as some species are able to tolerate salinities of up to three times that of seawater (Martens et al., 2008; Smith and Delorme, 2010; Martens, 2001). The ecology of ostracods is affected by a complex interaction of many environmental variables including but not limited to water chemistry, thermal regime, hydrogeology, soil structure, and food availability (Forester, 1991; Smith and Delorme, 2010; Mesquita-Joanes et al., 2012; Williams, 2016).

Most ostracods are free-living, benthic organisms and can be divided into swimming and nonswimming (or true benthic) forms. Swimming capacity is mainly determined by the presence of long, often plumose, setae on the antennulae and antennae (Martens and Horne, 2009; Smith and Delorme, 2010). Swimming forms occur most often between aquatic plants, using the macrophytes as shelter from predators, although some species will swim into the pelagic as well. In contrast, nonswimmers have strong, stout appendages and a more strongly developed carapace for protection from predation, and will crawl and/or burrow into the upper 2 cm of sediments (Martens and Horne, 2009; Smith and Delorme, 2010; Mesquita-Joanes et al., 2012; Li et al., 2010).

Although not considered a "keystone" group, ostracods nonetheless comprise an essential part of the animal biomass and productivity in most freshwater ecosystems (both permanent and temporary) (Mesquita-Joanes et al., 2012). Ostracods are preyed upon by numerous aquatic insects and invertebrates including larvae of Chironomidae, Tanypodinae, and Odonata as well as snails, water mites, other microcrustaceans such as copepods (Smith and Delorme, 2010; Vandekerkhove et al., 2012; Mesquita-Joanes et al., 2012) and vertebrates including amphibians, waterfowl, and fish (Lopez et al., 2002; Blanco et al., 2004; Smith and Delorme, 2010).

In most aquatic habitats, adult ostracods have a body size typically ranging from 0.3 to 2.0 mm. However, most will not grow larger than 1 mm in the presence of visual predators such as fish, dragonfly larvae, and predatory diving beetles (Martens and Horne, 2009). This relatively small size is an adaptation to avoid predation in larger, permanent habitats while also reducing resource demands and the probability of extinction in smaller, temporary systems (Valentine, 2009; Mesquita-Joanes et al., 2012). In "predator-free" (fishless) habitats, for example temporary ecosystems, gigantism has been recorded in Cyprididae in Australian lakes (Halse and McRae, 2004) and Indian and African temporary pools. Indeed, species as large as 8 mm have been recorded in temporary pools of South Africa (Martens, 2003; Martens and Horne, 2009).

Variations also exist in ostracod shape, color, and valve surface (Martens and Horne, 2009; Smith and Delorme, 2010; Ramos et al., 2017). Shapes may range from spherical, elongated, or compressed while epidermal pigmentation results in numerous color variations (Martens and Horne, 2009; Mesquita-Joanes et al., 2012). Little is known about the function of color variation although it has been suggested that it may offer some form of protection against visual predators and UV radiation (Mesquita-Joanes et al., 2012). On the surface, valves may be smooth or have various muscle scars and ornamentations (Martens and Horne, 2009; Smith and Delorme, 2010; Ramos et al., 2017). Variations occur as a result of differences in growth, environment, genetics, and sexual dimorphism (Van Harten, 1975; Yin et al., 1999; Danielopol et al., 2008; De Deckker and Martens, 2013; Ruiz et al., 2013) and are useful tools that aid in identification of species, but may also serve specific functions (Martens and Horne, 2009; Smith and Delorme, 2010; Karanovic, 2012; Halse and Martens, 2019). In some juvenile stages, ornamentation may be more pronounced than in the adult stage and act as potential deterrents toward (micro-) predators (De Deckker and Martens, 2013) while some adult stages, such as in *Sclerocypris jenkinae*, have large lateral spines that act as antipredator defences against fish (Van der Meeren et al., 2019). The composition of water may also affect ornamentation as nonmarine ostracods found in humic acid-rich water often have much more delicate ornamentation than their marine counterparts (Carbonel, 1988; Holmes, 2001; De Deckker and Martens, 2013). Stronger calcification and ornament reticulation are also evident in ostracods from slightly saline water (Ramos et al., 2017) or water with higher carbonate ion concentrations (Carbonel and Hoibian, 1988; Carbonel et al., 1990).

9.3.5 Life history

Nonmarine ostracods predominantly utilize asexual reproduction (parthenogenesis) such as in Darwinulidae considered an ancient asexual group as only females have been found for approximately 200 million years (Martens and Horne, 2009). However, some genera may reproduce sexually or use a mixed strategy depending on the habitat and/or geographic location (Martens et al., 2008; Martens and Horne, 2009; Mesquita-Joanes et al., 2012). In a phenomenon known as geographic parthenogenesis, individuals of *Eucypris virens* (Cypridoidea) reproduce asexually in temporary pools in Europe and sexually in circum-Mediterranean populations (Martens and Horne, 2009). Reproduction may also be affected by habitat type as parthenogenesis is more common in unstable habitats, for example temporary ecosystems, while sexual reproduction prevails in established or stable environments such as permanent and ancient lakes (Bell, 1982; Smith and Delorme, 2010; Mesquita-Joanes et al., 2012).

The life cycle of nonmarine ostracods generally consists of nine instars of which eight are juvenile and one adult (Benson, 1981, p 63; Martens and Horne, 2009; Mesquita-Joanes et al., 2012). Lifespan and number of generations vary greatly and depend on species as well as environmental factors and ecosystem type (i.e., permanent or temporary). Genera living in the variable environment of temporary ecosystems live between one to five months and produce only one or two generations before the pond dries. In contrast, genera from more stable permanent habitats, may live as long as four years and produce several generations (Martens and Horne, 2009; Smith and Delorme, 2010; Mesquita-Joanes et al., 2012). In both temporary and permanent habitats, egg hatching and juvenile development occur predominantly in spring and summer with little to no development in autumn and winter, while adults may be present until early winter (Martens and Horne, 2009; Smith and Delorme, 2010). Abiotic variables also affect the lifespan of ostracods. Whereas warm temperatures cause accelerated growth and development, and thus decreased lifespan, low pH, Ca, and bicarbonate (HCO_3) can slow growth and development by reducing shell calcification and molting capabilities (Higuti et al., 2010; De Deckker and Martens, 2013).

Most nonmarine ostracods in both permanent and temporary ecosystems are able to produce dormant propagules or enter a stage of dormancy (Horne and Martens, 1998; Brendonck et al., 2017). Adults and juveniles may enter a state of torpidity (Darwinulidae and some Cytheroidea) or produce desiccation-resistant resting stages, predominantly in the form of eggs (most Cytheroidea and all Cypridoidea), to avoid or tolerate adverse environmental conditions including drought or hypersalinity (Horne and Martens, 1998; Smith and Delorme, 2010; Mesquita-Joanes et al., 2012). These "resting stages" are able to persist for several months to years depending on surrounding conditions and the species involved (Hairston et al., 1995; Horne et al., 2004; Bird et al., 2019). *Cyprideis torosa* is able to survive for at least 30 days in a state of torpor under hypersaline conditions while desiccation-resistant eggs of Cypridoidea remain viable for up to 100 years (Martens, 1994). These resting stages also facilitate passive dispersal between habitats

(Meisch, 2000; Martens, 1994; Mesquita-Joanes et al., 2012) which may occur through wind, or by hitchhiking with mobile animals such as several invertebrates, amphibians, reptiles, and birds, or in mud carried by mammals and even humans (Vanschoenwinkel et al., 2008a,b, 2011; Mesquita-Joanes et al., 2012; Bird et al., 2019).

9.3.6 Feeding biology

In nonmarine environments, ostracods are most often considered as generalist deposit feeders, scavengers, or omnivores with a diet consisting largely of algae, detritus, and dead or living plant material (Martens and Horne, 2009; Smith and Delorme, 2010; Karanovic, 2012). As ethological studies on aspects of ostracod feeding activity are scarce (Mesquita-Joanes et al., 2012), this conclusion on feeding mode is based predominantly on the analysis of stomach contents and functional morphology (Cannon, 1933; Vannier et al., 1998; Lawrence et al., 2002). Several studies have, however, revealed that some ostracods may be active predators on not only plant material but animals as well (Mesquita-Joanes et al., 2012). Ostracods have been observed attacking and eating smaller ostracods as well as other zooplankton, insects, and snails (Sohn and Kornicker, 1972; De Deckker, 1983; Campbell, 1995; Meisch, 2000) and vertebrates such as fish (Stepien and Brusca, 1985). Ostracods appear to make use of chemoreception to detect both prey and predators and either move toward or away from them accordingly (Vannier et al., 1998; Mesquita-Joanes et al., 2012).

9.3.7 Threats and conservation

Although some ostracods are cosmopolitan in their distribution and/or tolerant to a wide range of environmental variables (Pieri et al., 2009; Meisch et al., 2019), others are highly endemic and sensitive to changes in water quality and anthropogenic inputs (Chial et al., 2003; Külköylüoğlu, 2004; Shuhaimi-Othman et al., 2011; Ruiz et al., 2013). Research has illustrated that the diversity and abundance of ostracods is far greater in ecosystems unaffected by human activities (Kiss, 2007; Stark et al., 2003; Külköylüoğlu, 2004). The persistence of ostracod populations is threatened by anthropogenic influences, environmental disturbance, habitat destruction, and changes in both water quality and quantity (Reeves et al., 2007; Ruiz et al., 2013).

Ostracods are unable to actively migrate to a new habitat if it becomes unsuitable as they rely on passive modes of dispersal to colonize new ecosystems (Vanschoenwinkel et al., 2008a,b; Brochet et al., 2010; Waterkeyn et al., 2010; Higuti et al., 2017). Alterations to their environment could, therefore, lead to premature death and other long-term effects and eventually even extinction, either locally or globally. One such example is the introduction of fish into Lake Naivasha, Kenya, which led to the complete disappearance of large ostracod species (Van der Meeren et al., 2019).

Ostracods also have an extensive fossil record as their valves readily fossilize (Park and Martens, 2001; Poquet et al., 2008) making them useful short and long-term bioindicators of, among other things, climate change, habitat loss, and water degradation.

The use of pesticides (e.g., DDT) and herbicides (e.g., dioxin) threatens ostracod populations as these pollutants accumulate in soft tissue and lead to intoxication, immobilization, or even mortality (Matsumura, 1977; Ruiz et al., 2013). Industrial pollution such as by various heavy metals has been found to be even more harmful to ostracod populations than pesticides (Samir, 2000). These harmful effects may have bottom-up cascading effects in the food web through bioaccumulation and biomagnification of these pollutants in biota that feed on ostracods. Climate change and its associated predicted effects on water quality, including increasing temperatures and changes in severe weather conditions such as drought (Woodward et al., 2012), may also affect performance and even persistence of ostracod populations since water temperature and salinity play a significant role in their survival, growth, and reproduction (Mesquita-Joanes et al., 2012; Ruiz et al., 2013). Habitat destruction, often destroying the macrophyte stands, also affects the survival of various biota (Malmqvist et al., 1997), including ostracods, since aquatic macrophytes are important substrates utilized by ostracods for egg deposition and shelter from visual predators (Martens and Horne, 2009; Mormul et al., 2010). Floating vegetation also acts as a source of passive dispersal (Higuti et al., 2017) and the loss of habitat complexity or total habitat destruction could therefore lead to local extinction of ostracod populations.

9.4 Copepods

9.4.1 Introduction

The Copepoda is one of the most species rich groups of metazoans on Earth (Humes, 1994; Brotskaya, 1963; Kikuchi, 1994). Copepods are capable of invading and surviving successfully in nearly every continental habitat and situation where sufficient moisture and organic matter are present (Reid, 2001). Although both parasitic and free-living copepods exist, this section only deals with the planktonic hence free-living component of the group. Free-living copepods typically range from 0.2 to 5.0 mm.

9.4.2 Systematics and general species richness

The phylogenetic position within Arthropoda and the relationships of the major evolutionary lineages within Copepoda is debatable (Khodami et al., 2017). Huys and Boxshall (1991) listed 10 orders of Copepoda based on homologies in the body plan, segmentation, and setation of copepod appendages. The resulting phylogeny divides Copepoda into three infraclasses: Progymnoplea Lang, 1948 (=Platycopioida Fosshagen, 1985); Gymnoplea Giesbrecht, 1892 (=Calanoida Sars, 1903); and Podoplea Giesbrecht, 1892. The Podoplea was divided into two main clades, the so-called "MHPSM-clade" containing Mormonilloida Boxshall, 1979; Harpacticoida Sars, 1903; Poecilostomatoida Thorell, 1859; Siphonostomatoida Burmeister, 1834; Monstrilloida Sars, 1901; and the "MCG-clade" including the Misophrioida Gurney, 1933; Cyclopoida Burmeister, 1835; and Gelyelloida Huys, 1988. Recent work based on morphological characteristics has revised the Huys and Boxshall (1991) phylogenetic concept. Martınez (2000) first revealed the paraphyletic status of Cyclopoida and Cyclopinidae Sars, 1913. He rejected the ordinal status of Poecilostomatoida and included all of its families in Cyclopoida. The Polyarthra Lang, 1948, order was considered a separate order with an uncertain phylogenetic position (Dahms, 2004) while Ho et al. (2003) proposed an ordinal level for the family Thaumatopsyllidae Sars, 1913. A molecular phylogenetic relationship among representatives of 10 copepod orders revised their taxonomy (Khodami et al., 2017). It demonstrated for the first time the monophyly of Copepoda (including Platycopioida Fosshagen, 1985) and rejected the polyphyletic Maxillopoda as a taxonomic unit. The molecular phylogenetic study supported the monophyly of the major subgroups of Copepoda (Fig. 9.2).

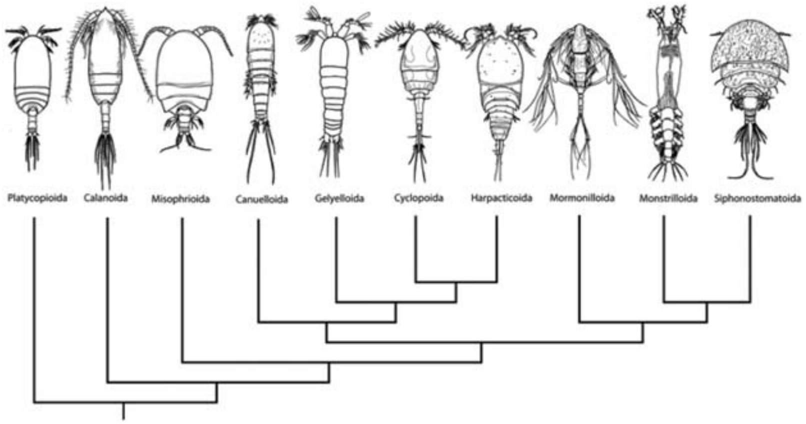

FIGURE 9.2 Most recent phylogram of copepod orders. *Adapted from Khodami, S., Mcarthur, J.V., Blanco-Bercial, L., Martinez Arbizu, P., 2017. Molecular phylogeny and revision of copepod orders (Crustacea: Copepoda). Scientific Reports 7, 9164.*

9.4.3 Comparison between tropical biogeographical regions

In Table 9.4, numbers of copepod genera and species for the considered biogeographical regions are presented. The Neotropical region has the highest copepod richness, with 561 recorded species. The major contributors are the Cyclopidae (31%), especially *Eucyclops*, *Metacyclops*, and *Mesocyclops*, the Canthocamptidae (19%), especially *Elaphoidella*, *Attheyella* (*Chappuisiella*), and *A.* (*Delachauxiella*), the Diaptomidae (15%), and Parastenocarididae (12%) (Boxshall and Defaye, 2008). The most speciose genera within the Diaptomidae are *Notodiaptomus* and *Argyrodiaptomus* which are both endemic to the region. The Afrotropical region has the second highest richness with 405 species. The major contributors are the Cyclopidae (41%), especially *Eucyclops* and *Thermocyclops*, and the Diaptomidae (18%), especially *Tropodiaptomus*, followed by the Lernaeidae (10%) (Boxshall and Defaye, 2008). The benthic families Canthocamptidae, particularly *Elaphoidella* and *Echinocamptus*, and Parastenocarididae contribute only 11% and 8% to the total, respectively. The diversity of the Oriental region is relatively low, with only 16 families represented by 381 species. The major contributors are the Cyclopidae (30%), especially *Mesocyclops* and *Thermocyclops*, the Diaptomidae (24%), especially *Tropodiaptomus* and *Heliodiaptomus*, the Canthocamptidae (15%), especially *Elaphoidella*, and the Lernaeidae (12%). The Oriental region is home to seven genera of Lernaeidae, three of which (*Indopeniculus*, *Pillainus*, and *Indolernaea*) are endemic (Boxshall and Defaye, 2008). The Australasian region has the lowest richness with 205 species. The major contributors to the overall species richness are the Cyclopidae (31%), especially *Mesocyclops* and *Eucyclops*, the Canthocamptidae (25%) especially *Canthocamptus*, and the Centropagidae (23%). The paucity of copepod species in the Australasian region is largely due to the aridity of large areas of the Australian continent. However, recent research into the subterranean fauna of arid Western Australia has revealed an unexpectedly high diversity and degree of endemism (Karanovic, 2004). The level of endemism in freshwater copepods is very high in the tropical region: Neotropical (89%), Afrotropical (85%), Australasian (82%), and Oriental (73%). Ancient lakes constitute prime hotspots for freshwater biodiversity. For copepods, Lake Baikal has over 120 species, the majority of which are endemic (Boxshall and Evstigneeva, 1994), and Lake Tanganyika with 69 species, of which 34 (49%) are endemic (Boxshall and Strong, 2006) (Table 9.4).

9.4.4 Ecology

Copepods are extremely abundant in freshwaters and comprise a major component of most planktonic, benthic, and groundwater communities. They occupy a variety of habitats including open water impoundments, a wide

TABLE 9.4 The number of genera and species level per copepod family, per tropical region based on Boxshall and Defaye (2008).

	Neotropical		Afrotropical		Oriental		Australasian		Endemics	Global
	Genera	Species	Genera	Species	Genera	Species	Genera	Species	Species	Species
Calanoida										**520**
Diaptomidae	18	82	7	72	22	92	2	2	231	441
Centropagidae	3	22			2	4	7	47	60	79
Harpacticoida										**1121**
Canthocamptidae	12	109	6	46	9	58	8	51	242	627
Parastenocarididae	6	65	1	34	1	16	1	2	122	249
Ameiridae	4	17	3	9	3	10	6	15	33	149
Miraciidae (Diosaccidae)	1	6	1	13	2	3	1	8	23	53
Ectinosomatidae					1	1			1	13
Phyllognathopodidae	2	3	1	3	2	3	1	3	6	10
Harpacticidae					1	1			0	4
Huntemanniidae	1	1	1	1	1				2	6
Laophontidae	2	1	2	2	2	2	3	3	1	7
Cletodidae					1	3			2	3
Cyclopoida										**1096**

Cyclopidae	30	174	25	167	19	115	19	64	364	800
Oithonidae	2	6			1	2			5	7
Ozmanidae	1	2							2	2
Lernaeidae	6	10	7	39	7	47	1	2	90	114
Ergasilidae	16	63	6	19	5	23	3	8	107	173
Total	***104***	***561***	***60***	***405***	***79***	***380***	***52***	***205***	***1291***	***2737***

range of temporary water bodies, vleis, and floodplain wetlands (Silva, 2008; Waterkeyn et al., 2008; Dube et al., 2017; Nhiwatiwa et al., 2017). Physical habitat factors (e.g., surface area) and water quality (e.g., conductivity and vegetation cover) have been demonstrated as the main factors structuring copepod species composition (Frisch et al., 2006). Ecologically, copepods play a role as a direct and efficient path for the transfer of energy to higher level consumers, which is pivotal to the functioning of tropical wetlands (Park and Marshall, 2000). Furthermore, accurate estimates of copepod abundance are fundamental for proper determination of biomass and productivity, which are crucial for the understanding of energy flow and the trophodynamics of tropical wetlands (Magalhães et al., 2015). Some copepods are predatory and have even been identified as key predators of mosquito larvae (Marten and Reid, 2007) and therefore have potential for natural biocontrol of disease vector mosquitoes (Cuthbert et al., 2018; Buxton et al., 2020).

9.4.5 Life history

Copepods are sexually dimorphic in size, with typically larger females than males. Parthenogenesis occurs when males are rare and has been demonstrated in some harpacticoid species such as *Elaphoidela bidens*, *Epactophanes richardi*, and *Canthocamptus staphylirmus* (Dole-Olivier et al., 2000). Dormancy is known exclusively from free-living taxa of the Harpacticoida, Cyclopoida, and Calanoida. Dormant instars may comprise resting eggs, naupliar stages arrested in their development, and free swimming or encysted copepodids and adults (Dahms, 1995). All cyclopoid taxa with a dormancy strategy belong to the Eucyclopinae (Cyclopidae). The three cyclopoid genera with encysting copepodids are *Cyclops*, *Microcyclops*, and *Metacyclops*. There are 16 species of freshwater Calanoida where there is proof for resting eggs (Dahms, 1995). They belong to the genera *Diaptomus*, *Onychodiaptomus*, *Leptodiaptomus*, *Aglaodiaptomus*, *Acanthodiaptomus*, *Scotodiaptomus*, *Eurytemora*, *Epischura*, *and Limnocalanus*. Both abiotic (e.g., desiccation, temperature, oxygen availability) and biotic (e.g., food availability, predation) environmental factors can trigger the onset of diapause (Spindler, 1971; Hairston, 1987; Hairston and Brunt, 1994; Johnson, 1979). Copepods inhabiting temporary water bodies produce resting eggs or dormant copepodid stages which allow survival of adverse conditions (Hairston and Brunt, 1994). Juvenile stages of copepods are the earliest zooplankters recolonizing temporary waters after the dry phase (Frisch et al., 2005; Badosa et al., 2010). They furthermore have short developmental times and a quick hatching response after dormancy (Brendonck and De Meester, 2003).

9.4.6 Feeding biology

Freshwater copepods occupy different trophic levels in the food web. Most freshwater copepods are free-living, but they have adopted parasitism in numerous independent lineages. About 330 species of freshwater copepods are parasitic, most commonly on fish hosts (e.g., *Lernaea cyprinacea*) (Barson et al., 2008; Fryer, 1968), but also on molluscs (Boxshall and Jaume, 2000; Boxshall and Strong, 2006). Copepods also live as commensal epibionts on freshwater invertebrates including crayfish, medusae, and sponges (Boxshall and Strong, 2006). Some calanoids are herbivores feeding on phytoplankton. Several large copepods are predatory eating rotifers, oligochaetes, dipteran larvae, and small crustaceans such as cladocerans (Fryer, 1993; Wasserman et al., 2015). The main food source for harpacticoids consists of particulate organic matter. Predatory behavior has been observed in some species such as *Heterocypros incongruenns* (Ottonello and Romano, 2011).

9.4.7 Threats and conservation

Freshwater copepods have not attracted much concern from the general conservationist community. The factors threatening copepods are common in tropical regions and include: salinization, draining of wetlands or conversion of temporary to permanent water bodies, mining, pollution, and damming of rivers (Reid et al., 2002; Dalu et al., 2017). For example, salinization of inland waters is a major factor in the disappearance of habitat for Australian freshwater crustaceans, especially in Western Australia (Yencken and Wilkinson, 2000). Draining of swamps may threaten certain species such as the vulnerable calanoids *Boeckella nyoraensis* and *Boeckella propinqua*, for which this type of habitat is important. Many of the wetlands in the Afrotropical region have been drained for agriculture and polluted by mining, industry, and informal settlements (Rayner and Heeg, 1994). Another major threat is the conversion of temporary into permanent wetlands, which is often even aggravated by the introduction of fish. Such drastic hydrological change does not only have a dramatic impact on specialist groups of temporary wetlands such as large branchiopods (Brendonck et al., 2022a,b), but also on specialized zooplankton, including some copepods (Dalu et al., 2017).

9.5 Rotifers

9.5.1 Introduction

Rotifers are acoelomate metazoan animals that are microscopic, ranging between 50 and 2000 μm in size, and are widely distributed in freshwater ecosystems (Fernando, 2002; Segers, 2008). Many rotifers have a transparent body, consisting of two specific organs: the rotatory organ (i.e., corona) and a mastax, which is the pharynx (Brain, 2002; Fernando, 2002). The two main freshwater Rotifera classes are Bdelloidea and Monogononta, with the latter being widely distributed in tropical ecosystems. In general, many rotifer species are benthic, living on the substratum and among submerged vegetation. Wetland habitats are favored by many of the Bdelloidea, as there they can shift from the active to the anhydrobiotic stage (i.e., cryptobiosis), enabling them to live in temporary wetland environments (Brain, 2002).

9.5.2 Systematics and general species richness

Reliable information on rotifer species numbers is sparse, but Segers (2008) estimates that there are about 2031 taxa, with many unidentified species. In turn, known distributions reflect more the biased prevalence of rotiferologists in Western Europe where most studies have been conducted rather than the real distribution of rotifers. Little is known about rotifer phylogeny, due to a lack of modern comprehensive studies (Mills et al., 2017), coupled with the lack of a robust fossil record. Recent decades of research have led to the hypothesis that subtropical floodplains are among the world's richest habitats for rotifers (Segers et al., 1993; Segers, 2008). There are several relatively complete surveys of rotifer taxa from different regions of the tropics (e.g., Africa, Amazonia, Australia, Central America and the Caribbean, Neotropics, and the Oriental regions) which are provided in detail by Segers (1996, 2001, 2003, 2007, 2008) and Fernando (2002).

Analysis of planktonic and littoral rotifer fauna from different tropical regions has shown endemism at the species level, however, with most being cosmopolitan. The most diverse rotifer group are the Notommatidae, with Cephalodella, monogeneric Lecanidae, and Dicranophoridae being the most speciose. All of these groups contain almost exclusively benthic-littoral or psammon-inhabiting species, with a majority inhabiting oligotrophic to mesotrophic, slightly acidic and soft waters (Segers, 1993; Kutikova and Fernando, 1995). Dumont and Segers (1996) calculated that a nonpolluted lake with developed, weedy littoral would harbor approximately 150 species in temperate, and up to 250 species in tropical regions.

Littoral-periphytic taxon richness of Lecanidae, Lepadellidae, Testudinellidae, and Trichocercidae reflect more the littoral-periphytic assemblages, while Brachionidae and especially *Brachionus* spp. and *Keratella* spp. usually attain a higher abundance and richness in limnetic fish pond environments. Recently, Luo and Segers (2020) reported that the Lepadellidae rotifers collected in the Congo Basin contained eight hitherto unknown species (i.e., *Colurella asymmetrica*, *Lepadella hanneloreae*, *L. jingruae*, *L. weijiai*, *L. wilungulai*, *L. yangambi*, *Squatinella curviseta*, *S. longipila*) among the 33 Lepadellidae taxa. This remarkable result illustrates previously unknown and largely endemic Congo Basin microfauna and refutes the "African anomaly" hypothesis on the purported African rotifer fauna poverty. In another study by Serafim et al. (2003) in the Pantanal Upper Paraná River Floodplain Wetland, 11 genera and 42 species including new rotifer records were observed. The study showed an increase in rotifer diversity in this particular ecosystem from 184 to 230 species. Thus, 37 species occurred in the littoral floodplain zones and 34 species in the pelagic floodplain zones. The lagoons had the highest richness due to greater stability, low current velocity, and extensive aquatic macrophyte cover in the littoral zones (Serafim et al., 2003).

Green (2003) showed that euplankters dominated in static waters, and also when the flow was very slow in the Okavango Delta. Where water flow was visibly stronger, euplankters were very sparse, and periphytic species dominated such as *Lecane bulla*. A study by Koste and Robertson (1983) in Brazil during the dry season, recorded 33 species and the number of species increased to 138 during the wet season. The sparse, diverse, wet season community may merely reflect rotifer species most easily dislodged during sampling. Thus in stagnant waters, periphytic species may remain among the macrophytes due to their inability to compete with euplankters in open water, or they may be vulnerable to predation by large euplankters such as *Asplanchna* spp. and copepods. Furthermore, the macrophyte diversity and varied architecture of wetlands provide a large number of physical niches, which are preferred by certain rotifers. For example, *Euchlanis dilatata* survives better on *Myriophyllum* spp. than on *Elodea* spp. and/or *Ceratophyllum* spp. when exposed to predation (Green, 2003). Serafim et al. (2003) observed that there were no great differences in rotifer species richness between habitats of the Paraná River Floodplain Wetland environments, with high species richness being observed in the littoral habitats due to the greater influence of shoreline vegetation, which allows for greater habitat diversification. The high rotifer diversity observed in the lagoons compared to river sites was related to some characteristics of these environments such as low stream velocity (Serafim et al., 2003). The Okavango Delta moving waters contained low abundances, but high species diversities of euplankters as compared to samples from stagnant waters (Green, 2003). When euplankters are washed away by water movement, some of the periphytic species are free to leave the macrophytes and free-floating algae and bacteria. Another key factor influencing species richness is the food variety and availability. For example, the complexity of epiphytic algae results in herbivorous rotifers developing foraging patterns which parallel their food distributions.

9.5.3 Comparison between tropical biogeographical regions

In Table 9.5, numbers of rotifer genera and species for the considered biogeographical regions are presented. Despite some increasing knowledge on diversity in the last few years, the fauna of tropical Asia, especially the Indian subcontinent, and Afrotropical regions warrant further study as there has been sampling bias. Studies in south-eastern Asia by Segers (2001), Athibai et al. (2013), and Sa-ardrit et al. (2017) have shed light on

TABLE 9.5 The number of genera and species level per rotifer family, per region based on Segers (2008).

	Afrotropical		Australasian		Oriental		Neotropical		Endemics	Cosmopolitan	Global
	Genera	Species	Genera	Species	Genera	Species	Genera	Species	Species	Species	Species
Monogononta											**1496**
Asplanchnidae	2	9	2	9	3	12	3	10	2	8	15
Atrochidae	1	1	2	2	3	3	1	1	0	1	4
Brachionidae	7	51	6	58	7	57	7	71	94	36	169
Collothecidae	1	14	2	12	2	8	2	15	24	10	47
Conochilidae	1	5	2	6	1	5	1	5	1	5	7
Dicranophoridae	5	19	8	24	5	15	6	21	98	9	181
Epiphanidae	4	9	5	8	5	9	3	10	4	9	16
Euchlanidae	4	15	4	18	5	15	4	14	8	11	27
Flosculariidae	6	22	7	30	6	23	7	37	7	19	50
Gastropodidae	2	8	2	7	2	6	2	8	2	6	12
Hexarthridae	1	8	1	6	1	4	1	7	7	4	18
Ituridae	1	2	1	5	1	3	1	4	0	2	6
Lecanidae	1	82	1	61	1	99	1	94	81	49	200
Lepadellidae	3	62	3	55	4	59	4	70	89	37	168
Lindiidae	1	2	1	7	1	3	1	4	4	3	13

Microcodidae	1	1	1	1	1	1	1	1	0	1	1
Mytilinidae	2	12	2	12	2	12	2	14	13	8	29
Notommatidae	9	29	11	72	9	48	10	70	149	45	277
Proalidae	3	10	3	14	2	7	3	7	20	6	47
Scaridiidae	1	4	1	3	1	4	1	4	3	2	7
Synchaetidae	3	13	3	17	3	15	3	18	16	12	45
Testudinellidae	2	18	2	17	3	15	2	19	19	9	40
Tetrasiphonidae	1	1	1	1	1	1	1	1	0	1	1
Trichocercidae	2	39	3	43	3	41	2	45	13	34	70
Trichotriidae	3	12	3	10	3	11	3	15	10	9	23
Trochosphaeridae	3	13	3	13	3	10	3	1	5	9	19
Bdelloidea											**460**
Adinetidae	1	7	1	12	1	5	1	6	7	5	20
Habrotrochidae	3	45	3	53	1	18	2	37	75	14	152
Philodinavidae	1	1	2	2	1	2	2	2	3	0	6
Philodinidae	10	85	10	109	6	33	9	71	152	41	282
Total	***85***	***591***	***96***	***6877***	***87***	***544***	***91***	***682***	***900***	***405***	***1956***

the diversity of rotifers, and Luo and Segers (2013, 2020) did the same for the Afrotropics. The latter studies described nine new rotifer species within the genera *Colurella*, *Lepadella*, and *Squatinella*, which refuted the African anomaly hypothesis on the purported rotifer species poverty. Within the Australia region, the number of known rotifer species was more than doubled to close to 500 species in the early 1980s by the research efforts of Russell J. Shiel. In the neotropical realm, as exemplified by the Amazon basin, several endemics in the *Brachionus*, *Anuraeopsis*, *Lecane*, and *Lepadella* genera have been characterized (see Serafim et al., 2003; Segers, 2007, 2008). Given the lack of rotifer studies within tropical wetlands, the rotifer diversity in this section is described in general, highlighting the diversity that exists within freshwater ecosystems across different tropical regions.

9.5.4 Ecology

Analysis of rotifer distribution and diversity is seriously hampered by lack of knowledge on the taxonomy and chorology of this group (Luo and Segers, 2020). However, ecological research on rotifers from interstitial waters has been neglected to date. Rotifers living in interstitial water within *Sphagnum* mats and *Sarracenia purpurea* pitchers are capable of regenerating large amounts of nitrogen and phosphorus, that is, ~3%–10% in Europe and 5%–7% in North America, and can be a major source of inorganic phosphorus (Błędzki et al., 2018). Thus a world estimate of rotifer nutrient regeneration is approximately 0.12 and 0.17 million tons of N and P, respectively, to wetlands every year (Błędzki et al., 2018). For example, *Habrotrocha rosa* can live between wet *Sphagnum* litter and is the most frequent rotifer species in wetland peatlands, responsible for about 40%–50% of N and P regeneration by rotifers. Rotifers provide food to many other aquatic animals, that is, adults and eggs may be parasitized by fungi, while some rotifers are symbiotic with, or parasitic on, other organisms. Some rotifers are endoparasitic mainly on invertebrates (e.g., algae, annelids, bacteria, brachiopods, bryozoans, crustaceans, protists, other rotifers) (Segers, 2007). Rotifer diversity is mainly explained by fluctuations in hydrological level (Bonecker and Lansac-Tôha, 1996).

9.5.5 Life history

The Monogononta and Bdelloidea have one and two gonads, respectively, and both reproduce parthenogenetically. In Monogononta, parthenogenetic reproduction periods are interspersed with sexual phases (i.e., heterogony), but in Bdelloidea reproduction is by diploid, mitotic parthenogenesis only, making them unique and the most diverse group of metazoans (Segers, 2008). The Monogononta propagules consist of single, hard-shelled, and durable encapsulated cysts, while those of Bdelloidea consist of anhydrobiotic individuals (Segers, 2008). The propagules produced are small and drought-resistant, making rotifers perfectly adapted to aerial, passive, and/or phoretic dispersal. The high dispersal capacity and their parthenogenetic reproduction enable them to establish or renew a population starting off from a single resting stage, and to reach viable population sizes relatively quickly, making them superb (re)colonizers (Brain, 2002; Segers, 2008). For these reasons, many rotifer species are cosmopolitan.

9.5.6 Feeding biology

In tropical freshwater food webs, rotifers are of particular importance, forming a key link between primary producers (i.e., phytoplankton, bacteria, detritus) and consumers (i.e., carnivorous zooplankton, fish). Nearly all planktonic rotifers are herbivores, feeding on phytoplankton and ingesting cells roughly 4–17 μm in size (see Fig. 9.3). Besides being heterotrophic, planktonic rotifers also consume organic detritus and bacteria. Obertegger et al. (2011) classified rotifers into two functional feeding guilds based on the feeding strategy they employed across genera: (1) *raptorial rotifers*

FIGURE 9.3 *Keratella* sp. identified from a temporary wetland (Malilangwe Reserve, Zimbabwe) feeding on a centric diatom. *Photo by Tatenda Dalu.*

(genera, e.g., *Ascomorpha*, *Asplanchna*, *Collotheca*, *Gastropus*, *Ploesoma*, *Polyarthra*, *Synchaeta*, *Trichocerca*), that exhibit active grasping, piercing, and/or pumping action to catch single food items and generally consist of cardate, forcipate, incudate, uncinate, and/or virgate trophi; and (2) *microphagous rotifers* (genera, e.g., *Brachionus*, *Conochilus*, *Euchlanis*, *Filinia*, *Floscularia*, *Kellicottia*, *Keratella*, *Lecane*, *Notholca*, *Testudinella*, *Trichotria*), that collect multiple food items and consist of malleate, malleoramate, and/or ramate trophi.

9.5.7 Threats and conservation

Human introduction coupled with inadequate taxonomic expertise/studies in tropical regions precludes accurate biogeographical classifications of zooplankton. This is also the case for rotifers where most taxa are currently classified as cosmopolitan when in effect that might not be the case and some can be considered as cryptogenic species. Rotifers in general are not considered endangered or threatened in any way. As mainly planktonic animals, rotifers are an important food source for many aquatic animals, including some economically important to humans. Indeed, particular environments such as wetlands deserve more intensive sampling across different seasons to uncover more detail about their peculiar microfauna. Due to the large dispersal and colonization capacities of many rotifer species, they are easily transported to new habitats by humans (Segers, 2008). For example, rotifers have been and continue to be introduced to regions where they did not naturally occur before. This phenomenon may have been going on for a long time and is thought to be responsible for isolated records of regionally common species outside their natural range. The same reasons explain why rotifers have hardly been used in biodiversity assessments and conservation, notwithstanding their economic relevance in aquaculture (Segers, 2008). Rotifers are mostly threatened by water quality changes due to anthropogenic influences.

9.6 General conclusions and conservation management

It is too early to draw far going conclusions on general patterns in richness and endemicity across tropical regions and wetland types (see Irvine et al., 2022, Chapter 19). Current data reflect mainly areas with higher research efforts, rather than natural patterns of species richness and endemicity. More studies are required covering large areas and time-integrated sampling as species succession and turnover in relation to environmental changes are typical to zooplankton communities. In addition to more explorative studies, more taxonomical research is needed. Particularly for southern continents, there is an overall lack in trained taxonomists for most aquatic invertebrate groups. Nearly every extensive study on zooplankton from tropical wetlands reveals new species or even higher order taxa, especially when applying molecular systematics as cryptic species are common.

Many zooplankton groups are widely distributed, can cope with variable environmental conditions, and occur in both permanent and temporary tropical wetlands. Functional feeding groups include detritus feeders, scavengers, predators, and filter feeders. They consequently sustain important ecosystem functions (e.g., nutrient cycling, clearing water) and form crucial components of the food web (Cuthbert et al., 2022, Chapter 17). Zooplankton is the main link of biomass transfer between primary producers and consumers (Setubal et al., 2020). Especially under often high temperature conditions in the tropics, accelerated processing of autochthonous and allochthonous organic matter takes place, which without the activities of zooplankton groups would quickly result in eutrophic systems with frequent (often toxic) algal blooms. An abundant and diverse zooplankton community can maintain the aquatic ecosystem in a clear water phase with ample vegetation and deliver crucial services to human populations (e.g., clean water, fish, recreational area).

Reproduction modes span the whole range in zooplankton, from obligate sexual to parthenogenetic reproduction, with sometimes different modes represented in a single species. In addition, in each of the zooplankton groups covered here, species are known that produce drought-resistant dormant propagules in variable developmental stages that allow persistence in temporary wetlands and facilitate passive dispersal.

Habitat characteristics that tend to impact zooplankton community composition, species richness, and diversity include wetland size, wetland type (permanent vs temporary), the presence of predatory fish (mainly in permanent wetlands) and macrophyte cover as biotic variables, and pH and salinity as for the abiotic environment. Fish predation not only selects for smaller species but also affects size structure and sometimes behavior of populations. The presence of a diverse and vegetated littoral zone offers extra food, shelter, and habitat heterogeneity supporting often high species richness and occurrence of particular plant dwelling species. For conservation of zooplankton diversity in tropical wetlands, it is therefore crucial to focus mainly on the maintenance of a well-vegetated littoral zone (Gebrehiwot et al., 2017). Some zooplankton groups seem to do well under (even hyper) eutrophic conditions in (subtropical) systems, so that indicators based on zooplankton richness sometimes are positively associated with trophic status, in contrast with the impact on macroinvertebrate richness (Azevêdo et al., 2015). In temporary wetlands, the community composition and species richness are mainly determined by the hydroperiod, that indirectly has an impact on water quality and the presence of invertebrate predators. Any change in temporary wetland hydrology due to direct anthropogenic impact and/or by climate change will therefore have a significant impact on community processes and dynamics. This topic is being dealt with in detail in the chapter on large branchiopods (Brendonck et al., 2022a,b, Chapter 10).

Zooplankton groups are usually not prime targets for conservation efforts as they are too small and lack the charism of other wetland invertebrates such as dragonflies. Due to their versatile feeding, reproduction, and life history strategies, they are usually abundant, quite widespread with limited documented cases of species extinctions. However, tropical zooplankton are crucial to maintain ecosystem functions and services, including suppression of harmful algal blooms and provisioning of food for rare insect, amphibian, and fish species.

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Chapter 10

Large branchiopods

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10.1 Introduction

Most large branchiopods occur in a variety of temporary, or seasonally astatic "waters" (hereafter referred to as "wetlands") which are rare in the tropics (between 23°26′11.6″ N and 23°26′11.6″ S), the focal region of this book (see Wasserman and Dalu, 2022, Chapter 1). We will therefore extend the study region of this chapter to also include the subtropical region (between the tropics and about 35°N and S of the equator) where such habitats are still abundant and diverse, especially in the (semi)arid regions (Brendonck and Williams, 2000). Besides natural and artificial wetlands typically characterized by hydromorphic soils and macrophytes, we here also include temporary rock pool systems that occur on eroded granite or sandstone bedrock (Fig. 10.1; Deemy et al., 2022, Chapter 3; Piedade et al., 2022, Chapter 7).

Large branchiopod crustaceans are often considered "the flag ship group" among residents of seasonally astatic wetlands (Brendonck et al., 2008). Since they are variably allocated to the arbitrary groupings of zooplankton or macroinvertebrates, we have chosen to devote a unique chapter to them while (sub)tropical wetland zooplankton (Brendonck et al., 2022, Chapter 9) and macroinvertebrates (Dube et al., 2022, Chapter 11) are presented in different chapters. In contrast to most macroinvertebrates that actively colonize wetlands during the wet phase, large branchiopods and zooplankton are permanent residents with strategies to cope with drought and variable hydrological disturbance regimes.

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FIGURE 10.1 Some typical temporary aquatic systems considered in this review. Top row left to right: rock pools in Comoe National Park (Ivory Coast) (by Mario Driessen), wetland in Save floodplain (Zimbabwe) (by Luc Brendonck); Bottom row left to right: Water Buffalo Wallows (Thailand) (by Christopher Rogers), Karingani Game Reserve (Mozambique) (by Tom Pinceel).

A main obstacle to studying temporary wetlands in drier areas is their remoteness and the fact that their wet phase is often unpredictable due to stochastic rainfall (Hamer and Brendonck, 1997). In the wet tropics, shallow ponds typically lack a dry phase, which, together with strong predatory trophic interactions, make such systems unsuitable for large branchiopods (Kerfoot and Lynch, 1987). Although in the last two decades there has been a renewed interest in large branchiopod ecology, distribution, and systematics, current knowledge is still scattered and limited.

Including the subtropical region in this chapter will allow us to compare patterns between entire biogeographical regions: the Neotropics, the Afrotropics, the Oriental, and Australasia. Although a general overview of numbers of taxa and their level of endemicity will be presented for the (sub) tropical biogeographical regions, we here mainly focus on the most studied regions across the (sub)tropics: South America, Southern Africa, the Indian subcontinent and Southeast Asia, and Australia. Due to the limited amount of landmass in the southern hemisphere and sometimes also the overlap in climate and taxa, we also include southern subtropical portions of South America, Africa, and Australia in our analyses.

Among these regions, southern Africa has historically received most attention for the study of large branchiopod diversity, systematics, and ecology. The region is considered a large branchiopod biodiversity hotspot (Bird et al., 2019; Meyer-Milne et al., 2020). Over the last 20 years large branchiopod research has also intensified in Australia (Schwentner et al., 2015a,b), central and South America (the Neotropics) (reviewed in Rogers et al., 2020). Despite this renewed interest, current knowledge on total species richness in the tropics is still limited and many promising regions remain unexplored. We therefore expect scientific description of many species and several genera in the next decades. After all, just about any exploration effort in previously understudied areas uncovered new taxa.

Through combining available systematic, ecological, and biogeographical information on large branchiopods from the (sub)tropics, we aim to offer an update on the reference work by Brendonck et al. (2008) on this important faunal component from wetlands.

10.2 Systematics

The class Branchiopoda is composed of three extant orders: Anostraca (fairy shrimp), Notostraca (tadpole shrimp), and Diplostraca (Rogers, 2009; Ahyong et al., 2011; Schwentner et al., 2018). The Diplostraca are further subdivided into the suborders Laevicaudata (smooth clam shrimp) and Onchyocaudata, which houses the Spinicaudata (spiny clam shrimp) and Cladoceromorpha (Schwentner et al., 2018). This last group, in turn, is composed of Cyclestherida (tropical clam shrimp) and the Cladocera (water fleas) (Olesen, 2007, 2009; Olesen and Richter, 2013). The noncladoceran branchiopods are usually descriptively indicated as "large branchiopods" (Fig. 10.2).

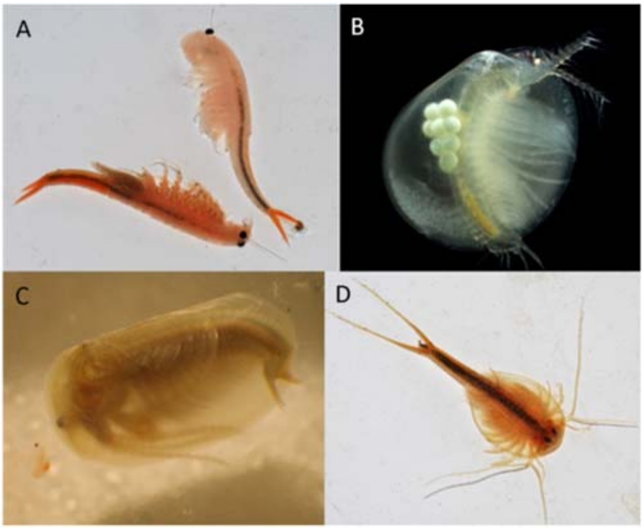

FIGURE 10.2 Images of (sub)tropical large branchiopods: (A) *Branchinella ondonguae* from (sub)tropical clay pans in Zimbabwe. (B) *Cyclestheria hislopi* from a temporary pond in Madagascar. (C) *Leptestheria rubidgei* from temporary wetlands in South Africa. (D) *Triops* cf. *granarius* from clay pans in Zimbabwe. *Photo courtesy Bram Vanschoenwinkel except* C. hislopi *by Jean Francois Cart.*

All large branchiopod groups are abundant and widespread in wetlands across arid zones. While fairy shrimps are taxonomically by far the most diverse group (see Rogers, 2013 for the most recent catalog), this at least partly results from poor systematic knowledge of clam shrimps and tadpole shrimps, which may hold many cryptic species. Molecular evidence indeed points to species complexes with high levels of cryptic diversity in tadpole shrimps (Korn and Hundsdoerfer, 2006; Korn et al., 2006; Vanschoenwinkel et al., 2012; Korn et al., 2013; Gálvez et al., 2022, Chapter 18; Meusel and Schwentner, 2017; Rogers et al., 2021a), clam shrimps (Rogers, 2020; Rogers et al., 2012; Schwentner et al., 2015a,b, 2020a,b), and even in the more studied fairy shrimps (Pinceel et al., 2013a; Reniers et al., 2013; Lukić et al., 2019). Limited systematic knowledge on clam shrimps and tadpole shrimps is mainly due to lack of apparent species-specific morphological features (except egg morphology in Limnadiidae) and high intraspecific morphological variation. The recent special issue on clam shrimp research (Hegna and Rogers, 2020) including an updated catalog (Rogers, 2020) and worldwide review (Schwentner et al., 2020a,b) of the Spinicaudata illustrates progress in clam shrimp biology, phylogeny, and systematics. The Spinicaudata, but also the Laevicaudata (Rogers and Olesen, 2014; Sigvardt et al., 2019), are considered in need of further revision based on morphological characters, combined with molecular data. Such an approach was recently already successfully adopted for the delineation of a spinicaudatan genus (*Ozestheria*), which occurs across Australia, Asia, and Africa (Schwentner et al., 2020a,b). With regard to tadpole shrimps, Naganawa (2018) presents a phylogeny of *Triops cancriformis*, *Triops longicaudatus*, and *Triops granarius* and recognizes a fourth species (*Triops strenuus*) occurring in Australia and Japan. The latter study is criticized by Rogers et al. (2021a), in a global review of the *T. granarius* species group. These authors suggest the resurrection of *Triops sakalavus* and a revision of the southern African forms. Recently, the complete mitogenome was sequenced in an anostracan (Tladi et al., 2020a) and clam shrimp species (Tladi et al., 2020b). Similar studies on large numbers of species should result in accurate phylogenies of large branchiopod taxa.

10.3 Comparison between (sub)tropical biogeographical regions

Although we mainly focus on some well-studied (sub)continents within the tropical and subtropical geographical regions, Table 10.1 summarizes the most recent status of numbers of large branchiopod taxa and their endemicity at global scale and for each of the biogeographical regions within the geographical delineation considered in this chapter. For each biogeographical region we will also compare species numbers and endemicity between tropical and subtropical regions.

TABLE 10.1 Estimated large branchiopod crustacean taxa (family, genus, species) and level of endemicity of anostracan and notostracan orders and clam shrimp clades on a global scale and for delineated biotropical regions.

Taxon	Global	Afrotropics		Australasian tropics		Neotropics		Oriental tropics	
		Taxa	Endemic	Taxa	Endemic	Taxa	Endemic	Taxa	Endemic
Anostraca: families	8	4	0	5	1	4	0	5	0
Artemiidae: genera	1	1(1)	0	1(1)	0	1(1)	0	1(1)	0
Artemia: species	7	2(2)	0	2(2)	0	2(1)	1	2(2)	0
Branchinectidae: genera	2	0	0	0	0	2(1)	1	0	0
Archaebranchinecta: species	2	0	0	0	0	2	2	0	0
Branchinecta: species	51	0	0	0	0	18	5(13)	0(2)	0
Branchipodidae: genera	6	4	3	1	1	0	0	1	0
Australobranchipus: species	2	0	0	0(2)	0(2)	0	0	0	0
Branchipodopsis: species	22	16(2)	16(2)	0	0	0	0	0(2)	0(1)
Branchipus: species	5	0(1)	0	0	0	0	0	0(1)	0
Metabranchipus: species	3	3	3	0	0	0	0	0(1)	0
Pumilibranchipus: species	1	1	1	0	0	0	0	0	0
Rhinobranchipus: species	1	1	1	0	0	0	0	0	0

(*Continued*)

TABLE 10.1 (Continued)

Taxon	Global	Afrotropics		Australasian tropics		Neotropics		Oriental tropics	
		Taxa	Endemic	Taxa	Endemic	Taxa	Endemic	Taxa	Endemic
Chirocephalidae: genera	9	1	0	0	0	0	0	1	0
Branchinectella: species	1	1(1)	0	0	0	0	0	0	0
Chirocephalus: species	52	0(1)	0(1)	0	0	0	0	1(7)	1(7)
Parartemiidae: genera	1	0	0	1	1	0	0	0	0
Parartemia: species	18	0	0	2(18)	2(18)	0	0	0	0
Streptocephalidae: genera	1	1	0	1	0	1	0	1	0
Streptocephalus: species	61	15(27)	14(26)	1(1)	1(1)	4(13)	2(10)	8(3)	8(3)
Tanymastigitidae: genera	2	1	1	0	0	0	0	0	0
Tanymastigites: species	5	0(5)	0(5)	0	0	0	0	0	0
Tanymastix: species	4	0(2)	0(1)	0	0	0	0	0	0
Thamnocephalidae: genera	6	3	0	1	0	4	1	2	0
Branchinella: species	47	2(1)	1(1)	4(37)	4(37)	0	0	3(1)	3(1)
Carinophallus: species	1	1	0	0	0	0	0	1	0
Dendrocephalus: species	19	0	0	0	0	16(4)	16(4)	0	0
Phallocryptus: species	5	1	0	0	0	1(1)	1(1)	0	0
Spiralifrons: species	1	0	0	0	0	1	1	0	0

Thamnocephalus: species	5	0	0	0	0	4(1)	4	0	0
Notostraca: families	1	1	0	1	0	1	0	1	0
Triopsidae: genera	2	1	0	2	0	2	0	1	0
Lepidurus: species	~10	0	0	1	1	1	1	0	0
Triops: species	~50	~6	~3	~26	~26	~2	~2	~3	~3
Laevicaudata: families	1	1	0	1	0	1	0	1	0
Lynceidae: genera	3	2	1	1	0	2	0	1	0
Lynceiopsis: species	2	2	2	0	0	0	0	0	0
Lynceus: species	35	7(4)	7(4)	1(7)	0(5)	2(2)	2(1)	3(2)	3(2)
Paralimnetis: species	3	0	0	0	0	0(3)	0(3)	0	0
Spinicaudata: families	4	4	0	4	0	2	0	4	0
Cyzicidae: genera	2	2	0	1	0	0	0	2	0
Cyzicus: species	~25	~4(~6)	~4	0	0	1(2)	1	2(6)	6
Ozestheria: species	~15	~0(1)	~0(1)	~5(~6)	~2(6)	0	0	~2(2)	~2(2)
Eocyzicidae: genera	1	1	1	1	1	0	0	1	1
Eocyzicus: species	~35	2(4)	6	~5 (~10)	~1(~10)	0(1)	0	1(~8)	1(~5)
Leptestheriidae: genera	3	1	0	1	0	1	0	1	0
Eoleptestheria: species	2	0(1)	0	1	0	0	0	0	0
Leptestheria: species	~33	6(9)	5(7)	0	0	5(1)	5	4(10)	3(8)

(Continued)

TABLE 10.1 (Continued)

Taxon	Global	Afrotropics		Australasian tropics		Neotropics		Oriental tropics	
		Taxa	Endemic	Taxa	Endemic	Taxa	Endemic	Taxa	Endemic
Limnadiidae: genera	8	3	2	4	2	1	0	2	0
Australimnadia: species	3	0	0	2(1)	2(1)	0	0	0	0
Calalimnadia: species	1	1	1	0	0	0	0	0	0
Eulimnadia: species	∼46	5(1)	5	7(6)	7(6)	8(8)	5(3)	5(2)	5(2)
Gondwanalimnadia: species	1	0(1)	0(1)	0	0	0	0	0	0
Limnadopsis: species	12	0	0	7(7)	7(7)	0	0	0	0
Paralimnadia: species	24	0	0	4(15)	4(15)	0	0	1	1
Cyclestherida: families	1	1	0	1	0	1	0	1	0
Cyclestheridae: genera	1	1	0	1	0	1	0	1	0
Cyclestheria: species	∼1	∼1	0	∼1	0	∼1	0	∼1	?
Total tropical species		∼62 (∼38)	∼55(18)	∼68 (138)	∼56 (∼133)	∼64 (∼26)	∼46 (∼25)	∼29 (∼45)	∼28 (∼31)
% Endemicity			88.7 (47.4)		82.4(96.4)		71.8 (96.2)		96.6 (68.9)

Note: Numbers in parentheses in columns represent numbers of subtropical taxa. There is overlap in the numbers of taxa found in both the tropics and subtropics.

10.3.1 Biogeography

As large branchiopods have an ancient history and were present before the split up of Gondwana and Laurasia, many families are widespread and not restricted to a particular biogeographical region (Brendonck et al., 2008; Schwentner et al., 2020a,b). The wide distribution of many spinicaudatan taxa, for example, is therefore largely based on vicariance with some transoceanic dispersal in *Eulimnadia* and Leptestheriidae (Bellec and Rabet, 2016; Schwentner et al., 2020a,b). The cyclestherid *Cyclestheria hislopi* (Fig. 10.2) currently is the only species with a circumtropical distribution, although whether all records indeed represent the same species is disputed (Olesen et al., 1996; Schwentner et al., 2013). All large branchiopod families occur in the (sub)tropics. Some families only occur in one (sub)tropical region, for example, the anostracan Parartemiidae in Australia (Brendonck et al., 2008). Other families are excluded from at least one of the focal regions. For instance, the anostracan Streptocephalidae and Branchipodidae have not been reported from the Neotropics (Rogers, 2020). Species richness of some families is region-specific with, for instance, most Thamnocephalidae being confined to Australia and the Neotropics, and Streptocephalidae to the Afrotropics. Based on a molecular phylogeny of the Streptocephalidae, Daniels et al. (2004) suggest a Gondwana origin of the only genus *Streptocephalus*, with current distribution patterns likely resulting from a combination of vicariance and limited dispersal.

10.3.2 Species richness patterns

Patterns of large branchiopod species richness among the four (sub)tropical regions vary widely, ranging from Australia with around 180 species, to the Oriental region with an estimated 62 species (Table 10.1).

The *Afrotropics* are mainly arid in the north and otherwise semiarid with large numbers of wetlands and a high associated large branchiopod diversity. Since the early work by G.O. Sars, R. Gurney, G.S. Brady, E. Daday, K.H. Barnard, and V. Brehm in the 19th to early 20th century, the knowledge of diversity and distribution of large branchiopods was significantly updated in the 1990s (see review by Bird et al., 2019), including the description of four new monotypic and endemic genera; in Anostraca: *Rhinobranchipus* (Brendonck, 1995) and *Pumilibranchipus* (Hamer and Brendonck, 1995); and in Spinicaudata: *Calalimnadia* (Rogers et al., 2012) and *Gondwanalimnadia* (Rogers et al., 2016c). Some genera are endemic to southern Africa, such as the anostracans *Metabranchipus*, *Rhinobranchipus*, and *Pumilibranchipus* and the clam shrimp *Gondwanalimnadia*. In total 66 species were known at that time; 46 anostracan species from six genera and four families (Hamer and Brendonck, 1997; Hamer, 1999); two notostracan (*Triops*) species (Hamer and Rayner, 1995); and 18 clam shrimp species (Brendonck, 1999). Since this last update six new anostracan species were described (Boumendjel et al., 2018; Hamer and Rogers, 2012; Nhiwatiwa et al., 2017; Rogers and Meyer-Milne, 2021), three notostracan species were resurrected (Rogers et al., 2021a), and two new notostracans were described (Korn and Hundsdoerfer, 2016). In addition, Baxevanis et al. (2014) for the first time genetically confirmed the presence of the invasive *Artemia franciscana* in the region (see Pegg et al., 2022, Chapter 16). Considering the vastness of the subcontinent and the many promising but largely unexplored regions, the above figures still are a serious underestimation of the real richness. More intensive monitoring and the use of molecular tools to detect cryptic species, especially in clam and tadpole shrimps, will likely lead to the identification of many more species. This expectation is consistent with some recent case studies of formerly ill-explored areas that resulted in serious expansion of known species ranges (Hamer and Rogers, 2012; Tuytens et al., 2015; Mabidi et al., 2016; Nhiwatiwa et al., 2017; Meyer-Milne et al., 2020).

Since virtually no taxonomic research was done on clam shrimps since the early studies, we expect many additional species in this group in particular. For instance, a worldwide revision of limnadid genera by Rogers et al. (2012) revealed the presence of eight genera, including two new ones (*Calalimnadia* and *Gondwanalimnadia* (originally named *Afrolimnadia*)). Although many more *Triops* species were previously recognized in Africa, Longhurst (1955) only accepted *T. cancriformis* and lumped all other southern African forms into *T. granarius*. Hamer and Rayner (1995), however, suspected the presence of many cryptic *Triops* species. This is now confirmed in recent revisions of the *T. granarius* species group (Korn and Hundsdoerfer, 2016; Korn et al., 2010; Rogers et al., 2021a). By combining morphological and molecular techniques, these authors resurrected two species within the *T. granarius* species group (*Triops namaquensis* and *Triops numidicus*) from southern Africa and a third species (*T. sakalavus*) from Madagascar.

The Oriental region has been studied far less. Mostly anecdotal reports mentioned 86 species from the Indian subcontinent. However, many of these species are not validated. In a conservative review of large branchiopod collections from the Indian subcontinent, Rogers and Padhye (2015) only recognized 42 species (16 anostracans, 2 notostracans, 3 laevicaudatans, 21 spinicaudatans, and 1 cyclestherid) with three endemics (Rogers and Padhye, 2014; Padhye and Dahanukar, 2015; Padhye and Kulkarni, 2019). In an updated account, Padhye and Lazo-Wasem (2018) increased the total number of confirmed large branchiopod species on the Indian subcontinent to 45 species. The validated number of Indian clam shrimp species stands at 8, while 15 more need re-examination (Padhye, 2020). Rogers et al. (2013a) mention eight described and several undescribed species from South East Asia, many of them endemic. Subsequent work on Southeast Asia has revealed a distinct large brachiopod fauna for the region (Shu et al., 2015a,b, 2018, 2019; Rogers et al., 2013b, 2016a,b, 2017; Sanoamuang et al., 2020). Rogers and

Padhye (2014) furthermore present a key for all Asian streptocephalids, and Sanoamuang et al. (2020) provide a key to all Asian *Eulimnadia*. These works have increased the large known branchiopod diversity of the Oriental region to 63 species (26 anostracans, ~3 notostracans, 7 laevicaudatans, ~30 spinicaudatans, and ~1 cyclestherid) with around 30 being endemic. The fact that the Oriental region has the lowest large branchiopod species diversity recorded among the four biogeographical regions, is most likely an artefact of the limited survey work in that region.

The *Neotropics* have also been poorly studied. Rogers et al. (2020) recently reviewed all of the available literature and summarized distributional information on species from the Neotropical and Antarctic bioregions. Anostracans appear again as the most prevalent group with high endemicity; of the 14 large branchiopod genera and 25 reported species, only 4 genera and 9 species are known outside of this region. The notostracans of the region are likely in need of revision as all Neotropical forms are currently treated as *T. longicaudatus*, while also only one species of *Lepidurus* (*L. patagonicus*) is reported from South America. Spinicaudatans are currently represented by 4 genera and about 17 species. The Neotropical Laevicaudata are represented by two genera; *Lynceus* with seven species and three *Paralimnetis* species. Sigvardt et al. (2019) present a key to laevicaudatan species in the Americas (including a new species from Chile) and a first molecular phylogeny of the genus *Lynceus*. Interestingly, the closest relatives appear to be Australian species. A biogeographic link between Australia and North America was previously suggested for notostracans by Vanschoenwinkel et al. (2012), based on genetic analyses. This link was presumably mediated by historic long-distance dispersal via birds.

The *Australian* continent consists of 70% arid to (semi)arid regions. Therefore most aquatic habitats are of a temporary nature and potential habitat for large branchiopods. Over two decades of intense study have resulted in updated patterns of species diversity and distribution, especially in clam shrimps (e.g., in *Paralimnadia* by Timms 2016; Timms and Rogers, 2020; Timms and Schwentner, 2020; spinicaudatans in general by Schwentner et al., 2014, 2015). This also resulted in the description of a new endemic clam shrimp genus (*Australimnadia*) (Timms and Schwentner, 2012, 2017) and many clam shrimp species (e.g., Richter and Timms, 2005; Timms and Richter, 2009; Timms, 2009a, 2015, 2018; Schwentner et al., 2012; Weeks et al., 2012; Tippelt and Schwentner, 2018), some on neighboring islands (Olesen et al., 2016). Schwentner et al. (2015b) also established a new spinicaudatan genus (*Ozestheria*) to accommodate the Australian Cyzicidae species, and at least seven cryptic species in the Australian *Eocyzicus* were revealed (Schwentner et al., 2014). The updated Australian large branchiopod fauna is very rich with about 180 species and has an unparalleled diversity of spinicaudatan clam shrimps, both at regional scales and within water bodies (Schwentner et al., 2015a). After extensive sampling and by making use of molecular tools, these authors conservatively estimated the occurrence of 55 spinicaudatan clam shrimp species in central and eastern Australia, and a total of 70 spinicaudatan species for the whole of Australia (i.e., just over 1/3 of the known global spinicaudatan diversity). Also, knowledge on Anostraca systematics and diversity was updated in the last decade, including the description of a new endemic genus (Rogers et al., 2007). In Australia, 5 anostracan genera occur (*Branchinella*, *Parartemia*, *Streptocephalus*, *Australobranchipus*, and *Artemia*) with at least 59 species, of which about 40% is endemic to Western Australia (Timms, 2012; Pinceel et al., 2013a). *Branchinella* is a strikingly species rich genus in Australia, accounting for 60% of all known Australian anostracan species and several new species have been described in the last decade (Timms, 2012). Pinceel et al. (2013a) suspect the occurrence of at least three more cryptic *Branchinella* species based on their phylogenetic study. The remaining anostracan species are mostly salt lake specialists belonging to *Parartemia*, of which six new species were described in the last decade (Timms, 2010). Based on an integrated morphological and molecular approach, Meusel and Schwentner (2017) suggest that the previously known notostracan species (*Triops australiensis*) might actually represent a complex of (26) species, which was also suggested in previous studies (Vanschoenwinkel et al., 2012; Mathers et al., 2013). Australia houses several endemic genera such as *Australobranchipus* and *Parartemia* in anostracans and *Australimnadia*, *Limnadopsis*, and *Paralimnadia* within the clam shrimps.

10.3.3 Hotspots

Based on accumulating information, several (sub)tropical regions were indicated as "hotspots" for large branchiopod diversity. Southern Africa is currently considered a global hotspot (Bird et al., 2019). In a relatively small protected area (150 km^2) in SE Zimbabwe, Nhiwatiwa et al. (2014) discovered about 35% of all southern African species, together with a new anostracan species. Most species were first records for Zimbabwe. Mabidi et al. (2016) reported 23 species from the Eastern Cape Karoo region in South Africa. In Australia, extensive monitoring revealed the middle Paroo catchment as a hotspot for large branchiopods (especially of the Limnadiidae) (Timms and Richter, 2002; Timms and Sanders, 2002; Timms, 2012; Schwentner et al., 2015a,b; Meusel and Schwentner, 2017). Pinceel et al. (2013a) also consider SW Australia as a diversity hotspot, mainly for anostracans with at least 34 *Branchinella* species for the region.

10.3.4 Endemicity

Large branchiopod endemicity in the (sub)tropics follows a similar pattern to species diversity, with approximately 178 endemic species in Australia down to around 55 in the Oriental region (Table 10.1). However, the fraction of endemism among the estimated species diversity is very high across all four biogeographical regions, varying from 96.4% in the Oriental tropics to 71.8% in the Neotropics. While some species do have a wide distribution, most are known only from a small range, sometimes even only from the type locality. Rogers (2015) reported that 56.2% of anostracan species globally are known from 10 or fewer localities, while 28.7% globally are known only from the type locality.

Among the widespread species, the circumtropical clam shrimp *C. hislopi* currently is the champion. However, recent molecular studies have demonstrated that this circumtropical species probably comprises numerous localized species (Schwentner et al., 2013). The halophilic anostracan *Phallocryptus spinosa* has a vast distribution, reported from Europe, Africa, and occidental Asia (Ketmaier et al., 2008; Amarouayache and Derbal, 2010). In contrast, species of the southern African anostracan genus *Branchipodopsis* and the New World *Branchinecta* display rather high levels of endemicity. Also, Spinicaudata species currently exhibit high endemicity with about 22% of the 194 valid species known only from the type locality (Rogers, 2020). Such high endemicity could result from poor systematics (e.g., in spiny clam shrimps), type of habitat (ephemeral rock pools in *Branchipodopsis*), high degrees of specialization, limited successful long range dispersal, or lack of sampling.

10.4 Functional groups

Most large branchiopods develop into (or a combination of) filter feeders, scavengers, scrapers, or predators. Most anostracans remain opportunistic suspension feeders throughout their life cycle (Brendonck, 1993). Because of their relatively large size and a large number (usually 11 pairs) of filtering appendages, they are dominant filter feeders and outcompete the smaller zooplankton such as cladocerans and rotifers. Anostracans are increasingly considered as omnivorous (Lukić et al., 2018), feeding on both phytoplankton and small zooplankton (including larval stages), with ratios impacted by the turbidity of the water (Lukić et al., 2020). Sometimes adult anostracans are also found scraping the pond basin or margin. Few real raptorial anostracans are currently known (Rogers et al., 2006), of which one Australian *Branchinella* and two North American *Branchinecta* species (Rogers et al., 2006; Rogers and Timms, 2017) are active predators on other branchiopods and insects. Adult clam shrimps are mainly benthic feeders where they disturb the sediment and feed on resuspended sediment and phytoplankton, sometimes combined with scraping of the sediment (Liu et al., 2020). Many species are also commonly observed to swim freely through the water (Schwentner et al., 2015a). After a filter feeding period, all tadpole shrimps become predatory and feed on other invertebrates and small vertebrates (e.g., small fish and tadpoles). Coexisting species sometimes reveal differences in functional feeding structures which can indicate resource partitioning among large branchiopod species (Liu et al., 2020).

10.5 Life history strategies

Similar to other Cladoceromorpha but in contrast with the other large branchiopods, *Cyclestheria* has a heterogonous life cycle with gamogenetic production of resting eggs alternated with a parthenogenetic phase during which subitaneous eggs are produced (Fritsch and Richter, 2015). In *Cyclestheria*, subitaneous eggs have a pseudodirect development inside the female brood chamber, while resting eggs develop in a direct way, both with release of juveniles. In all other large branchiopods, resting eggs hatch as nauplius larvae and only develop into juveniles after subsequent molts. It should be noted that resting eggs actually are shelled dormant embryos (Brendonck, 1996). This particular life cycle in *Cyclestheria* may be the reason why this genus is more common in the tropics and permanent wetlands compared to the other large branchiopods. In large branchiopods specialized to temporary wetlands, the drought resistant resting eggs help to bridge the dry period and terrestrial phase of the wetland (Fig. 10.3). In some clam shrimps and tadpole shrimps not only males and females are known, as is the case for most anostracan species, but also hermaphrodites (Zierold et al., 2007; Weeks et al., 2009).

After hatching from the egg bank, growth and maturation rates are often spectacular, depending on the species and local environmental conditions, with the first eggs being produced in less than one week (Rogers et al., 2007; Vanschoenwinkel et al., 2010b). After production, some eggs may float (Pinceel et al., 2013c), while most sink and accumulate in the sediment (Brendonck and De Meester, 2003). Both fractions contribute to a persistent and mixed egg bank. Depending on sedimentation rates and the type and intensity of sediment mixing, eggs can become buried and covered by layers of variable thickness. During the dry period, eggs are exposed to sometimes high soil temperatures and to wind. Wind erosion was shown to potentially be an important natural loss factor in the egg bank budget (Pinceel et al., 2020),

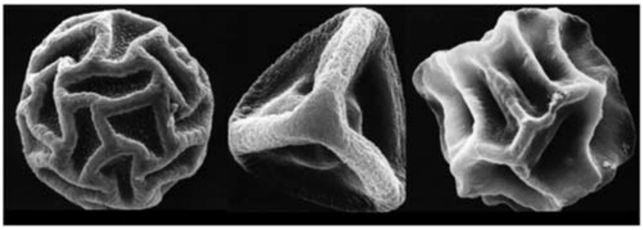

FIGURE 10.3 Pictures of resting eggs of (left to right) *Streptocephalus proboscideus*, *S. (Parastreptocephalus) zuluensis*, and *Eulimnadia cylindrova*. *Photo courtesy Luc Brendonck.*

an effect which is reduced by the presence of plants in the wetland basin (Brendonck and Riddoch, 2000). Depending on size, shape, and external ornamentation of the resting eggs (see Fig. 10.3), some species-specific egg types are more apt for wind dispersal (Pinceel et al., 2016b), while others may stick better to bird feathers or mammal fur (Vanschoenwinkel et al., 2011a; Rogers et al., 2021b).

When ponds are filled by rains, only a variable part of the available active egg bank will hatch, while the remaining unresponsive part postpones hatching until later (Brendonck et al., 1998; Pinceel et al., 2017). Similar to seed germination in annual dessert plants, the fraction of large branchiopod eggs that hatches with each inundation should theoretically correspond with the probability of completing the life cycle with the successful production of resting eggs. This delayed hatching is likely part of a risk-spreading strategy (bet-hedging) for which also empirical evidence is accumulating (Pinceel et al., 2017). In addition, as eggs require light for hatching (Pinceel et al., 2013d; Tladi et al., 2020c), only eggs in the top soil layer ("the active egg bank") will hatch upon inundation, while deeply buried eggs are lost or may resurface only after disturbance and turnover of the sediment. Some studies revealed protection mechanisms to prevent egg hatching under unsuitable growing conditions. At least eggs of (sub)tropical rock pool species show reduced hatching with increased water conductivity (Vanschoenwinkel et al., 2009), especially when combined with increased temperatures (Brendonck et al., 1998). Such conditional hatching will prevent abortive egg hatching when only partially flooded wetlands are likely to dry before hatchlings mature. It is currently not sufficiently known to what extent hatching requirements are species-specific. Yet, an improved understanding of these mechanisms could facilitate field surveys and diversity studies since they may strongly determine species distribution and temporal occurrence patterns.

Large branchiopods rely on vectors for passive dispersal of their eggs (i.e., propagules). Being subject to vectors, this type of dispersal is often rather unreliable and many propagules do not reach a new suitable habitat but are lost in the matrix (Brendonck et al., 2017). With excessive rains, floating eggs can for instance be lost with spilling water or may end up in connected wetlands, for example, by erosion channels. While passive dispersal by wind is blind, with eggs generally landing in unsuitable places (Brendonck and Riddoch, 1999; Vanschoenwinkel et al., 2008), transport by water birds, livestock, and mammal wildlife, is more directed as transported eggs may ultimately arrive in other wetlands when animals come to drink or wallow when ponds are filled (Green et al., 2008; Vanschoenwinkel et al., 2011a). Furthermore, hatching rates may increase in eggs consumed and excreted by predators (Rogers, 2014a).

High dispersal rates can result in homogenization of aquatic communities among nearby wetlands as concluded by Dube et al. (2019). However, despite the potential for dispersal, population genetic studies usually reveal differentiation among often nearby populations, indicative of limited successful long range dispersal (Brendonck et al., 2000; Vanschoenwinkel et al., 2011b; Pinceel et al., 2013b). This is in contrast with the study by Schwentner et al. (2012) that showed limited population structure in four Australian *Limnadopsis* species and by Schwentner et al. (2014) in Australian *Eocyzicus*, indicative of effective recent long range dispersal in their study region. Meusel and Schwentner (2017) found a similar pattern of limited genetic differentiation over large spatial scales for Australian *Triops* and Schwentner et al. (2015b) for Australian *Ozestheria*. Schwentner and Richter (2015) even observed similar genetic differentiation between successive active populations in one pool as between populations at the same time and attributed this to stochastic effects related to hatching from the egg bank.

Despite loss factors due to unsuccessful hatching, wind erosion, and overflows, egg densities in the active egg bank are usually high (Thiéry, 1997; Brendonck and Riddoch, 2000) but expected to vary with wetland characteristics such as the hydrology, the presence of plants, and type and intensity of loss factors (Brendonck and De Meester, 2003).

10.6 Habitat preferences

While knowledge of large branchiopod systematics is starting to balance out among (sub)tropical regions, knowledge of the ecology of large branchiopods is still heavily biased toward Southern Africa (overview in Bird et al., 2019) and to a lesser extent Australia (reviewed in Brendonck et al., 2017).

Depending on regional climate, pond size, and volume, wetlands display large natural variation in environmental conditions to which inhabitants are adapted. Inhabitants are therefore usually considered as habitat generalists (Mabidi et al., 2020). In rare cases, large branchiopods were discovered in semipermanent systems that only dry out occasionally (Ferreira et al., 2011, 2012). In contrast to what is often stated, large branchiopods sometimes also occur in temporary wetlands with fish. A number of predatory aquatic vertebrates (e.g., lungfish, killifish, and some tadpoles and urodelans) have indeed developed strategies to survive in temporary waters and can coexist with large branchiopods, at least in an early successional stage of the inundated wetland (Brendonck and Pinceel, personal observations).

Most large branchiopods inhabit freshwater systems. However, some anostracan species from the genera *Artemia*, *Branchinella*, *Streptocephalus*, *Thamnocephalus*, and *Parartemia* thrive in inland brackish or saline waters. This is especially the case in Australia where besides halophilic *Artemia*, *Branchinella*, and *Parartemia* species, several spinicaudatans (e.g., *Eocyzicus parooensis*) and *Triops* spp. also thrive in saline waters (Timms, 2009b). As rock pools are usually very transparent, fresh, and often very ephemeral, they require special adaptations of the inhabiting communities.

Therefore compared to depression wetlands, they often house a very specialized set of species. In the neotropics, several anostracan and clam shrimp species have currently been reported exclusively from rock pools (*Branchinecta valchetana*, *Branchinecta vuriloche*, *Dendrocephalus orientalis*, and *Eulimnadia ovilunata*) (Rogers et al., 2020). In India, seven large branchiopod species have been shown to inhabit freshwater rock pools (Padhye and Dahanukar, 2015). In southern Africa, rock pools are primarily dominated by species of the anostracan genus *Branchipodopsis* and members of the genus are considered true rock pool specialists (Brendonck et al., 2001) but also some *Streptocephalus* populations have been found in rock pools in South Africa (De Roeck et al., 2010) and Zimbabwe (B. Vanschoenwinkel *pers. obs*.). In Australia, not only some specialized *Branchinella* species are known from granite outcrops but also several spinicaudatans (belonging to *Limnadopsis*, *Eulimnadia*, and *Ozestheria*) and even occasionally tadpole shrimps (Zofkova and Timms, 2009; Brendonck et al., 2016; Timms, 2017, 2018; Timms and Hales, 2020; Timms and Schwentner, 2020).

Wetlands are not necessarily endorheic but can also occur in a floodplain where they depend at least to some extent on natural flooding of an associated river for their filling. In this case, lateral hydrological connectivity can significantly impact the community composition of such floodplain wetlands, with reduced diversity of large branchiopods when river connections are frequent due to fish predation (Dube et al., 2019; Nhiwatiwa et al., 2009, 2014).

10.7 Important local habitat characteristics

It is generally accepted that local habitat characteristics and associated species sorting processes are the main filter for shaping large branchiopod communities (Vanschoenwinkel et al., 2007; 2013), although regional processes should also be considered, especially when pools are geographically isolated (Nhiwatiwa et al., 2011).

Probably the most important complex variable having an impact on water quality and quantity, hatching success and resulting community structure is the hydroregime of the respective wetland, often used as synonym of disturbance regime (Vanschoenwinkel et al., 2013; Brendonck et al., 2017). This variable entails the timing and predictability of inundation, the duration and frequency of inundations, and the variance on these variables. Depending on soil structure and composition, pond size, and the regional climate, ponds can maintain water for almost an entire rainy season or fill and dry out intermittently. A positive association between hydroperiod and invertebrate richness and diversity was shown in several studies (Nhiwatiwa et al., 2011; 2017). Longer hydroperiods tend to provide more extensive opportunities for temporal niche segregation (Jocque et al., 2010) providing reproduction opportunities for organisms with short and longer aquatic life cycles but also for the development of aquatic vegetation which in turn may provide habitat for additional biodiversity. Hydrological models are valuable tools for unraveling the impact of historic climate regimes on current life history patterns and community structure but also to test predictions of changing hydroregimes under climate change. Such progressively optimized models have been used for rock pools on several occasions in Hulsmans et al. (2008), Vanschoenwinkel et al. (2009), and Tuytens et al. (2014). As these models are tuned to rather simple rock pool systems, the challenge remains to design similar hydrological models for soft bottomed temporary wetlands.

Several studies have reported significant positive species richness and pond area relationships for both plants and animals in wetlands (Nhiwatiwa et al., 2014; Mabidi et al., 2020). Larger wetlands are more easily colonized and usually offer higher habitat heterogeneity and buffering capacity. Yet, such relationships are not always clear. For instance, the association between large branchiopod richness and diversity with aquatic macrophytes has been researched on several occasions and while Dube et al. (2020) revealed a positive association of taxon richness with macrophyte cover, Mabidi et al. (2020) only found significant differences between vegetated and unvegetated wetlands, but not between different categories of macrophyte cover. The lack of association between macrophytes and macroinvertebrate assemblages in general could result from the high turbidity of many temporary wetlands that can prevent macrophyte establishment (Mabidi et al., 2020).

Soil structure and composition is not often considered to explain large branchiopod community composition and diversity. Rogers (2014b), however, revealed an association between sediment geochemistry and the distribution of North American anostracan species. Depending on geology and soil structure after an initial turbid phase due to stirring of the sediment by often torrential seasonal rains, ponds can become more clear allowing plants to germinate. Where clam shrimps and/or tadpole shrimps occur, the water can turn turbid again due to disturbance of the sediment by their benthic feeding activities (Waterkeyn et al., 2016). In contrast to filter feeding cladocerans and rotifers, anostracans do not seem to be negatively impacted by high concentrations of suspended particles, and probably feed on the sediment associated bacterial communities. An association between large branchiopods and turbid systems has been explained in terms of less effective visual predation (Lukić et al., 2019).

10.8 Community assembly and dynamics

After inundation, large branchiopods, together with other permanent wetland inhabitants hatch from the egg bank and are usually first to recolonize the habitat. In ponds with a sufficiently long hydroperiod, invertebrate predators (e.g., odonates, corixids, notonectids) establish later and have a dramatic impact on large branchiopod richness, especially on the unprotected anostracans (Brendonck et al., 2017). This heralds a next phase in the succession during which also the less efficient filter feeders (cladocerans and rotifers) have the opportunity to grow and reproduce (Lahr et al., 1999; Jocqué et al., 2007, 2010; Vanschoenwinkel et al., 2010a).

It is hard to reliably estimate the numbers of large branchiopod specimens and species per pond or in a region, especially based on short-term snapshot sampling. Firstly, they are hard to catch with dip nets. As a result, large branchiopod community analyses are often qualitative and based on the presence/absence of data. In addition, researchers sometimes arrive too early (only larvae present) or too late (adults already consumed by predators) during an inundation. In both cases, it can be incorrectly concluded that large branchiopods are absent from the study pond. However, even when species are present, it is possible that relative abundances or even species composition are different from the previous and next inundation as hatching conditions and requirements may be species-specific and seasonally different. It is therefore recommended to sample several times during a single inundation and across a number of subsequent seasons. An alternative method to integrate temporal variation in community composition is the collection and hatching of egg banks under controlled conditions (Brendonck and De Meester, 2003). Still, it is possible that hatching conditions are not favorable to all species and a rather large mortality can occur after hatching. To compensate for incomplete hatching and early mortality of hatchlings, it is common practice to also isolate and study unhatched eggs from the sediment (Thiéry, 1997; Wang et al., 2014). In contrast to species-specific egg morphology in most Limnadiidae (Timms and Schwentner, 2012, 2017, 2020), however, many anostracan species, even from different genera, can have remarkably similar egg types (Brendonck and Coomans, 1994a,b; Brendonck and Riddoch, 1997; Takahashi et al., 2018) reducing the effectiveness of such additional egg bank analysis. This rather labor intensive method therefore proved to be not always as effective as in the study of zooplankton from permanent lakes and ponds (Vandekerkhove et al., 2005).

It should be noted that it is not unusual to find several (even congeneric) large branchiopod species coexisting in the same habitat. Thiéry (1991) collected up to 10 species from a single pond in Morocco, and 12 coexisting species (mainly Anostraca) are recorded from a single pool in the southeastern Zimbabwe lowveld (Nhiwatiwa et al., 2014). Hamer and Rayner (1996) mention the unusually high number of coexisting congeneric species (including five anostracan *Streptocephalus* species) in one temporary wetland in the Northern Cape (South Africa). Other remarkable cooccurrence patterns in Australian limnadiids and other large branchiopod taxa are summarized in Schwentner et al. (2015a).

10.9 Role of large branchiopods in ecosystem function and services

In addition to the taxonomic approach in large branchiopod community analysis, it is also recommended to adopt a functional feeding approach which is more related to ecosystem processes (Ferreira et al., 2012). As they fill in all recognized functional feeding groups known from invertebrates, large branchiopods play an important role in temporary wetlands and as such are often key to maintain ecosystem functioning and services. Wetlands in (semi)arid areas are a major source of water for agriculture and household use. Being dominant filter feeders, anostracans help to control algal blooms, among which potentially toxic blue–green algae (cyanobacterians) (Yang and Park, 2017). Likewise, these ecosystems are essential sources for water in many protected areas across Africa. Large branchiopods also are an important link in the food chain between primary producers and higher trophic levels, such as fish, birds (Horváth et al., 2013), and amphibians (see Cuthbert et al., 2022, Chapter 17).

10.10 Threats and conservation

10.10.1 Threats

Wetlands are usually shallow and depend on direct capture of rainfall, runoff water, and sometimes groundwater discharge for replenishment. Therefore their hydrology is easily impacted by changes in local anthropogenic activities and climate and due to their relatively small volume, they are often poorly buffered. Major threats of temporary wetlands and their inhabitants include agriculture, mining, urbanization, drainage, habitat destruction, invasive species, pollution, and climate change. An emerging threat to many temporary wetlands is the hydraulic fracturing for shale gas in, for example, South Africa. This may change the hydrology of the system and lead to increased salinity (Mabidi et al., 2017, 2018). Increasing salinity of pond water due to climate change, pollution, or secondary salinization (Pinceel et al., 2013a) may negatively impact large branchiopod communities. Although adult large branchiopods can cope with rather large variation in ionic concentration during the pond hydrocycle, hatching of some species is cued by the conductivity at the start of the inundation phase (Vanschoenwinkel et al., 2010b), and increased salinity could prevent hatching.

Gradual slow historical climate change with increasing aridification appears to have been the motor for diversification in certain large branchiopod groups such as the Australian *Branchinella* (Anostraca) genus (Pinceel et al., 2013b) but this happened over hundreds of thousands to millions of years. However, current changes in temperature and rainfall occur at a pace that probably prevents local adaptation and may ultimately result in depletion of the egg bank on which demographic resilience and persistence of populations depends. Besides shortening growing seasons (hydroperiod of pools), ongoing and predicted climate change may also negatively impact local populations by prolonged exposure of the egg banks during the dry phase to wind erosion and increasing soil temperatures. As temporary rock pools are among the first to be affected by climate change, they were used to model the impact of different scenarios of climate change on persistence of local anostracan populations in southern Africa (Hulsmans et al., 2008; Tuytens et al., 2014; Pinceel et al., 2016a, 2018). According to Tuytens et al. (2014), a shift toward a drier climate will result in reduced permanence, increased conductivity, and reduced connectivity of temporary rock pools. This would not only impact the probabilities for successful reproduction of permanent inhabitants, but also impact metapopulation dynamics. Demographic modeling suggests that persistence of large branchiopods under these scenarios of climate change will hinge on hatching strategies and long-term survival of resting eggs (Pinceel et al., 2016a). However, these very traits may be compromised by exposure to temperature extremes as forecasted for regions such as southern Africa under climate change (Pinceel et al., 2018).

10.10.2 Conservation status

Despite their ecological significance, temporary wetlands are usually not prioritized for conservation (Dalu et al., 2017). In line with this, also the conservation status of large branchiopod species in (sub)tropical regions remains largely unknown, mainly due to a lack of knowledge on their diversity and ecology (Brendonck et al., 2008). This complicates development of science-based conservation strategies. Lack of information also inhibits proper categorization of the conservation status of large branchiopods according to IUCN (1996) criteria in most regions considered here. In South Africa, where rather good background information is available, some attempts were made to categorize anostracan species (Hamer and Brendonck, 1997; De Roeck et al., 2007). Of the 46 anostracan species assessed by Hamer and Brendonck (1997), 13 species were data deficient, 2 were considered critically endangered, 4 endangered, and 3 were considered vulnerable. In South Africa, progress is also made toward a framework for the assessment of the ecological integrity of temporary wetlands (Bird and Day, 2016).

It is not sure how many known species have gone extinct since their first description. However, species extinctions are highly likely given that a good number of species are only known from their type locality or have a limited distribution. An iconic example of species loss due to habitat alteration is the loss of the anostracan *Rhinobranchipus martensi*, of which the type locality was transformed in a permanent fish pond even before the species description was published (Martens and de Moor, 1995; Brendonck, 1995).

10.10.3 Protected areas

Several studies reported high branchiopod richness in wetlands located in nature reserves (Ferreira et al., 2012; Nhiwatiwa et al., 2014; Lumbreras et al., 2016; Dube et al., 2020). About 50% of the then known large branchiopod species from southern Africa were collected in protected areas (Hamer and Brendonck, 1997). Dube et al. (2020) reported a significantly higher species richness of large branchiopods in a conservation area (Ndumo Game Reserve) in South Africa compared to the wetlands in surrounding communal lands and underlined the need for the continued protection of areas (Dube et al., 2020). Malan et al. (2015) compared the overall environmental condition of 65 wetlands in the Western Cape Fynbos biome over a 25 years period. Improvement of the ecological health in about 30% of studied wetlands was mainly due to protection of these wetlands within new conservation areas, while deterioration of a similar fraction of wetlands was mainly due to invasion of alien plants and urban and agricultural development. The authors also underlined the importance of a citizen science approach to educate and incentivize land-owners about the benefits wetlands supply. Even within protected areas, wetlands are sometimes modified and made permanent to, for instance, supply water sources to resident big game or to accommodate fish populations (Martens and de Moor, 1995).

10.10.4 Biomonitoring

As permanent and exclusive inhabitants of temporary wetlands, large branchiopods have potential as focal groups for biomonitoring (Nhiwatiwa et al., 2014; Bird et al., 2019; Greenfield, 2022, Chapter 20). However, living in dynamic systems with major daily and seasonal fluctuations in abiotic conditions, large branchiopods are quite robust and have limited indicator value for habitat quality. Furthermore, several species seem to be generalists and can occur in vegetated versus nonvegetated and turbid versus clear wetlands. The lack of easy diagnostic characters, especially in clam shrimps and notostracans, make quick in situ identification of species problematic. Although several biomonitoring tools based on macroinvertebrates have proven to be efficient and relevant for assessing the status of river systems, similar approaches are less developed or found less reliable for temporary wetlands (Bird et al., 2013, 2019; Van den Broeck et al., 2015).

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Chapter 11

Macroinvertebrates

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11.1 Introduction

Wetlands are lands that are characterized by the presence of water on the surface or within the root zone, permanently or temporarily during the year (Mitsch and Gosselink, 1986; Wasserman and Dalu, 2022, Chapter 1). The period in which the soil can retain water above or below ground is the dominant factor determining the occurrence of wetlands as well as the types of plant and animal communities living in them. The occurrence of wetlands is therefore tied to the presence or absence of water, which also is a reflection of the global environment where they occur (Mitsch and Gosselink, 1986). The dominant wetland types in semiarid and arid areas are temporary systems which constitute an important category of wetlands (Fig. 11.1, Jones and Day, 2003). Temporary wetlands are often ignored because of their small size and temporary presence of water. It is for this reason that they have often been overlooked or even regarded as unimportant when compared to permanent wetlands (De Meester et al., 2005). Temporary wetlands are an example of hydro-geomorphic units of inland aquatic systems that are further distinguished on the basis of their level of permanence and connectedness to a river (Ollis et al., 2013, 2015). Among the temporary wetland types, playas, depression, and floodplain wetlands are common in tropical regions, especially in arid and semiarid areas. Depression wetlands (also known as endorheic wetlands) are inland aquatic ecosystems with closed (or near-

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FIGURE 11.1 Examples of permanent wetlands (left) from Ndumo Game Reserve South Africa, and temporary wetlands from Tembe Elephant Park, South Africa (middle right), near Ndumo Game Reserve (bottom right) and rock pool from Botswana (top right). *Pictures of permanent wetlands by Trevor Dube, temporary wetlands by Wayne Matthew, and rock pools by Luc Brendonck.*

closed) basins in which water accumulates by precipitation and runoff (Cowardin et al., 1979; Ollis et al., 2015; Job et al., 2022, Chapter 2). The depression wetlands are aquatic habitats within a terrestrial matrix. Endorheic wetlands are distinguished from floodplain wetlands that occur mostly on flat or gently sloping land formed by an alluvial river channel, and are subject to periodic connection with a river channel.

11.2 Diversity of macroinvertebrates in depression and floodplain wetlands

Although macroinvertebrates dominate the faunas of wetlands worldwide, in terms of species diversity, abundance, and biomass, they have historically been understudied (Williams, 2006; Bird et al., 2019). Early research to understand the ecology and diversity of wetland invertebrates started mainly because of the realization of their importance as food sources for waterfowls and potential vectors of disease (e.g., Tabanidae and Culicidae) (Murkin and Wrubleski, 1988; Batzer et al., 1999). Subsequently, several regions of the world now have produced reviews on the taxonomic and ecological aspects of major macroinvertebrate taxa from permanent and temporary wetlands; North America (Batzer et al., 1999), Europe (Bazzanti et al., 1996; Bazzanti, 2015), and southern Africa (Bird et al., 2019).

The tropics house some of the world's largest wetland systems, including Amazon River Basin, Congo River Basin, Pantanal, Lake Chad Basin, and Nile River Basin (Fraser and Keddy, 2005). Unlike the riverine wetlands of the Afrotropical Congo and Nile River basins, the macroinvertebrates of Lake Chad have been intensively studied (Carmouze et al., 2012). The Congo River Basin is largely unknown (Keddy et al., 2009), lacking information on biotic communities in wetlands (Fraser and Keddy, 2005). Similarly, in the Neotropics, macroinvertebrates of the Pantanal Floodplain Wetland have been better studied (Molina et al., 2011; Wantzen et al., 2016) than those of the riverine Amazon River Basin. In the Afrotropics, the Pongolo Floodplain in South Africa (Smit et al., 2016) and the Okavango Delta in Botswana (Davidson et al., 2012; Dallas and Mosepele, 2020), are globally important wetland systems. The macroinvertebrate community dynamics of Pongolo and Okavango Floodplain Wetlands have been studied extensively (Davidson et al., 2012; Dube et al., 2019, 2020; Dallas and Mosepele, 2020; De Necker et al., 2020). Invertebrate communities in floodplain wetlands throughout the tropical and subtropical regions have high diversity reflecting abundant food resources and complexity of these habitats (Davidson et al., 2012; da Silva and Henry, 2020).

Studies of invertebrate communities from small, isolated, temporary wetlands have been historically limited until recently; especially in Afrotropics (see Bird et al., 2019, for a review of southern Africa). In contrast, the invertebrates of lakes (Muli and Mavuti, 2001; Mengistou, 2016; Odountan et al., 2019) and large permanent wetland systems (Mhlanga and Siziba, 2006; Ferreira et al., 2012) have been extensively studied, because of the ecosystem services they provide. The tropical permanent wetland systems generally have higher diversity than their temporary counterparts (de Ávila et al., 2011; Hart et al., 2014). Similar results are observed in the temperate (Collinson et al., 1995) and Mediterranean regions (Waterkeyn et al., 2008; Slimani et al., 2019), where the taxonomic identification level is highly advanced compared to the tropics. Caution is, however, urged in making a direct comparative assessment between temporary and permanent wetland systems and among different regions due to differential taxonomic identification level and sampling intensity.

Macroinvertebrates in temporary wetlands are typically classified as either transient or permanent resident species (Hall et al., 2004). Transient resident species are usually highly mobile taxa, such as flying insects, that can emigrate to nearby water bodies when conditions in the wetland becomes inhospitable and return when they improve (Wissinger, 1999). Insect communities dominate the diversity and biomass of macroinvertebrate communities of these wetlands, as well as, most freshwater wetlands systems (Batzer and Wissinger, 1996), except for inland saline wetlands (Seaman et al., 1991). Working in the rock pools of the southeastern Botswana, Jocque et al. (2007, 2010) demonstrated that insects (i.e., culicids, chironomids, dytiscids, and odonates) mainly composed of transient taxa, while noninsects (i.e., flatworms, water mites, and crustaceans) were permanent residents. Lahr et al. (1999) showed that predatory insect taxa, aquatic beetles and bugs in Senegalese wetlands, increased toward the end of the hydroperiod, taking advantage of the plentiful food resources.

Permanent resident species, on the other hand, are less-mobile taxa, such as crustaceans and mollusks, that cannot emigrate and must persist in the wetland throughout the inhospitable dry periods (Hall, 1997; Hall et al., 2004). They persist through the dry period by producing desiccation resistant or dormant propagules (e.g., eggs, cysts, or spores) to survive periods of alternating wet and dry phases (Incagnone et al., 2015). Propagules play an important role in the re-establishment of biotic communities once the conditions are favorable. While permanent resident taxa, like crustacea and mollusca, have well-known strategies for surviving drying (Vera et al., 1995; Benvenuto et al., 2015); one insect clade, that generally has transient resident species, is a unique example of a higher metazoan that can survive almost complete desiccation. "sleeping" chironomid (Diptera), *Polypedilum vanderplanki* (Hinton, 1951), is the species that can undergo extreme desiccation through anhydrobiosis, whereby it can lose 97% of body water and can survive up to 17 years (Hinton, 1960). The biochemical and physiological mechanisms allowing this incredible phenomenon are detailed here in Cornette and Kikawada (2011) and Ryabova et al. (2020). Other "sleeping chironomid" species have been described in the Afrotropical region in the last few years (Cornette et al., 2017). Another example of a species that survive the dry phase associated with temporary wetlands is *Aedes aegypti* (Linnaeus), a mosquito native to central Africa but currently widely distributed throughout the world (Soper, 1967; Kraemer et al., 2015; Buxton et al., 2019). This species is involved in the transmission of arboviral diseases such as dengue, zika, and chikungunya in Latin America (Kraemer et al., 2015; Vanhove et al., 2022, Chapter 15). Several studies have shown that other species of *Aedes* are highly adaptable, increasing the risk of movement to non-endemic regions of the world (Bonizzoni et al., 2013; Ryan et al., 2019). Furthermore, the ability of a mosquito egg to resist desiccation during long-distance transport increases the likelihood of incursions and subsequent establishment in nonnative habitats (Faull et al., 2016), including temporary wetlands. For example, Buxton et al. (2020a) sampled larvae of invasive *A. aegypti* from temporary wetland habitats in Botswana.

Using 447 permanent and temporary wetlands from across the world, Batzer and Ruhí (2013) showed that wetland macroinvertebrate assemblages are dominated by about 40 widely occurring taxa at family level that tend to occur idiosyncratically (Table 11.1; Fig. 11.2). However, their study did not include data from wetlands in the Afrotropical region, which has one of the highest densities of temporary wetlands in the world (Brendonck and Williams, 2000). A comparison of macroinvertebrates composition from

TABLE 11.1 A comparison between the macroinvertebrate taxa from temporary and permanent wetlands from a worldwide study and case studies from the Afrotropical region.

		Batzer and Ruhí (2013) ($n = 447$)	Mlambo et al. (2011) ($n = 138$)	Burger et al. (2019) ($n = 17$)	Dube et al. (2019) ($n = 47$)
Order/Class	**Family**	**FOC (%)**	**FOC (%)**	**FOC (%)**	**FOC (%)**
Acarina	Acarina	49.2			
Acarina	Eylaidae		25.4		
Acarina	Hydrachnidae			5.6	
Acarina	Pionidae		8.7		
Bivalvia	Sphaeriidae	38.9			
Coleoptera	Dytiscidae	87.5	95.7	55.6	90.0
Coleoptera	Gyrinidae	20.4			
Coleoptera	Haliplidae	39.6		5.6	4.3
Coleoptera	Hydrophilidae	67.1	50.0	55.6	56.5
Coleoptera	Scirtidae		11.6		
Coleoptera	Hydraenidae		25.4		4.3
Coleoptera	Elmidae			5.6	2.2
Coleoptera	Noteridae			44.4	43.5
Coleoptera	Staphylinidae			5.6	

(*Continued*)

TABLE 11.1 (Continued)

		Batzer and Ruhí (2013) (*n* = 447)	Mlambo et al. (2011) (*n* = 138)	Burger et al. (2019) (*n* = 17)	Dube et al. (2019) (*n* = 47)
Order/Class	**Family**	**FOC (%)**	**FOC (%)**	**FOC (%)**	**FOC (%)**
Coleoptera	Chrysomelidae				6.5
Coleoptera	Curculionidae				15.2
Coleoptera	Erirhinidae				13.0
Coleoptera	Hydrochidae				2.2
Coleoptera	Spercheidae				34.8
Coleoptera	Tipulidae				2.2
Decapoda	Atyidae				23.9
Diptera	Ceratopoginidae	46.5			
Diptera	Chaoboridae	33.8			
Diptera	Chironomidae	97.3	78.3	83.3	49.8
Diptera	Culicidae	46.5	55.1	5.6	52.3
Diptera	Dixidae	18.1			
Diptera	Stratiomyidae	16.1	15.9		10.9
Diptera	Tabanidae	17		5.6	6.5
Diptera	Tipulidae	26.8			
Diptera	Ceratopogonidae				2.2

Diptera	Dolichopodidae				8.7
Diptera	Ephydridae				10.9
Diptera	Syrphidae				2.2
Ephemeroptera	Baetidae	36	67.4	16.7	47.8
Ephemeroptera	Caenidae	13.8			
Ephemeroptera	Lynceidae	11.9			
Ephemeroptera	Polymitarcyidae			5.6	
Gastropoda	Lymanaeidae	28.6	13.8	5.6	56.5
Gastropoda	Physidae	38.3	23.9	5.6	
Gastropoda	Planorbidae	37.6	22.5	11.1	
Gastropoda	Pomatiopsidae		32.6	5.6	
Gastropoda	Thiaridae				4.3
Gastropoda	Ampullariidae				10.9
Gastropoda	Paludomidae				6.5
Hemiptera	Belastomatidae	10.3		22.2	54.3
Hemiptera	Corixidae	69.1	65.9	83.3	71.7
Hemiptera	Gerridae	26.8	15.9	5.6	8.7
Hemiptera	Notonectidae	45.9	59.4	72.2	95.7
Hemiptera	Pleidae	10.5	29.0	16.7	28.3
Hemiptera	Mesovelidae			11.1	45.7

(*Continued*)

TABLE 11.1 (Continued)

		Batzer and Ruhí (2013) (*n* = 447)	Mlambo et al. (2011) (*n* = 138)	Burger et al. (2019) (*n* = 17)	Dube et al. (2019) (*n* = 47)
Order/Class	**Family**	**FOC (%)**	**FOC (%)**	**FOC (%)**	**FOC (%)**
Hemiptera	Velidae			5.6	
Hemiptera	Ochteridae			5.6	
Hemiptera	Naucoridae				19.6
Hemiptera	Nepidae				67.4
Hemiptera	Gelastocoridae				2.2
Hirudinea	Erpobdellidae	14.8			
Hirudinea	Hirudinidae			5.6	
Hirudinea	Glossiphoniidae	22.1		22.2	
Hirudinea	Hirudinae				39.1
Lepidoptera	Nymphulinae				6.5
Malacostraca	Asellidae	17.4			
Malacostraca	Crangoynyctidae	10.3			
Odonata	Aeshinidae	19.2		22.2	41.3
Odonata	Coenagrionidae	38	16.7	55.6	39.1
Odonata	Lestidae	29.5			30.4
Odonata	Libellulidae	45.2		5.6	56.5

Odonata	Gomphidae				2.2
Odonata	Platycnemididae				17.4
Oligochaeta	Lumbriculidae	28.2			
Oligochaeta	Oligochaeta	58.6			45.7
Oligochaeta	Tubificidae	17.9			
Trichoptera	Leptoceridae	10.7			
Trichoptera	Limnephilidae	41.6			
Trichoptera	Echnomidae			11.1	
Turbellaria	Turbellaria	27.5			
Turbellaria	Pseudoceros			11.1	
Crustacea	Paramelitidae	6			
Platyhelminthes	Planariidae			22.2	
Trombidiformes	Hydrachnellae				41.3

FOC, Frequency of Occurence.
Source: Adapted and modified from Batzer, D.P., Ruhí, A., 2013. Is there a core set of organisms that structure macroinvertebrate assemblages in freshwater wetlands? Freshwater Biology 58, 1647–1659; Mlambo, M., Bird, M., Reed, C., Day, J., 2011. Diversity patterns of temporary wetland macroinvertebrate assemblages in the South-Western Cape, South Africa. African Journal of Aquatic Science 36, 299–308; Dube, T., Pinceel, T., De Necker, L., Wepener, V., Lemmens, P., Brendonck, L., 2019. Lateral hydrological connectivity differentially affects the community characteristics of multiple groups of aquatic invertebrates in tropical wetland pans in South Africa. Freshwater Biology 64, 2189–2203; Burger, M., van Vuren, J.H.J., de Wet, L., Nel, A., 2019. A comparison of water quality and macroinvertebrate community structure in endorheic depression wetlands and a salt pan in the Gauteng Province, South Africa. Environmental Monitoring Assessment 191, 1–21.

FIGURE 11.2 Examples of typical macroinvertebrates found in wetlands from left to right then top to bottom Notonectidae (Hemiptera), *Lethocerus* (Hemiptera), *Enochrus* (Coleoptera), *Laccotrephes* (Hemiptera), and *Appasus* (Hemiptera). *Photos by Trevor Dube.*

Afrotropical temporal and permanent wetlands using small data sets collected from depression and floodplain wetlands in South Africa shows similarities with widely occurring macroinvertebrate taxa (Mlambo et al., 2011; Burger et al., 2019; Dube et al., 2019). This shows that wetland macroinvertebrate assemblages share similarities in composition between regions at family level. However, individual wetlands may miss several core taxa, at any given moment especially in the temporary systems, but the composition of core taxa does not readily change regardless of whether the wetlands are permanent or temporary (Batzer and Ruhí, 2013). In the temporary wetlands, macroinvertebrates appear within days of inundation and quickly become abundant, occupying many trophic levels (Williams, 1996). The fauna in temporary wetlands are characterized by taxa adapted to withstand the dry periods or are good migrants that are capable of colonizing nearby permanent wetlands when conditions deteriorate (Williams, 1996, 2006).

Insect groups dominate the composition of core taxa in permanent wetlands, with most aquatic insect families/orders represented (Batzer and Ruhí, 2013). In the temporary wetlands, insects (e.g., hemipterans, coleopterans, and dipterans) survive the dry phase through timely dispersal by moving away from drying temporary wetlands to nearby systems that still hold water (e.g., rivers, lakes, or permanent wetlands) (Strachan et al., 2015; Boix et al., 2016). This movement is energetically costly which might negate movement by certain species. Further, dipterans (and other taxa) that occur are typically juvenile stages that cannot self-disperse until maturation. The dipteran family, Chironomidae, contributes almost the same biomass as other insect taxa in both Neotropical and Afrotropical wetlands (Frouz et al., 2003; Armitage et al., 2012) and this increases with longer hydroperiod (Siziba et al., 2013). For example, chironomids occurred in over 90% of wetlands ($n = 447$) studied by (Batzer and Ruhí, 2013). Similarly, chironomids are reported in

50%–83% of temporary and permanent wetlands in the Afrotropical region (Mlambo et al., 2011). Coleopteran dytiscids and hemipteran corixids have the second and third highest occurrence record after chironomids in both the temperate (Burger et al., 2019) and Afrotropical regions (Mlambo et al., 2011; Burger et al., 2019; Dube et al., 2019).

The dipteran culicids are associated more with freshwater temporary and permanent wetlands than lotic systems (Hanford et al., 2020), occurring in 47% of the wetlands studied by Batzer and Ruhí (2013) and Hanford et al. (2020) and 6%–55% of the wetlands in the Afrotropical region (Mlambo et al., 2011; Burger et al., 2019; Dube et al., 2019). The dipterans contributed a total of eight families to the core list of wetland taxa (Chironomidae, Ceratopogonidae, Culicidae, Chaorbidae, Tipulidae, Dixidae, Tabanidae, Stratiomyidae), which is higher than other taxa, demonstrating the importance of dipterans in wetland invertebrate assemblages (Keiper et al., 2002; Frouz et al., 2003; Batzer and Ruhí, 2013). The Afrotropical region has four additional dipterean taxa (Ceratopogonidae, Dolichopodidae, Ephydridae, and Syrphidae). The production of the manual of Afrotropical diptera should greatly assist in understanding the distribution, taxonomy, and ultimately, ecology of dipterans in tropical wetlands (Kirk-Spriggs and Muller, 2017). The hemipterans Corixidae (69%) and Notonectidae (46%) are common in the temperate region. Similarly, in the Afrotropical region, the corixids and notonectids occur in 66%–83% and 59%–95% of the wetlands (Table 11.1). In addition to insect groups, mollusc taxa, together with water mites and oligochaetes contributed significantly to the core taxa of wetland invertebrate assemblages (Mlambo et al., 2011; Batzer and Ruhí, 2013; Dube et al., 2019).

In contrast to depression wetlands, floodplain temporary wetlands tend to have additional riverine macroinvertebrates such as the shrimp *Caradina* sp., hydrophiloid beetles *Allocotocerus* sp., *Berosus* sp. during flooding and Leptophlebia (Junk et al., 1989; Galatowitsch, 2010; Dube et al., 2017), an indication of invertebrate dispersal from the river into the floodplain wetlands. Also, winged insects (e.g., *Derovatellus* sp., *Hyphydrus* sp., *Hydrochus* sp., *Regimbartia* sp., *Spercheus* sp., *Hydrocanthus* sp.) take refuge in floodplain wetlands from the high velocity of the river (Batzer and Boix, 2016; Dube et al., 2017).

11.3 Ecological processes and factors structuring macroinvertebrate assemblages in temporary wetlands

Metacommunity ecology and its processes have emerged as key factors in understanding the spatial distribution of organisms in isolated habitats such as temporary depression wetlands embedded in a terrestrial matrix (Leibold et al., 2004, 2017). A metacommunity is a set of local communities that are linked by dispersal of multiple and potentially interacting species (Leibold et al., 2004; Gálvez et al., 2021, Chapter 18). Metacommunity ecology is defined principally by four main models, namely patch-dynamics, species-sorting, mass-effects, and neutral models (Leibold et al., 2004). Several studies have contributed significantly to the application of these concepts in temporary wetlands (Vanschoenwinkel et al., 2007, 2008; Nhiwatiwa et al., 2011, 2017b; Dube et al., 2019). In addition to metapopulation and metacommunity dynamics, other processes that may influence species composition in temporary wetlands include habitat selection in heterogeneous environments, species-specific ecological requirements (Nhiwatiwa et al., 2017b), and biotic interactions (Vonesh and Blaustein, 2010). Several studies on temporary wetlands show the importance of both local environmental and spatial variables in structuring macroinvertebrate communities (Hancock and Timms, 2002; Ferreira et al., 2012; Foster et al., 2015; Mabidi et al., 2017).

Connectivity in depression wetlands in a terrestrial matrix is defined by spatial distances between individual wetlands. The connectivity between aquatic systems can influence dispersal of organisms within an area. Dispersal is recognized as an important regional factor influencing the composition of temporary wetlands in a metacommunity context (Cottenie and De Meester, 2004; Vanschoenwinkel et al., 2009; Gálvez et al., 2021, Chapter 18). Therefore by moving from one habitat patch to another, the dispersal of an individual has implications not only for individual fitness, but also for population dynamics, population genetics, and species distribution (Nhiwatiwa et al., 2017b; Haileselasie et al., 2018; Schwentner et al., 2020). In contrast, connectivity in floodplain wetlands refers to links between the main course of a river and the various waterbodies lying in the alluvial floodplain (Amoros and Bornette, 2002). According to the flood pulse concept, hydrological connectivity is the main driver of habitat and aquatic community characteristics in floodplain wetlands (Junk et al., 1989; Amoros and Bornette, 2002). Hydrological connectivity of floodplain wetlands to the main river channel allows dispersal of organisms, nutrients, and sediments between interconnected habitats thereby influencing the biodiversity of the whole floodplain (Junk et al., 1989; Tockner et al., 1999; Amoros and Bornette, 2002; Dube et al., 2019). Dispersal is, therefore, a critical process for proper understanding of both patterns of gene flow and current geographic distributions of macroinvertebrates in depression and floodplain wetlands. Consequently, temporary wetland species assemblages will not only depend on local habitat characteristics but also on the geographical setting and density of wetlands and the ability of specimens to disperse from one wetland habitat patch to another.

The transient nature of temporary depression wetlands and the absence of a direct connection with permanent water sources, excludes most fish. Only annual killifish species are able to persist as they also produce drought resistant dormant eggs (Martin and Podrabsky, 2017; Reichard, 2022, Chapter 12). Being generally fishless, however, does not mean that these temporary systems are "enemy free" (Brendonck et al., 2002). Predation by amphibians and some invertebrates is an important biotic regulating mechanism of temporary wetland communities (Herwig and Schindler, 1996; Brendonck et al., 2002; Boix et al., 2006; Wasserman et al., 2018). For example, notonectids and odonates are top invertebrate predators in temporary wetlands (Brendonck et al., 2002). Further information on food-web structure and complexity of temporary wetlands has more recently been derived using a stable isotopes approach, highlighting the variable nature of the systems (Dalu et al., 2016, 2017b,c; De Necker et al., 2020; Cuthbert et al., 2022, Chapter 17).

Besides the alternating dry−wet periods, local physical environmental variables such as habitat morphometry (Artois et al., 2004; McCulloch et al., 2008), water quality (Hamer and Appleton, 1991; Mabidi et al., 2016; Dube et al., 2017), hydroperiod (Therriault and Kolasa, 1999; Kulkarni et al., 2019), soil structure and composition (Tuytens et al., 2015; Mabidi et al., 2016) jointly constitute a template along which macroinvertebrate communities develop in temporary wetlands (Wellborn et al., 1996; Wissinger et al., 2009). The combination of physical environment and biotic interactions such as predation limits species distributions and success (Schneider and Frost, 1996; Nhiwatiwa et al., 2009; Deemy et al., 2022a,b, Chapters 4 and 6). Among the local environmental factors, hydroperiod (duration, timing, predictability) is the most cited driver of macroinvertebrate community assembly in both the tropical and subtropical areas (Waterkeyn et al., 2008; Boven and Brendonck, 2009; Hill et al., 2016). Hydroperiod directly and indirectly affects wetland macroinvertebrate communities because it influences other abiotic (dissolved oxygen, pH, nutrients, salinity) and biotic (primary production, detritus breakdown, predation, competition) factors that affect invertebrates (Mabidi et al., 2018; Waterkeyn et al., 2008; Wissinger, 1999).

Furthermore, the effects of macrophytes are known to increase the abundance and diversity of macroinvertebrates in temporary wetlands by providing structural complexity and food (Ferreira et al., 2012; Bird and Day, 2016; Mabidi et al., 2020). Macroinvertebrate richness and abundances in temporary wetlands tends to be positively associated with macrophyte abundance (De Szalay and Resh, 2000; Dube et al., 2017; Mabidi et al., 2020). The importance of macrophytes as refugia against predators has been observed in field studies and demonstrated in mescosom experiments (Trochine et al., 2006; Lopes et al., 2015; Dube et al., 2019). The submerged plant parts (i.e., leaves, roots, and stems) increase habitat complexity and food resources by providing a substrate for algae and attachment of other microorganisms and invertebrates (Mabidi et al., 2020; Dalu et al., 2022, Chapter 8; Piedade et al., 2022, Chapter 7). Vegetative habitat complexity effects can also interact with temperature when driving interaction strengths in temporary ponds (Buxton et al., 2020c), and sex demographics (Cuthbert et al., 2020b). The increase in algal abundance and organic matter could explain the attraction of other invertebrates through a positive feedback mechanism (Thomaz and Cunha, 2010; Schneider et al., 2015).

In contrast to depression wetlands, fishes and other riverine vertebrates are present in floodplain temporary wetlands that colonized the wetland during flooding (Junk et al., 1989; Dube et al., 2017). When fish are present, they structure the invertebrate community assemblages through selective predation, especially of larger prey (Williams, 1996; Nhiwatiwa et al., 2017b). Other temporal inhabitants, for example, the aquatic beetle genus *Tropisternus*, dragonfly species of *Enallagma* and *Palaemon* shrimp species alter their behavior to reduce predation risk (Resetarits, 2001; Gancedo and Ituarte, 2017).

11.4 Macroinvertebrates as biological indicators of habitat quality in temporary wetlands

Human activities tend to influence the community composition of aquatic invertebrates in wetlands (Ferreira et al., 2012; Nhiwatiwa et al., 2017a; Buxton et al., 2020d). In general, disturbance of habitats is followed by a change in the composition of organisms occupying the original habitat. In this respect, organisms tolerant or intolerant to the changes in their habitat can be used as indicators of habitat disturbance (Van den Broeck et al., 2015b). Macroinvertebrates are used to assess the condition of the aquatic environment or to monitor trends in condition over time (Siddig et al., 2016). Biological indicators integrate overall habitat quality over long time periods and therefore document how episodic and cumulative disturbances impact the ecological integrity of an ecosystem (Dale and Beyeler, 2001; Li et al., 2010; Siddig et al., 2016). Among the potential bioindicators available for aquatic biomonitoring, macroinvertebrates are the most widely used for assessing aquatic ecosystems (Barbour et al., 1999; Aschalew and Moog, 2015), including temporary wetlands (Van den Broeck et al., 2015b). This is because they are ubiquitous and abundant, are taxonomically diverse, show taxon-specific differences in sensitivity to pollution, and have lifecycles long enough to provide a record of environmental quality (Barbour et al., 1999; Ollis et al., 2006). A number of families or genera of water beetles (Coleoptera) have shown to be potential bioindicators for fast and cost-efficient monitoring of the overall quality of wetland ecosystems in the temperate (Boix et al., 2005; Oertli et al., 2005; Sánchez-Fernández et al., 2006) and tropical (Foster et al., 2015; Malherbe et al., 2015) regions. For example, Gutiérrez-Estrada and Bilton (2010) found that the diversity of aquatic Coleoptera was highly correlated with conductivity, turbidity, and depth in temporary waters of southern England. Several studies have shown that macroinvertebrate diversity in temporary wetlands located in protected areas such as national parks is generally high compared to areas exposed to agricultural activities (Chawaka et al., 2018; Dalu and Chauke, 2020; Dube et al., 2020). For example, dragonflies and damselflies (Odonata) larvae have shown to be good biological indicators of grazing impacts on wetlands (Lee Foote and Rice Hornung, 2005). The removal of emergent vegetation by grazers decreased odonate abundance and reproductive effort in the Prairie wetlands (Kostecke et al., 2005; Lee Foote and Rice Hornung, 2005). Empididae and *Mystacides*, were also identified as indicator taxa of early grazed temporary wetlands, north of Strathmore, Alberta (Silver and Vamosi, 2012). The dipterans (i.e., *Aedes*) are indicators of highly disturbed temporary wetlands (Schneider et al., 2015). Similarly, several genera of the subfamily Orthocladiinae such as *Cricotopus*, *Thienemanniella*, *Synorthocladius*, and *Tvetenia* were shown to be good indictors of pond degradation (with preferences for degraded ponds and highly perturbed sites) in Mediterranean flatland ponds, North Iberian Plateau (Trigal et al., 2007). Other studies in the Afrotropical regions have shown that macroinvertebrates are poor indicators of habitat quality in the wetlands (Bird et al., 2013).

11.5 Ecosystem functions and services provided by macroinvertebrates in wetlands

Macroinvertebrates provide a number of important functions and services in temporary aquatic habitats (Mlambo, 2018). These include decomposition of organic matter, energy flow through food webs, nutrient cycling, and transformations (Covich et al., 2004; Cooper et al., 2009; Cuthbert et al., 2022, Chapter 17). In many cases, they are the primary trophic link between aquatic producers and consumers (Batzer and Boix, 2016). They provide food supply for both aquatic and terrestrial vertebrates such as fishes, amphibians, and birds (Boros et al., 2006; Van den Broeck, 2016). Detritivores such as the haliplid beetles and limnephilid caddisflies are critical in nutrient transformations and decomposition of organic matter (van der Valk, 2006; Wissinger et al., 2018). Burrowing macroinvertebrates such as notorid beetles, naidid worms *Tubifex* sp., and chironomids release bound nutrients into the water column, accelerating microbial, algal, and plant growth (Cooper et al., 2009; Adámek and Maršálek, 2012), that in turn are consumed by herbivorous and omnivorous invertebrates and vertebrates. Predatory macroinvertebrates such as wrestling water bug *Lethocerus* sp., water scorpions *Laccotrephes* sp., predaceous diving beetle *Hydaticus* sp., and great water bug *Hydrocyrius* sp. are important in structuring the abundance and sizes of their prey (Batzer and Boix, 2016). Filtering collectors such as filter-feeding water beetles (Spercheidae) and the fairy shrimps (anostracans) improve the water quality by filtering suspended particulates from the water column (Van den Broeck et al., 2015a; Batzer and Boix, 2016; Brendonck et al., 2022, Chapter 10).

In Afrotropical context, wetlands macroinvertebrates are immensely relevant for human welfare and health, given the vectorial capacity of certain species (Malan et al., 2009; Appleton and Madsen, 2012; Buxton et al., 2020b). Recently, experimental studies (Buxton et al., 2020e; Cuthbert et al., 2020a) have shown that natural fauna of temporary wetlands such as notonectids *Anisops sardea* Herrich-Schäffer, 1850 and *Enithares chinai* Jaczewski, 1927, and calanoid copepods such as *Lovenula raynerae* (Suárez-Morales et al., 2015) can be useful in the control of vector mosquito populations. Similarly, biological control of pulmonate snails, especially those that serve as intermediate hosts for bloodflukes responsible for the schistosomiasis (i.e., bilharzia), has been explored using both native and nonnative invertebrates (Appleton et al., 2004; Maharaj et al., 2005). In fact, most of the invasive crayfish (Decapoda) species that have been introduced in sub-Saharan Africa were for aid in the control of bilharzia-causing snail populations (Mikkola, 1996; Madzivanzira et al., 2020; Pegg et al., 2022, Chapter 16), even though these species have had further impact (de Moor, 2002; Weyl et al., 2017).

11.6 Threats to temporary depression and floodplain wetlands

Temporary wetlands have long been overlooked as habitats in conservation management due to their temporal nature and often small size. This has contributed to their rapid disappearance worldwide (Brendonck et al., 2008). A combination of socio-economic (e.g., agriculture and urbanization) and climatic factors (e.g., climate change) are a threat to the functioning and existence of temporary wetlands (Dalu et al., 2017a).

Wetlands are highly vulnerable to climate change and might be affected in different ways: by changes in the hydrological regime; changes in precipitation patterns and local changes in temperature (Mitsch et al., 2010; Junk et al., 2013; Barros and Albernaz, 2014; Fay et al., 2016). A decrease in precipitation especially in arid and semiarid areas will result in a general decrease in inundation length of temporary wetlands due to their small size which has direct and indirect impacts on the wetland invertebrates (Brooks, 2009; Tuytens et al., 2014; Fay et al., 2016). Future projections of climate change in arid and semiarid regions indicate that they will become drier (IPCC, 2014; Valdes-Abellan et al., 2020) which would entail a decrease in inundation length of temporary wetlands thereby affecting the life cycles of aquatic invertebrates. Due to the exacerbation of time stresses associated with reduced hydroperiods, macroinvertebrate communities in wetlands may have less time to reach maturation and reproduce, thus potentially threatening population persistence. Furthermore, climate change is associated with increasing temperatures of aquatic ecosystems (Saintilan et al., 2019). Water temperature has been shown to affect the distribution, physiology, and morphology of many aquatic invertebrates (Bhowmik and Schäfer, 2015). For example, elevated water temperatures significantly affect the survivorship of odonate (Insecta: Odonata) early stages and surviving adults (Starr and McIntyre, 2020). Similarly, elevated temperatures can compromise hatching success of invertebrates reliant on resting eggs for population success (Sukiato et al., 2019; Tladi et al., 2020). Therefore climate change can have far-reaching consequences on the structure and functioning of temporary wetlands.

Habitat fragmentation due to agricultural expansion is another human activity contributing to the decline of natural wetlands throughout the world, with severe consequences for species conservation (Gomes and MagalhãesD. Jr, 2004). For example, the macroinvertebrate abundance, richness, and composition was shown to reduce during the rice cultivation cycle in southern Brazil wetlands (Maltchik et al., 2011). The conservation of the species in rice field channels may be an important alternative for biodiversity conservation, where more than 90% of wetland systems have already been lost (Maltchik et al., 2011, 2012). Other studies show that macroinvertebrates are poor indicators of agricultural activity in wetlands (Hornung and Rice, 2003; Gleason and Rooney, 2017).

In contrast to depression wetlands, the ecological integrity of floodplain wetlands is sustained by the natural variability of a river's flow regime (Poff and Zimmerman, 2010; Richards et al., 2020). The features of streamflow regime (timing, frequency, duration, and magnitude) tends to influence hydrological connectivity of the floodplain to the river and can thereby affect aquatic floodplain diversity and communities (Tockner et al., 1999; Talukdar and Pal, 2019). For example, hydrological connectivity affected both taxonomic and trait community composition, and reduced local taxa diversity of tropical floodplain wetlands (Dube et al., 2019). It is therefore important to maintain the natural variability of water flow in floodplain ecosystem by releasing water from the dam walls.

11.7 Conclusion

The macroinvertebrates diversity in wetlands of different regions is generally high. In the Afrotropical region, some species have unique traits that enable them to survive the dry phase of temporary wetlands. Globally, the permanent wetlands have been more extensively studied than temporary wetlands, with the Afrotropical region being no exception. There is also still much need for further research on tropical wetlands in general, as they are largely understudied compared to temperate systems (see Irvine et al., 2022, Chapter 19). This is particularly relevant for Afrotropical wetlands, as there are major gaps on the ecology and macroinvertebrates distribution record for these systems. Much of the research work on wetland macroinvertebrates in the region is concentrated in southern Africa, specifically in South Africa.

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Chapter 12

Fish

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12.1 Introduction

Fish diversity in tropical freshwater wetlands mirrors diversity and heterogeneity of available habitats and their dynamic connectivity. This leads to functional, life history, and taxonomic diversity of local fishes. Wetland fish have to cope with dynamic environmental and ecological conditions and local fish communities contain a mix of species loosely associated with wetlands and wetland-specialized species. When strictly defined, wetlands are characterized by the existence of relatively shallow water or water-saturated soil (often with anaerobic conditions) (see Wasserman and Dalu, 2022, Chapter 1; Job and Sieben, 2022, Chapter 2; Deemy et al., 2022a,b, Chapter 3). However, deeper water habitats are often considered a part of wetlands (e.g., Alho and dos Reis, 2017) and they are especially relevant for fish, as they typically require some shelter from desiccation. In this chapter, both temporary and permanent wetlands are considered, including floodplain systems of large tropical rivers.

High global diversity of tropical wetland fishes is also associated with the fact that this environment is widespread in Africa, the Neotropics (Central and South America) and southeast Asia, and relatively common in northern Australia and New Guinea. Given the poor long-range dispersal abilities of freshwater fishes, tropical wetland fish communities are dominated by different taxonomic groups across continents and biogeographical regions. Several clades of characiform (tetras), siluriform (catfish), and cichlid fishes taxonomically dominate Neotropical regions. In Asia, cypriniforms replace characiforms, while local perciform taxa (such as anabantoids and ambassids) replace cichlids. African wetland ichthyofauna is composed of all main taxonomic groups and cypriniform fishes coexist with characiforms, anabantoids with cichlids, and catfishes are common. Given the much longer

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(although more ancient) link between Africa and Neotropics, fish fauna of the two regions is more similar than to Asia. In northern Australia and New Guinea, wetland ichthyofauna is severely taxonomically depauperated. Rainbowfishes (Melanotaenidae: Atheriniformes) occupy niches taken by cypriniforms and characiforms, percichthyids occupy niches inhabited by cichlids and anabantoids elsewhere, and catfishes (Siluriformes) are relatively common. The diverse origin of continental ichthyofaunas enables interesting comparisons of convergent evolution of functional and life-history traits of tropical wetland fishes across regions. To this end, wetland fishes appear especially suitable for a quantitative comparative study on niche space and use within the concept of "periodic table of niches" (Winemiller et al., 2015), which classifies five primary niche dimensions. Those are habitat use, reproductive and life history, trophic ecology, defense mechanisms, and metabolic strategies.

12.2 Flood pulse: dynamic connectivity

The flood pulse concept characterizes how seasonal dynamics in water level connect river channels with associated habitats in the floodplain (oxbow lakes, backwaters, temporary pools, and flooded terrestrial ground), resulting in maintenance of high functional and organismal diversity (see Deemy et al., 2022a,b, Chapter 6). Flood pulse and associated interconnection of habitats is critical for the functioning of most wetlands worldwide, including the functioning of fish communities. It redistributes nutrients and increases primary productivity, creates new habitats and enables spatial redistribution of organisms, including fishes (Junk, 1999). In the tropics, flood pulses are often highly predictable on a seasonal basis and wetland ecosystems, communities and organisms are adapted to those predictable changes. For example, the annual flood pulse of the upper Paraguay River is the major driver of the changes in the fish communities within diverse Pantanal habitats, as it enables species turnover between periods of low and high water (Da Silva et al., 2010).

The flood-pulse concept predicts a greater diversity of trophic resources available for fish species during floodplain inundation. Pool et al. (2017) used stable isotopic data from 17 fish species from Tonle Sap Lake, an extensive seasonal wetland in central Cambodia which is dependent on substantial annual flooding from the Lower Mekong River, to demonstrate that fish indeed expanded their trophic niches during the flood phase, with broader within-species trophic niches and larger interspecific overlaps. In the Rio Grande (southwestern USA), seasonal flooding extended the narrow algivorous trophic niche of an endangered cyprinid (*Hybognathus amarus*) in streams to exploit rich invertebrate resources in adjacent wetland habitats (Magana, 2013). Wetland habitats are often critical for reproductive activities (spawning) and offspring survival (nursery zones) of tropical fishes.

12.3 Wetland habitat types and associated fish fauna

A larger wetland area often translates into a greater diversity of its habitats and hence increases functional and taxonomic richness of its fish community. Tropical wetlands range from extensive areas such as Pantanal (in the Paraguay River Basin), Okavango Delta and Tonle Sap (in the River Mekong Basin) through intermediate size floodplain systems of many tropical rivers to small, isolated habitat patches such as seasonal marshes, and vernal, rain-fed pools of grassland landscapes, exemplified by temporary pools in semiarid southern Mozambique and wetland marshes in southern Brazil. Consequently, the Great Lake of Tonle Sap Wetland supports at least 150 fish species (Campbell et al., 2006) and the estimated fish species richness in Pantanal is over 300 species (Alho and dos Reis, 2017). In contrast, small seasonal wetlands in savanna regions of Africa and southern Neotropics support few (1−9) fish species (Maltchik et al., 2010; Reichard et al., 2017).

Large wetlands are typically associated with a large river system composed of a river channel, backwaters, oxbow lakes (which are disconnected from the main river for most of the year), and a multitude of small, temporary streams and pools (Fig. 12.1). In large, complex wetlands, the main river channel serves as a refuge and central migratory pathway for wetland fish (Fig. 12.1A). Tributaries (Fig. 12.1C) and side channels are generally shallower and may be more prone to seasonal changes in environmental and biotic conditions—from water level and temperature, flow conditions and oxygen availability, to the presence of vegetation and predators. Tributaries and side channels may play a similar role to the main river channel but create a finer habitat structure. They also play an important role in fish migrations to flooded temporary habitats of a wetland. Wetlands associated with large rivers may be dominated by forests (e.g., in the Amazon Basin) or shrubs and grasses (e.g., freshwater wetlands in savannas and pampas of southern Brazil), with consequences for the composition of their ichthyofaunas. Backwaters are nonflowing sections of the river channel, connected directly to the main river system. Oxbow lakes (Fig. 12.1B) are former river meanders that lack permanent connections to the flowing section. Oxbow lakes, in particular, harbor seasonally very dynamic fish communities, in response to seasonal fluctuation in water level (Fig. 12.1B, D, and F) and associated conditions and resources (White et al., 2012). Finally, temporary streams (Fig. 12.1E), pools and marshes are exploited by many fish species for feeding and reproduction, utilizing their short-term but high resource availability during the inundated phase. They also act as refuges from predation by larger fishes and provide elevated water temperatures during the daytime, which may increase metabolic activity and growth rates of resident fish. Few species have evolved to be permanent residents of temporary pools.

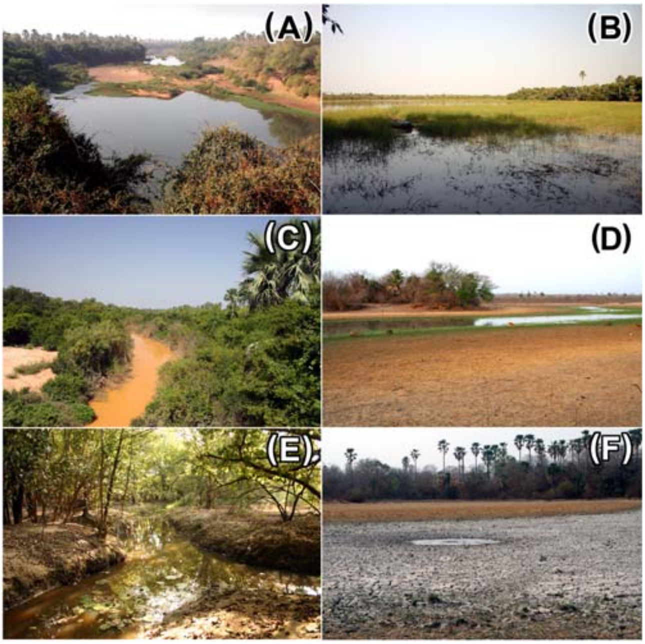

FIGURE 12.1 Wetland habitats associated with the middle reach of the Gambia River. The system consists of fluvial habitats (left panel), with main river channel (A), a series of tributaries (C), and temporary streams (E) and stagnant water habitats (right panel). Oxbow lakes were highly dynamic, with large expanse in area during the wet season (B), shrinking in dry season (D) and occasional desiccation in the driest weeks (F). *Photo courtesy: Martin Reichard.*

To demonstrate the dynamic nature of fish communities associated with wetland systems, I provide examples of fish communities from an extensive wetland system in the middle Gambia River Basin in Senegal, a series of isolated wetland pools in Pantanal, and a small wetland associated with seasonal marshes in southern Brazil.

12.3.1 Example 1: wetland system associated with the middle reach of the River Gambia

The Gambia River is the last of the large West African rivers with a natural flood regime, with no impoundments along its 1120 km long stretch. Its large floodplain is seasonally inundated by river floodwater, creating a network of habitats and allowing fish to move freely across the wetland. A 5-year study was conducted in the Niokolo Koba National Park in the middle reaches of the river. The flow regime of the river is natural, with a peak discharge in September ($\sim 1500\,\mathrm{m^3\,s^{-1}}$) and minimal flow in May to June ($\sim 4.5\,\mathrm{m^3\,s^{-1}}$). In the study area, the main river channel never desiccated, but formed a set of disconnected isolated pools during periods of the lowest flow. A total of 62 fish species from 22 families were recorded over the 5 years (Blažek et al., 2012; White et al., 2012).

In a multiyear analysis, estimates of fish species richness in the main channel (width of approximately 100 m) increased by 50% during the wet season (White et al., 2012). Only one large mormyrid *Mormyrus hasselquisti*, a malapterurid catfish *Malapterurus occidentalis* and a riverine cichlid *Tylochromis intermedius* were recorded exclusively in the main river channel (Blažek et al., 2012), while other species regularly used a wider spectrum of habitats.

Fish species richness in tributaries of the main river, represented by three permanent streams 2–30 m wide, increased in the wet season almost twofold. A claroteid catfish *Chrysichthys mauri*, mochokid catfish *Synodontis schall*, a syngnathid pipefish *Enneacampus ansorgii*, and a gobiid *Porogobius schlegeli* were associated with tributaries and the main river channel (Blažek et al., 2012), indicating their associations with more fluvial conditions. Other species, such as *Ctenopoma petherici* (Anabantidae) (Fig. 12.2D), were present only in temporary floodplain pools in the wet season, and in oxbow lakes and tributaries in the dry season (White et al., 2012).

Oxbow lakes, connected to the main river via temporary channels in the wet season, demonstrated the highest (fourfold) increase in species richness between wet and dry seasons. *Polypterus senegalus* (Polypteridae) (Fig. 12.2H), *Heterotis niloticus* (Osteoglossidae), and *Brienomyrus niger* (Mormyridae) were highly associated with oxbow lakes, though also occurred in other habitat types. During the dry season of some study years, several oxbow lakes desiccated. The last species recorded in such habitats was *Heterobranchus longifilis* (Clariidae) (Fig. 12.2F) that were trapped in desiccating mud and predated by large flocks of marabou storks *Leptoptilos crumeniferus*. Smaller temporary habitats, such as seasonal pools and streams, had diverse ichthyofauna that exploited this seasonal habitat with rising water level. Only an annual killifish *Pronothobranchius gambiensis*, a specialist in desiccating wetland pools, was recorded exclusively in temporary habitats (Blažek et al., 2012; White et al., 2012).

All other species recorded in the wetland used multiple habitats across seasons, despite various affinities to particular habitat types. For example, a small barb *Enteromius niokoloensis* and a small distichodontid *Nannocharax ansorgii* were recorded only in flowing water habitats, be it main river channel, tributary or a temporary stream during the wet season. A large number of species (e.g., *Papyrocranus afer*: Notopteridae, *Schilbe intermedius*: Schilbeidae, *Auchenoglanis occidentalis*: Bagridae (Fig. 12.2C), *Clarias anguillaris*: Claridae, *Brycinus leuciscus* (Fig. 12.2E) and *Rhabdalestes septentrionalis*: Alestidae, *Labeo coubie*, *Enteromius macrops* and *Enteromius baudoni*: Cyprinidae; Fig. 12.2A, *Synodontis nigrita*: Mochokidae, *Hemichromis bimacultus*: Cichlidae and *C. petherici*: Anabantidae; Fig. 12.2D) were common across all wetland habitats (Blažek et al., 2012).

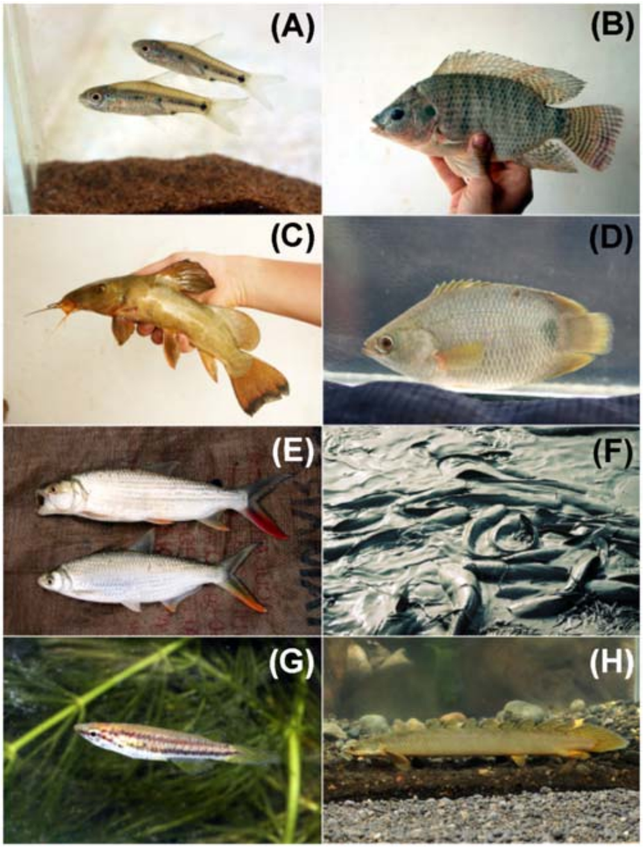

FIGURE 12.2 Characteristic fish species in wetlands of the middle Gambia River. (A) *Enteromius baudoni* (Cyprinidae) and (B) *Oreochromis niloticus* (Cichidae), (C) *Auchenoglanis occidentalis* (Bagridae), (D) *Ctenopoma petherici* (Anabantidae), and (E: lower) *Brycinus leuciscus* (Alestidae) are examples of species widespread across all wetland habitats. Body shape and colouration of *Alestes baremoze* (Alestidae) (E: upper) is an example of aggressive mimicry of *B. leuciscus*. (F) *Heterobranchus longifillis* are often the last surviving fish in desiccating habitats. (G) *Epiplatys bifasciatus* (Nothobranchiiidae) is an example of an invertivore associated with flooded river margins. (H) *Polypterus senegalus* (Polypteridae) are associated with oxbow lakes, often found in dense vegetation, and adapted to frequent hypoxia. *Photo courtesy: Radim Blažek.*

12.3.2 Example 2: seasonal wetland pools of Northern Pantanal in Brazil

Seasonal pools are characteristic habitats for wetland fishes. Tondato et al. (2013) compared fish communities from ten temporary pools and linked species presence to habitat characteristics. The composition of fish communities (based on a sample of 8735 individuals from 29 species) varied among ponds but was not associated with the level of isolation from other aquatic habitats. Instead, fish communities were structured by water depth, macrophyte vegetation richness and cover. Beta diversity was high, with only 14 species detected in more than three pools. Characids such as *Markiana nigripinnis* and *Moenkhausia sanctaefilomenae* and a cichlid *Crenicichla vittata* were associated with deep water. In contrast, *Hoplias malabaricus* (Erythrinidae), *Aequidens plagiozonatus* (Cichlidae) and *Synbranchus marmoratus* (Synbranchidae) lived in shallow and nonvegetated areas. A catfish *Trachyleopterus striatulus* (Auchenopteridae), a gymnotiform *Eigenmannia trilineata* (Sternopygidae) and a small characiform *Psellogrammus kennedyi* (Characidae) inhabited pools and areas with greater richness and extent of macrophyte cover. Finally, many smaller fish species were generally widespread across the pools and habitats, especially *Hypessobrycon elachys* and *Serrapinnus calliurus* (Characidae), which composed 54% and 31% of all collected fish individuals, respectively (Tondato et al., 2013). Representative species are illustrated in Fig. 12.3.

12.3.3 Example 3: pools associated with shallow marshes in southern Brazil

The region with the highest abundance of small wetlands is located between the permanent lakes Lagoa do Peixe and Laguna dos Patos in a coastal plain of Rio Grande do Sul state in Brazil. A total of 25 fish species were recorded in 9 small wetland pools formed on flooded grassland vegetation (Maltchik et al., 2010; Lanés et al., 2016). Three of the species were annual killifishes (*Austrolebias minuano* (Fig. 12.4D), *Austrolebias wolterstorffi*, and *Cynopoecilus fulgens* (Fig. 12.4C): Rivulidae), surviving habitat desiccation as diapausing embryos in dry mud. Of the other species, adult *H. malabaricus* (Erythrinidae), *Callichthys callichthys* (Callichthyidae) (Fig. 12.4F), and *Synbranchus marmoratus* (Synbranchidae) (Fig. 12.4E) are reported to temporarily survive desiccation in mud, a clear adaptation to life in wetlands. Many species used the pools opportunistically and could not have survived habitat desiccation. One half of fish diversity in wetland pools was composed of characiform fishes, with dominant species being small-bodied *Astyanax eigenmanniorum* (Fig. 12.4H), *Hyphessobrycon igneus*, and *Cheirodon interruptus*. Another very common species was a live-bearing poecilid *Phalloceros caudimaculatus* (Lanés et al., 2016). In general, population density of annual species declined throughout the season, from high abundance in the wettest period (when annual killifishes hatched) to very low abundance near pool desiccation. In contrast, population densities of nonannual species varied greatly, as fish entered and left small wetland pools during periods of connection within the grassland matrix (Lanés et al., 2016). Such broad coexistence between specialized annual fish species and nonannual fish species is in contrast with the occurrence patterns of six annual killifish

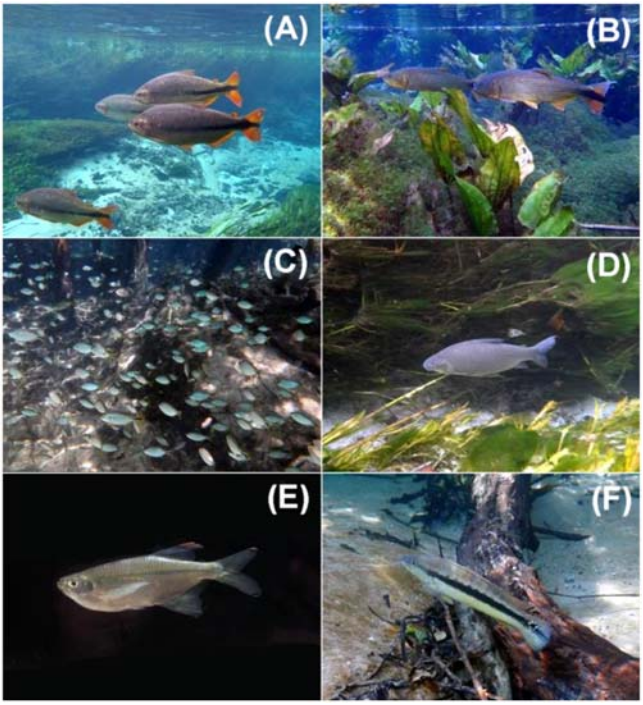

FIGURE 12.3 **Characteristic fish species of Pantanal.** Underwater photographs of (A) a frugivorous *Brycon hilarii* (Characidae), (B) its aggressive mimic *Salminus brasiliensis* (Characidae), (C) large shoal of omnivorous *Astyanax lacustris* (Characidae), (D) detritivorous *Prochilodus lineatus* (Prochilodontidae), (E) *Pseudocorynopoma doriae* (Gasteropelecidae) specialised on feeding terrestrial insects from water surface (Alestidae), and (F) *Crenicichla lepidota* (Cichlidae), a resident invertivore with equilibrium life history and parental care. *Photo courtesy: Martin Reichard.*

species from ephemeral wetland pools in Venezuelan Llanos. There, arrival of nonannual fishes to pools formerly disconnected from the permanent water bodies during elevated water level resulted in the complete disappearance of annual fish species (Nico and Thomerson, 1989).

12.4 Reproductive strategies and spawning migrations

Reproductive strategies of wetland fishes, and their association with flood pulse dynamics, can be exemplified by fishes from the Pantanal (Alho and dos Reis, 2017). Four main types of reproductive strategy were classified. Long-distance migratory species annually migrate upstream to spawn, their eggs and larvae being passively carried down by the water current. Juveniles feed on resources from highly productive lowland wetlands. In Pantanal, catfishes such as *Pseudoplatystoma reticulatum* and *Pseudoplatystoma*

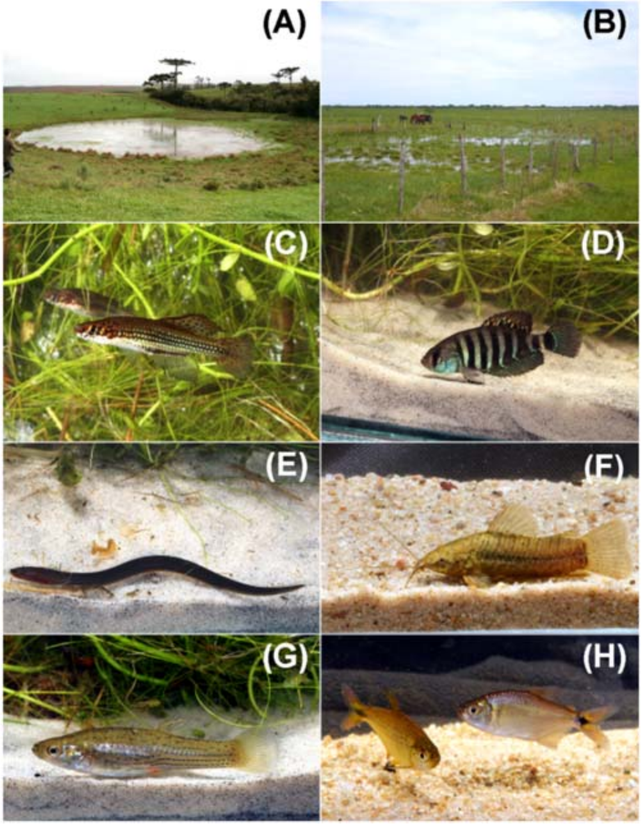

FIGURE 12.4 Shallow marshland pools in southern Brazil and associated fish species. Highland (A) and lowland (B) wetland habitats are associated with pastures. Annual killifishes *Cynopoecilus fulgens* (C) and *Austrolebias minuano* (D) (Rivulidae) survive habitat desiccation as dormant embryos. *Synbranchus marmoratus* (Synbranchidae) (E) and *Callichthys callichthys* (Callichthyidae) (F) are species with adaptations to hypoxia. *Jenynsia multidentata* (Poecilidae) and *Astyanax eigenmanniourum* (Characidae) are frequent visitors of small seasonal wetlands. *Photo courtesy: Martin Reichard (A, B) and Radim Blažek (C−H).*

corruscans (both Pimelodidae) or characiforms *Salminus brasiliensis* (Fig. 12.3B), *Brycon hillari* (Characidae), *Megaleporinus macrocephalus* (Anostomidae), and *Prochilodus lineatus* (Prochilondontidae) (Fig. 12.3D) are typical examples of long-distance upstream migrants (Alho and dos Reis, 2017).

The second strategy includes fish species that perform small migratory movements between flooded wetland habitats such as oxbow lakes and the river channel to spawn in the rivers during seasonal floods. Examples from Pantanal include a characiform *Mylossoma duriventre* (Serrasalmidae) and gymnotiform knife fishes *Gymnotus* spp. (Gymnotidae). The third strategy includes fish that migrate from the river to flooded wetlands to spawn, such as piranhas (i.e., *Serrasalmus* spp., and *Pygocentrus* spp.: Serrasalmidae) and another predatory fish *H. malabaricus* (Erythrinidae). The fourth reproductive strategy includes fishes that do not perform any spawning migrations, such as many cichlids (Alho and dos Reis, 2017).

The Mahakam River in East Kalimantan, Indonesia, supports a complex wetland composed of river channels, lakes, pools, and swamps (Christensen, 1992). Fish reproductive strategies like those in the Pantanal can be defined in the local fish community. An example of a long-distance migratory behavior associated with reproduction is reported for a cyprinid *Thynnichthys vaillanti*, which migrates 300−400 km upstream to spawning grounds. Another common cyprinid fish in the region, *Leptobarus hoevenii*, lays its eggs on flooded wetland vegetation at the peak of the wet season. Their juveniles grow in shallow, plankton-rich areas of the lakes. *Barbonymus schwanenfeldii* inhabit the main river during the dry season and migrate to the small tributaries to spawn on gravel and sand substrates as water levels rise during the wet season. Staying in breeding areas for extended periods, they produce successive egg batches continuously throughout most of the wet season and their offspring drift downstream to grow in shallower and warmer stagnant waters. Finally, an anabantoid fish (*Helostoma temminckii*: Helostomatidae) migrated only short distances into flooded forest where spawning occurred and juveniles left that habitat with decreasing water level (Christensen, 1992).

12.5 Latitudinal aspects

Position on latitudinal gradient greatly affects regional seasonality in precipitation, flooding, and wetland connectivity. While subtropical regions experience a single rainy season and major seasonal dynamics, equatorial wetlands may be less seasonal or exhibit two phases of rainy and dry seasons every year. This has consequences for life history, migration and timing of reproduction for many wetland fish species. For example, annual killifishes of the genus *Nothobranchius* inhabit seasonal wetland pools in African savanna. In equatorial regions with two rainy seasons, *Nothobranchius* fishes may complete two generations per year, separated by desiccation of their habitats and population persistence in the form of diapausing eggs buried in dry sediment. In more subtropical wetlands, a single generation is produced per year, because habitats only appear during a single rainy season (Reichard, 2015). Similarly, in south India, Sri Lanka and Sumatra, two monsoonal floods per year translate into two reproductive seasons of local fishes (Dudgeon, 2000).

Large wetlands are associated with seasonal flood pulses and they appear to possess higher alpha diversity (more locally coexisting species) and beta diversity (species turnover across local habitats) but a lower gamma (between regions) diversity estimate. Migratory behavior and subsequent dispersal of juveniles support larger ranges and many fish species of seasonally variable wetlands have wider distributions. For example, in Africa, species-rich small barbs (i.e., *Enteromius* spp., Cyprinidae) do not rely on flood pulses and have often evolved into local endemics. In contrast, other cyprinid fishes, *Labeo* spp., exploit larger rivers associated with flood pulses, resulting in wider distributions of certain species but lower taxonomic diversity (Paugy et al., 2003).

In addition to lower seasonality and hence higher benefit from narrower specialization to particular ecological niches, long-term climate and habitat stability maybe responsible for generally greater species richness of tropical wetlands. Local communities in the less-seasonal tropics may be saturated while fish communities at higher (but still tropical) latitudes may have been depauperated in the past due to climate-driven extinctions (droughts), with too little time since recolonization to saturate their communities (Hugueny and Paugy, 1995). To what extent ecological or historic contingencies are responsible for taxonomic diversity gradients is hotly debated, with data on wetland-associated fishes providing important contributions to this debate (Oberdorff et al., 2019).

12.6 Life history strategies

Life-history strategies of wetland fishes are best described by a triangular life-history continuum (Winemiller and Rose, 1992). In this classification system, species are divided according to reproductive strategies and consequent demographic structure. Fishes from each of the three main strategies use resources in their specific manner.

Periodic strategy is perhaps the most characteristic for species that utilize seasonally dynamic connectivity of wetland habitats. The periodic strategy is characterized by short and synchronized reproductive periods, typically coinciding with the peak of the rainy season, increase in main channel discharge and high connectivity across the floodplain. Species with the periodic strategy have high fecundity (number of eggs) and relatively smaller eggs, with little energetic investment into individual offspring. Those species often live in large shoals and migrate to spawning places. Their mating system is promiscuous, with multiple spawners of both sexes releasing their gametes synchronously. It contains many species with a lifespan expectancy of one year, resulting from major mortality that occurs soon after reproductive season. Alternatively, longer-lived species with a periodic strategy survive across several breeding cycles. This strategy is associated with density-independent (environmental) mortality of egg and juveniles and periodic availability of resources and developmental conditions. Species employing this periodic reproductive strategy are capital breeders. Capital breeders store energy acquired over long term and allocate it into their short reproductive bouts.

Many larger cypriniform (e.g., *Thynnichthys vaillanti* and *Labeo senegalus*) and siluriform (e.g., *Pangasius pangasius*) fishes in Asia and Africa, and characiform (e.g., *P. lineatus*) (Fig. 12.3D) and siluriform (*P. corruscans*, Pimelodidae) fishes in the Neotropics are typical representatives of species with a periodic strategy.

Equilibrium strategy is characterized by less pronounced reproductive seasonality, with breeding distributed almost continuously over the seasonal cycle, irrespective of environmental fluctuations. There is much higher investment into individual offspring, either in terms of resources (nutritional value of the egg yolk) or in parental care. Fishes with equilibrium strategy have larger eggs and overall lower fecundity, divided into more frequent batches. Parents employ various modes of active contribution to offspring survival. This often leads to formation of stable pairs that share parental care duties. Alternatively, harem systems are established with dominant males guarding a territory with resources needed for reproduction (i.e., a substrate or habitat patch) and females protect their clutches. Equilibrium strategy results in less fluctuating population dynamics as recruitment is often driven by density-dependent processes and because recruitment and mortality are continuous. Equilibrium strategy is not associated with upstream or lateral spawning migrations.

Cichlid fishes are perhaps the most known examples employing equilibrium life history strategy, from guarding eggs and offspring in a nest to elaborate cases of parental care such as mouthbrooding. Many catfishes (e.g., loricarids in the Neotropics), basal teleosts (e.g., *Gymnarchus* and *Polypterus* in Africa; Fig. 12.2H) or labyrinth fishes in Asia (*Channa*, *Betta*, *Trichopterus*: Anabantidae) also employ equilibrium strategy with extensive parental care.

Opportunistic strategy is described by high investment into rapid sexual maturation and production of offspring, often at the expense of potential late-life fecundity and survival. Seasonality of reproductive effort is typically low but may be associated with availability of habitat or resources that are needed for successful reproduction. This strategy appears common in fishes that suffer strong mortality from predation or frequent habitat disturbance that is less predictable than a seasonal flood pulse. Fish species with an opportunistic strategy have low fecundity, because they reproduce at small size and are income breeders. Income breeders convert energy acquired during their reproductive period into immediate reproductive effort.

Small species associated with marginal wetland habitats are typical opportunistic breeders. Cyprinodontiforms, such as killifishes (Nothobranchiidae in Africa, Rivulidae in the Neotropics, and Aplocheiliidae in Asia) (Fig. 12.2G) or livebearers (Poecilidae in the Neotropics) (Fig. 12.4G) are representative examples of this strategy. Some of the smallest fishes in the world belong to this life history category, including Asian *Danionella* and *Paedocypris* from peat swamp forest wetlands. Small cypriniforms (such as *Rasbora* in Asia and *Enteromius* in Africa) or characiforms (such as *Hyphessobrycon* in the Neotropics) (Fig. 12.4H) are other typical examples of fishes with an opportunistic life history.

It is important to emphasize that this triangular life-history continuum has three endpoints but there is a lot of variation in the life history space that falls into intermediate regions. Given the triangular shape, some species would be characterized as a transition between two of the three strategies, with a mix of traits and features representative of those two endpoints. For example, a species that blends features of periodic and opportunistic strategy would have a temporally constrained reproductive season that spans a period of several weeks or months but is not year-round (e.g., *B. schwanenfeldii*). Consequently, stored energy (capital breeding) may be utilized at the start of reproductive season, with a contribution of new resources (income breeding) as the reproductive season progresses. Overall, wetland fishes represent the full spectrum of life-history strategies, with a periodic strategy typical for seasonal migrants to large wetland habitats and an opportunistic strategy most typical for long-term residents in small wetlands.

12.7 Trophic ecology

Wetland fishes are characterized by high plasticity in the composition of their diet. As tropical wetlands are dynamics systems, many fishes opportunistically expand their trophic niche during periods of food availability (Pool et al., 2017). In a Pantanal pool fish community, herbivory and planktivory disappeared during the dry season, while detritivory, invertivory, piscivory, lepidophagy (scale consumption), and generalist omnivorous strategies persisted throughout the year cycle (Novakowski et al., 2008).

There is a tight link between trophic ecology and morphological features. Feeding habits can be estimated from stomach contents, stable isotopic signature, but also inferred indirectly from dentition, mouth and jaw morphology, and gut length (Keppeler et al., 2020). These morphological features are convergent across main tropical wetland regions and strongly correlate with realized trophic niche. Generalized predatory body shape (slender body, posterior position of dorsal fin) or herbivorous and detritivorous species with very long guts have evolved across disparate regions with tropical wetlands. In addition to typical trophic niches, tropical fishes in general, and species inhabiting larger wetlands in particular, employ some trophic specialization (e.g., frugivory) that are not commonly observed in other fishes. Tropical wetland fishes also occupy trophic niches that are usually taken by aquatic invertebrates in temperate regions. For example, there are more detritivorous fishes in the tropics compared to temperate regions (Winemiller et al., 2007) and some miniaturized cypriniform species (*Paedocypris*, *Danionella*) feed on meiofauna such as rotifers (Kottelat et al., 2006). In the following paragraphs, I outline some typical trophic guilds of tropical wetland fish species.

Invertivory: Feeding on aquatic invertebrates is a common trophic habit among tropical wetland fishes. Insects and crustaceans are the most common prey given their generally high abundance, compared to other aquatic invertebrates. In approximately 25% of fish species in a Pantanal pool, insects were main prey consumed during both the dry and wet season (Novakowski et al., 2008). In addition to aquatic invertebrates, many species feed on terrestrial invertebrates that fall or land on the water surface. Some species specialize on such a diet using upturned (superior) mouths, including the cypriniform *Aplocheilus lineatus* (Aplocheilidae) from Asia, the osteoglossiform *Pantodon buchholzi* (Pantodontidae) from Africa and the characiform *Pseudocorynopoma doriae* (Gasteropelecidae; Fig. 12.3E) from the Neotropics. Archerfishes (*Toxotes* spp., Toxotidae: Perciformes) are capable of shooting down their aerial and terrestrial insect prey by spitting jets of water. Many other fish species consume invertebrates when they become abundant.

Herbivory and detritivory: Herbivorous fish can exploit various plant resources of the wetland. Aquatic vegetation, when available, is the most widely consumed plant resource. Terrestrial plants are accessible seasonally in flooded habitats and are only consumed by specialized species that resort to other food in the dry season. In Africa, *Coptodon rendalli* (Cichlidae) is an example of a species that feeds heavily on floating and emergent vegetation. In the Neotropics, *Pterodoras granulosus* (Doradidae) seasonally consumes large quantity of macrophytes, though it is classified as a feeding generalist (Winemiller et al., 2007). A lot of vegetation is consumed during its decay, as detritus. Several species of Curimatidae in the Neotropics (Fig. 12.3D) and Distichodontidae in Africa feed heavily on plant detritus and contribute significantly to organic matter transfers and nutrient cycling within wetlands. Finally, phytoplankton is consumed by some specialized fish species (e.g., the small cypriniform *Pectenocypris balaena* [Cyprinidae] from the Kapuas, Borneo), though this resource is not stable or available across longer time periods in typical tropical wetlands. The fact that phytoplankton feeding requires morphological specialization (such as specialized gill rakers), which limits exploitation of other resources, constrains its wider utilization among tropical wetland fishes.

Frugivory: Many wetland fishes feed on seeds and fruits that become more available during floods. The most known and studied species from this trophic guild is *Colossoma macropomum*, but at least 275 fish species are reported to feed on fruits and seeds (Horn et al., 2011). Frugivory is very common in the Neotropics (at least 150 species), dominated by herbivorous serrasalmids (*Myleus*, *Colossoma*, *Metynnis*, *Piarctus*; Characiformes), large omnivorous catfishes (Doradidae, Pimelodidae) and generalist small- and medium-sized characids and cichlids (Horn et al., 2011), including *Brycon hilarii* (Fig. 12.3A). Fruit-eating fishes can play important roles as seed dispersers, with considerable consequences for plant-recruitment dynamics in some wetlands. In the Peruvian Amazon, two large fruit-eating fish species (*C. macropomum* and *Piaractus brachypomus*, Serrasalmidae) consumed 35% of the fruit species available to fishes (Anderson et al., 2009). Hence, frugivory is not an exclusive feature of larger characiforms. A study from a savanna stream in Central Brazil reports that fruits and seeds were an important component of the diet of eight species, being most abundant in four species of *Astyanax* tetras (Characidae) whose diets contained 45%–73% of this item (de Melo et al., 2004).

In Africa, less information is available on fruits and seeds in the diet of wetland fishes. However, they are consumed at least by some larger catfish species (e.g., *Clarias* spp. and *Schilbe* spp.) and morphological features such as the muscular gizzard of *H. niloticus* (Osteoglossidae, Osteoglossiformes) or the special oral dentition of some characiforms (e.g., *Brycinus* and *Alestes* spp.: Alestidae and *Distichodus* spp.: Distinchodontidae) from the Congo Basin suggests that these fishes are likely foraging on fruits and seeds (Horn et al., 2011). In tropical Asia, at least 55 species of freshwater fishes from nine families are known to consume fruits regularly or occasionally, including many cyprinids (e.g., *Tor* spp., *Barbonymus* spp., *Leptobarbus* spp.) and *Pangasius* catfishes (Horn et al., 2011).

Piscivory: Predation on other fish is also a relatively widespread trophic specialization among wetland fishes, often combined with invertivory. Many species opportunistically feed on small juvenile fish. In fact, fish were the dominant prey of 31% of the species in dry and wet periods in a Pantanal pool, with the characiforms *Acestrorhynchus pantaneiro* (Acestrorhynchidae), *Plagioscion ternetzi* (Sciaenidae), *Raphiodon vulpinus* (Cynodontidae), *S. brasiliensis* (Characidae), *Serrasalmus marginatus*, and *Pygocentrus nattereri* (both Serrasalmidae) being exclusive piscivores (Novakowski et al., 2008). Specialized larger piscivorous species may employ a sit-and-wait strategy (e.g., *Hepsetus* spp. in Africa, *Hoplias* spp. in the Neotropics or *Channa* sp. in Asia) or pursue their prey (e.g., *Hydrocynus* spp. in Africa and *Pygocentrus* spp. in the Neotropics). *S. brasiliensis* is an example of aggressive mimicry, whereby a predatory species blends within shoals of its prey, *B. hilarii* (Fig. 12.3A and B) (Bessa et al., 2011).

Specialists: Several species of *Roeboides* (Characidae) and *Catoprion* (Serrasalmidae) feed on fish scales (lepidophagy). Few species are specialist lepidophages. For example, *Roeboides prognathus* feeds almost entirely on scales (and possesses highly specialized tooth and jaws to dislodge scales) while *Roeboides bonariensis* combines invertivory with occasional lepidophagy (Sazima, 1983). At least one wetland lepidophagous species, a small characid *Probolodus heterostomus* employs aggressive mimicry, similar to piscivorous *S. brasiliensis*. Other extreme diet specializations of wetland fish include selective feeding on hard incrustations of cyanobacteria by adult *Annamia normani* (Balitoridae) from Vietnam (Herder and Freyhof, 2006), molluscivory by a catfish *Nedystoma dayii* (Ariidae) from New Guinea

(Hyslop, 1999) and specialized feeding on microcrustaceans by *Moenkhausia dichroura* (Characidae) (Novakowski et al., 2008).

12.8 Community perspectives on trophic ecology

Several tropical wetland fish communities have been thoroughly investigated in relation to trophic ecology of individual species and their coexistence, including seasonal shifts in diet, interspecific diet overlaps and the extent of specialization. Overall consensus highlights that body size is not directly linked to trophic level in wetland fishes while some functional traits like body form and dentition enable adequate prediction of trophic level for particular fishes (Keppeler et al., 2020). For example, two related small *Aphyocharax* species (2–5 cm long) coexisting in Pantanal substantially vary in their diet, with *Aphyocharax dentatus* being consistently piscivorous over the entire season while *Aphyocharax anisitsi* was consistently invertivorous (Corrêa et al., 2009).

Regular sampling over a 1-year period in the Pantanal identified two strict herbivores (*P. granulosus* and *Piaractus mesopotamicus*) and several strict piscivores (e.g., *S. brasiliensis*, *P. nattereri*, *Serrasalmus* spp., *Rhaphiodon vulpinus*) (Corrêa et al., 2011). However, the diet of most fishes varied seasonally among periods of large-scale flooding. *Gymnogeophagus balzanus*, for example, fed on other fishes during the wet phase and switched to aquatic invertebrates during the dry season (Corrêa et al., 2011). Invertivorous *A. anisitsi* switched between aquatic insects (mainly dipteran larvae) in the wet season and terrestrial insects (mainly Hymenoptera) during the dry season (Corrêa et al., 2009). Most variability, however, is associated with the expansion of trophic niches during the wet season. Seasonal variation in trophic specialization and resource partitioning was reported to be higher during the wet season when food was more diverse (Corrêa et al., 2011; Polačik et al., 2014; Pool et al., 2017) while others reported greater resource partitioning during dry periods when food was scarce, with individual species feeding on a diet they specialize on (e.g., Prejs & Prejs, 1987).

In another study from Pantanal, omnivory was most common (29 out of 101 fish species), 16 species were fish predators, 12 herbivorous, 18 detritivorous, 8 fed on zooplankton, 7 were invertivorous, 2 were lepidophagous, 4 species fed on a diet composed from small fish and invertebrates and 4 combined zooplankton and aquatic insects (de Resende, 2000). For the Neotropics in general, Araujo-Lima et al. (1995) reported that all trophic guilds, except planktophagous, are well represented in wetlands, with the detritivorous species having the largest biomass in 8 of the 10 studied floodplains. Planktivorous species are not lacking from tropical wetlands and Novakowski et al. (2008) listed a small characid *M. dichroura* as a specialist consumer of microcrustaceans. Herbivory (combined with frugivory) is much more common in the wet season. *Astyanax abramis* (Characidae), *Loricaria* sp. (Loricariidae) and *Trachydoras paraguayensis* (Doradidae) fed predominantly on fruits and seeds, but also consumed small portions of leaves, and filamentous and unicellular algae (Novakowski et al., 2008).

In Africa, data from two Okavango Delta oxbow lakes (madibas) revealed that *C. rendalli* (Cichlidae) was a strict herbivore, *Hepsetus odoe* (Hepsetidae: Characiformes) and *Hemichromis fasciatus* (Cichlidae) were strictly piscivorous and *Schilbe mystus* was an invertivore. *Marcusenius macrolepidotus* was an invertivore, feeding on insects and zooplankton. Other species, including small cyprinids (*Enteromius* spp.) and a small alestid *Brycinus lateralis* fed on a range of diet items with a preference for aquatic and terrestrial insects. Finally, *Serranochromis* spp. (Cichlidae) also fed opportunistically, but often had smaller fish in their stomach (Gilmore, 1979).

In wetlands of the upper Zambezi basin, 10 coexisting catfish species were grouped into four main trophic categories. The largest species (*Clarias gariepinus* and *C. ngamensis*: Clariidae) were piscivorous, smaller clariids and *S. intermedius* (Schilbeidae) combined piscivory with invertivory, while six *Synodontis* species (Mochokidae) scavenged on fish remains and further fed on aquatic insects, seeds and detritus. Finally, *Chiloglanis neumanni* (Mochokidae), *Amphilius uranoscopus* and *Zaireichthys rotundiceps* (both Amphiliidae) were small omnivores that inhabited smaller streams rather than wetlands (Winemiller and Kelso-Winemiller, 1996).

In Angabanga River Wetlands in New Guinea, two introduced species dominated local fish communities (Hyslop, 1999). Asian *Trichogaster pectoralis* (Osphromenidae) was a detritovore feeding on detritus, diatoms and higher plant material. Invasive African *Oreochromis niloticus* (Cichlidae) was classified as a microherbivore, feeding predominantly on unicellular green algae. Native species often fed on benthic invertebrates (e.g., *Neosilurus brevidorsalis*: Plotosidae and *Ophioeleotris aporos:* Eleotridae), while others were herbivorous (*Cestraeus goldiei*: Mugilidae) or piscivorous (*Lates calcarifer*: Latidae) (see Pegg et al., 2022, Chapter 16). Two species were diet specialists—a molluscivore catfish *N. dayii* (Ariidae) and a microcrustacean specialist pipefish *Hippichtys spicifer* (Syngnathidae) (Hyslop, 1999).

12.9 Specific adaptations of wetland fishes

12.9.1 Low oxygen conditions (hypoxia)

Many wetland habitats are, at least temporarily, oxygen-depleted. Declines in dissolved oxygen levels leading to hypoxia are a natural component of many swamps and backwater habitats within tropical wetlands. Hypoxia arises due to poor water circulation, stratification and decay of flooded organic matter. In deeper wetland habitats, thermal stratification may exacerbate hypoxic conditions in the lower part of the water column. In small shallow wetland water bodies, diel-cycling hypoxia develops when microbial and vegetation respiration at night depletes oxygen levels and normoxic conditions are restored once aquatic vegetation and phytoplankton start photosynthesizing during the light phase (Díaz and Breitburg, 2011).

Wetland fish possess various anatomical, physiological and behavioral adaptations to cope with hypoxia. Increased ventilation rate is employed during mild hypoxia in species such as zebrafish, *Danio rerio* (Danionidae). A more efficient response is aquatic surface respiration when fish skim the water surface and breath in the oxygen-enriched layer of water. Surface respiration is used only after increased gill ventilation rate is inefficient to sustain oxygen levels because it increases the risk of predation as fish leave their refugia. Some species associated with hypoxic wetland habitats can facultatively breathe air. For example, many loricariid and callichthyid catfish species in the Neotropics breathe air during periods of hypoxia (Perry, 2011). Other species are obligate air breathers, including African lungfishes (*Protopterus* spp.), Neotropical *Arapaima gigas* (Arapaimidae) and many Asian anabantoids (e.g., *Trichogaster* spp., *Anabas testudinus*). Air-breathing has evolved in fishes independently at least 38 times (Graham, 2011) and represents a trait more common than generally assumed. In some cases, air-breathing even enables wetland fish to survive long-term exposure to drying mud, with African (*Protopterus* sp.) and Neotropical (*Lepidosiren paradoxa*) lungfishes seasonally aestivating in dry mud. Long-term survival of adult fish in mud is also reported in callichthyid catfishes of the Neotropics (*Callichthys* spp., *Hoplosternum* spp.; Fig. 12.4F), anabantiods (*Ctenopoma* spp.; Fig. 12.2D) and clariids (*Clarias* spp. *Heterobranchus* spp.) in Africa, and *Channa* spp. in Asia.

Anatomically, adaptations to hypoxia maybe associated with the presence of lungs (*Polypterus* and *Erpetoichthys* from Africa) or a respiratory gas bladder (e.g., African *Heterotis*, *Papyrocranus*, *Notopterus*, and *Gymnarchus*, Neotropical *Arapaima*, *Erythrinus* or *Lebiasina*, and Asian *Chitala* and *Pangasius*). In many fishes, the ancestral connection between alimentary canal and swim bladder was lost. To enable air respiration, those fishes evolved various, often very specialised, anatomical and physiological adaptions to cope with hypoxia. Neotropical *Electrophorus electricus* became an obligate air breather, possessing extensive respiratory epithelium which covers its mouth, branchial arches and the inner part of its operculum, while *Synbranchus marmoratus* (Synbranchidae) (Fig. 12.4E) evolved similar respiratory epithelium but retained the capability to extract oxygen from water. In Africa, three clariid catfish genera (*Clarias*, *Heterobranchus* and *Dinotopterus*) evolved large paired suprabranchial chambers that extend from skull to pectoral girdle, with a similar adaptation present in Asian *Heteropneustes fossilis* (Heteropneustidae). Neotropical loricariid catfishes swallow air and extract oxygen in their stomach, while some Neotropical callichthyids and Asian cobitids (*Misgurnus*, *Lepidocephalichthys*) extract oxygen in the posterior part of their gut (Graham, 2011). In Africa and Asia, anabantoid fishes (e.g., *Ctenopoma* and *Trichopterus*) possess a labyrinth organ formed by vascularized expansion of the epibranchial bone of the first-gill arch. Comparing three Neotropical wetland species that coexist in Pantanal, Jucá-Chagas (2004) observed that *Hoplosterum littorale* (extracting oxygen in intestine) was 2–3 times more efficient in oxygen extraction than *L. paradoxa* (obligatory air breather with lungs) and *Hoplerythrinus unitaeniatus* (with vascularized swim bladder), and *H. unitaeniatus* had to take twice as many breaths to retrieve sufficient oxygen compared to the other two species (Jucá-Chagas, 2004).

12.9.2 Habitat desiccation

Many wetland habitats combine aquatic and desiccated phases over their annual cycle. The most typical response of wetland fishes is to leave the desiccating habitat with receding water. Fish can sense gradients in oxygen levels and water flow and typically follow receding waters to leave desiccating habitats. Many fish are trapped in desiccating pools and predated by piscivorous birds when their density and catchability are high, providing a considerable nutrient transfer link between aquatic and terrestrial components of wetland habitats.

Various species survive short-term desiccation in wet mud, including callichthyid catfish in the Neotropics and clariid catfishes in Africa. These species have well-developed organs for air-breathing to survive receding water levels that are often associated with hypoxia. African lungfishes (*Protopterus* spp.) survive dry periods by burrowing into the mud and aestivating in a subterranean cocoon or even inside a cocoon made of dried mucus on bare land (Chew et al., 2015). Neotropical lungfish (*L. paradoxa*) are not tolerant to body desiccation and dig deep burrows that retain water throughout the dry phase of the habitat (de Almeida-Val et al., 2015).

Annual killifishes survive desiccated phases of their habitats as dormant embryos encased in egg envelopes with thick chorion to protect them from water loss. Annual killifishes have repeatedly evolved annual life cycles in the Neotropics (Fig. 12.4C and D) and in Africa, perhaps 3–4 times on each continent (Furness et al., 2015), though it is also possible that a shared preadaptation enabled them to switch to a developmental mode that includes diapauses (Reichard, 2015). In these fishes, an entire generation can survive for up to 11 months per year as dormant embryos (Vrtílek et al., 2018). During the wet phase, annual killifish develop rapidly. They utilize the aquatic period of their pools until it dries up, with daily reproduction starting in as few as two weeks after hatching (opportunistic life history strategy). They may sustain populations in pools that are inundated for as few as three weeks, though inundations of one to three months are more typical even in the driest region of their range (Vrtílek et al., 2018). Their embryos develop in aquatic habitat for a few days before the first diapause (Diapause I) is initiated by anoxic conditions in pool sediments. Greater oxygen availability during habitat desiccation initiates re-establishment of the active development and its halt at Diapause II. Another bout of development occurs when the substrate is disturbed and wetted during the initial rains of a new rainy season. Embryos reach Diapause III which apparently serves to slow down metabolism until conditions for hatching are optimal (wetland inundation) (Reichard and Polačik, 2019). It is notable that all clades of annual killifishes (in Africa and Neotropics) undergo the same system of three diapauses. This adaptation enables annual killifishes to colonize wetlands which lack regular connection to permanent water bodies. Other species colonize such habitats by overland migration (e.g., African *Claris gariepinus* and Asian *A. testudinus*). Recently, colonization of isolated wetlands through endozoochory (as eggs transported in the alimentary canal of wetland birds) was confirmed in various fish species (Silva et al., 2019; Lovas-Kiss et al., 2020).

12.10 Summary and conclusions

Tropical wetlands provide a rich network of habitats for freshwater fish. While most wetland fish diversity is connected to large alluvial systems, some fish species are adapted to periodic desiccation of their habitats. Tropical wetlands are subject to strong seasonal fluctuations and therefore even trophic specialists expand their diet temporarily. Functional traits associated with trophic niches are convergent across continents (see Cuthbert et al., 2022, Chapter 17; Gálvez et al., 2022, Chapter 18). Wetland fish fauna have evolved characteristic adaptations associated with particular life histories, including the ability to breath air during hypoxia, survive desiccation, and having characteristic body shapes to energetically maximize resource acquisition. The threats to wetland fishes through habitat degradation, impoundments, water pollution, water extractions, and arrival of non-native species are detailed in Chapters 13 (Moraes et al., 2022), 14 (Tarakini et al., 2022), 16 (Pegg et al., 2022), 19 (Irvine et al., 2022), 20 (Greenfield, 2022), and 22 (Marambanyika et al., 2022).

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Chapter 13

Amphibians and squamates in Amazonian flooded habitats, with a study on the variation of amphibian assemblages along the Solimões River

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Amphibians and squamates are ectothermic vertebrates, whose spatial and temporal distribution across the landscapes are notably influenced by thermo-hydraulic gradients (Pough et al., 2015). The number of species (species richness) of these vertebrates frequently increase in microhabitats close to water bodies, since many species depend on the microclimatic and structural conditions present in these microhabitats to complete their reproductive cycles or to maintain homeostasis (Uzarski et al., 2009). At the same time, aquatic interface and lateral overflow of rivers might pose challenges for other amphibians and squamates, for example, by reducing dispersal or affecting nests and clutches viability (Ocock et al., 2014). Consequently, a trade-off between positive and negative impacts of water bodies interact shaping amphibians and squamates occurrence in wetlands (Junk et al., 2006). In this sense, the global wetlands, here broadly defined as aquatic and palustrine habitats, and its transition with terrestrial zones, are relevant repositories for the origin and maintenance of these vertebrates diversity (Junk et al., 2006; Keddy, 2010; Keddy et al., 2009; Wasserman and Dalu,

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2022, Chapter 1). Depending on the different types of vegetation associated with these wetlands (e.g., forest or open habitats), the variation in species composition may be evident or subtle (Piedade et al., 2022, Chapter 7). In some cases, assemblages of these habitats acquire a nested structure, in which species composition is a subset of the assemblages at enclosing habitats, due to the combined influence of local extinctions and selective colonization processes (Tockner et al., 2006; Ramalho et al., 2018).

The species richness inhabiting wetlands increases in tropical regions, following the broadly recognized pattern of increase in overall species richness from high latitudes to the Equator (Junk et al., 2006; Wiens et al., 2006). In tropical South America, a dynamic seasonally flooded wetland system develops on the margins of large Amazonian rivers (Junk et al., 2011). A unique biota occupies these river-created habitats, contributing to the high species richness known for this bioregion (Cohn-Haft et al., 2007; da Fonte et al., 2021; Remsen and Parker, 1983; Wittmann et al., 2006). Amphibians and squamates are highly diverse vertebrates occupying these Amazonian flooded habitats, and show remarkable adaptations to inhabit them, such as an external morphology well suited to swimming ability, and temporal synchronicity of their life cycles with seasonal flooding (Mesquita et al., 2006; Villamarin et al., in press). However, overall diversity and spatial structuring of amphibian and squamate assemblages in these flooded habitats are poorly characterized and wait a knowledge summary. Here, we combine previous knowledge with novel data on species occurrence to summarize and investigate the amphibian and squamate species diversity in Amazonian flooded habitats, considering two distinct geographic scales. Therefore, this chapter is structured in two main sections; in the first one we explore the origins of Amazonian flooded habitats, and how their dynamics and structural characteristics lead to the occurrence of a distinct biota of amphibians and squamates. In the second section, we present a case study on the longitudinal variation of species richness and composition of amphibian assemblages in these habitats along one of the largest Amazonian rivers, in Brazil.

13.1 Origin, dynamics, and environmental heterogeneity of Amazonian flooded habitats

The megadiverse Amazonia is drained by the largest river basin in the world, composed of the transcontinental Amazon River and its many tributaries, covering an area of more than 6,000,000 km^2 (Junk et al., 1989, 2011, 2012; Junk and Piedade, 2005). Located over a historically dynamic landscape, this system acquired its current configuration after the uplift of the Andean mountain range in western South America, during the course of the Cenozoic (Hoorn et al., 2010; Bicudo et al., 2020). Andean uplift created an extensive "dammed" wetland in western Amazonia for some million years, and the sediment influx in this system culminated in the inversion of the entire drainage system into the Atlantic Ocean (Hoorn et al., 2010; Bicudo et al., 2020). Another consequence of the Andean uplift was the regional climate change, which also suffered variation during the Earth's glaciation periods, changing the morphology and dynamics of Amazonian habitats, and consequently affecting the biotic distribution patterns (Cheng et al., 2013; Bicudo et al., 2019, 2020). Even after the establishment of the drainage system, recent geological reconfigurations (late Pleistocene and Holocene) likely promoted significant rearrangements in the river's network (see Ruokolainen et al., 2019). This history of combined tectonic and climatic changes has generated a bioregion currently characterized by a generalized high annual rainfall, unequally distributed between rainy and dry seasons. Such a precipitation regime leads to largely predictable oscillations in the rivers discharge across the basin, resulting in extensive seasonally flooded habitats along the riverbanks (Junk et al., 2011). The seasonal flood pulse and the consequent cyclical dynamics have generated a transitional habitat between aquatic and terrestrial interfaces, representing one of the most influential components for the origin and maintenance of environmental heterogeneity, biotic diversity, and ecological processes within Amazonia (Junk, 1997; Wittmann et al., 2006; Cohn-Haft et al., 2007). In this sense, it is possible to draw a parallel between the relevance of the flood pulse in this extensive drainage system with cyclical pumping in a circulatory system.

The extensive geomorphological heterogeneity of Amazonian landscape directly influences the physicochemical variation of its rivers, and consequently affects the environmental conditions of adjacent flooded habitats. For instance, rivers with headwaters in the Amazonian Craton are mostly embedded in the Precambrian rocky bed (Sioli, 1968, 1984; Junk et al., 2011). Because of the origin of these rivers in such ancient and highly eroded terrains, the volume of suspended sediments in their systems is relatively low, and their oligotrophic waters usually are less turbid and greenish colored, being known as "clear-water" rivers (e.g., Tapajós River; Sioli, 1984). Due to the rocky bed and greater terrain slope, water flow increases in some courses of these rivers, creating extensive waterfalls and rapids (Sioli, 1984). Amazonian river basins with headwaters on sandy soils also have low amounts of suspended sediments in their systems (Sioli, 1984). Due to incomplete decomposition of chemical compounds at their headwaters, these rivers have more acidic waters and acquire a brownish coloration, being known as "black-water" rivers (e.g., Negro River; Sioli, 1984). As a consequence of geomorphological characteristics and low amounts of suspended sediments circulating in their systems, alluvial plains are scarcely represented on the banks of clear-water and black-water rivers, with the flooded interface being dominated by relatively oligotrophic forest habitats (known as *igapó*; Sioli, 1984; Junk et al., 2011) (Fig. 13.1A and B).

Conversely, rivers with headwaters in relatively recently uplifted regions (mainly the Andean region) have high amounts of suspended sediments,

FIGURE 13.1 Flooded habitats at the margins of large Amazonian rivers, depicting the *igapó* flooded forests along a black-water river (Negro) (A) and a clear-water river (Tapajós) (B), as well as some distinct habitats from the *várzea* of a white-water river (Solimões) floodplains (C–L). *Várzea* habitats depicted includes smaller tributaries with high densities of macrophyte banks (C–E), a fragment of macrophytes banks being carried downstream (F), a exposed sand bank (G), mud bank covered by herbaceous vegetation (H), and different landscapes of the heterogeneous mosaic of flooded forests, including the low and high *várzea* (I–L). For color version of this figure, the reader is referred to the electronic version of this chapter. *Photos courtesy Erik Choueri (A), Dante Pavan (B), Marcelo Gordo (C–D, L), and Leandro J.C.L. Moraes (E–K).*

generating turbid and yellowish-brown colored water (Sioli, 1984). These eutrophic systems are known as "white-water" rivers (e.g., Amazon River; Sioli, 1984), and most of them run through the sedimentary basin of western Amazonia. In this geomorphological context, these rivers are embedded in extensive nutrient-rich alluvial plains (known as *várzea*; Sioli, 1984; Junk et al., 2011) (Fig. 13.1C–L), in which their meandric channels remain constantly unstable due to the simultaneous action of erosive and sedimentary processes (Sioli, 1984). A wide range of distinct habitats develops at the *várzea*, generating an evident successional landscape ranging from exposed sand/mud banks and steep shores to herbaceous, arbustive, and forest habitats

(Fig. 13.1C–L) (Albernaz, 2007; Junk et al., 2012). The development of each of these habitats in the landscape is directly influenced by the period the terrain remains flooded during the seasonal cycle. Habitats that spend much of the year flooded are known as "low *várzea*" and the ones subjected to shorter flooding periods are the "high *várzea*" (Junk et al., 2012) (Fig. 13.1I–L). In the nonflooded interface, some terrains are no longer influenced by the flood pulse only recently (in geological time), due to the lowering of the river channel (Pupim et al., 2019). In these unique terrains, a distinct type of nutrient-rich forest develops (known as *paleovárzea*; Junk et al., 2011). In addition, due to the greater amount of nutrients carried in the white-water rivers, extensive banks of aquatic macrophytes grow on their margins (Junk and Piedade, 1993). Eventually, fragments of these macrophyte banks disconnect and are carried downstream, contributing as a way of geographic dispersal of the associated biota by passive transportation (da Fonte et al., 2021; Junk, 1997; Schiesari et al., 2003) (Fig. 13.1F). Such macrophyte banks are less diverse and abundant in the oligotrophic black-water and clear-water rivers (Junk, 1997; Piedade et al., 2010).

Although the primary productivity varies among habitats flooded by these river types as a result of the different amounts of dissolved nutrients, the flood pulse is a fundamental component for all of them in the cyclical supply of these nutrients to the terrestrial interface (Junk, 1997). It is also worth mentioning that this discrete classification traditionally applied to describe Amazonian rivers is quite simplistic and more useful for comparative purposes. In fact, variation in physicochemical characteristics of Amazonian rivers are part of an environmental continuum that depends on the landscape context of the drainage systems (Ríos-Villamizar et al., 2013), and usually, more than one river type can be found within a single major basin (see Junk et al., 2011).

13.2 Biotic patterns in Amazonian flooded habitats: amphibians and squamates

Amazonian flooded habitats have historically been treated as harboring biotic assemblages with: (1) lower species richness in contrast to interfluvial nonflooded habitats (*terra firme*), due to the intense cyclic dynamism to which they are subjected (Hoogmoed, 1993; Junk et al., 2006, Wittmann et al., 2006), and (2) relatively homogeneous species composition, because flooded habitats are supposed to be "linearly" connected and promote the flow of genes and individuals while decreasing the genetic diversity (Aleixo, 2006; Cadena et al., 2011; Harvey et al., 2017). Mounting evidence of biodiversity data has only partially corroborated both assumptions. Species richness actually substantially increases in the more stable and geographically broader nonflooded habitats (Wittmann et al., 2006; Vale et al., 2017; Ramalho et al., 2018). In addition, for some wetland species the flooded interface is favorable for a dendritic-like dispersal (Cadena et al., 2011), tending to homogenize the assemblages composition throughout the basin. However, those assumptions are not currently treated as universally applicable, and the knowledge gaps associated with flooded habitats have historically masked various biotic patterns (Cohn-Haft et al., 2007). High local/regional species richness has continuously been reported for the assemblages of flooded habitats with increased sampling effort and taxonomic resolution (Assis et al., 2017; Dayrell et al., 2021; Ramalho et al., 2016). Species endemic to these habitats have also been evidenced, especially plants, birds, and primates (Remsen and Parker 1983; Wittmann et al., 2012; Barnett, 2019), but also lizards (Marques-Souza et al., 2020). Similarly, some phylogeographic breaks and compositional turnovers have been recently evidenced in flooded habitats (Cohn-Haft et al., 2007; Choueri et al., 2017; Thom et al., 2020), indicating that they have their own "areas of endemism", similarly to the historically recognized for nonflooded habitats (Albernaz, 2007; Cohn-Haft et al., 2007).

This knowledge advance suggests that the real diversity of Amazonian flooded habitats is largely underestimated, and some aspects of the spatial and temporal distribution of this diversity are poorly understood (Laranjeiras et al., 2019). Amphibians and squamates are among the most historically neglected vertebrates in broad-scale studies addressing biotic regionalization in Amazonian flooded habitats (da Fonte et al., 2021). Thus, to understand their general patterns of spatial occurrence in these flooded habitats, as well as their variation within the different *várzea* habitats, we compiled species lists based on our primary data from these habitats at the Solimões and Negro River basins since 2001. We expanded these species lists with secondary data from local/regional inventories focused on flooded habitats or that explicitly discriminated where species were recorded (Hödl, 1977; Hoogmoed, 1993; Schiesari et al., 2003; Gordo, 2003; Neckel-Oliveira and Gordo, 2004; von May et al., 2010; Pantoja and Fraga, 2012; Bernarde et al., 2013; Waldez et al., 2013; Barros et al., 2014; Upton et al., 2014; Moraes et al., 2016; Ramalho et al., 2016; Böning et al., 2017; Debien et al., 2019). To avoid bias considering species with historical gaps in their taxonomic and distributional resolutions, we kept them in broader taxonomic categories. (e.g., species groups or complexes) or lumped in single operational units some morphologically similar sister-species. The species lists are available in the online supplementary material of this chapter (Appendices I and II).

Based on the compiled lists, we detected at least 232 taxa of amphibians and squamates somehow exploiting Amazonian flooded habitats, being 137 amphibians, 40 lizards, and 55 snakes (some representative examples pictured in Figs. 13.2 and 13.3). As expected, due to the greater spatial extent and primary productivity, a greater number of species (212) has been recorded in flooded habitats adjacent to eutrophic white-water rivers, when compared to the oligotrophic river types (54 species at black-water rivers and 75 at clear-water rivers). Most of the species recorded in a single

FIGURE 13.2 Examples of some representative amphibians from Amazonian flooded habitats: (A) *Rhinella marina*, (B) *Boana boans*, (C) *Boana lanciformis*, (D) *Boana punctata*, (E) *Boana raniceps*, (F) *Dendropsophus haraldschultzi*, (G) *Dendropsophus triangulum*, (H) *Dendropsophus walfordi*, (I) *Lysapsus bolivianus*, (J) *Scarthyla goinorum*, (K) *Sphaenorhynchus lacteus*, (L) *Sphaenorhynchus dorisae*, (M) *Trachycephalus typhonius*, (N) *Leptodactylus petersii*, and (O) *Pipa pipa*. For color version of this figure, the reader is referred to the online version of this chapter. *Photos courtesy Leandro J.C.L. Moraes (A, E–G, I–N) and Marcelo Gordo (B–D, H, O).*

river type were from the margins of white-water rivers (88%), whereas a considerable proportion of species occupy the flooded habitats of more than one river type (34%). These results are biased at some extent by the taxonomic resolution, species' detectability, and lower number of inventories carried in clear-water and black-water flooded habitats. However, it indicates that the species composition and richness of amphibian and squamate assemblages varies among the flooded habitats of distinct river types, as evidenced

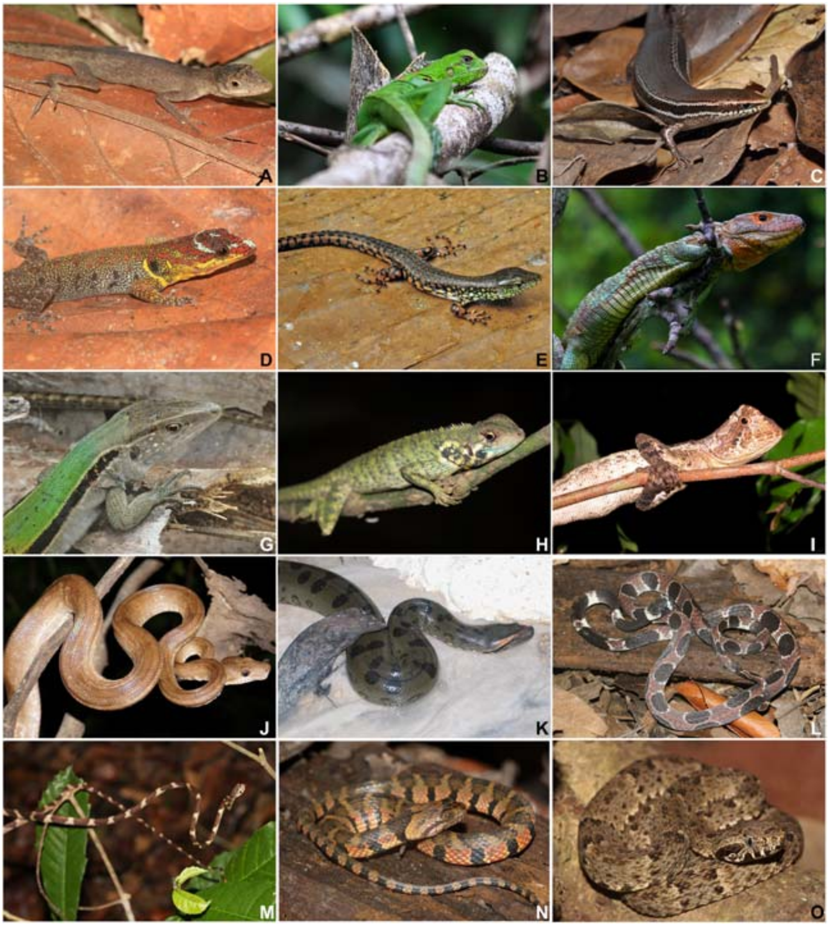

FIGURE 13.3 Examples of some representative squamates from Amazonian flooded habitats: (A) *Anolis fuscoauratus*, (B) *Iguana iguana*, (C) *Varzea bistriata*, (D) *Gonatodes humeralis*, (E) *Crocodilurus amazonicus*, (F) *Dracaena guianensis*, (G) *Kentropyx altamazonica*, (H) *Plica umbra*, (I) *Uranoscodon superciliosus*, (J) *Corallus hortulana*, (K) *Eunectes murinus*, (L) *Dipsas catesbyi*, (M) *Imantodes cenchoa*, (N) *Helicops angulatus*, and (O) *Bothrops atrox*. For color version of this figure, the reader is referred to the online version of this chapter. *Photos courtesy Leandro J.C.L. Moraes (A, D, H, L–O), Jéssica dos Anjos (B, F), Alexandre P. Almeida (C), Laurie Vitt (E, G), Marcelo Gordo (I, K), and Renata M. Pirani (J).*

for bird assemblages (Laranjeiras et al., 2019). Such variation can be attributed to the geomorphological and climatic variation across Amazonia, which generates the different environmental conditions already mentioned for the *igapó* and *várzea* (Junk et al., 2011), allowing the occupation of distinct assemblages with variable species richness, abundances, and functional groups. Thus, considering the aforementioned biases and the fact that

Amazonian diversity is still severely underestimated for these vertebrates (Ribeiro-Júnior et al., 2020; Vacher et al., 2020), it seems reasonable to predict that far more than these 232 species of amphibians and squamates exploit the flooded habitats of this bioregion.

13.3 Diversity and spatial variation of amphibians and squamates at the *várzea*

Focusing on the historically best-studied *várzea*, we classified the level of species association with these flooded habitats by the regularity of their presence in the compiled inventories. In a finer scale, we investigated the main habitats of the *várzea* mosaic occupied by the species, based on the information provided in the inventories and our primary data. We detected some species rarely represented in inventories at flooded habitats, which likely correspond to immigrant species from adjacent habitats that eventually use this interface (da Fonte et al., 2021; Junk et al., 2006), or species geographically restricted to an Amazonian subregion. The presence of such rarely recorded species indicates the occurrence of some relevant species turnover throughout flooded habitats across the basin, instead of a tendency of homogenization in assemblages' composition. In contrast, other species were repeatedly recorded in the compiled inventories and can be considered as typical members of amphibian and squamate assemblages of the *várzea* (Figs. 13.4 and 13.5). According to habitat preferences and geographic distributions, this typical assemblage is composed of four main functional groups (numbered according to the level of association with the *várzea*): (1) widely-distributed species, indistinctly occupying Amazonian habitats and other bioregions; (2) typical Amazonian species but habitat-generalist, with geographic distribution encompassing other habitats adjacent to the flooded ones; (3) widely-distributed species, occupying other bioregions but absent or rare in Amazonian nonflooded forests; and (4) Amazonian species typical from the flooded interface, with some also occupying open habitats and ecotonal regions of adjacent bioregions (Figs. 13.4 and 13.5). While species of groups 1–3 seem to represent cases of geographic distribution expansion among habitats and bioregions due to the wide breadth of their ecological niches, species of the group 4 present stronger association with Amazonian flooded habitats and are potential cases of *in situ* diversification. In fact, a very similar functional segregation of the amphibian assemblages within the *várzea* was recovered by a recent study (da Fonte et al., 2021). A fifth group is also considered: Amazonian species typical of the flooded interface but with low density or detectability and consequently rarely recorded in the compiled inventories by sampling biases (da Fonte et al., 2021) (Figs. 13.4 and 13.5). Due to the presence of these functional groups with varying geographic ranges and levels of association with the flooded habitats, we consider that the *várzea* has a unique fauna of amphibians and squamates. Such

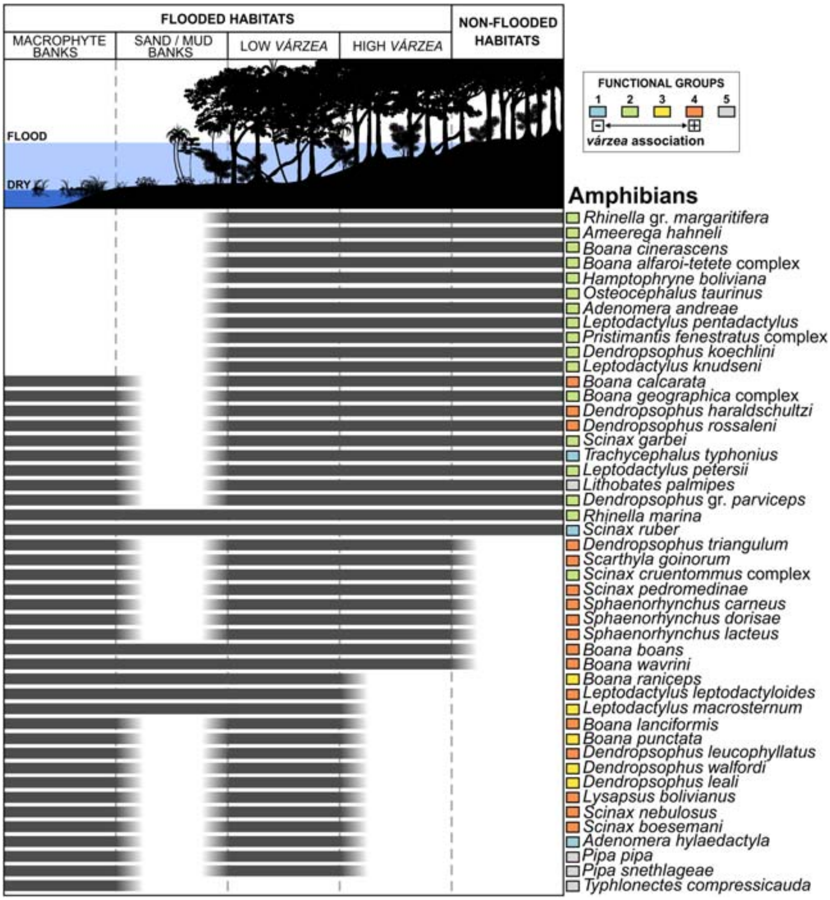

FIGURE 13.4 Typical assemblage of amphibians occurring in flooded habitats at the margins of white-water Amazonian rivers (*várzea*), with their respective environmental association within this mosaic (horizontal bar corresponds to species presence). Functional groups 1−4 represent distinct levels of species association with the *várzea*, and group 5 represent typical species from this habitat but rarely recorded in compiled inventories due to lower detectability. List summarized of a more comprehensive compilation of amphibians inhabiting Amazonian flooded habitats (see text for details). For color version of this figure, the reader is referred to the online version of this book.

a presence of many species typically associated with the flooded interface reaffirms the significant contribution of these habitats to the species pool inhabiting this megadiverse bioregion (Schiesari et al., 2003; Ramalho et al., 2016; Böning et al., 2017). However, it is important to highlight that many of these typical species have a certain degree of environmental plasticity, and/or are spatially restricted to a single or few habitats within the *várzea* (Ramalho et al., 2018). Therefore members of this typical assemblage should

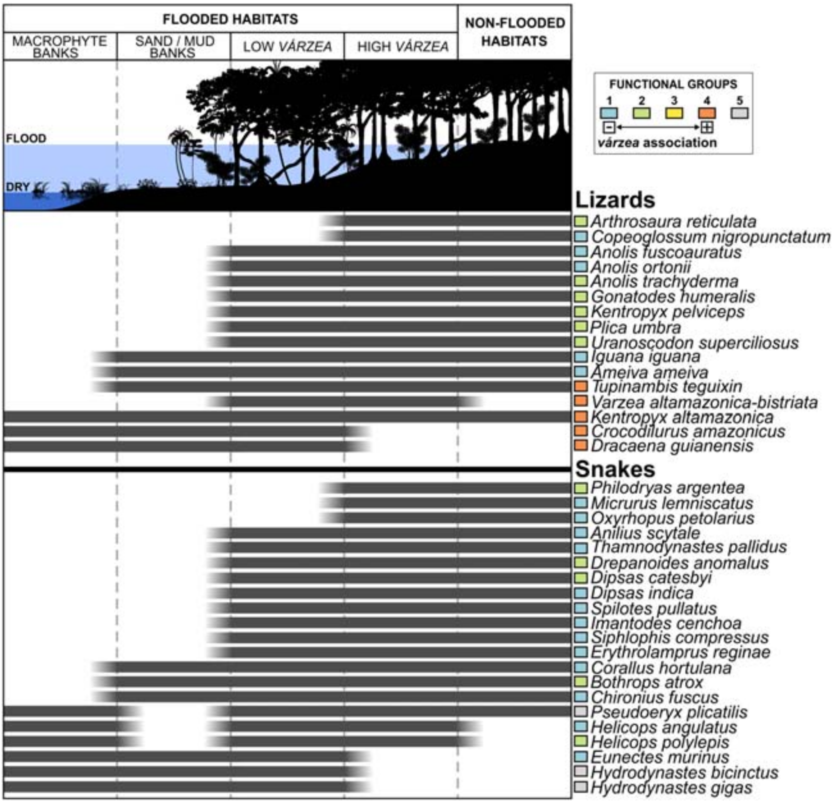

FIGURE 13.5 Typical assemblage of squamates occurring in flooded habitats at the margins of white-water Amazonian rivers (*várzea*), with their respective environmental association within this mosaic (horizontal bar corresponds to species presence). Functional groups 1–4 represent distinct levels of species association with the *várzea*, and group 5 represent typical species from this habitat but rarely recorded in compiled inventories due to lower detectability. List summarized of a more comprehensive compilation of squamates inhabiting Amazonian flooded habitats (see text for details). For color version of this figure, the reader is referred to the online version of this chapter.

be considered case-by-case as model organisms in biogeographic and ecological studies.

Amphibian and squamate diversity is heterogeneously distributed among the different habitats within the *várzea*, in such a way that the flood pulse promotes a high species turnover along the flooding gradient and increases regional species richness (Waldez et al., 2013; Ramalho et al., 2016). For example, higher rates of species turnover are detected between amphibian assemblages from flooded forests and macrophyte banks (da Fonte et al., 2021; Ramalho et al., 2018). This result occurs because several amphibians species that are typically found in open habitats use macrophyte banks as breeding sites, although some of these species are also recorded in lower densities in flooded forests (Schiesari et al., 2003; Böning et al., 2017). Macrophyte banks also represent important refuges for several amphibian species that do not necessarily reproduce in this habitat, as well as for some lizards and snakes, especially during the high-water phases (Schiesari et al., 2003; Böning et al., 2017). Similar species partition occurs at the interface between flooded and nonflooded forests (*paleovárzea* or *terra firme*) since species typical of nonflooded habitats usually invade the flooded ones in search of seasonal resources during the low-water phases (Tockner et al., 2010). The seasonal flood pulse also creates aquatic microhabitats used as breeding sites by these vertebrates and new refuge opportunities in flooded forests (Martins, 2006; Ramalho et al., 2018). Arboreal amphibians and squamates are particularly common in Amazonian flooded habitats, including several species from open and forest habitats that exploit the flooded forests in search of prey or refuge along the seasonal variation (da Fonte et al., 2021; Ramalho et al., 2018; Waldez et al., 2013). Terrestrial heliothermic lizards are also especially diverse and abundant due to the increase of solar incidence at the forest floor compared to the nonflooded forests with closer canopies (Vitt et al., 1997; Waldez et al., 2013). Fossorial or cryptozoic species from all of these groups, as well as amphibians that lay their eggs in the leaf-litter, are absent or occupy these habitats only seasonally (Waldez et al., 2013; Ramalho et al., 2018), due to the impact of flood pulse over the terrestrial layer. According to our study, the proportion of species typically associated with the *várzea* is low for snake assemblages while increases sequentially for lizards and amphibians (Figs. 13.4 and 13.5). Such patterns indicate that species turnover between the flooded and nonflooded habitats is higher for amphibian assemblages, while squamate assemblages acquire a predominant nested structure in the flooded interface. Focusing only on the *várzea* flooded forests, the composition of amphibian and squamate assemblages can be interpreted as a mixture of species typical of other habitats such as the macrophyte banks and/or open habitats, and generalist species from nonflooded habitats. Thus, these seasonally flooded forests act as functional links between aquatic and terrestrial Amazonian habitats, enhancing its overall diversity and levels of biological interactions.

13.4 Case study: variation of amphibian assemblages along the *várzea* of the Solimões River

Most of the studies addressing the spatial variation of amphibian assemblages in flooded habitats are geographically restricted and mainly investigate how the assemblages vary perpendicularly to the river channel and toward the nonflooded habitats (Waldez et al., 2013; Ramalho et al., 2018). Moreover, the only few studies that aimed to compare the spatial variation of these assemblages along the longitudinal axis of large rivers had to deal with large sampling gaps (Böning et al., 2017). Based on primary data, we aim to expand this knowledge by investigating the spatial variation of composition and richness of amphibian assemblages from the flooded habitats along the Solimões River (hereafter, Solimões). This large white-water river has its headwaters in the Andes and carries high amounts of suspended nutrients (Espinoza-Villar et al., 2018). It represents the middle course of the Amazon River *sensu lato*, which is named "Solimões" when it crosses the triple boundary between Brazil, Colombia, and Peru, at the confluence of the upper Amazon River *sensu lato*

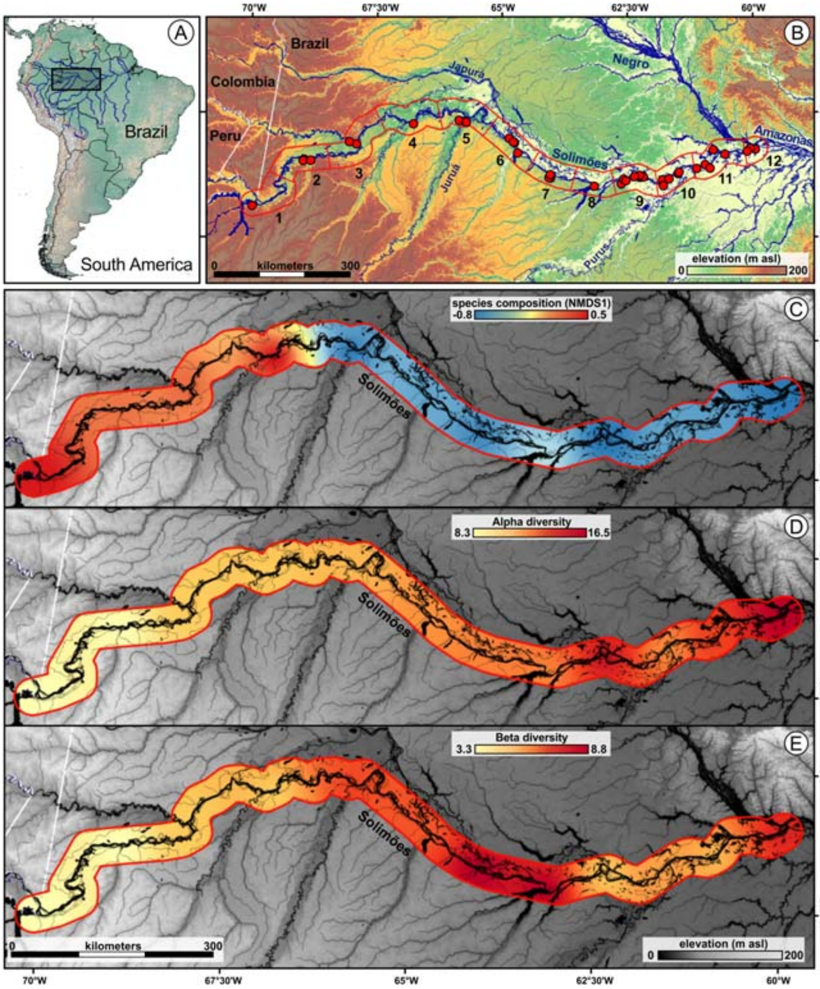

FIGURE 13.6 Geographic location of the Solimões River in relation to South America and Brazil (A), spatial distribution of the localities sampled for amphibian occurrences (red dots) and the summarized 12 sampling units (B), as well as the results of spatial variation in species composition (C), alpha diversity (D), and beta diversity (E), the last two estimated from standardized species richness under two distinct approaches (see text for details). Plates B–E with a background of fine-scale terrain elevation, showing the geomorphological variation along the river basin. For color version of this figure, the reader is referred to the online version of this chapter.

with the Javari River (Fig. 13.6). The Solimões runs longitudinally through much of the Brazilian state of Amazonas, for c.1400 km in length and reaching more than 5 km in width, until its confluence with the Negro River, in the region of Manaus municipality, central Amazonia (Junk and Piedade, 2005). The confluence of these two large rivers generates the Amazon River (=lower Amazon River *sensu lato*) (Sioli, 1984). The Solimões is located in the sedimentary basin of western Amazonia, and extensive alluvial plains develop on its margins, harboring the most diverse habitats of the *várzea*, as well as some patches of land not currently subject to the flooding (Junk et al., 1989; Pupim et al., 2019; Fig. 13.1B). The flood pulse along this river varies annually in a predictable manner, with a high-water season fluctuating longitudinally from April to July and a low-water season from September to November (Junk et al., 2011). The Solimões also crosses an extensive climatic and geomorphological gradient (Fig. 13.6B), mostly influenced by the Andean uplift and the sequential West–East terrace exposition after the draining of the wide lacustrine system in this region during the Cenozoic (Pupim et al., 2019, Tuomisto et al., 2019).

Such broad and fine-scale environmental heterogeneity likely influences the occupation of distinct amphibian assemblages along the flooded habitats of the Solimões, but generalist species could potentially homogenize the variation (Harvey et al., 2017). To investigate what is the predominant pattern in the spatial variation of the composition and richness of these amphibian assemblages, we compiled our occurrence data collected from 2001 to 2018 in 39 localities along the entire length of the Solimões (Fig. 13.6). Individuals were visually or acoustically recorded, through diurnal and nocturnal active surveys (Heyer et al., 1994). We considered sampling localities contained within a 25 km buffer from the center of the river channel (Fig. 13.6B). To uniformly distribute the sampling units along the river, we included data collected within approximately 100 km sections of the river (Fig. 13.6B). This sampling design resulted in 12 sampling units (Table 13.1), allowing an increase in the robustness of the biotic data while accounting for the environmental heterogeneity of the river margins. To mitigate potential biases caused by variations in sampling effort and period (Table 13.1), we based our compositional analysis solely on qualitative data (presence–absence). The compositional variation was summarized by extracting the values of the first axis (NMDS1) of a Non-Metric Multidimensional Scaling (NMDS) ordination, based on the *Jaccard* similarity measure (Anderson, 2005).

Richness variation was standardized by sampling effort, under two approaches: (1) dividing the sum of local richness from each locality of a sampling unit by the total of sampled localities within this unit (as a proxy for alpha diversity); (2) dividing the richness of each sampling unit by the total of sampled localities within this unit (as a proxy for beta diversity). A higher beta diversity value for a given sampling unit, which approximates the corresponding alpha diversity value, indicates a greater amount of species turnover among sampled localities, while lower beta diversity values indicate greater

TABLE 13.1 Sampling units and variation in effort and period among our surveys for amphibian species occurrence at the *várzea* habitats on the Solimões River margins.

Sampling unit	Municipalities	Sampling localities	Riverbank	Date	Flooding season	Samplers
1	Benjamin Constant	1	N	2018: 07–10 May	HW	1
2	São Paulo de Olivença	3	S, I	2018: 11–14 May	HW	1
3	Santo Antônio do Içá	2	N, I	2018: 15–18 May	HW	1
4	Jutaí	2	S	2018: 20–22 May	HW	1
5	Juruá	3	S	2018: 18–20, 23–28 July	LW	3
6	Uarini (RDS Mamirauá), Tefé	3	N, S	2017: 24–27 October; 2018: 24–26 May	LW, HW	1 (May); 3 (October)
7	Coari	3	S, I	2017: 29–31 October	LW	3
8	Coari	1	S	2002: 16 June	LW	2
9	Coari, Codajás	8	N, S, I	2001: 24 May, 17 August, 26 October, 17–19 November; 2002: 18 June; 2017: 02–04 November	LW, HW	2 (2001, 2002); 3 (2017)

(*Continued*)

TABLE 13.1 (Continued)

Sampling unit	Municipalities	Sampling localities	Riverbank	Date	Flooding season	Samplers
10	Anori, Beruri	5	N, S	2001: 25 May, 18 August, 25 October; 2017: 05–08 November	LW, HW	2 (2001); 3 (2017)
11	Manacapuru	6	N, S	2001: 26 May, 19 August, 28 October; 2002: 19–20 June; 2017: 09–11 November	LW, HW	2 (2001, 2002); 3 (2017)
12	Iranduba	3	N, I	2001: 27 May, 20–21 August	LW, HW	2

See Fig. 13.6 for geographic location of the sampling units. *Riverbanks*: *N*, north; *S*, south; *I*, Fluvial Island. *Flooding season*: *HW*, high-water; *LW*, low-water.

homogeneity in species composition. Data from sampling units containing a single locality were merged with adjacent ones ($1+2$, $3+4$, $7+8$). We tested for the statistical significance of the variations with linear regressions comparing the dependent variables composition (NMDS1) and richness (alpha and beta diversity) with the longitude. Their variation along the river were spatially projected using interpolation by the Inverse Distance Weighting at the software QGIS version 2.14 (QGIS Development Team, 2021). The NMDS calculation and the statistical tests were conducted in R (R Core Team, 2021) using the package "*vegan*" (Oksanen et al., 2019). The list of taxa by sampling units is available in the online supplementary material of this chapter (Appendix III).

We recorded 52 amphibian taxa along the *várzea* of the Solimões, with 42 nominal species and 10 broader taxa with lower taxonomic resolution. Raw richness among the 12 sampling units varied from 8 to 38 species. The most widely-distributed taxa in our sampling were *Boana raniceps*, recorded in all sampling units, and *Boana punctata*, *Dendropsophus* gr. *leucophyllatus*, and *Sphaenorhynchus lacteus*, recorded in 11 sampling units. Twelve taxa were recorded in single localities. Species composition was not homogeneous along the longitudinal axis of the river, nor subtly changed along it. In fact, a drastic compositional change was detected in the transition between the upper and middle Solimões ($F_{1,10} = 22.83$, $R^2 = 0.69$, $P < 0.001$) (Fig. 13.6C). Based on the gaps in the spatial arrangement of our sampling localities, the precise location for this compositional change is uncertain, but likely occurs around the region of the confluence with the Juruá River. This sharp change in composition is mainly caused by the absence of some taxa (*Boana alfaroi-tetete*, *Rhinella marina*, *Osteocephalus taurinus*, *Scinax* gr. *ruber*, *Trachycephalus typhonius*, *Rhinella* gr. *margaritifera*, *Adenomera andreae*, *Leptodactylus macrosternum*, *Scarthyla goinorum*) in the upper Solimões localities. Since there are historical records of these taxa in the upper Solimões, this result is probably biased by our sampling and most likely represent false absences. However, our result might also indicate that these species were less detected in the upper Solimões because they share lower densities in this region. In fact, our preliminary observations indicate that the abundance of some species typical from the *várzea* decreases toward the upper Solimões, and further studies including quantitative data may reveal hidden patterns of distribution. The drastic compositional change between the upper and middle Solimões is also supported by a turnover between two species of *Dendropsophus* (*D. riveroi* and *D. walfordi*). *Dendropsophus riveroi* is spatially restricted to the upper Amazon basin (Frost, 2021) and this turnover region may represent the eastern limit of its range. Meanwhile, *D. walfordi* is more widely-distributed across Amazonia (Frost, 2021). These species are typical from the flooded interface, locally abundant, similar-sized, and phylogenetically closely related (Orrico et al., 2021). Such traits are likely to promote a high overlap in their occupied ecological niches, and the inference of segregation between their populations in this region seems to represent a robust biological pattern.

Spatial variation according to the two species richness indexes also showed heterogeneous patterns along the Solimões, but not similar to each other or the compositional variation. Alpha diversity was negatively related with longitude ($F_{1,7} = 32.50$, $R^2 = 0.82$, $P < 0.001$) (Fig. 13.6D), indicating a continuous increase in species richness by sampled localities from the upper to the lower Solimões (Fig. 13.6D). This result is counterintuitive considering one of the best known patterns of Amazonian diversity gradient, where species richness increases in the opposite direction (east—west) for terrestrial and aquatic assemblages (Wittmann et al., 2006; Hoorn et al., 2010; Oberdorff et al., 2019). Although unexpected, this result was also found in a recent study investigating the spatial patterns of amphibian diversity from macrophyte banks in this river basin (da Fonte et al., 2021), and may be caused by a downstream increase in habitat availability, in accordance with the classical hypothesis that species and genetic diversity increase downstream of riverine systems (Muneepeerakul et al., 2007; Paz-Vinas et al., 2013). In the Solimões, the West—East decrease in terrain slope also decreases the energy in the system, and increases the proportion of terrains subjected to the seasonal flooding (Pupim et al., 2019) (Fig. 13.6B). These geomorphological changes generate more extensive floodplains downstream from the Solimões, which probably harbor a greater abundance of macrophytes, consequently generating ecological opportunities for a greater amphibian diversity. Some species only recorded in the lower Solimões in our sampling support this hypothesis (e.g., *Scinax nebulosus*, *Dendropsophus* cf. *minusculus*), and should be more common in the Amazon River.

Beta diversity was not related with longitude ($F_{1,7} = 0.94$, $R^2 = 0.12$, $P = 0.202$) (Fig. 13.6E), instead, highest values were observed in specific regions of the Solimões. This result indicates a greater homogeneity in species composition among localities in the upper Solimões and closer to its lower course, while species turnover reached maximum values among localities in the middle Solimões (Fig. 13.6E). Such a result is likely generated by the heterogeneous mosaic of habitats on the margins of the Solimões, which combines different geomorphological characteristics and flood pulse influences (Pupim et al., 2019). In the upper and middle Solimões, the proportion of *paleovárzea* patches increases near its margins, following an elevational gradient and the sequential historical abandonment of floodplain terraces toward the lower course (Pupim et al., 2019). On the southern bank of the Solimões, these patches of higher terrains advance further east than on its northern bank (Fig. 13.6B). Therefore the possibility of overlap between distributions of species typical of flooded habitats and generalist immigrants from nonflooded ones increases along the southern margin of the middle Solimões. The occasional presence of some immigrant species from the nonflooded habitats in our sampling (e.g., *Osteocephalus leprieurii*, *Allobates* spp.) may have contributed to the high species turnover detected in this region. An analogous pattern might also occur in the environmentally similar upper Solimões (Fig. 13.6B), where additional distributional overlap with species typical from Andean foothills may occur. A high beta diversity value was also detected in the extreme lower Solimões (Fig. 13.6E) and may be a result of overlap between distributions of species typical from the *várzea* of the Solimões and the Amazon River.

Although affected by sampling biases, the combined results of our exploratory analyses around the amphibian variation along the longitudinal axis of the Solimões indicate that: (1) amphibian assemblages at the flooded habitats are heterogeneously distributed along this river; (2) this variation is likely influenced by geomorphological and environmental heterogeneity both in the west−east direction and between the river margins (north−south direction). Investigating such little-known biogeographical patterns of flooded habitats is essential, as the future of these habitats is worrying (Vale et al., 2008; Davidson, 2014; Irvine et al., 2022). In addition to being historically exploited by human occupation and extremely sensitive to anthropogenic impacts (Keddy et al., 2009), many new hydroelectric dams are planned to be built in Amazonia (Latrubesse et al., 2017). These dams may negatively and irreversibly affect the seasonally flooded habitats before we can better elucidate the spatial variation and levels of ecological dependence of their associated biota (Dayrell et al., 2021; Latrubesse et al., 2021; Ribas and Aleixo, 2019). We envision that this chapter encourages new research on the historical and ecological processes that shaped the biotic patterns evidenced here, as well as new studies with amphibians and reptiles in these threatened Amazonian flooded habitats.

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Chapter 14

Management of waterbirds in a Kalahari pan ecosystem

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14.1 Wetlands in southern Africa

Southern Africa extends south of the Kunene River in the west and the Zambezi River in the east, along the latitudes of 17°S and 16°S. It encompasses four large countries, two small enclaves, and the southern half of Mozambique. Southern Africa holds a large number of natural wetlands and artificial reservoirs. There are said to be up to 11,000 reservoirs (larger than 1 hectare) in Zimbabwe alone (Verheust, 1997). Zimbabwe too shares the enormous Kariba reservoir on the Zambezi River with Zambia to the north; it covers nearly 5500 km^2, and is 281 km long (Hughes, 2006). At the time of its completion, Kariba was the "world's biggest man-made lake" (Gillies, 1999), and apparently it still in terms of volume (185 billion m^3).

The definition of wetlands by the Convention on Wetlands of International Importance especially as Waterfowl Habitat (Ramsar Convention) is broad (Smart, 1996) and it includes "artificial" and "permanent" wetlands (see Irvine et al., 2022, Chapter 19; Laltaika, 2022, Chapter 23; Marambanyika et al., 2022, Chapter 22; Wasserman and Dalu, 2022, Chapter 1). Here we prefer a more restricted view, which is naturally flooded land by means of rainfall, a river, and/or the sea. Southern Africa has numerous large natural wetlands. In Namibia, there is the Etosha Pan, in Botswana the Okavango Swamps and the Makgadikgadi Pans, in South Africa the St Lucia estuarine system, and in Mozambique the Zambezi River Delta. By contrast, in Zimbabwe the only

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natural wetland of any size is the Kazuma Depression on the western boundary, which covers 23 km^2 (Beattie and Bing, 1990). The local names of some of these areas are descriptive of the nature of the wetlands, but suffice to say that the Etosha and Makgadikgadi Pans are salt pans which mostly fill up from rainfall at the onset of the wet season.

There are numerous wetlands in southern Africa, both on the coastlines (e.g., in Namibia, Simmons, 1992) and inland. Most of the inland wetlands are called pans occurring on Kalahari sands, dambos, or vleis. In Hwange National Park (HNP), western Zimbabwe, for example, there are almost 39,000 Kalahari pans (hereinafter called pans), at an average density of about 2.7 pans per km^2 (Fig. 14.1; Bowler, 1995). The pans extend from northern South Africa (about Upington) through half of Namibia and most of Botswana, and a small part of western Zimbabwe, and through half of Angola and western Zambia, into the south and west of the Democratic Republic of Congo, as far as capital city Kinshasa on the Congo River (Mendelsohn et al., 2002). In semi-arid Botswana, there are "numerous small pans and seasonally inundated wetlands"; also several large reservoirs have been built (Tyler and Bishop, 1998). As mentioned above, Zimbabwe is endowed with countless small wetlands, which have been mapped at a large scale of 1:6.8 million (Matiza, 1994). Matiza (1994) distinguished between dambos and pans, dambos being "palustrine wetland(s)" mostly on the granite shield of the country; they cover about 3.3% of Zimbabwe. Pans in Zimbabwe also occur in the southern end of the Gonarezhou National Park; in the west they are at an altitude of about 1000 m above sea level (asl), whereas in the south they are closer to 300 m asl (Matiza, 1992).

By contrast, much of Mozambique is in the low-lying coastal plain of south-east Africa. The Save and Limpopo Rivers flow through Mozambique at low gradients for 270 and 400 km, respectively, before joining the Indian Ocean. Floodplains, swamps, and pans are a feature of the landscape from the Zambezi River Delta coming south. Mangroves hug much of this

FIGURE 14.1 An aerial photograph of a cluster of pans from Hwange National Park, with some of them drying up (bottom right). *Photo by Hugo Valls.*

coastline and these are considered a subtype of coastal/marine wetlands under the Ramsar. As the Zambezi River leaves Zambia and Zimbabwe at the confluence with the Luangwa River, it forms the Cahora Bassa reservoir, Mozambique's "largest body of freshwater" (Parker, 2005). The reservoir extends westward for about 240 km from the dam wall near Songo and has a surface area of about 3000 km^2.

There are also peatlands in the Angolan Highlands that help in maintaining the large source lakes that feed into the Okavango Delta (Goyder et al., 2018). In Lesotho, the natural wetlands of the eastern highlands are bogs and fens, known as "mires or peatlands" (Schwabe, 1995). These alpine mires are the only ones in southern Africa, and do not occur at altitudes below 2750 m (Schwabe, 1995). Eswatini (formerly Swaziland), similarly to Lesotho, has a few wetlands that have all suffered from "erosion and degradation" (Barnes and Monadjem, 2001).

South Africa is the largest country in southern Africa, and enjoys three coastlines: against the Atlantic (west) and Indian (east) Oceans, and a southern coastline facing Antarctica. In spite of its southern location, south of 22°S, it hosts the full range of wetland types, namely riparian including some development of floodplains; mangroves on the east coast from East London (33°S) northward; and endorheic pans (see below) that occur in much of the country; the coastal "lakes" such as Zeekoevlei near Cape Town; Wilderness lakes at Sedgefield, Lake St Lucia, coral reefs in Maputaland north of Lake St Lucia; and Aliwal Shoal just south of Durban.

14.2 The formation and ecology of pans in southern Africa

A common feature of dry regions within southern Africa is endorheic pans. Endorheic pans are small closed basins, typically circular/oval or shallow, where inundation is ephemeral. They have no outlet as a drainage, and the average slope of the land is less than one degree (Allan et al., 1995; Job et al., 2022, Chapter 2). Allan et al. (1995) use a cut-off point of 1 hectare as the minimum size for a pan, just as Verheust (1997) does for his inventory. However, most pans in HNP are smaller than 1 hectare, hence we suggest that the definition may be too restrictive.

The distribution of pans in southern Africa (Fig. 14.2) is affected by four main factors: drainage, slope gradient, bedrock, and climate (Le Roux, 1978). Animals concentrate around areas with available surface water and essential salts which lead to localized overgrazing. In areas of low precipitation, vegetation is limited and the land surface is left highly susceptible to deflation (Goudie and Thomas, 1985). The substrate under the soil is very important in pan formation, with the landscape in regions such as the western part of Zimbabwe (Bowler, 1995) and northern Cape (Ferreira, 2010) having layers of clay in depressions that collect rain water during the wet season thereby forming pans. In the central Kalahari basin, pans are often associated

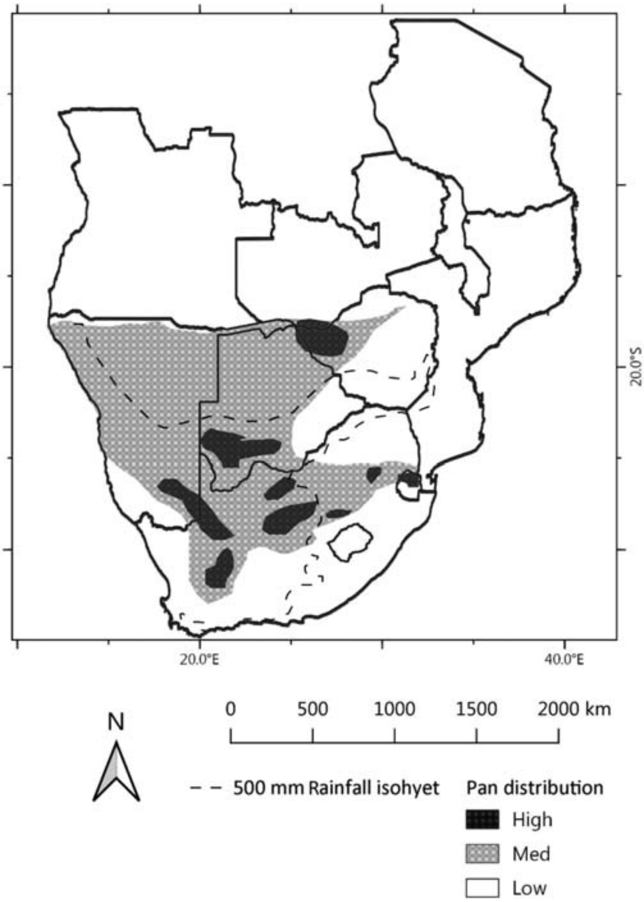

FIGURE 14.2 Distribution of pans in Southern Africa. The areas with high pan densities have densities exceeding 1 km^{-2} while those with medium (Med) is 0.8 km^{-2}. *Adapted from Goudie, A.S., Thomas, D.S.G., 1985. Pans in southern Africa with particular reference to South Africa and Zimbabwe. Zeitschrift für Geomorphologie NF 29, 1–19.*

with a high concentration of minerals, forming salt pans, that are utilized by a variety of ungulates (Parris, 1984), as well as birds. In the southern Kalahari dune veld, pans are usually found on flat ground (Leistner, 1967).

The changing limnology of a pan, through to its eventual and normal drying out, will influence the kind of life forms that are able to survive in the pan or to invade it seasonally. Vegetation will include flora such as sedges, grasses, reeds and bulrush, waterweeds, ferns, as well as phytoplankton and cyanobacteria (Dalu et al., 2022, Chapter 8; Piedade et al., 2022, Chapter 7). Indeed, these last are likely to be the first invaders into a newly wet pan (Msiteli-Shumba et al., 2017), as they utilize the available nutrients in the water (Deemy et al., 2022, Chapter 6). The plant dynamics are also conditioned by the influx of nutrients coming from the excreta of large mammals around these pans (Hulot et al., 2019). Among animals there will be a list of aquatic invertebrates that will increase due to abundant food, including a variety of zooplankton (see Brendonck et al., 2022a,b, Chapters 9 and 10). Most fish are unlikely to survive in pans that dry up with the excpetion of killifish and lungfish but will certainly be present in permanent pans and those with artificial water provisioning (see Reichard, 2022, Chapter 12). Amphibians should appear, such as the African Bullfrog *Pyxicephalus adspersus* coming out of estivation after sufficient rain. Maybe some reptiles could arrive; the Nile crocodile *Crocodylus niloticus* is well known for finding its way to newly inundated pans from other permanent water bodies; and possibly the water monitor (Lizard) *Varanus niloticus* to feed on frogs and catfish in the pans (see Cuthbert et al., 2022, Chapter 17; Moraes et al., 2022, Chapter 13). Both of these reptiles are predators of birds' eggs and young chicks. The greatest users of these ephemeral pans are undoubtedly birds, also known to arrive quickly at newly wet pans (Herrmann et al., 2004; Simmons et al., 1999), and even to breed there. Indeed the pans in HNP were described as "duck factories" (Godfrey, 1992).

Numerous studies have been focused on the different bird species found at pans (Geldenhuys, 1982), and many of the counts are now incorporated into the biannual waterbird surveys of Wetlands International (Dodman and Diagana, 2003) as well as published separately in various publications (Tyler, 2001). Waterbirds can breed successfully in pans, given that surface water is available long enough for chicks to develop until fledging, but short enough not to be preyed upon by reptiles. Perhaps the most spectacular birds to take advantage of the pans, especially if they become salty, are the greater and lesser flamingos (see Latin names of waterbirds in Appendix 4).

Much of the pan ecosystem type in southern Africa is contained in the newly established (from 2006) Kavango–Zambezi Transfrontier Conservation Area (KAZA TFCA). Not only is it the largest TFCA in Africa, at 520,000 km^2 in size, but it also holds the largest population (approximately 230,000) of African Savanna elephants *Loxodonta africana* in Africa (Chase et al., 2016). Elephants are ecosystem engineers as they alter vegetation structure and cover in and around pans. Other mammals include the hippopotamus *Hippopotamus amphibius* and Sitatunga antelope *Tragelaphus spekei* (both probably found mostly in protected areas in southern Africa) to the Cape clawless otter *Aonyx capensis* and water mongoose *Atilax paludinosus*, to various rodents. The hippopotamus is known for maintaining short grass swards around pans, while the Cape clawless otter and water mongoose prey not only on fish and frogs but also on waterbirds and their eggs. One species of waterbird, the slaty egret, is endemic to the TFCA. The shoebill stork has been seen on a few occasions in different areas but it is not yet included on the area's check list. Among passerine waterbirds the *Luapula Cisticola* is also close to being endemic to the TFCA.

Macrophytes are central to the diversity and abundance of macroinvertebrates in the pans (Meintjes, 1996). The type of vegetation is known to be dependent on pan size, or density of pans in a particular locality (Ferreira, 2010). Most of the pans in northern Botswana have been described as having muddy edges and occupied by few macrophytes (Herremans, 1999). With advancement in geospatial technologies it should be possible to estimate more precisely the number of pans in a system. Such technologies can also allow for modeling the available habitat for breeding waterfowl, given that the minimum period required for most waterfowl species to complete a breeding attempt is longer than 110 days (Godfrey, 1992; Meintjes et al., 1994).

A variety of macroinvertebrates utilize pans. For example, macroinvertebrate communities in and around pans in HNP were dominated by Chironomidae, Corbiculidae, Dytiscidae, Hydrophilidae, Notonectidae, and Oligochaetes (Hulot et al., 2020), while Meintjes (1996) found Anostraca, Notostraca, Cladocera, Ostracoda, and various insect larvae in South Africa (also see Brendonck et al., 2022a,b, Chapters 9 and 10; Dube et al., 2022, Chapter 11). These organisms need to reach reproductive maturity or metamorphose into non-aquatic stages before the water in pans dry up (see Fig. 14.3 for an example of a pan drying up). A particular type of invertebrates is the phyllopods, which are primarily referred to as "temporary water taxa" in arid regions (Meintjes, 1996), because they are able to reproduce quickly before pans dry up, and hence have been common in these systems. They thus form important components of the food webs in the pans (see Cuthbert et al., 2022, Chapter 17).

FIGURE 14.3 An illustration of a pan drying up, with visible tracks of elephants. *Photo supplied by Hugo Valls.*

14.3 Waterbird communities and breeding in the pan ecosystem

There are variations to the definition of waterbirds, with some authorities adopting a family-based approach (Rose and Scott, 1997; Underhill et al., 1999) and others use ecological association of birds to wetlands (e.g., Mundy, 2000). Here, we define a waterbird (or wetland bird) as one that is ecologically dependent on water habitats for important processes such as feeding and breeding. We have provided the list of these species in Appendix 4, but have also included a few nonwaterbird species that we often encountered when carrying out counts in HNP.

Each pan may be a seemingly unimportant wetland, but their combined numbers scattered over the arid interior of southern Africa, make this system undoubtedly the most important for wetland birds in the region (Herremans, 1999). Pans are part of the larger savanna, grassland, and desert biomes, and contribute immensely to the ecology of surrounding habitats. The contribution of pans to waterbird diversity is high, for example, surveys conducted at all major wetlands in the Kalahari Basin in Botswana showed that waterbird diversity and densities were highest at small ephemeral pans (Herremans, 1999). The curlew sandpiper, ruff, little stint, and wood sandpiper (see Fig. 14.4 for examples of these waders) are all considered to have substantial inland populations in southern Africa during their austral summer

FIGURE 14.4 Examples of waders found on pans in southern Africa, illustrating the Caspian Plover (A), Common Ringed Plover (B), Little Stint (C), and the Three-banded Plover (D). *Photos supplied by Jean-Michel Blake.*

nonbreeding visit, occupying a variety of freshwater wetland types including pans (Underhill, 1995). The pans in northern Botswana host very high densities of waterbirds during the wet season, especially Anatidae (ducks and geese) which had densities that were more than double than those at sewage works (Herremans, 1999).

While a pan may provide food for waterbirds, it may not provide sufficiently well-protected nesting areas, and vice versa. Thus most waterbird species in southern Africa are opportunistic and highly mobile in various wetland matrices and this results in them being widely distributed (Herremans, 1999). The mechanisms used by waterbirds to move to pans soon after flooding have not been fully explored given the episodic nature of such events, and the low observer density in arid areas (Simmons et al., 1999). It has been suggested that waterbirds move with the rainfall fronts and so arrive at pans shortly after flooding, and this is presumably related to the other ecological events triggered by the rains (i.e., the emergence in massive numbers of frogs, termites, and dragonflies) (Simmons et al., 1999).

Some analyses of waterbird counts conducted at various sites in Namibia (Kolberg, 2012, 2013) reveal the importance of pans in maintaining species' populations. Some sites are considered important when they host more than 1% of the world populations. Although some of the Namibian pans support high densities of waders such as the little stint, curlew sandpiper, and sanderling, which have surpassed the 1% threshold of their world populations on several occasions (Kolberg, 2013), however, most other waterbirds are below this threshold. An example is the red-billed teal which is considered one of southern Africa's most abundant duck on Namibian ephemeral pans, but had not surpassed the 1% level between 1991 and 2008 (Kolberg, 2012).

The Makgadikgadi salt pans in Botswana (a complex covering about 35,000 km^2) are believed to be among the most important breeding sites for the lesser and greater flamingos, and flamingo numbers recorded at Sua Pan sometimes exceed the total estimated southern African population (McCulloch and Borello, 2000). In the late 1980s, approximately 44,000 greater flamingos successfully raised more than 25,000 chicks at Sua Pan (Mcculloch and Borello, 2000). In July 2001, (Mcculloch et al., 2003) tagged five lesser flamingos and three greater flamingos with satellite trackers at the Sua Pan. Information recovered from these trackers revealed that flamingos migrate from different parts of southern Africa to feed and breed at the Makgadikgadi. One of the greater flamingos flew west to the coast of Namibia, and the other birds moved to pans in several parts of South Africa and the Mozambican coast.

The contribution of pans to the breeding of waterbird species in southern Africa cannot be ignored as there is much evidence of the importance of pans for duck breeding when compared to reservoirs (Geldenhuys, 1976; Geldenhuys, 1982). A recent analysis of waterbird trends over 20 years in HNP revealed a general increase in populations of most waterbird species, contrasting with the rest of Zimbabwean waterbird trends (Tarakini et al., 2020b). We have included these trends for species presented in Appendix 4, alongside their global status and breeding season.

14.4 The pan ecosystem in western Zimbabwe – protected areas and nonprotected areas

Conservation strategies in southern Africa will not be complete without giving attention to the large areas of western Zimbabwe, which have been set aside for wildlife conservation because of their aridity (mean annual rainfall about 600 mm, Chamaillé-Jammes et al., 2006) and where rain-dependent agriculture is non-viable. These areas make up the southern part of the KAZA TFCA, and are mainly covered by Kalahari sands, which support many pans (Table 14.1). For this region, the highest densities of pans (i.e., 1,65 waterpans km^{-2}) were recorded in HNP (Godfrey, 1992), which also hosts one of the highest densities of free-ranging elephants in Africa (Chamaillé-Jammes et al., 2016).

TABLE 14.1 Areas, activities, and administration of land categories in the south-east KAZA TFCA.

Name of area	Activities	Size (km^2)	Responsible authority
HNP	Photography	14,651	PWMA
Sikumi Forest Area	Photography, hunting	544	FC
Matetsi Safari Area	Photography, hunting	2918	PWMA
Kazuma Pan National Park	Photography	313	PWMA
Pandamasue Forest Area	Photography	350	FC
Zambezi National Park	Photography	560	PWMA
Hwange District	Urban and rural settlements, mining, hunting under CAMPFIRE	8198	Hwange Rural District Council
Tsholotsho District	Urban and rural settlements, hunting under CAMPFIRE	7844	Tsholotsho Rural District Council

Abbreviations: *FC*, Forestry Commission; *HNP*, Hwange National Park; *PWMA*, Parks and Wildlife Management Authority.

Pans in areas set aside for photography are protected from both subsistence and commercial hunting. In high tourist hotspots, a number of seasonal pans' water is augmented through boreholes to attract various animals and birds. As a result, the pressure exerted on waterbirds from human presence on pans can be high especially during peak tourist seasons. Our studies in some of these photographic areas reveal that wildfowl species generally increased their wariness in presence of humans but the current levels of disturbance do not seem to affect their probability of occupying these pans (Tarakini et al., 2020a). Pans in the hunting areas probably experience less pressure from human disturbances (when compared to those in photography areas) as hunting is seasonal (Crosmary et al., 2012) as fewer tourists visit them. Also, there is less effort directed to providing artificial water in these areas and waterbird abundance is generally lower on seasonal pans.

While entry into areas under Zimbabwe Parks and Wildlife Management is restricted and controlled through a photography/hunting permit system, those under the Forestry Commission allow local people from neighboring communal areas to extract thatching grass (in April—May), firewood (every Thursday), and livestock grazing 3 km from the forest area boundary (Guerbois et al., 2013). Access to pans in communal areas (rural settlement areas) is governed loosely by traditional leaders and the local people sometimes hunt/trap waterbirds at the pans. The communal areas are administratively under the Rural District Councils but have Communal Areas Management Programme for Indigenous Resources (CAMPFIRE) wards in Hwange and Tsholotsho districts. The CAMPFIRE was developed to ensure that significant financial earnings from natural resources (e.g., from trophy hunting in communal areas) revert to rural communities for their benefit, but it has been facing several challenges as discussed by Neumann (2005).

Before 1970s, in the pans on the northern side of the Tsholotsho District (areas bordering HNP), duck shooting was practiced. Indeed the gamebird hunting hotspots identified by Griffiths (1998) also included this area. However, because individual pans did not host large numbers of ducks to sustain the hunting activity, it was stopped. Also, the exploitation of ducks especially for human consumption had other challenges including quality of meat produced (Geldenhuys et al., 2013) and disease risks (Cumming et al., 2015; Vanhove et al., 2021, Chapter 15), although some viewed the hunting activities as a way of reducing the damage to crops by species such as Egyptian geese.

Villagers in communal areas often rely upon areas close to pans for crop production, livestock grazing, and supplementary protein from fish. As a result, relatively large changes in vegetation composition and productivity due to livestock grazing have been reported to occur around pans (Strauch et al., 2009). The heavy grazing near pans can reduce or even eliminate important grasses that are useful to waterbirds (Raeside et al., 2007), in addition to the trampling risk to the nests of ground nesting species. The livestock drive ecosystem processes especially vegetation richness, standing biomass, soil microbial communities, water quality, vertebrate and invertebrate abundance and richness (Cumming et al., 2013; Msiteli-Shumba et al., 2018; Russell et al., 2014). Also, domestic dogs *Canis familiaris* that usually accompany the local people often disturb waterbird activities at pans.

Our work in this area suggests spatiotemporal variation in waterbird communities. For example, ducks were more abundant inside HNP during the wet season, but during the dry season the proportion of ducks in the communal areas was greater than those inside the protected areas. Livestock in the communal areas attracts large numbers of cattle egrets, and these would contribute to greater waterbird abundances. There are therefore distinctive functional capacities of pans outside core conservation zones in meeting specific requirements of waterbird guilds.

14.5 Trends and drivers of waterbird communities

As the pan system in southern Africa is mostly found in arid areas, some of these areas have also been set aside for wildlife conservation purposes. Thus waterbirds utilizing pans are subject to interactions with other wildlife species, including but not limited to, herbivores (mostly elephants, buffaloes, and cattle); terrestrial predators (such as jackals and mongooses); a wide variety of birds of prey; and humans with their pets (see Fig. 14.5 for an illustration of animals on pans). The interaction of waterbirds with other wildlife species on pans can have beneficial or detrimental effects to waterbird feeding and breeding.

Evidently, the amount of water contained in pans is an important driver of waterbird communities. Our surveys in the south-east KAZA TFCA suggest that ducks and waders have a preference for large pans compared to small ones. Also, diversity of waterbirds seems not to be affected by vegetation attributes in and around HNP, which supports the observation that the waterbirds in the pans will be following inundated areas after rains for feeding and breeding (Herremans, 1999). The management intervention of supplementing water into pans may affect waterbird spatiotemporal use of pans

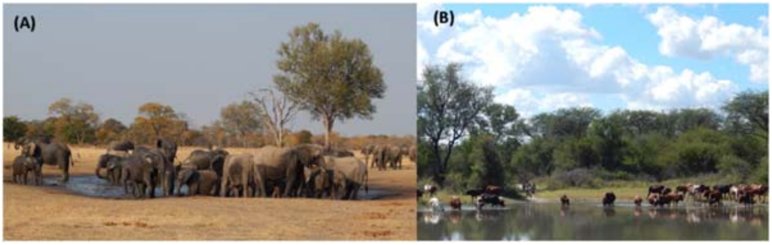

FIGURE 14.5 African elephants (A) and cattle (B) drinking water from pans. *Photos by Tawanda Tarakini.*

in the landscape. The waterpans with artificial water provisioning may become more attractive in general for the waterbird communities as previously documented (Li et al., 2013), probably because they remain relatively large for longer periods.

There are studies that have illustrated how predation can be detrimental to waterbird populations, but there are few studies pertaining to southern African pans (Coetzer and Bouwman, 2017). Although waterbirds may suffer negative effects of noise from humans and hunting in the communal areas (Tarakini et al., 2018), the presence of terrestrial predators (mainly wild carnivorous mammals and crocodiles) does not seem to influence waterbird abundance in the south-east KAZA TFCA. However, disturbances from stimuli such as human/vehicle noise and domestic dogs caused waterbirds to fly away from their feeding/resting patches (Tarakini et al., 2020a). Most duck species may often swim into the pan interior when sensing danger (Ndlovu et al., 2014).

Some studies provide evidence that population trends are not random with respect to life history traits and ecological traits (see Gálvez et al., 2022, Chapter 18). Barshep et al. (2017) found that brood size, type of chick development, and mating system were related to population trends of resident and migrant species in South Africa. While chick rearing in colonial nesting waterbirds may be more successful compared to solitary nesters on pans (McNeil et al., 1993), they can be more vulnerable to disease outbreaks (Kushlan, 1993). The species that migrate long distances may also be prone to more global threats compared to short distance migrants (Barshep et al., 2017). An attempt to understand the possible effects of life history traits, human activities such as hunting and habitat modifications and disturbances on the population trends was done by Tarakini et al. (2020b) using 20 years of data from pans in north-western Zimbabwe. It seems that the trends are more reflective of the large-scale pressures such as the utilization of waterbirds by people at regional/continental/global levels and habitat disturbances than species' ecological and life history traits (except for body mass). Body mass, which is a correlate of many life history traits, interacted with large-scale pressures (i.e., species' susceptibility to hunting and habitat disturbances) resulting in greater chances of declining population trends for small waterbird species. However, it was established that some of the pans are still supporting mostly stable or increasing trends when compared to other wetland types (Tarakini, 2019).

14.6 Threats to waterbirds inside and outside protected areas

Despite pans being fairly well-utilized habitats for waterbirds in southern Africa, there are processes that threaten waterbird populations not only in these pans but in other wetlands. First, wetlands rank high in the list of habitats that are currently being converted to other uses. BirdLife International has attempted to describe the major threats to individual species. For the species presented in Appendix 4, their global threats are summarized in Table 14.2.

Some pans are important stop-over sites for migratory waterbirds (e.g., the Makgadikgadi Salt Pans in Botswana and Etosha Pan in Namibia) and the use of the "hop, skip and jump" (i.e., the pans are used for resting and replenishing energy reserves before flying to another site along the migration flyway) as described by Piersma (1987). Processes occurring at such key sites thus become important to migratory waterbirds. Kirby et al. (2008) showed that Palearctic—Afrotropical migrants breeding in Europe had declining status more than increasing during the 1970—2000 period. Data from BirdLife International indicate that Palearctic—African migrants have the highest proportion of threatened waterbirds (i.e., 16% of all migrating birds) (Dodman and Diagana, 2007).

The declines in almost 80% of bird species that are threatened or near threatened globally are attributed to land use changes from commercial agriculture (Kirby et al., 2008). The drainage and reclamation of wetlands for commercial agriculture has been widespread globally (Wood and van Halsema, 2008). In Africa, agriculture has long been practiced on the floodplains of major rivers, such as the Nile, Niger, and Zambezi and in other

TABLE 14.2 **A summary of dominant threats to waterbirds in southern Africa and examples of waterbird families affected.**

Threats	Percentage of species affected	Examples of families affected
Poisoning	22.0% (*n* = 39)	Phoenicopteridae, Accipitridae, Ardeidae, and Rallidae
Hunting	40.1% (*n* = 71)	Anatidae, Scolopacidae, and Phalacrocoracidae
Diseases	29.9% (*n* = 53)	Anatidae, Scolopacidae, and Charadriidae
Habitat disturbances	59.3% (*n* = 105)	Ciconiidae, Laridae, Gruidae, and Phalacrocoracidae
Land cover changes	88.1% (*n* = 156)	Anatidae, Rallidae, Accipitridae, and Ardeidae
Invasive species	7.3% (*n* = 13)	Anatidae, Rallidae, Gruidae, and Laridae
Persecution	13.6% (*n* = 24)	Anhingidae, Ardeidae, Laridae, and Accipitridae

types of wetland such as dambos and bas-fonds (shallow areas of the sea) or inland valley bottoms (Wood and van Halsema, 2008). The dambos and pans in southern Africa are playing an important role in helping human communities survive during the long dry season and avoid seasonal hunger through small-scale agriculture (McCartney et al., 2010). Some of the impacts include, but are not limited to, eutrophication, undesirable effects of pesticides and herbicides, and trampling of areas around pans.

Grazing by livestock under free-ranging conditions (Scoones and Cousins, 1989; Wood and van Halsema, 2008) as well as wildlife particularly in the protected areas (Valeix et al., 2007) remains a major threat to pans. Inside protected areas, pans are heavily trampled by herbivores during the dry season as the animals lick the soil around sites with high mineral content (salt pans). In communal areas, where resources inside and around pans are treated as common goods (Murombedzi, 1994), the levels of grazing and waterbird disturbances are very high. Herbivore congregations around pans may negatively affect not only the nesting waterbirds (risk of nest trampling), but also foraging waterbirds. A study by Tarakini et al. (2020a) to investigate responses of waterbirds to various forms of stimuli revealed that birds did not make high escape behaviors when disturbed by herbivores compared to noise from humans/vehicles, but their levels of vigilance increased. Thus, waterbirds seem to be making mostly behavioral adjustments, with no impact on population numbers, but if herbivore pressure intensifies with aridity it may have a more significant effect on waterbird numbers as well as diversity.

Many waterbird species are utilized in sport hunting in southern Africa, especially in South Africa and Namibia (Harmse, 2019; Viljoen, 2005). The common species targeted are the yellow-billed duck, red-billed teal, South African shelduck, spur-winged goose, and Egyptian geese. In Zimbabwe, between 1968 and 1973, the waterfowl hunting statistics showed a steady increase of waterbirds being hunted corresponding to more people buying gamebird hunting licenses (Woodall, 1974). During the 1972–1973 season, about 14,000 waterfowl were shot by licensed hunters in Zimbabwe (Shackleton, 1979). These statistics excluded ducks which were killed illegally especially in communal areas. Hunting has however declined sharply in Zimbabwe, owing to various factors including deteriorating wetland habitats, more so after the land reform program in the year 2000 which resulted in humans settling close to some of the wetlands.

Recent work by Pain et al. (2019) shows that there has been an increase of species being affected after ingesting lead from ammunition used in waterfowl hunting. The effect of lead is expected to be high where waterfowl hunting is intense, and practiced for longer periods. There are limited assessments to establish the percentage of pans in southern Africa on which waterfowl are hunted for commercial purposes. Also, the general decline of waterfowl hunting (e.g., in Zimbabwe) may imply a declining effect of commercial waterfowl hunting on southern African pans. In fact, other authorities think that this region has not developed the potential for gamebird hunting or wing-shooting (shooting of birds in flight) (Geldenhuys et al., 2013).

In sub-Saharan Africa, the human communities living in arid under-developed areas are plagued by drought and crop and animal diseases, and often with high levels of vulnerability to food insecurity (Seoraj-Pillai and Pillay, 2017). As a result, people resort to subsistence hunting on pans. Waterfowl meat helps in improving nourishment and the food security situation (Geldenhuys et al., 2013). Studies are also lacking to estimate the numbers of birds that are being harvested on pans. People use various methods including dogs, catapults, poisoning, snares, and traps to capture waterbirds (Miima, 2006). In north-western Zimbabwe species such as spur-winged geese, Egyptian geese, knob-billed duck, red-billed teal, and African pygmy goose could be facing more hunting pressure from locals compared to other species (Tarakini et al., 2018). Due to the opportunistic nature of the breeding of many waterfowl species in southern Africa especially on pans (Hockey et al., 2005), the subsistence hunting pressure can be very localized.

Infrastructural developments associated with energy production and mining are also threatening waterbird welfare. Currently, South Africa is leading in terms of the development of wind energy in southern Africa, followed by Namibia and Zambia, which this activity posing a significant threat to waterbirds. Although in the Mpumalanga province of South Africa, Ferreira (2010) cited the establishment of power and telecommunication lines (especially around the coal fields) as a threat to flying waterbirds, the level of threat is believed to be still small in comparison to other places in the world (Allanson et al., 2012).

Pans have been polluted in areas where minerals are being extracted. For example, the mining activities in the Mpumalanga province of South Africa often result in toxic chemicals being washed into pans which in turn compromise the water quality as there is oxidation of sulphite-containing waste associated with mining activities, known as the acid mine drainage (AMD) (Ferreira, 2010). Sensitive macroinvertebrate and plant species may disappear under AMD, and the toxins in the precipitate may end up accumulating in top predators of the ecosystem. Although there are less pans in the northern part of HNP, the coal mining activities nearby have resulted in the water in the surrounding surface waters being polluted with sulfur and carbon rich compounds.

Another form of pollution, associated with urban settlements is wastewater treatment sites. A lot of plastics are also found at sites receiving water from sewage treatment plants. A recent study by Reynolds and Ryan (2018) revealed that ducks ingest microplastics if they are present in freshwater systems, and it has also been proven that the ducks carry the microfibers on their feathers. Birds that ingest microplastics may have their gastrointestinal tracts obstructed and such obstructions lead to increased mortality. Another challenge of partially treated sewage is eutrophication, which is the increase of nutrient concentration (e.g., phosphorus, nitrogen, sulphur). Eutrophication disrupts waterbird communities on affected wetlands. Usually, vegetation on eutrophic sites will be dominated by weeds and due to the limited oxygen in the water, some aquatic forms of life (e.g., fish) die-off. Thus, eutrophication will have cascading effects on food chains of the systems. These threats emanating from urbanization can be worsened by noise pollution, which may disturb the foraging patterns of waterbirds as birds may constantly react to sounds. The sub-Saharan Africa region is considered the world's fastest urbanizing area in the world, with projections that by year 2050, about 54.8% of its population will be living in urban areas (Saghir and Santoro, 2018).

Persecution of species remains a threat, particularly at important waterbird migration locations in southern Africa. Reasons for persecution vary, but include killing birds because of superstitious beliefs through associating some species to witchcraft such as the hamerkop and marsh owl. Also, another reason for persecution is competition for common resources such as wild fruit/fish. The greater flamingo, African fish eagle, and grey heron are persecuted among fishing communities while the Egyptian geese is persecuted by farmers (Seoraj-Pillai and Pillay, 2017; Zisadza-Gandiwa et al., 2013). Some species (such as blacksmith lapwing) make displeasing noises resulting in people chasing them from their habitats (Tarakini et al., 2018). Due to the small size of pans and also their occurrence in arid/semi-arid regions (which are sometimes protected), the persecution pressure on waterbird species tends to be small. However, for those that have high persecution pressure in certain localities, important activities like breeding could be compromised.

Waterbirds in southern Africa have not been spared from the negative effects of climate change and severe weather events. For waterbirds, at both species' and population levels, models by Amano et al. (2019) suggest general declines of waterbird abundance in the tropics, but increases at higher latitudes, with increasing temperature. As wetlands are among the most threatened ecosystems, species thriving on them have not been spared from climate change impacts. For the major threats presented in Table 14.2, it can be argued that these would worsen given the declines in precipitation and increasing temperatures. Hot climatic environments cause pans to dry up faster. When pans dry up there can be a sudden exodus of waterbirds to other wetlands where other pressures such as stiffer competition for food, noise, and pollution, exist at greater magnitudes (Dodman and Diagana, 2007). Although some birds can exploit the last shrinking pans until they dry up completely (e.g., Kittlitz's plover) (Tyler, 2001), most species would be forced to leave drying pans earlier. Climate change is likely to lead to some major changes in the way water resources are used and this will also have major implications for waterbirds. As temperatures increase, demand for land under irrigation will increase; this may cause low flow in rivers, over-abstraction of other surface waters, lowering of water tables, leading to degradation of water resources and aquatic ecosystems with general negative effects on biodiversity.

Severe weather conditions can also impact waterbird species, for example, Clark (2004) found that the number of dead, ringed individuals of several migratory wader species including the Redshank, increased during winters with periods of extreme cold. The African-Eurasian Waterbird Agreement lists species according to levels of threat from impact of climate change, into critically, highly, and moderately threatened.

Although temperature increases on tropical ecosystems are projected to have widespread species-wide declines, the analysis by Amano et al. (2019) suggests that temperature alone generally explained only a small proportion of yearly abundance changes in waterbirds. Also, range shifts due to temperature in Africa are less certain partly as there is less information, and partly because the upper temperature tolerance limit of species which occur in the tropics is unknown (Maclean et al., 2007). The work by Hole et al. (2009) also suggests that the protected area network in southern Africa can play a key role in mitigating the impacts of climate change on biodiversity although there is greater likelihood of significant waterbird community disruption.

Projections that were made more than a decade ago suggested that southern Africa was not going to be affected in the same way. As an illustration of this regional disparity, of the 58 important bird areas (IBAs) within Botswana, Zimbabwe, and Zambia, 83% are projected to retain suitable climate space for more than half of their whole avian community complement by year 2085. A further 24% of these IBAs would retain suitable climate space for more than half of their complement of priority species (Hole et al., 2009). These percentages were significantly higher than those projected for IBAs in Nigeria, Cameroon, and the Central African Republic where only 43% were projected to retain suitable climate space for half of their whole avian community (*op. cit.*). However, the important question is the proportion of pans that are part of areas with IBA designation. Also, these projections ignore local factors that could have a greater influence such as local illegal hunting, land use changes in neighboring wetlands, and changes in management approaches of the IBAs.

Infectious diseases limit waterbird populations and changes in weather conditions may lead to shifts in the rate of reproduction of pathogens, or in the distribution of vectors carrying these pathogens. For example, Epstein and Defilippo (2001) suggested that warm winters and spring droughts might have contributed to the spread of West Nile Virus (WNV) through avian populations in Europe and North America. The prevalence of avian malaria is also dependent on temperatures. Avian Influenza Virus (AIV) epidemiology has been shown to be inseparable from the ecology of reservoir hosts, being closely linked to diet, foraging behavior, habitat type and use, movement patterns, population size, group size, and frequency of aggregation (Engering et al., 2013; Hoye et al., 2012; van Dijk et al., 2018). It is worth noting that although the construction of large dams in southern Africa has benefited most waterbirds, these areas become focal habitats with a greater risk of the viruses being spread, especially during the dry season when other wetlands dry up.

14.6.1 Avian Influenza Virus (AIV)

The AIVs have their natural reservoir in Anseriformes (ducks, geese, and swans) and Charadriiformes (gulls, terns, and waders) (Olsen et al., 2006; Webster et al., 1992). Outside of the natural reservoirs, the AIV also infects passerine and nonpasserine birds (Caron et al., 2017b; Mundava et al., 2016), poultry and other mammalian species including humans (Brown, 2010). Under experimental conditions, the AIVs have been shown to remain infectious for several months in the environment (Nazir et al., 2011). The re-emergence of zoonotic, highly pathogenic avian influenza virus (HPAI) H5N1 (bird flu) and many other HPAI subtypes in Asia, the Middle East, Europe, and Africa has led to an increased focus on the role of wild birds, particularly waterbirds, in the persistence of both low pathogenic avian influenza viruses and HPAI influenza viruses (Poen et al., 2018; Venkatesh et al., 2018; Belser et al., 2018). The spread of some of these viral diseases (e.g., H5N1 strain, and the WNV) is capable of crossing over into humans after undergoing mutations (Hill et al., 2017; Reed et al., 2003; Siembieda et al., 2008).

The southern African region generally experiences high temperatures, and this has a direct impact on the tenacity of AIV. Environmental factors such as temperature and evapotranspiration are poor predictors of AIV seasonal infection dynamics in southern African waterbirds (Gaidet, 2016), thus the host ecology could play a more important role in transmissions. Direct interindividual transmission therefore possibly plays a major role (Caron et al., 2017a; Lowen et al., 2008) as environmental conditions are not conducive for the extended pathogen persistence. As the diversity of waterfowl on pans is reliant on rainfall (rather than temperatures), its fluctuations/patterns directly influence host density (Simmons et al., 1999).

As waterbird movements increase the risk of disease transmissions, influxes of migratory waterbird species particularly waders, but possibly including rails, terns, herons, and storks could be important in introducing novel strains to waterfowl in the region. The nomadism of waterbirds across southern Africa could also affect distribution and maintaining strains as they move around, particularly in the pan system. However, the southern African region does not receive Eurasian Anatid species (Hockey et al., 2005) as these stop north of the equator hence there could be a lower risk of direct transfer of AIV strains between the northern and southern hemispheres. Also, infectivity may be reduced by warmer temperatures, radiation, and desiccation, thereby reducing virus persistence and the efficacy of indirect transmission.

14.6.2 Avian malaria

It appears that only few studies have evaluated the impact of avian malaria on freshwater waterbird species in southern Africa. The vectors of the disease are mosquitoes (*Culex quinquefasciatus* and *C. univitattus)* and their abundance is influenced by environmental factors such as temperature, rainfall, water quality, and habitat (Valkiunas, 2004). In southern Africa, areas with high rainfall have a high prevalence of the vectors, and high nutrient values within wetlands were also shown to be key in the breeding of the vectors (Okanga et al., 2013). Avian malaria prevalence may be directly influenced by anthropogenic activities that influence these environmental factors. More studies are needed to assess the potential risks of avian malaria and waterbirds on pans, as they are often nutrient hotspots, in order to prevent catastrophic episodes.

14.6.3 West Nile Virus (WNV)

The WNV belongs to the *Flavivirus* genus which has a growing number of zoonotic viruses that are transmitted by mosquitoes and ticks (Gould and Solomon, 2008). The WNV clusters with viruses that are transmitted by the *Culex* spp. mosquitoes, and birds are the main vertebrate host to this pathogen (see Vanhove et al., 2021, Chapter 15). Cases in southern Africa have been recorded in South Africa, Namibia, and the Democratic Republic of Congo and involved waterbird groups such as egrets (Sule et al., 2018). Migratory birds have been associated with the spread of the WNV across the globe (Hubálek, 2004), and the host ecology plays an important role in WNV transmission. In southern Africa, exposure to WNV would most likely occur in wetlands where there is the presence of both the vector mosquitoes and the reservoir hosts. There are many published cases of WNV from sub-Saharan Africa that suggest that the virus is endemic across the region. There is also limited availability of diagnostic methods across large areas of the continent, thus some of the risks both to humans and waterbirds are poorly understood. The presence of multispecies reservoir hosts possibly increases the success of the pathogen – with wild waterbirds providing a wider reservoir base.

14.7 Benefits of waterbirds to local people

People have always co-existed with wildlife species, and they have exploited waterbirds for several uses. Green and Elmberg, (2014) have tried to document all the ecosystem services provided by waterbirds, this section is narrowed to the services that people living with (or close to) the waterbirds obtain from them. Use of waterbird species varies with culture, religion, and ethnicity. Anatids have a major cultural value in many parts of the world, and have important amenity values for the human population, both in rural and urban landscapes (Green and Elmberg, 2014).

A survey conducted by Tarakini et al. (2018) in north-western Zimbabwe offered some insights into some uses of waterbirds in this area by focusing on the ethnolinguistic groups of people particularly the Nambya, Ndebele, Dombe, Tonga, and Shona. The most common use is consumption of the meat as a source of protein (see Fig. 14.6 for examples of species consumed). All duck and geese species were consumed (the four most cited species were Anatids), and the list also included birds of prey such as the African Fish Eagle; waders (e.g., black-winged stilt, blacksmith lapwing); herons, storks, and egrets (e.g., cattle egret, saddle-billed stork, and grey heron); and others as listed in Appendix 5. The same species are reportedly consumed in countries such as Botswana, Zambia, Namibia, and South Africa (Hockey et al., 2005). Eggs of waterbirds are collected from their nests for consumption, and the large eggs such as those of Spur-winged Geese and Egyptian Geese are commonly targeted. This egg collecting for consumption was historically common-place in many countries. The feathers are also used for making arrow flights, some grease can be extracted from the preen gland and is used for waterproofing, lubrication, ointments, and as oil for lamps (MaMillan and Leader-Williams, 2008). There are also species whose chicks are captured from wetlands to try and domesticate them (or collection of eggs for later incubation using chickens). These domestication

FIGURE 14.6 Examples of waterbird species that are consumed for protein in southern Africa (White-faced Duck and Red-billed Teal). *Photo by Tawanda Tarakini.*

attempts are usually done by young boys, and species targeted include the spur-winged goose, Egyptian geese, red-billed teal, and little grebe.

Body parts from various waterbirds are used in belief-based superstitions. Tarakini et al. (2018) in western Zimbabwe highlighted that some species are believed to have medicinal properties such as the African fish eagle, grey heron, hamerkop, white-faced duck, Egyptian geese, African pygmy goose, and knob-billed duck. The African jacana was reported to be used in making love potions in the Ndebele and Nambya cultures. Other species including the blacksmith lapwing, grey crowned crane, cattle egret, and little grebe are reported to be useful in different witchcraft rituals in the Tonga culture.

Humans clearly feel a special reverence for birds such as swans, flamingos, and ibises as reflected through their artistic and religious importance. Feathers from waterbirds such as herons, terns, and grebes became highly prized for fashion items in the 19th century with consequences to the species' conservation states (Doughty, 1975). In north-west Zimbabwe, various storks, kingfishers, and geese (see examples in Appendix 5) are exploited for their colorful feathers that are used in various fabric designs and decoration of the interior of houses. The use of feathers, especially down feathers for bedding and insulation is common in southern Africa, similar to other places in the world.

14.8 Measures for the conservation of waterbirds in the pan wetland system

There are several measures that can be taken to improve the conservation of waterbirds in southern African pans. The first observation is that there are no criteria under the Ramsar that specifically include pans. This means that their conservation will take individual countries to implement actions toward protecting them. The fact that several pan systems in southern Africa occur in the arid/semi-arid areas, which are already designated as protected areas, has benefited some pans in this regard. After efforts for pan recognition under Ramsar are successful, the next stage could be to establish a pan classification system, which permits monitoring by remote sensing to overcome challenges of scale and remoteness (Herremans, 1999). Such classification system could be based on aspects such as pan depth, size (surface area), and aquatic vegetation. Long-term inventories and monitoring of waterbirds can then be done in these strata. Also, the Ramsar requirement stipulating the inclusion of sites into monitoring programs to only those that "hold a certain number of birds" could also be revised because pans are generally small, at least in HNP.

The magnitude of future impacts of climate change on waterbirds is likely to be affected by human habitat modification which may offer considerable opportunities for adaptive management. Adaptive management options include site management (manipulation of vegetation structure) to ensure cooler microclimates or managed realignment (Abdu et al., 2018; Hancock and Timms, 2002). Adaptive management will also allow humans to use results from ongoing research while correcting past mistakes.

Efforts are also needed to establish a coherent network of protected areas (and aligning some governance principles/regulations across the units which promote waterbird conservation). Such efforts may also result in coordinated research and monitoring programs across protected areas which will be critical in making decisions at country or regional levels. This will also benefit management of the wider countryside and conservation funds can be equitably distributed across the protected area network (Maclean et al., 2007).

As long-term monitoring in north-west Zimbabwe is not suggesting major negative effects of water supplementation on pans, this option should carefully be considered for each protected area in a holistic manner. Also, it is important to ensure a coherent network of sites that could buffer populations against climate change not only by increasing the overall available area of habitat but also by facilitating dispersal between sites. An example could be to establish protected areas at the beginning or end of arduous migration stages or in areas where there is a paucity of protected areas at present.

There is also a good proportion of pans occurring in communal areas where there are various forms of community-based natural resources management (such as the Communal Areas Management Programme for Indigenous Resources (CAMPFIRE) in Zimbabwe). Since it is acknowledged that any meaningful conservation action should not exclude local people, educational campaigns and inclusion in conservation should be extended to them with particular focus on pans and waterbird conservation. A suggestion made by local people in Zimbabwe involves fencing off pans for the welfare of ducks to reduce the effect of livestock trampling of vegetation (Tarakini et al., 2018). Negotiation with local leadership can also be made to reduce access of domestic dogs to pans and also use of catapults that may be used to kill birds. Local people involvement could also include negotiation of spatiotemporal access by livestock to pans and their participation in waterpan-monitoring programs. Such monitoring data could be useful in forming national conservation strategies. Fishing practices by local people often involve use of nets, and some birds are strangled in the nets, or when the nets are discarded. This is also common in protected areas where fishing is practiced illegally, and also on other wetlands such as dams and rivers.

Hunting is a topical debate, with several sustainable use options existing. These include promotion of ecotourism in areas outside protected areas. However, there are cases where hunting outweighs other options. There is a need to quantify species' specific hunting exploitation for southern African waterbirds. Such evaluations should be prioritized for large species (especially wildfowl) which are more prone to anthropogenic predation and also those in population declines due to various threats. The effect of lead poisoning on waterbirds is likely to occur wherever lead ammunition is used in hunting and pathways of exposure have been demonstrated (Pain et al., 2019), but we know little on species being impacted in southern Africa. We however advocate for use of alternative non-toxic ammunition.

Control of pests, such as red-billed quelea *Quelea quelea* colonies, with toxic chemicals potentially disrupts processes in wetlands, particularly when there are reeds. There are records where breeding colonies of herons, egrets, cormorants as well as associated fish and amphibians have been destroyed by such spraying in some wetland systems (Whigham et al., 2013), but currently spraying on pans is not a common activity. We therefore believe that the effect of such chemicals is not currently a problem in southern Africa. As areas around pans are often cultivated, eutrophication can be a challenge. There have also been concerns over excessive use of inorganic fertilizers on agricultural lands, and organic fertilizers are therefore encouraged. As highlighted before, educational campaigns to all stakeholders could help in reducing the eutrophication challenge.

There is no “one-size-fits-all” solution to the control of alien vegetation (i.e., waterweeds) on wetlands (see Pegg et al., 2022, Chapter 16). The mechanical, chemical, biological, or a blend of these methods needs to be considered for each problem, all actions being scientifically based. It should also be noted that waterbirds are vectors in transmission of some alien vegetation species (through ingestion of seeds, or attachment to plumage, bills, or feet), thus some control programs may need to be coordinated across wetlands and regions.

In the rural communal areas themselves, usage comes mostly from domestic water usage from the pans, livestock watering as mentioned above, cropping, and in particular perhaps market gardening. Murombedzi (1994) has called for a redefinition of the land tenure system in communal lands, in an effort to have better control of the resources, and we agree with that.

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Chapter 15

A snapshot of parasites in tropical and subtropical freshwater wetlands: modest attention for major players

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15.1 Introduction

The high productivity and biotope diversity of wetlands renders them important to the conservation of biodiversity, for example, migrating birds and fishes as well as endemic species. High organism density and interaction levels enable parasites to complete their life cycles whether they require one (simple or monoxenous cycles; e.g., amoebae) or multiple hosts (complex or heteroxenous cycles; e.g., many trematodes pass through an aquatic snail before infecting a fish, a bird, or a human). This is among the reasons why wetlands are considered to have a high parasite diversity, having impacts on their stability and evolutionary ecology, for example, by exerting control and selective pressures on host populations and communities. Wetland parasites are, however, currently better known as disease agents potentially devastating to humans or their livestock (Thomas et al., 1997 and references therein). Blood-feeding (vector) arthropods (e.g., biting flies), vector-borne diseases (e.g., malaria), and infections by helminths (e.g., liver flukes) have historically been linked to wetlands. Many such diseases have shaped human land colonization, impacted military campaigns, and even influenced traditional

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human migration patterns and herding practices of nomadic pastoralists (Schillhorn van Veen, 1997). Such disease risks obviously fostered an unfavorable view of wetlands sometimes leading to serious and consequential habitat modifications such as intentional wetland drainage campaigns (Carver et al., 2015).

Health risks ascribed to wetlands are copiously covered in fiction. Children display, as they age, an increasingly negative attitude toward wetland habitats, which may be perceived as dirty, scary, and dangerous Anderson and Moss (1993) leading to the need for a correct and positive youth education for wetland conservation. Negative perceptions are unfortunate, especially since healthy wetland systems provide regulating ecosystem services, which can mitigate vector populations and hence disease risk (Carver et al., 2015). Adequate understanding of parasites and their vectors in wetlands would therefore benefit not only the conservation of these ecosystems, but also the health of surrounding human and animal populations.

Wetlands are vulnerable (see Wasserman and Dalu, 2022, Chapter 1). Cromie (2018) calls wetlands "meeting places" between a species-rich wildlife, and humans and their livestock, supporting a concentration of activities such as trade, agriculture, recreation and aquaculture. If wetlands are not managed appropriately, (re)emergence and transmission of infectious agents are facilitated, and wetlands may foster host-switching, and new host—parasite interactions. Like other ecotones, they generate novel interspecies interactions and alter food webs (Cuthbert et al., 2022, Chapter 17). This interface is broadened by typical high connectivity between wetland sites and severe anthropogenic influence including frequent nonnative invaders. Particularly relevant are parasites with aquatic and terrestrial hosts, vectors, or life stages. Weinstein et al. (2019) showed that in Californian aquatic-terrestrial ecotones, raccoons *Procyon lotor* harbored parasite communities different from their conspecifics foraging away from water. The Totsu River Basin in Japan offers a fitting subtropical example. In one of its headwaters, nematomorph parasites belonging to *Gordionus* manipulate their orthopteran insect hosts to seek water, where they become an important part of the diet of an endangered trout species, Kirikuchi charr *Salvelinus leucomaenis japonicus*. This influences, significantly, the terrestrial energy input into the water, the community composition of benthic aquatic invertebrates, and the food subsidy from stream to riparian forest (Sato et al., 2011; Dube et al., 2022, Chapter 11). There are other abundant illustrations of how important parasites are in (sub)tropical ecosystems with strong aquatic-terrestrial coupling, for example, relatively high trematode prevalence associated with mangroves in Puerto Rico (Lafferty et al., 2005) and the biomass of parasites, especially trematodes, exceeding that of hosts in Californian estuaries (Kuris et al., 2008). Therefore, we argue wetland parasitology can fundamentally help our understanding of wildlife health, disease ecology, and emerging infections.

In freshwater wetlands, however, parasites and their hosts only receive scant attention, as illustrated in several seminal books on freshwater wetland ecology and management. Only the mere occurrence of plant parasites, parasitic fungi, and human diseases is mentioned by van der Valk (2012), next to the concept of the enemy release hypothesis and the lack of knowledge on pathogenic bacteria and viruses in wetlands. Mitsch and Gosselink (2015) include a single mention of parasites and vectors each, further unspecified, in addition to brief mentions of human or plant disease and biocontrol of vectors. Batzer and Boix (2016), apart from a couple of references to agents of human disease or their vectors, only mention a handful of parasitic organisms. Regional volumes about tropical wetlands often do not render parasitology more visible either. For South Asia, Prusty et al. (2017) only refer to human diseases and parasitism in birds, while in Africa, Crafter et al. (1992) mention some challenges regarding human or crop disease surrounding Kenyan wetlands. Only the comprehensive book of Roggeri (1995) devotes considerable attention to parasites and vectors of tropical freshwater wetlands, albeit focused on public or cattle health threats. As parasite diversity in general is expected to be high, but most likely understudied in many tropical countries (Carlson et al., 2020), ecological and evolutionary parasitology in the tropics deserve more attention.

Management of health risks, conservation of wetlands, and parasitology in general would benefit from better knowledge of wetland-dwelling parasites, hosts, vectors and their life cycles, but mostly remains under the radar in tropical freshwater wetlands. This chapter introduces the diversity of wetland parasites and interactions with their hosts, and highlights some promising parasitological avenues for future tropical wetland research and management.

15.2 A multitude of lifeforms and lifestyles: major parasite taxa in freshwater wetlands

Many potential host species depend on wetlands. However, wetlands being ecotones, it is not trivial to delineate observed parasites and vectors as typical or unique to them. Thus, this section cannot strive for a comprehensive overview. Rather, it is intended to set the scene and introduce the reader to the major taxa of parasites with an aquatic phase, using examples from wetlands. We have left out taxa that we do not treat further, such as Hydrachnidia (water mites, which have a parasitic larval stage), unionid bivalves with their parasitic glochidia stage, and Entocytheridae, a family of ostracods living on other crustaceans. We mainly consider parasites with at least one fully aquatic life stage; hence we do not discuss arthropods infecting terrestrial vertebrates, for example, ticks and fleas of mammals that visit wetlands. Lastly, we do not include vector taxa in this systematic overview, for example, insects or ticks, as these very large taxa would deserve their own chapter.

15.2.1 Viruses

Viruses can be defined as obligate intracellular parasites unable to produce any independent biosynthetic processes outside their host cells (Maclachlan et al., 2010) (Fig. 15.1A). They are also some of the smallest (about 20−400 nm in diameter) agents of infectious diseases infecting all forms of life, including plants, fungi, bacteria, protozoan parasites, and helminths (Korsman et al., 2012; Barrow et al., 2020). The general structure that makes up a virus consists of a genome, made up of the nucleic acids (DNA or RNA), and a protein shell or capsid (Korsman et al., 2012; Roossinck, 2016). In some viruses, a surrounding membrane, or envelope, is present and acquired from budding through the host cell membrane (Korsman et al., 2012). Although the number of known viruses are thought to only represent a small fraction of their true diversity, the ICTV (International Committee on Taxonomy of Viruses) recognizes 16 phyla, 55 orders, 8 suborders, 168 families, 1421 genera, and 6590 species (ICTV, 2021).

In (sub)tropical wetlands worldwide, mosquito vectors (Fig. 15.2A) are major players in the spread of several viruses often referred to as arboviruses ("arthropod-borne viruses") (Dale and Knight, 2008). Dengue is a mosquito-borne viral infection; the virus is transmitted to humans by the mosquito

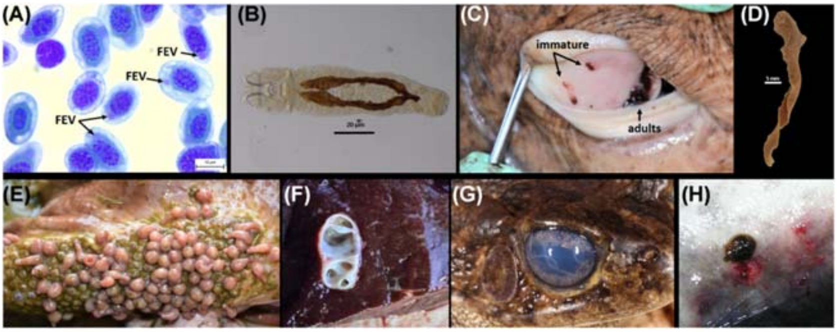


FIGURE 15.1 Examples of parasites occurring in (sub)tropical freshwater systems. (A) Frog Erythrocytic Virus (FEV) in red blood cells of Natal tree frog *Leptopelis natalensis* (Anura, Arthroleptidae), iSimangaliso wetland at Sodwana Bay, South Africa. (B) *Macrogyrodactylus* sp., a gyrodactylid monogenean, skin of snake catfish *Clarias theodorae* (Teleostei, Clariidae), Okavango Delta, Botswana. (C) *Oculotrema hippopotami* (Monogenea, Polystomatidae) with left more whitish immature individuals and redder adults on the right, eye of hippopotamus, small dam in Mpumalanga, South Africa. (D) *Fasciola nyanzae*, a liver fluke of hippopotamus, Lake Kariba, Zimbabwe. (E) Amphistome digeneans causing inflammation resulting in nodules, stomach of hippopotamus, small dam in Mpumalanga, South Africa. (F) Hydatid cyst of the cyclophyllidean cestode *Echinococcus* sp., liver of hippopotamus, small dam in Mpumalanga, South Africa. (G) *Neofoleyellides boerewors* (Nematoda, Onchocercidae), eye of guttural toad *Sclerophrys gutturalis* (Anura, Bufonidae), iSimangaliso stream wetland at Sodwana Bay, South Africa. (H) Individual of *Dolops ranarum* (Crustacea, Argulidae) and the lesions it causes, skin of North African catfish *Clarias gariepinus*, Nwanedi dam, South Africa. See Luus-Powell et al. (2016) for background on (C), (E), and (F), and Schols et al. (2021) for background on (D).

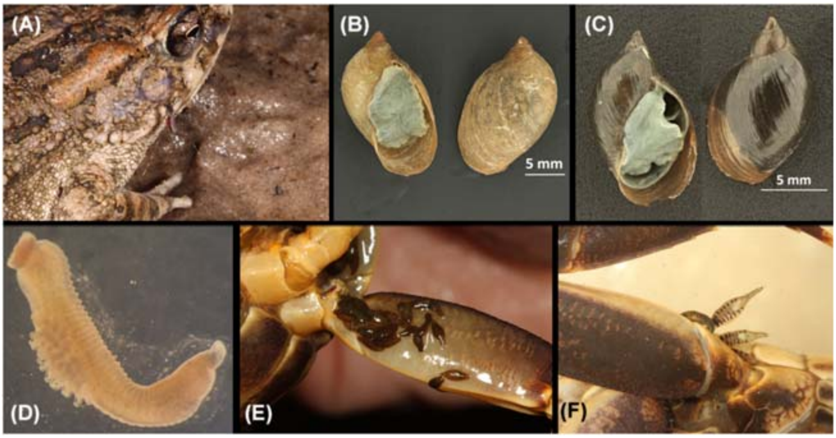


FIGURE 15.2 Examples of invertebrate vectors occurring in (sub)tropical freshwater systems. (A) Culicid mosquito belonging to *Uranotaenia* taking a bloodmeal on guttural toad *Sclerophrys gutturalis* (Anura, Buffonidae), iSimangaliso wetland stream at Sodwana Bay, South Africa. (B) *Radix natalensis*, Mwenje reservoir, Zimbabwe. (C) *Pseudosuccinea columella*, Lake Chivero, Zimbabwe, in Africa, respectively, a native and nonnative lymnaeid snail vector for *Fasciola gigantica*, *F. hepatica*, and *F. nyanzae* (see Smyth, 1994; Carolus et al., 2019; Schols et al., 2021). (D) Glossiphoniid leech probably belonging to *Helobdella*, exhibiting brood care, skin of *Clarias gariepinus* (Teleostei, Clariidae), Olifants River, South Africa. (E) and (F) Glossiphoniid leech *Marsupiobdella* sp. on Cape River crab, *Potamonautes perlatus* (Decapoda: Potamonautidae), small urban wetlands adjacent to the Mooi River in Potchefstroom, South Africa.

Aedes aegypti, also infamous for carrying the Yellow fever virus. Outbreaks of dengue occur in Africa, Asia, Australia, and the Americas (Dale and Knight, 2008; Roossinck, 2016) but now threaten to extend to Europe (Rogers et al., 2014). Other common mosquito-borne viruses of humans linked to wetlands include the West Nile virus, Ross River virus, and the Zika virus (Lee et al., 2016; Roossinck, 2016). Although the Yellow fever virus is also a mosquito-borne virus, its link specifically to wetlands is not well documented (Dale and Knight, 2008). Ectotherms associated with wetlands also host a number of viruses; for example, freshwater fish and amphibians are host to various iridoviruses and ranaviruses (Duffus et al., 2015; Price et al., 2017; Torrence et al., 2010; Whittington et al., 2010; Reichard, 2022, Chapter 12; Moraes et al., 2022, Chapter 13). Furthermore, a recent study using large-scale *meta*-transcriptomics discovered over 200 previously unknown RNA viruses from ectotherms, and although these were not connected to wetlands specifically, this provides an idea of the viral diversity associated with hosts that commonly inhabit wetlands (Shi et al., 2018). Since freshwater viruses mostly occur in surface biofilms, for example, on plants, submerged wood, or in sediments, the scarce body of virological research in natural wetlands has focused on this microhabitat. Viral ecology and diversity in wetlands are poorly understood (Jackson and Jackson, 2008). The effect of viruses in tropical freshwater wetlands can be expected to be substantial: in the Murray River Basin (Australia), Bonetti et al. (2021) demonstrated how wetland management can impact viral communities and their role in regulating greenhouse gas emissions by inland wetlands.

15.2.2 Bacteria

Most bacteria consist of a cell wall surrounding a cell membrane that encloses the cytoplasm, a single circular strand of DNA, and ribosomal structures that perform the cell's biological protein synthesis (Hollar, 2011). Bacteria are 10–100 times larger than viruses, and are typically between 1 and 5 μm in size. Bacterial cells come in one of three basic shapes: spherical (coccus), rod-like (bacillus), or curved (vibrio, spirillum, or spirochete) (Rogers, 2010). Although most bacteria, including free-living and symbiotic forms, are beneficial ecological agents whose metabolic activities sustain higher life-forms, some cause diseases in many animals and plants (Brockhurst et al., 2005; Rogers, 2010).

Pathogenic bacteria associated with aquatic environments severely impact the aquaculture industry, mainly due to the shear diversity of bacteria found in these systems, the diseases they cause, and their efficiency to spread among different individuals (Loch et al., 2013; Buller, 2014). Flavobacteriosis, although a common disease occurring in aquaculture conditions globally, is also responsible for causing disease and mortality of several species of fish from wild populations. Columnaris is an example of flavobacteriosis, caused by *Flavobacterium columnare*, and one of the most prevalent fish diseases (Loch et al., 2013; Buller, 2014; Loch and Faisal, 2017; LaFrentz et al., 2018).

15.2.3 Unicellular eukaryotes

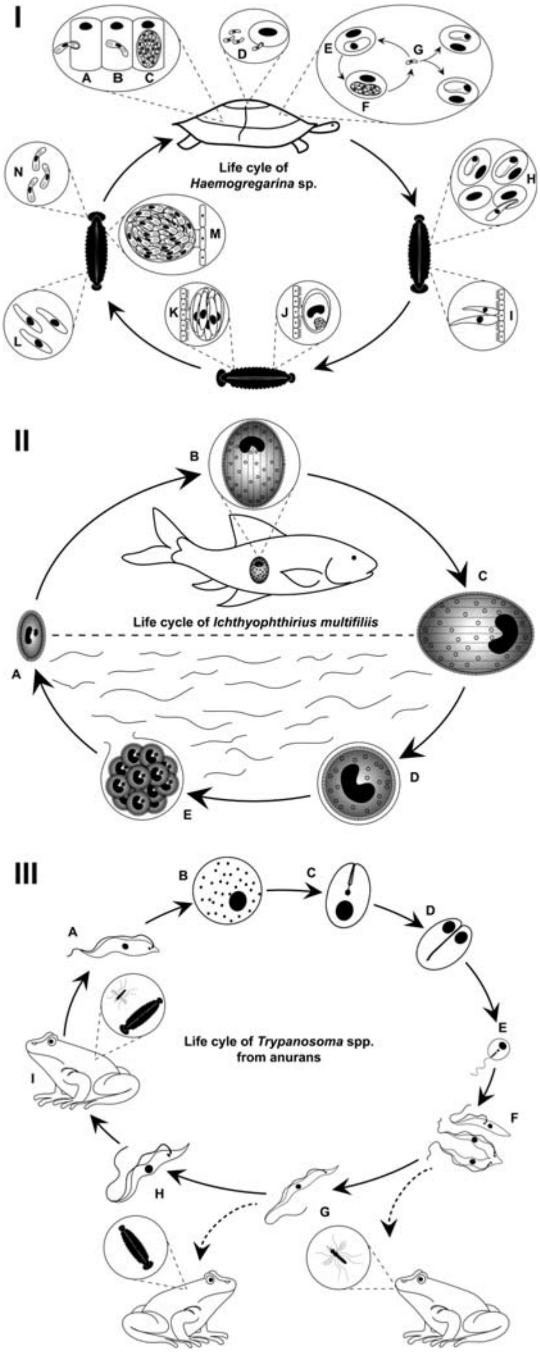
Protozoa is a group of single-celled eukaryotic microorganisms from a diverse range of lineages (Lucius and Roberts, 2017). The most abundant parasitic representatives in freshwater wetlands belong to Apicomplexa and Ciliophora, Diplomonadida and Euglenozoa, and Amoebozoa, which themselves belong to one of the three major eukarytic supergroups, namely SAR ("Stramenopiles, Alveolates, and Rhizaria"), Excavata, and Amorphea, respectively.

Apicomplexans are obligatory intracellular parasites characterized by the presence of an apical complex in at least one of their life stages (Morrison, 2009). There are four clearly defined groups: the coccidia, gregarines, haemosporidia, and piroplasmids. They may have either a heteroxenous or a monoxenous life cycle and they are known to infect representatives of all the vertebrate classes as well as of numerous invertebrate classes. Apicomplexans undergo a number of transformations with a series of asexual and sexual reproductive processes to complete their cycle. For example, *Haemogregarina balli*, a heteroxenous blood parasite of snapping turtle (*Chelydra serpentina*) uses the leech *Placobdella ornata* as its vector (Siddall and Desser, 1991). The vertebrate is the intermediate host in which asexual reproduction takes place, and the invertebrate is the definitive host where asexual and sexual reproduction take place (Fig. 15.3I). Perhaps the most infamous apicomplexan genus is *Plasmodium*, the agent of malaria.

Ciliophorans, or ciliates, are characterized by a pellicle with many cilia used for locomotion or food gathering. Parasitic ciliates have a monoxenous life cycle mostly populating the skin, gills, or digestive tract of their hosts and are generally, but not always, nonpathogenic (Lynn, 2012). Reproduction of ciliates is almost exclusively asexual by means of fission or budding (Adl et al., 2012). For example, the parasite *Ichthyophthirius multifiliis* (Fig. 15.3II) commonly referred to as "ich" induces the white spot disease. A free-swimming infective stage (theront) attaches to the skin of its fish host and develops into the fish-associated feeding stage (trophont) that obtains nourishment from its host's tissue, grows in size (Dickerson and Clark, 1998) and can be highly pathogenic.

Diplomonads ("two units") (Excavata, Metamonada, Diplomonadida) are free-living or endobiotic anaerobic flagellates defined by a bilateral symmetric cell body, each part possessing a karyomastigont consisting of a single nucleus with four basal bodies (kinetosomes) each from which a flagellum usually emerges for locomotion (Adam, 2017). Most are extracellular and infect the intestine where active trophozoites reproduce via binary fission before forming cysts that pass with faeces into the external environment. Transmission is direct, typically via the ingestion of cysts (Woo, 2006). Species of *Giardia* are common parasites in the intestinal tract of various vertebrates (Thompson and Monis, 2004). This important enteric disease agent at the human—animal—environment interface likely thrives in wetlands. *Giardia agilis* is found parasitizing several frog species; for instance, Lyu et al. (2020) showed occurrence of this parasite in 25 species of frogs from five provinces of China.

Euglenozoans (Excavata, Discoba, Euglenozoa) form a prominent monophyletic group of single-celled flagellates with different lifestyles and modes of nutrition, including predation, osmotrophy, photoautotrophy, and parasitism (Cavalier-Smith, 1993; Butenko et al., 2020). The flagella, used for locomotion, contain a unique heteromorphic structure that characterizes the group and is made up of a network of protein filaments known as the paraxial rod (Lucius and Roberts, 2017). Life cycles can be monoxenous or heteroxenous (Fig. 15.3III) with asexual reproduction occurring by longitudinal binary fission (Lange and Lord, 2012). In some species sexual reproduction takes place in the arthropod host (Lucius and Roberts, 2017). Various species of *Trypanosoma* are commonly found parasitizing vertebrate and invertebrate hosts from tropical freshwater wetlands. In the subtropical lower Phongolo Floodplain (KwaZulu-Natal, South Africa), *Trypanosoma mukasai* is reported


I
A
B
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Life cyle of
Haemogregarina sp.
H
N
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Life cycle of *Ichthyophthirius multifiliis*
A
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Life cyle of *Trypanosoma* spp.
from anurans
I
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from various fish hosts including *Clarias gariepinus*, *Coptodon rendalli*, *Oreochromis mossambicus*, and *Synodontis zambezensis*. The Phongolo Floodplain is also home to a number of *Trypanosoma* species that infect frogs including *Afrixalus fornasini*, *Hemisus marmoratus*, *Hyperolius argus*, *H. marmoratus*, *H. tuberilinguis*, *Ptychadena anchietae*, *P. mossambica*, *Sclerophrys gutturalis*, and *S. pusilla* (see Acosta et al., 2020). Representatives of *Trypanosoma* are well-studied in the Pantanal Wetlands, where a diverse set of mammal hosts serves as a complex reservoir system (Martins Santos et al., 2019) and where these parasites are known to affect the health of domestic mammals as well as carnivores (Martins Santos et al., 2018), pigs, and peccaries in the wild (Herrera et al., 2008). Furthermore, various Pantanal fishes (Pádua et al., 2011; Lemos et al., 2015) and caimans (Fermino et al., 2015) harbor members of *Trypanosoma* transmitted by leeches.

◀ **FIGURE 15.3** Life cycle of representative protozoan parasites.
I Apicomplexan: *Haemogregarina* sp. (A–B) Infective merozoite from leech enters endothelial cells of the freshwater turtle. (C) Pre-erythrocytic meront in cells of the liver, lung, and spleen yielding up to 18 merozoites. (D) Merozoites enter erythrocytes. (E–F) Immature erythrocytic gamonts (E) and meronts (F). (G) Merozoites formed in erythrocytic meronts infect other erythrocytes to produce either gamonts or more meronts. (H) Micro- and macrogamonts in the peripheral blood are ingested with leech blood meal; gamonts then exit erythrocytes. (I) Gamonts (micro and macro) join in syzygy in intestine of leech. (J) Microgametogenesis where microgametes fertilize the associated macrogamete. (K) Sporogony produces oocysts with eight naked sporozoites. (L) Sporozoites migrate to the anterior end of the leech, and give rise to primary meronts (M) each containing hundreds of merozoites. (N) Merozoites migrate to proboscis of the leech and are released to host during subsequent blood feeding.
II Ciliophoran: *Ichthyophthirius multifiliis*. (A) Free-swimming theront penetrates surface epithelia of skin and gills of fish host. (B–C) Theront forms into trophont on fish host. (D) Trophonts leave the fish host transforming into free-swimming tomont that subsequently attaches to a free surface where they encyst. (E) After encystement and division, tomites rupture the cyst, break free, and transform into theront.
III Euglenozoan: *Trypanosoma* spp. infecting a frog through a leech or dipteran vector. (A) Peripheral blood trypomastigotes multiply by binary fission in (leech crop or dipteran midgut of) the invertebrate vector. (B) Rounded trypomastigotes form without undulating membrane or flagellum. (C) Spherical, cystlike amastigote with large vacuoles. (D) Dividing amastigote from leech crop or dipteran midgut. (E) Mono- and biflagellate spheromastigotes from leech crop or dipteran end-gut. (F) Spheromastigotes transform into epimastigotes, in leech crop or dipteran endgut. In dipterans, epimastigotes are apparently the infective stage released upon ingestion of the invertebrate vector by the vertebrate host. (G) In leech crop, epimastigotes transform into infective metacyclic trypomastigotes, which are injected into peripheral blood of vertebrate host by its leech vector during feeding. *Adapted from (I) Siddall, M.E., Desser, S.S., 1991. Merogonic development of Haemogregarina balli (Apicomplexa: Adeleina: Haemogregarinidae) in the leech Placobdella ornata (Glossiphoniidae), its transmission to a chelonian intermediate host and phylogenetic implications. Journal of Parasitology 77, 426–436; (II) Dickerson, H., Clark, T., 1998. Ichthyophthirius multifiliis: a model of cutaneous infection and immunity in fishes. Immunological Reviews 166, 377–384; (III) Desser, S.S., McIver, S.B., Ryckman, A., 1973. Culex territans as a potential vector of Trypanosoma rotatorium. I. Development of the flagellate in the mosquito. Journal of Parasitology 59, 353–358.*

Amoebozoa is a division of amoeboid or amoeboflagellate organisms that possess morphologically variable forms with extending pseudopodia or lamellipodia, and can be uninucleate, binucleate, or multinucleate (Schilde and Schaap, 2013; Simpson and Eglit, 2016). Most amoebae are free-living and nonparasitic. Free-living amoebae are common in wetland soils, also in the tropics (Smith and Wilkinson, 2007; Sigala et al., 2016). Some free-living types are opportunistic and adapted to a pseudoparasitic lifestyle, with a parasitic or free-living phase, neither dependant on the other. Although most amoebae are "naked" (lacking any hard covering), testate amoebae are enclosed within a hard shell known as a test (Schuster and Visvesvara, 2004). Amoebozoans commonly have a trophozoite feeding stage followed by a dormant cyst stage. Sexual fusion is also common, forming either dormant zygotic cysts or multinucleate cells of varying sizes (Schilde and Schaap, 2013). Many taxa produce a sporocarpic (single amoeboid cell that develops into a usually stalked subaerial structure enclosing one to many spores) or sorocarpic (amoebae that aggregate into a multicellular mass) fruiting body (Adl et al., 2005, 2012). Alternatively, fruiting bodies of myxomycetes (myxogastrids), often classified as amoebozoans, are large multinucleate structures used for reproduction from a single individual (Simpson and Eglit, 2016). Free-living amoebae such as species of *Acanthamoeba* are reported from a range of habitats including various freshwater systems and are known to infect several species of freshwater fish globally (Dyková et al., 1999; Zilberg and Munday, 2006; Visvesvara, 2013). Species of *Entamoeba*, which are anaerobic and mostly intestinal parasites of animals, are generally more widely known, mainly due to the common human water- and foodborne disease amoebiasis caused by *Entamoeba histolytica* (see Wertheim et al., 2012). A number of other species of *Entamoeba* are also known from freshwater habitats; for example, the Asian swamp eel from wetlands in northern Thailand (*Monopterus albus*) is host to *Entamoeba chiangraiensis* (see Jinatham et al., 2019).

15.2.4 Myxozoans

Myxozoans are the epitome of paradigm shifts; for the longest time considered to be protists, monoxenous, and almost exclusive parasites of fishes, the past ~40 years righted both their taxonomy and biology. Myxozoans are miniature cnidarians, that are endoparasitic (histozoic or coelozoic), heteroxenous (except rare exceptions), and they may infect terrestrial homeotherms. One species was recently shown to lack a mitochondrial genome spearheading the concept that some eukaryotes may exclusively sustain anaerobic metabolism (Yahalomi et al., 2020). Myxozoans are characterized by presenting cell-within-cell division and polar capsules, which are considered homologs of nematocysts (Americus et al., 2020). Myxozoa is comprised of two clades: Malacosporea and Myxosporea. Very few species (four) of malacosporeans are known and they all infect fish and freshwater bryozoans. To this day, none are reported from tropical wetlands. Myxosporeans are much more speciose with over 2200 species described; they use annelids as invertebrate definitive hosts and a variety of vertebrates as intermediate hosts, albeit fish are the best known (Hallett et al., 2015a) and sole hosts reported from tropical wetlands. Myxospores develop in plasmodia in the vertebrate host. Diversity is presumed highly underestimated as myxozoans may display a certain specificity for both infection sites and hosts (Molnár and Eszterbauer, 2015). Typically, myxozoans are innocuous. However, some species are highly pathogenic and most of our knowledge is based on those particular species such as the malacosporean *Tetracapsuloides bryosalmonae* that induces proliferative kidney disease and the myxosporean *Myxobolus cerebralis* that causes whirling disease, both in salmonid fishes. Difficulty in unraveling myxosporean life cycles in particular, is in part due to current lack of knowledge of the vertebrate-infecting stage (actinospores) that are released by the annelids. Myxozoans can induce severe fish diseases, may affect human health, and can establish in new environments either via human-induced translocations or natural disseminations (Hallett et al., 2015b). Thus, they attract high interest and are quite often surveyed in wetlands with *Henneguya* and *Myxobolus* being very common (e.g., Carriero et al., 2013 for the Neotropics). Regardless, the biology of several reported myxozoan species remains unknown.

15.2.5 Flatworms

Neodermatan flatworms form an exclusively parasitic metazoan clade with worldwide occurrence. Their estimated species richness goes along with a plethora of life-history strategies (Littlewood et al., 1999). As aquatic hosts and/or life stages are typically an obligate part of their life cycle, parasitic flatworms are abundant in wetland habitats (Poulin and Morand, 2000).

Unlike most other flatworm parasite taxa, **monogeneans** display a direct life cycle (Fig. 15.4) and often high levels of host specificity. As such their diversity is estimated in relation to the number of host species. They are always associated with an aquatic environment; most are parasites of fishes but some of them infect other groups, such as amphibians, turtles, crocodiles, waterfowl and hippopotamus (Poulin, 2002) (Fig. 15.1B and C). Monogeneans generally do not cause substantial harm to their fish hosts but they can pose threats by facilitating secondary infections. Also, crowded conditions in captivity (mainly driven by aquaculture and fisheries) and anthropogenic cotranslocation of parasites to susceptible wild host populations have led to fish mortalities caused by severe monogenean infections (Buchmann and Bresciani, 2006). In tropical freshwater wetlands, monogeneans are severely understudied with available data restricted to very few host taxa and areas. Examples of monogeneans reported from tropical freshwater wetlands include representatives of the dactylogyrid genera

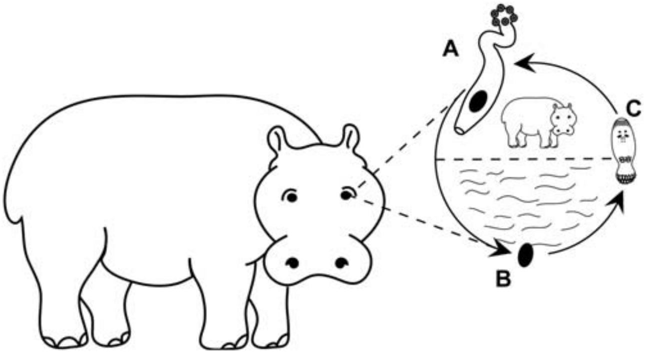


FIGURE 15.4 Life cycle of (A) *Oculotrema hippopotami* attached to eye of hippopotamus host. (B) Eggs released in the water. (C) Oncomiracidium (which is ciliated) swims and attaches to host eye. Images not drawn to scale.

Cichlidogyrus (African cichlids: Muterezi Bukinga et al., 2012; Vanhove et al., 2013), *Quadriacanthus* (African catfishes: Modise et al., 2009), *Anacanthorus* (Neotropical characids: Pereira et al., 2020), a species of the cosmopolitan genus *Gyrodactylus* described from the Okavango Delta in Botswana (Christison et al., 2005) and polystomatid parasites of amphibians (Shen et al., 2013).

Two groups are recognized in Trematoda (flukes) of which members of Aspidogastrea are restricted to marine areas, while over 12,000 species (Littlewood et al., 2015) of Digenea parasitize all major vertebrate groups as definitive hosts (Cribb et al., 2001) (Fig. 15.1D and E). **Digeneans** display an indirect life cycle and typically have molluscs (gastropods or bivalves) as their first intermediate hosts (Fig. 15.2B and C). Remarkable exceptions, albeit thus far known only from marine hosts, include some blood flukes (Schistosomatoidea) of fishes (Aporocotylidae; Power et al., 2020) and turtles (Spirorchiidae; de Buron et al., 2018) that use polychaetes as intermediate hosts. Regardless of their vertebrate host class, blood flukes are often pathogenic (e.g., *Schistosoma* spp.) and those of nonhuman hosts are conspicuously understudied. Various mechanisms of host manipulation by digeneans to facilitate transmission have been recorded (Paperna and Dzikowski, 2006). Host specificity in digeneans has evolved mainly toward the invertebrate host rather than the vertebrate host taxa in the life cycles. Infections of migratory animals such as birds have resulted in spectacular geographical distribution of some digenean representatives in wetland areas (Ashrafi et al., 2021; Tarakini et al., 2022, Chapter 14). As snails are often the first obligate intermediate hosts, wetland habitats provide ideal conditions for some of the widespread human tropical diseases caused by digeneans, such as schistosomiasis, opisthorchiasis, and fascioliasis. Also, digenean infections are highly prevalent in wild and domestic animals in tropical wetland ecosystems (Sithithaworn et al., 2012; Toledo and Fried, 2019).

Cestodes (tapeworms), of which Littlewood et al. (2015) report almost 4700 species, show a loss of structural complexity compared to other parasitic flatworms (e.g., absence of a digestive tract) and are considered some of the animals most adapted to a parasitic mode of living. Like digeneans, they have a heteroxenous life cycle in which representatives of various freshwater taxa can be involved, but always with a vertebrate as definitive host (Hoberg et al., 1999) (Fig. 15.1F). While tapeworm species are underreported from tropical freshwater wetlands, an Asian fish tapeworm, *Schizocotyle acheilognathi*, is an invasive species with a worldwide occurrence. It may cause severe infections of fish in the fragile ecosystems of freshwater wetlands (De Souza et al., 2018; Kuchta et al., 2018; Pérez-Ponce de León et al., 2017).

15.2.6 Leeches

Hirudinea (leeches) is the most specialized of the major groups within Annelida and includes the only important fish pathogens from this phylum. The subclass Hirudinea comprises two orders (Arhynchobdellida and Rhynchobdellida) based on the morphology of the vascular system and proboscis (Sivachandran et al., 2015). They are dorsoventrally flattened with posterior and anterior suckers for attachment, have 34 segments, which are externally divided into a number of annuli. Leeches are important components of food webs serving as prey, parasites, as well as vectors, with little overlap in the species they feed on, for example, either fish, amphibians, reptiles, birds, or mammals. Leeches are hematophagous and thus potentially affect their host health; they are known to transmit hemoflagellates (e.g., *Trypanosoma* and *Cryptobia*) and intracellular hemogregarines and piroplasmids as well as to harbor, as second intermediate hosts, larval stages of some digeneans of fish and birds (Burreson, 2006). They may also transmit viruses and bacteria and the feeding/attachment wounds may lead to secondary infections (Sawyer, 1986). Leeches are protandric hermaphrodites and do not self-fertilize (Hadfield and Smit, 2018). Eggs are enclosed in a cocoon and some species display parental care with eggs and young being brooded on the ventral surface (Fig. 15.2D). Leeches have a worldwide distribution but are more abundant in temperate lakes and ponds in the northern hemisphere with approximately 680 species described globally of which 480 are from freshwater. They prefer shallow, vegetated areas and very few species tolerate fast flowing water. In wetlands, the members of the rhynchobdellid family Piscicolidae parasitize many different fish species and infrequently crustaceans (Fig. 15.2E and F). Individuals of *Batracobdelloides tricarinatus* and *B. amnicolus* (Rhynchobdellida, Glossiphoniidae) are known to parasitize a range of fish species from wetlands in Africa and were also noted in the mantle cavities of freshwater snails but seemingly not feeding on the latter hosts (Oosthuizen, 1989; Chiangkul et al., 2021) while *B. bangkhenensis* recorded from wetlands in Thailand feed exclusively on snails (Chiangkul et al., 2021).

15.2.7 Acanthocephalans

All known thorny-headed worms (Acanthocephala) are gonochoristic parasites of vertebrates. Traditionally a phylum, Acanthocephala is now widely considered a clade within Rotifera of the larger protostome group Gnathifera (Garey et al., 1996, 1998; Brusca et al., 2016). Adult worms have a proboscis armed with hooks that can be withdrawn and invaginated into the body itself. A gut is absent, and nutrients are absorbed from the host via the syncytial body tegument (Miller and Dunagan, 1985). They occur exclusively in the digestive tract of their vertebrate definitive hosts, usually the small intestine. Females release embryonated eggs in the environment via the host's feces. Arthropod intermediate hosts (mostly crustaceans and insects) consume eggs, and larval development from acanthella through cystacanth occurs in their body cavity. Transmission to definitive hosts occurs via ingestion of intermediate hosts or vertebrate paratenic hosts harboring the fully developed cystacanth (Schmidt, 1985; Kennedy, 2006). Numerous species are reported as modifying their invertebrate host behavior (Bethel and Holmes, 1973; Gotelli and Moore, 1992; Kennedy, 2006). Acanthocephalans are a fairly small and poorly known group compared to other endohelminths, but appear to have reached their highest diversity in birds and freshwater fishes, although members of all vertebrate classes are infected. In wetlands, while some aquatic or semiaquatic amphibians (Campião et al., 2016), sauropods (Smales, 2007), and mammals (Gomes et al., 2015) may be infected, fishes (Chemes and Brusa, 2013) and migratory waterfowl (McDonald, 1988) are likely to harbor the vast majority of the acanthocephalan species present.

Species diversity of acanthocephalans is undoubtedly underestimated in wetlands the world over. New discoveries regularly occur even in groups that receive little attention. *Pandosentis napoensis* was described from the intestine of Gunther's banded tree frog (*Boana fasciata*) from the rainforest regions of Ecuador (Smales, 2007). This was just the second species recorded from the genus, the other being typically a parasite of fishes in the Neotropics. Gomes et al. (2015) described *Prosthenorchis cerdocyonis* from crab-eating foxes (*Cerdocyon thous*) as part of an ongoing conservation effort of the carnivores of the Pantanal wetlands of Brazil. Although more typical of primates and felids, the new species demonstrates that *Prosthenorchis* also includes species infecting canids.

15.2.8 Nematodes

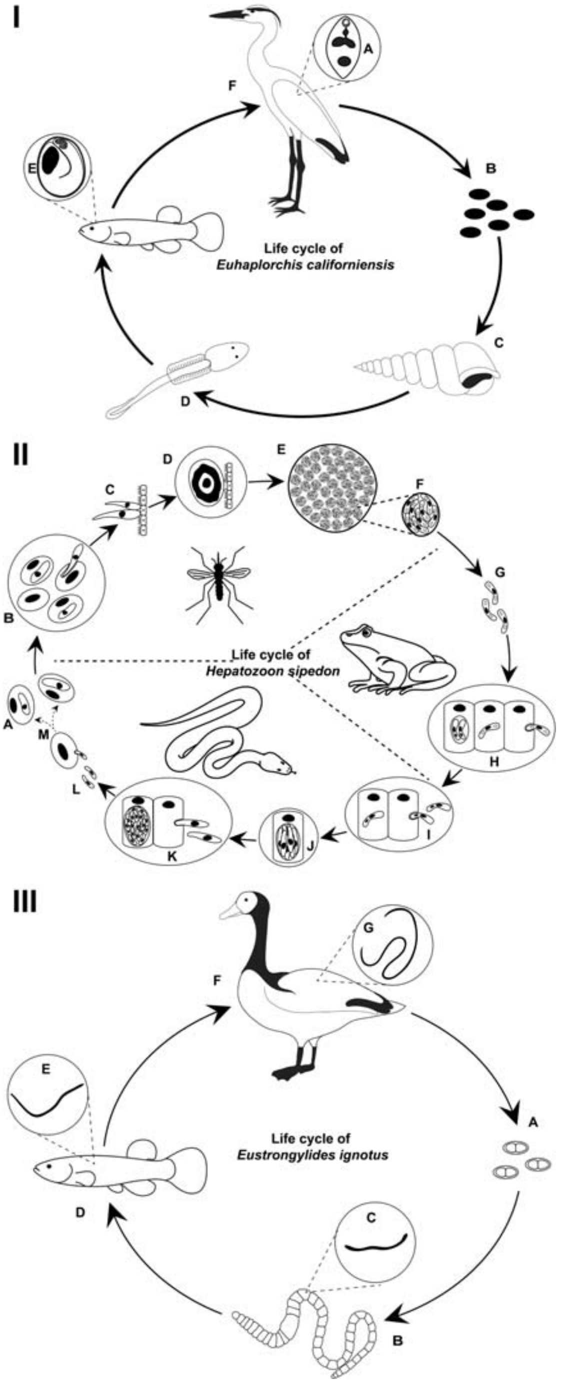
Nematodes (phylum Nematoda or Nemata), roundworms, are unsegmented blastocoelomates with affinities to horsehair worms (Nematomorpha) (see

Section 15.2.10) and are part of the ecdysozoan clade of protostomes (Brusca et al., 2016). Nematodes are diverse, understudied, and seemingly ubiquitous in the biosphere, occurring in nearly every habitat. Parasitic nematodes are among the most important etiological agents of disease in humans, their domesticated animals, their crops, and in organisms of conservation concern. Members of all classes of vertebrates and many (if not most) invertebrates host nematode parasites, and those occurring in wetlands are no exception (Fig. 15.1G). This diversity precludes any singular description of their life cycle, but often vertebrates are the definitive hosts and become infected via consumption of infected intermediate hosts, which can be invertebrates or vertebrates, depending on the nematode species. Still, others have direct life cycles, and many parasitize important aquatic invertebrates and exclude vertebrate hosts in their life cycles.

A telling example for our focal ecosystems is *Eustrongylides ignotus* (Fig. 15.5III), an intestinal parasite of waterfowl that uses oligochaetes as first intermediate hosts and fish as second intermediate hosts (Coyner et al., 2002). Piscine intermediate hosts are diverse, and thus piscivorous birds are at high risk of infection. This nematode causes moderate to severe pathology in some wading birds (Spalding and Forrester, 1993), is responsible for nestling morbidity and mortality (Locke et al., 1964; Spalding et al., 1994), and has been implicated in bird mass mortalities (Wiese et al., 1977; Winterfield and Kazacos, 1977; Roffe, 1988; Spalding et al., 1993). Although not strictly a "wetlands parasite" in the sense of being restricted to such ecosystems, *E. ignotus* appears to occur broadly enough that it commonly affects animals utilizing wetlands and is likely a permanent member of some wetland ecosystems (see Section 15.3).

15.2.9 Crustaceans

Crustaceans constitute the second-largest subphylum in Arthropoda and are considered to be the most morphologically diverse arthropods with 19 parasitic orders (Hadfield, 2019). The freshwater parasitic orders include Poecilostomatoida, Cyclopoida, Siphonostomatoida, Porocephalida, Isopoda, and Arguloida (see Smit and Hadfield, 2018). Freshwater parasitic crustaceans are mostly associated with fishes for which they infect the gills, fins, body, eyes, nares, cloaca, and buccal cavity, with some representatives (e.g., within the cyclopoid family Lernaeidae) lodged with their anterior end in a host's muscle tissue while their posterior trunk protrudes from the host's body surface. Sexual dimorphism is evident and in several species only the female attaches to the host and is parasitic while the male is free-living. Although not as common as other crustaceans, branchiurans (Arguloida), with only four genera described, are very intriguing. Some act as vectors of viruses (Ahne, 1985) and nematodes (Molnár and Székely, 1998) for instance, and they range from temporary parasites (e.g., *Argulus* spp. and


I
A
F
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Life cycle of
Euhaplorchis californiensis
C
D
II
C
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E
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Life cycle of
Hepatozoon sipedon
A
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III
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Life cycle of
Eustrongylides ignotus
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(*Continued*)

Dolops spp.) who can move from hosts to host because of their well-developed swimming legs to more permanent parasites (*Chonopeltis* spp.) that cannot swim. The latter complete their entire life cycle on the host while *Argulus* spp. leave their hosts to lay eggs on the substrate. Highly infected fish may be severely affected and attachment and feeding sites of some crustaceans may lead to pathology (Fig. 15.1H) and secondary infections. Several crustaceans have been reported from tropical freshwater wetlands including the branchiuran *Chonopeltis liversedgei* and the copepod *Lamproglena hepseti* from the Okavango Delta in Botswana (Van As and Van As, 1999, 2007).

◀ **FIGURE 15.5** Life cycles illustrating the diverse host interactions of heteroxenous wetland parasites.
I Digenean: *Euhaplorchis californiensis*. (A) Adult trematode in piscivorous birds' gut. (B) Eggs released with bird faeces. (C) Trematode eggs ingested by first intermediate California horn snail host. (D) Larval cercariae emerge from snail host and penetrate the skin of their second intermediate California killifish host. (E) Cercariae migrate to brain and encyst as metacercariae. (F) Infected killifish ingested by final piscivorous bird host. Images not drawn to scale.
II Apicomplexan: *Hepatozoon sipedon*. (A) Gamonts in erythrocytes of snake host. (B) Gamonts ingested by mosquito vector (the definitive host) with blood meal from the snake host, are released in the gut. (C) Microgamonts and macrogamonts undergo syzygy (paring) in fat bodies of the mosquitoes' hemocoel. (D) Gamonts then undergo gametogenesis (fertilization between micro- and macrogametes), forming a zygote and then into an immature oocyst. (E) The mature oocyst, contains hundreds of sporocysts. (F) Each sporocyst contains eight sporozoites. (G) Sporozoites are released into the gut of a frog when an infected mosquito is ingested. (H) Dizoic cysts form in frog hepatocytes. (I) Cystozoites are released into the snake's gut and enter the hepatocytes after ingestion of an infected frog by the second intermediate host. (J) Macromeronts in snake hepatocytes and other cells of visceral organs. (K) Macromerozoites released from macromeronts invade the bloodstream of the snake and reinfect hepatocytes and other cells of visceral organs. (L) Micromerozoites released from micromeronts and infect erythrocytes of snake host. (M) Micromerozoites form into micro- and macrogamonts, circulating in the peripheral blood cells and infective to mosquitoes during feeding.
III Nematode: *Eustrongylides ignotus*. (A) Eggs are released with feces into external environment. (B) Eggs containing first stage larvae, are eaten by oligochaetes. (C) Eggs hatch within oligochaetes to produce second-stage larvae. (D) Fish ingest infected oligochaetes. (E) Third stage larvae become encapsulated within body of fish. (F) Waterfowl ingest infected fish. (G) Larvae develop to adult nematodes. Images not drawn to scale. *Adapted from (I) Martin, W.E., 1950. Euhaplorchis californiensis n.g., n. sp., Heterophyidae, Trematoda, with notes on its life-cycle. Transactions of the American Microscopy Society 69, 194–209; (II) Smith, T.G., Desser, S.S., Martin, D.S., 1994. The development of Hepatozoon sipedon sp. nov. (Apicomplexa: Adeleina: Hepatozoidae) in its natural host, the Northern water snake (Nerodia sipedon sipedon), in the culicine vectors Culex pipiens and C. territans, and in an intermediate host, the Northern leopard frog (Rana pipiens). Parasitology Research 80, 559–568 Smith, T.G., 1996. The genus Hepatozoon (Apicomplexa: Adeleina). Journal of Parasitology 82, 565–585; Smith, T.G., Desser, S.S., 1998. Ultrastructural features of cystic and merogonic stages of Hepatozoon sipedon (Apicomplexa: Adeleorina) in northern leopard frogs (Rana pipiens) and northern water snakes (Nerodia sipedon) from Ontario, Canada. Journal of Eukaryotic Microbiology 45, 419–425; (III) Friend, M., Franson, J.C., Friend and Franson, 1999. Field Manual of Wildlife Diseases: General Field Procedures and Diseases of Birds. US Geological Survey, Washington, DC.*

15.2.10 Nematomorpha

Members of the phylum Nematomorpha (horsehair worms or Gordian worms stemming from the legendary Gordian knot as these worms often tie themselves in knots) are aschelminth aquatic parasitoid animals whose morphology resembles that of nematodes. Besides wetlands, nematomorphs might be present in damp areas such as streams, puddles, watering troughs, and even swimming pools. The adult worms are free-living but the larvae are parasites of a variety of arthropods such as cockroaches, grasshoppers, mantids, beetles, crustaceans, and orthopterans. They are long and slender and range in length from 50–200 mm, some reaching 2 m, with a diameter of ~1 mm (Schmidt-Rhaesa, 1997). They are gonochoristic; internal fertilization takes place and eggs are laid in gelatinous strings in water. The larvae hatch and have cuticular hooks and terminal stylets that they may use to penetrate into the hemocoel of the host. There they absorb nutrients, molt several times, and become adults within weeks or months (Hanelt et al., 2005). Nematomorphs are known as "brain controllers" (Biron et al., 2005) because infected hosts unnaturally seek water where adult nematomorphs must be released to complete their life cycle. There are about 350 freshwater species worldwide (Poinar, 2008). Freshwater species are rarely recorded but one species, *Euchordodes nigromaculatus* (Chordodidae), is often found in large numbers along forest streams on the South Island of New Zealand (Poinar, 2008). There is paucity of literature on the nine species known from southern Africa, but they are suspected to be widespread in the region, including in temporary wetlands (Bird et al., 2019).

15.2.11 Fungi

Compared to other aquatic habitats, the diversity and function of fungi in lakes and wetlands are relatively well known (Grossart et al., 2019). For example, peatlands are known to harbor a wide array of fungi and fungi-like protists, the diversity of which is closely associated with substrate diversity (Finlayson and Milton, 2018). Outbreaks of pathogenic fungi, which probably abound on tropical floodplains, are often opportunistic infections concomitant with natural or anthropogenic stressors (waterfowl: Traill et al., 2009). Several early diverging fungal lineages have parasitic representatives. Studying those is challenging: they are phenotypically often similar to fungi-like protists (e.g., oomycetes), and it is often difficult to determine whether their host interactions are mutualistic, parasitic, or saprophytic (Grossart et al., 2019). The nature of these interactions is often context-dependent, as are the proportion of parasitic fungi in tropical wetland soil microbiota (Panamanian peatlands: Morrison et al., 2021) and the host-specificity of tropical wetland fungi (Micronesian flooded forests: Gilbert et al., 2008). Examples of parasitic fungi found in (sub)tropical freshwater include species of *Zygorhizidium* (Chytridiomycota), which infect algae and diatoms (Seto et al., 2017), *Coelomomyces* (Blastocladiomycota), which alternate between dipteran and crustacean hosts and have biocontrol potential (Subramanian, 2013), and *Batrachochytrium dendrobatidis* (Chytridiomycota), a well-known parasite of amphibians contributing to their worldwide decline (Warne et al., 2016). Coinfection of *B. dendrobatidis* with *Ranavirus* (Iridoviridae) is often reported in (sub)tropical wetlands (Horner, 2019). The resulting patterns and effects are unclear, making this a promising topic for research on emerging infectious diseases in wetlands (Warne et al., 2016).

Related to fungi (Wadi and Reinke, 2020), microsporidians are spore-forming unicellular and microscopic obligate endocellular parasites (Capella-Gutiérrez et al., 2012) whose biology is not well known. Microsporidians are reported from all major invertebrate and vertebrate taxa. Many species infect insects and as such may be good candidates as biocontrol agents of insect pests (Bjørnson and Oi, 2014), a role that recently extended to aquatic invasive pests for other species (Bojko et al., 2013; Stentiford et al., 2013). Humans are infected by zoonotic species (e.g., *Enterocytozoon bieneusi*) and may be at serious risks if immunocompromised (Mathis et al., 2005; Stentiford et al., 2016). Despite being known for over a century, there are still very large gaps in our understanding of this group of parasites (Han et al., 2020), and it is no surprise that terrestrial microsporidians are better known than those in the aquatic environment. Nevertheless, microsporidians are thought to be ubiquitous in aquatic hosts, with a diversity currently considered largely underestimated (Stentiford et al., 2013). An increasing interest in fish diseases led to investigations in the potential usage of some microsporidian hyperparasites (Freeman and Sommerville, 2011). Transmission occurs horizontally (via predation or food or water-borne spores) and/or vertically (typically transovarian), depending on species (and likely on our status of knowledge). Importantly, a better understanding of microcrustacean microsporidian life cycles (Vávra et al., 2005) and recent discovery of microsporidian transmission between invertebrates and vertebrates (Nylund et al., 2011) in the aquatic environment raise concerns about the potential for additional emerging zoonotic infections (Stentiford et al., 2013, 2016).

15.3 Animals as vectors and hosts: some stories of conservation and parasite ecology

Seeing as tropical wetland parasites have received scant scientific attention, ecological parasitology of tropical freshwater wetlands is mainly fallow ground. As we have seen above, defining a "wetland parasite" is not straightforward. In terms of parasite ecology, however, tropical freshwater wetlands do present a peculiar environment. For instance, it has been shown that their unique hydroregime may influence parasite community composition (Costa-Pereira et al., 2014 for the Brazilian Pantanal).

For want of overarching ecological theory on tropical wetland parasites, we provide a primer on types of interplay between the biology and ecology of parasites and vectors or hosts, centered around a number of (in)vertebrate host taxa. These kinds of host–parasite relationships may seem anecdotal, fascinating, but disconnected from the larger forces at play in regulating communities and ecosystems (Lafferty and Kuris, 2012). However, increasing research on parasites from an ecosystem perspective has led to fundamental shifts in how parasites ought to be approached. Seemingly, minor and transient interactions among hosts and parasites can scale up to ecosystem levels (Marcogliese and Cone, 1997; Thomas et al., 1998; Hudson et al., 2006; Lafferty, 2008; Frainer et al., 2018; Timi and Poulin, 2020) and play important roles in determining the structure and function of ecosystems. For an engaging introduction to the potential of parasites, in general, to affect ecosystem processes, see Lafferty and Kuris (2012). For example, even though so far mostly neglected in tropical wetlands, cercarial stages of digeneans are an abundant and important food source as part of zooplankton communities (Morley et al., 2012; Preston et al., 2013, 2021; Brendonck et al., 2022, Chapter 9). Consequently, the introduction of predators including cichlid species of *Astatoreochromis* in Africa (Mvogo and Bard, 1964), various fish species in the Senegal River Basin (Arostegui et al., 2019), the prawn *Macrobrachium vollenhoveni* in Senegal (Sokolow et al., 2015), and the ostracod *Candonocypris novaezelandiae* (see Yousif et al., 2013) has been considered to decrease transmission success of *Schistosoma* spp. by targeting the cercariae as well as the snail vectors.

Fishes represent focal hosts for the community of parasites with complex life cycles found in wetlands, integrating important ecological interactions with most of the other animal groups. Fishes host the adults of many helminths, are vital intermediate or/and transport hosts for others, and of course, harbor a plethora of arthropod, myxozoan, protistan, bacterial, viral, and fungal parasites. Coinfections are common, and interactions between micro- and macroparasite communities (e.g., Hennersdorf et al., 2016 for Indonesian marine habitats) certainly deserve more scientific attention in tropical freshwater systems. A parasitological survey of fishes can reveal more about the total parasite fauna in a wetland than for any other host group because the fishes are integral to the life cycles of such a large fraction of the local parasite biota. Furthermore, when compared to other vertebrate groups, the fishes are most likely to be permanent resident in the wetland of interest. Therefore their parasite communities will include both that fraction dependent entirely on other resident species, and those that occur in more wide-ranging species, like birds and mammals, which move among ecosystems. Their lifespan causes them to accrue infections, rendering them powerful bioindicators integrating the influence of past food sources, migration, or anthropogenic impacts over time.

Although often viewed as either passive hitchhikers or pathogens (particularly in farming conditions), parasites of fishes play active roles in the lives of their hosts and their ecosystems overall. Nezhybová et al. (2020) document an interesting case in the larval trematodes infecting killifishes (*Nothobranchius furzeri*) in summer pools across the Mozambique savannah. Metacercariae of the digenean, *Apatemon* sp., localize in the brain of killifish and are transmitted to piscivorous birds when consumed. Uninfected killifish spend most of their time deep in the water column and avoid predation by swimming down in the water column. Nezhybová et al. (2020) document that *Apatemon*-infected killifish spent most of their time near the water surface and engage in erratic jumping and rolling behavior when disturbed, for example, by a predator strike. Their own field observations verified this behavior in the wild, where they observed killifish stranded on floating vegetation such as lily pads. The parasite-induced altered host behavior appears to be one that places infected killifish at increased risk of predation, favoring transmission and completion of this parasite life cycle. A similar situation occurs with the digenean *Euhaplorchis californiensis* (Fig. 15.5I) who uses three hosts in its life cycle, the California horn snail (*Cerithidea californica*), the California killifish (*Fundulus parvipinnis*), and several species of piscivorous birds (Martin, 1950; Shaw et al., 2009). Infected killifish display altered swimming behavior, rendering them more likely to be predated upon by the parasite's final bird host (Shaw et al., 2009).

The life history of many **amphibians and reptiles**, especially those with some association to aquatic adjoining terrestrial environments, provides certain parasites with pathways to easily infect their hosts or to be transmitted from one host to the next. *Hepatozoon sipedon* (Apicomplexa: Adeleina) (Fig. 15.5II) is a blood parasite with a complex life cycle, involving the **mosquito vector** (*Culex pipiens*) and two vertebrate hosts, namely the Northern leopard frog (*Rana pipiens*) and the Northern water snake (*Nerodia sipedon*). This life cycle is an example of how wetland parasites are able to alternate between terrestrial and aquatic/amphibian hosts.

Blood parasites of wildlife as models for human or cattle blood parasites

Parasites influence food web structures in an ecosystem and are drivers of speciation. To understand the role parasites play, one needs also to study the host's biology and behavior. Thus knowledge obtained from studying parasites has broader implications contributing to our basic understanding of the way the biological world functions. Relevant to tropical wetlands are the blood parasites of ectotherms. These have coevolved over millions of years with their vertebrate hosts and invertebrate vectors, forming balanced relationships that do not lead to the same degree of disease severity that their close relatives cause in their mammalian and avian hosts (Davies and Johnston, 2000). Whereas human parasites may often be popular research subjects, studies on medically relevant parasites

(*Continued*)

(Continued)

are often focused on host individuals. In contrast, ecological research on ectotherm blood parasites with comparable life cycles can provide complementary and valuable information regarding the ecology of parasites (Netherlands, 2019).

For example, haemosporidians, trypanosomes, and filarial nematodes are parasites of clinical or economic importance with similar life histories in endotherms and ectotherms (Fig. 15.6). Thus gaining insights from ectotherms' blood parasites (somewhat easier to study) does not only provide information on the natural world, but also usable data when designing policies to mitigate human parasite outbreaks and epidemics (Marcogliese, 2004). For instance, avian haemosporidians played an important role as models in the study of human malaria. Breakthrough investigations such as the study of the life cycles, malaria parasite cultivation in vitro, and malaria vaccinations, etc., were initially carried out with models of bird haemosporidians (Valkiūnas, 2004).

Although it seems unlikely that evolution may favor parasites that require multiple successive hosts to complete their life cycles, there are many different parasite taxa that have evolved this strategy independently (Auld and Tinsley, 2015). Parasites with complex life cycles often infect phylogenetically very different hosts within their cycle, with variable host or vector specialization or specificity, and they usually have at least one highly mobile host (Auld and Tinsley, 2015). For instance, **birds**, with their ability to fly, are hosts for a range of parasites, especially those with complex life cycles. Birds are also often apex predators in food webs allowing for parasite transmission through consumption of representatives of numerous intermediate and paratenic host taxa. In general, parasites persist in birds for several years or even for the remainder of their life, being thus a continuous source of infection for vectors (Valkiūnas, 2004).

Avian malaria is a vector-transmitted disease caused by different haemosporidians (Apicomplexa: Haemosporida) and is responsible for major die-off in captive and wild populations. The avian malaria agent develops in two groups of hosts, the intermediate vertebrate host (birds) and the definitive host that is the vector (blood-sucking dipterans) (Valkiūnas, 2004). Transmission success of bird parasites is also attributed to certain strategies that have evolved; for example, *Plasmodium relictum* induces an increased parasitemia in avian hosts exposed to feeding mosquitoes (thus, "ensuring" parasite transmission) as compared to hosts not exposed (Cornet et al., 2014). Furthermore, the relapse of parasitemia that commonly occurs during the reproductive cycle of the avian host facilitates the vertical parasite transfer to offspring (Valkiūnas, 2004).

The potential of *E. ignotus* (see Section 15.2.6) to impact species of conservation concern, most notably ciconiiform wading birds, and its association

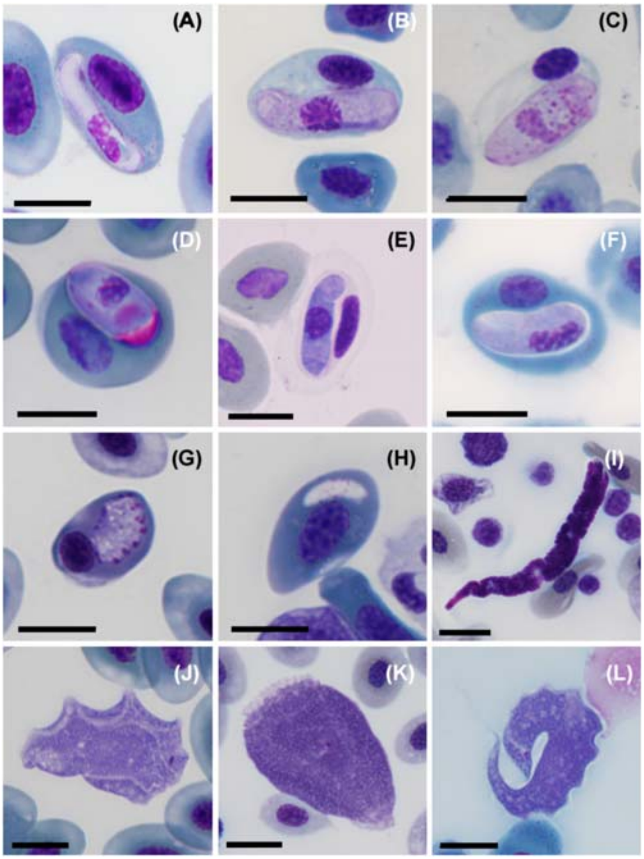

FIGURE 15.6 Photomicrographs of various blood parasites from aquatic reptiles and amphibians from South Africa. (A) *Hepatozoon tenuis* (Apicomplexa, Adeleorina, Hepatozoidae), *Afrixalus fornasini* (Anura, Hyperoliidae), iSimangaliso Wetland at Sodwana Bay. (B) *Hepatozoon* sp. (Apicomplexa, Adeleorina, Hepatozoidae), *Ptychadena anchietae* (Anura, Ptychadenidae), Lower Phongolo River and floodplain. (C) *Hepatozoon theileri* (Apicomplexa, Adeleorina, Hepatozoidae), *Amietia delalandii* (Anura, Pyxicephalidae), wetland in Vhembe Biosphere reserve. (D) *Hepatozoon ixoxo* (Apicomplexa, Adeleorina, Hepatozoidae), *Sclerophrys pusilla* (Anura, Bufonidae), Lower Phongolo River and floodplain. (E) *Hepatozoon cecilhoarei* (Apicomplexa, Adeleorina, Hepatozoidae), *Philothamnus natalensis* (Serpentes, Colubridae), Lower Phongolo River and Floodplain. (F) *Haemogregarina* sp. (Apicomplexa, Adeleorina, Haemogregarinidae), *Pelusios sinuatus* (Testudines, Pelomedusidae), Lower Phongolo River and floodplain. (G) *Dactylosoma kermiti* (Apicomplexa, Adeleorina, Dactylosomatidae), *P. anchietae*, Lower Phongolo River and floodplain. (H) *Lankesterella* sp. (Apicomplexa, Eimeriorina, Lankesterellidae), *A. fornasini*, iSimangaliso wetland. (I) *Neofoleyellides steyni* (Nematoda, Spirurida, Onchocercidae), *A. delalandii*, wetland in Vhembe Biosphere reserve. (J) *Trypanosoma* sp. (Euglenozoa, Kinetoplastea, Trypanosomatidae), *A. fornasini*, iSimangaliso wetland at Sodwana Bay; (K) *Trypanosoma* sp., *A. delalandii*, wetland in Vhembe Biosphere reserve. (L) *Trypanosoma* sp., *P. sinuatus*, Lower Phongolo River and floodplain. Scale bar 10 μm.

with human alterations of the physical, chemical, and biological characteristics of wetlands, makes it a particularly intriguing example of how parasites are intricately interwoven into the fabric of ecosystems (Fig. 15.5III). Coyner et al. (2002) found relatively high prevalence and intensities of larvae of this nematode in fishes from sites in Florida, United States that were durably altered by humans, often excavated sites receiving wastewater effluent that provide ample habitat for rapidly reproducing small fish (such as mosquitofish) and therefore attractive hunting locales for wading birds. The altered physicochemical properties of the substrates and overlying water column of these sites are thought to further enhance the transmission success of *E. ignotus* by promoting population growth of oligochaetes. In contrast to the human-dominated landscapes of northern Florida, prevalence was much lower in the southern regions of the state, including the areas encompassing the Everglades. It is certainly possible that alterations in the relatively pristine Everglades will lead to increases in this harmful parasite, as well. Increasingly, studies are finding parasites as useful metrics for various aspects of ecosystem quality (Huspeni et al., 2005; Hechinger et al., 2007; Bush et al., 2013; Dutton and Barger, 2017; Morton and Silliman, 2020) (see Section 15.5.1). Further research on species such as *E. ignotus*, will no doubt reveal even more powerful ways in which an understanding of an ecosystem's parasite fauna can lead to greater insights into the processes that influence the ecosystem as whole. Since members of *Eustrongylides* occur worldwide and are also implicated in zoonotic infections in humans (Narr et al., 1996; Eiras et al., 2018), research on these nematodes is likely to grow in the future.

Several wetland parasites of **mammals** are of medical and veterinary importance because wildlife share parasite species or genera with livestock and/or humans. The blood fluke genus *Schistosoma*, for example, has been reported from humans (e.g., *S. haematobium*, *S. intercalatum*, *S. guineensis*), livestock (e.g., *S. margrebowiei*, *S. leiperi*, *S. mattheei*, *S. bovis*, *S. curassoni*) and a wetland mammal we will zoom into, the hippopotamus (*S. hippopotami* and *S. edwardiense*) (see Webster et al., 2006). Several species of *Schistosoma* are known to hybridize and some of these hybrids (e.g., *S. haematobium* × cattle-infecting *S. bovis*) infect humans (Huyse et al., 2009). Within *Fasciola* (liver fluke), the host range of *F. hepatica* and *F. gigantica* includes both humans and wild and domestic ruminants, whereas their congener *F. nyanzae* infects hippopotami in southern Africa (Carolus et al., 2019). *Echinococcus felidis* is a cestode of terrestrial mammals that uses herbivores (although only confirmed in warthogs; see Hüttner et al., 2009) as intermediate host and carnivores (e.g., lions and hyenas) as definitive host. Although the hippopotamus is not a well-known prey of lions, a recent study confirmed the infectivity of *E. felidis* in the former (Halajian et al., 2017). This is not, however, the only surprising hippopotamus parasite. *Oculotrema hippopotami* is the only monogenean reported from mammals; it was discovered about 100 years ago and infects the eyes of the hippopotamus (Stunkard, 1924; Du Preez and Moeng, 2004) (Figs. 15.1C and 15.4). This is so unique that parasitologists questioned the host type and suggested that it must have been mislabeled or that it was an accidental infection as monogeneans normally occur on/in fish and herptiles (Thurston and Laws, 1965); this parasite was only accepted as a valid species four decades after its description. Adults and subadults occur together, often in clusters and high numbers, under the eyelid of the hippopotamus where they induce low pathogeny (Rubtsova et al., 2018).

15.4 Plant(s) (and) parasites in tropical freshwater wetlands

Plant and animal parasitology have their own, typically separate, research scenes, with different traditions, conferences, journals, and approaches. This is unfortunate since animal host–parasite and plant–herbivorous arthropod interactions conceptually have much in common, and a shared research program would substantially further understanding of infectious diseases (Nylin et al., 2018). A systematic overview of plant pathogens is beyond the scope of this text. Instead, we highlight plant-related examples illustrating the importance of tropical freshwater wetland parasitology for conservation and human health, drawing from taxonomically diverse examples of parasitic plants, fungi, nematodes, and flatworms.

Hemiparasitic (photosynthetic plants that only obtain water and nutrients from their host) and holoparasitic plants (heterotrophs that rely on their hosts for water, nutrients but also carbon) are known to influence vegetation composition in temperate and Mediterranean-type wetlands (Grewell, 2008; Kilgore, 2017; Piedade et al., 2022, Chapter 7). Such important ecological interactions, even in natural ecosystems, are not without consequences for agriculture. Mohamed et al. (2001) explain for instance, how an increasing number of species of *Striga* (Orobranchaceae) infect crops as agriculture expands into areas where these hemiparasites are native, hence a need for information about their taxonomy and distribution. An example from tropical freshwater wetlands is *S. lanceolata*, a pest of sugarcane in East Africa. While typical to dryer areas, the genus has some other representatives in tropical wetlands such as *S. junodii*, *S. pubiflora*, *S. angolensis*, *S. angustifolia*, and *S. forbesii*, the latter two also being potential agricultural pests. Other orobranchacean genera with (sub)tropical wetland species are *Buchnera* and *Alectra* (see Burgoyne et al., 2000; Catarino et al., 2001; Bridgewater et al., 2002). The most well-known parasitic flowering plants worldwide are probably mistletoes, of which *Korthalsella* (Santalaceae) in tropical inland wetlands (Heide-Jørgensen, 2008).

The most devastating invasive plant species worldwide have a Neotropical origin, for example, water hyacinth *Eichhornia crassipes* (Pontederiaceae), water lettuce *Pistia stratiotes* (Araceae), and aquatic ferns belonging to *Azolla* and *Salvinia* (Salviniaceae) (see Pegg et al., 2021, Chapter 16). Apart from arthropods, fungi have been proposed as biological control agents for these invasive plants. Criteria in selecting fungi with biocontrol potential include the ability to have a pathogenic effect on the targeted plant and a narrow host-specificity to avoid demise of native plants. This is not trivial, hence a challenging process: Monteiro et al. (2003) describe a search in Brazil for fungal parasites of the grass *Hymenachne amplexicaulis*, invasive in Australia and Florida, United States. One of the fungus species, *Curvularia lunata* (Pleosporaceae), retrieved on native *H. amplexicaulis* in Brazil where it causes necrotic lesions, was found to be insufficiently host-specific. Moreover, it also occurs naturally in Australia but is not known to affect *H. amplexicaulis* there. The other fungus recovered in the Brazilian search, a species of *Phyllachora* (Phyllachoraceae), hardly induced damage in native *H. amplexicaulis*. Therefore clearly neither of these two fungi had much of the biocontrol potential sought. Barreto et al. (2000) provide an overview of plant-pathological field survey efforts in the Neotropics with the goal of identifying agents against invasive aquatic plants. Similar to the above-mentioned case, most often only a few fungal species are retrieved. Therefore identifying the respective plant's center of origin, where a higher diversity of (fungal) specific pathogens is expected, is key to identify potential biocontrol species. The authors describe how in the Dominican Republic, wetland drainage done to get rid of vectors of human pathogens, destroyed most accessible habitats of pathogenic fungi of water hyacinth. Hence, provisioning and understanding candidate biocontrol agents against invasive aquatic plants is not only an argument in favor of parasite conservation, but of wetland conservation as well.

Another example where a better understanding of the parasite diversity is policy relevant, is the suggested potential for bioindication in wetlands of various plant-parasitic nematodes, among which members of Tylenchida. Tylenchid genera reported from (sub)tropical wetland plants include *Hirschmanniella* (Pratylenchidae) and *Meloidogyne* (Meloidogynidae) (Siddiqi, 2000; Brito et al., 2016).

A particular scenario of wetland plants impacting human health, is the transmission of some plant-borne fasciolid, gastrodiscid, and paramphistomid trematodes. Six species of these flatworms use snails as intermediate hosts. Humans become infected when they ingest the metacercarial stage, typically attached to water plants, though other sources such as contaminated water are possible, too. Fascioliasis (caused by *Fasciola gigantica* or *Fasciola hepatica*) occurs in temperate and tropical climates, from below sea level to high altitudes; fasciolopsiasis (caused by *Fasciolopsis buski*) is typical to Asia. *Fasciola* spp. use a wide range of host plants: wild and cultivated, freshwater and terrestrial ones (Mas-Coma et al., 2007). The snail hosts may show a certain plant host preference but are able to utilize a systematically broad plant spectrum (e.g., Giraldo and Álvarez, 2013, for Colombian mountain wetlands).

15.5 Anthropogenic influences on parasites in tropical freshwater wetlands

15.5.1 Environmental parasitology: a promising research field for tropical wetlands?

Parasites may be highly informative "tags" for their hosts and ecosystems, for example, to elucidate host migration patterns (Hoberg, 1997; Criscione and Blouin, 2006; Criscione et al., 2006; Barson et al., 2010) . Intestinal parasite communities were used to identify migratory and resident individuals of endangered double-crested cormorants partially residing in swampy areas in the Mississippi River Delta (Sheehan et al., 2016). Another field of study where parasites are an information source is environmental parasitology, which utilizes parasites to provide insights into environmental issues such as pollution. Most of this work has occurred in aquatic systems, although there is no logical barrier to applying it to terrestrial landscapes, as well. Recognition of the potential application of parasitological data to environmental questions was pioneered in the mid-late 1990s (Sures et al., 1994, 1997, 1999). In particular, the use of helminths as indicators of heavy metal environmental contamination has broadened our perspective to consider parasites as providing not only new bioindicators (Lafferty, 1997; Sures, 2001, 2003) but also potential health benefits to their hosts, hence shifting the paradigm that parasites are harmful organisms to be systematically eliminated (Malek et al., 2007; Molbert et al., 2020).

Parasites are both a rich source of potential bioindicators on their own, and it has largely escaped the attention of non-parasitologists that the presence of parasites in hosts utilized as bioindicators can influence and confound results of traditional assays (Grabner and Sures, 2019). Recently, Vidal-Martínez et al. (2010), Sures et al. (2017), and Vidal-Martínez and Wunderlich (2017) have summarized research over the past several decades and provide insightful information on the field and its applications.

Wetlands research naturally includes a conservation component because of the severe alterations and degradation that human activities continue to inflict on these ecosystems. Most wetlands of the world have never been surveyed for their parasite fauna. Hence, in most cases, then, research on these systems will have to proceed without the knowledge of true baseline data, and contextualizing the parasite communities currently present in these areas to some sort of pristine state will be all but impossible. One may not emphasize enough the usefulness of museum collections in such cases. Jorissen et al. (2020) demonstrate the potential of historical host collections to reconstruct a baseline for the situation prior to the anthropogenic impact in question; in this case, introduction of nonnative tilapias in the Congo Basin. Environmental parasitology uses a set of logical and empirical tools that can help integrate data from many sources to produce a fuller understanding of the impacts of pollution and other ecological aberrations in wetlands (because heteroxenous parasites depend on the presence of several host species), and therefore provides opportunities to mitigate ongoing destruction of these ecosystems. Parasite life cycles are often woven into the most stable strands binding free-living species together in an ecosystem (Lafferty et al., 2008). A lack of parasites may not necessarily mean an ecosystem is unhealthy and we therefore call for increased awareness and further investigations.

15.5.2 Climate change may impact wetland parasite dynamics in various ways

Tropical wetlands and their ecosystem (dis)services are often at center-stage in the climate debate, in view of their potential in mitigating climate change, their global importance as carbon sinks (Murdiyarso et al., 2012), and the link between climate change and outbreaks of water-borne infectious diseases (e.g., fasciolasis in South America: Mas-Coma et al., 2007). Since ecological fitting allows many parasites to increase their host range under changing environmental conditions, it is indeed predicted that global climate change events should lead to new parasite—host associations and thus, to a redistribution of parasite diversity with unpredictable ecological consequences (Brooks and Hoberg, 2007; Carlson et al., 2017).

The most direct effect of global climate change on parasite biota in wetlands is the potential for increased surface-water temperatures to amplify the rate of parasite reproduction, maturation, and transmission through straightforward physiological effects on both the parasites and their hosts. This effect has the most salience for those researchers focused on human pathogens such as the parasites belonging to *Plasmodium* causing malaria, because the population dynamics of their mosquito vectors can be influenced immensely by changes in water temperature. Such direct effects might occur for other parasites as well, including most of the viral, bacterial, and protistan pathogens of fishes and other wetland vertebrates. Otherwise nonpathogenic wetland fungi such as *Candida auris* can adapt to higher temperatures, be selected to tolerate avian or mammalian body temperatures, allowing them to be transmitted by birds to humans and thus become zoonotic (Casadevall et al., 2019). In a nutshell, both recent research and the complexity of many parasite life cycles argue for a more sophisticated view of the potential for climate change to alter parasite population and community dynamics.

Cohen et al. (2020) used existing datasets from across the globe to model how temperature changes could affect parasite prevalence in the context of the thermal mismatch hypothesis. Warming temperatures represent a far greater departure from long-term norms for cold-adapted hosts (and parasites) than they do for those with long evolutionary histories in the tropics and subtropics. Not surprisingly, Cohen et al.'s (2020) models predicted near uniform increases in overall parasitism in cold-adapted hosts in a warming world, but a mixed picture in those hosts from perennially warm locales: helminth infections were predicted to increase slightly, but bacterial, viral, and especially fungal parasitism were predicted to decline dramatically. Directly transmitted parasites were expected to suffer losses in warm areas of the globe, whereas the models predicted modest increases in the prevalence of indirectly transmitted parasites in those same areas. Overall, global projections from the Cohen et al. (2020) study suggest declines in parasite prevalence in a warming world among wildlife in most tropical and subtropical areas, including in aquatic ecosystems. Cizauskas et al. (2017) and Carlson et al. (2017) even suggest that certain parasite species may be driven to extinction by climate change.

In view of the complex multispecies interactions in a parasite's life cycle, a less-than-straightforward relationship between temperature changes and parasite dynamics may be expected. Both Lõhmus and Björklund (2015) and Marcogliese (2016) provide accessible summaries on these topics, Studer et al. (2010) and Paull et al. (2015) are excellent case studies, and Byers (2020) provides, for coastal and estuarine environments, an overview of the multifaceted influence that changes in temperature and other factors associated with global change may have on host—parasite interactions. Since parasite life cycles may involve free-living and parasitic stages of ectothermic and/or endothermic hosts, there are many points in the life history of parasites where temperature changes may modulate parasite success. A few examples generalized from the literature illustrate some of the difficulties anyone attempting to predict the effects of global climate change on parasite populations and communities will face:

1. Larval development of trematodes inside their molluscan first intermediate hosts might be faster under warmer waters, leading to possible increased cercarial production both in time and quantity. However, those same conditions in other species may induce a decrease in cercarial production (Poulin, 2006), and could decrease the longevity of the nonfeeding free-living cercariae that emerge from the snails and provide the link to the next host in the life cycle. Similarly, the snail population may boom or on the opposite decline.
2. Increased water temperatures could speed the development and reproduction of helminths in ectothermic definitive hosts. However, this could lead to a change in the temporal pattern of egg release in the environment, which may be asynchronous with the presence of the next host in their life cycles.
3. Higher temperatures might render some hosts more resistant to infection on a per capita basis because of enhanced specific immune responses. However, higher temperatures could also induce shifts in hosts' habitat to areas where they may be more exposed to infection, and perhaps to new pathogens.

In these examples, then, the actual effect might be opposite of what would be predicted by an oversimplified view (see also Paull et al., 2015 for the freshwater snail-borne trematode *Ribeiroia ondatrae*). Furthermore, there are numerous consequences to climate change, especially concerning water resources that are critical to both humans and wildlife. Increased dryness leading to fragmentation of wetlands (Nielsen et al., 2020) into smaller, discrete wetted areas could be particularly detrimental to all biota, including parasites. How monoxenous and heteroxenous parasites will fare in those changing conditions is the object of discussions. For instance, Carlson et al. (2017) and Cizauskas et al. (2017) mention various reasons why several monoxenous parasites may fare worse than heteroxenous parasites. Other authors predict some monoxenous parasites might experience short-term increases in transmission and therefore a boom in population size, whereas heteroxenous parasites are likely to be exposed to a mosaic of newly formed habitats, potentially insufficiently supplied with intermediate and/or definitive host populations, water quality suitable for free-living life stages, etc. to support transmission and completion of their life cycles. If temporal and functional relationships among hosts and environment are altered by climate change as well, then many parasites with complex life cycles may even be extirpated locally. Collapsing parasite faunas have been documented (Russell et al., 2015), including in wetlands (Sitko and Heneberg, 2020), although to our knowledge not in climate change-induced scenarios or in tropical wetlands. However, this may reflect a lack of research rather than a lack of effect. As in most human-dominated ecosystems, by the time research has documented a so-called baseline, the ecosystem has already been fundamentally altered from its pristine state (Jackson, 2001; Jackson et al., 2001), and what is being described already carries the stamp of decades or centuries of anthropogenic influence. Hence, occurrence in wetlands of a community dominated by just one or two directly transmitted parasite species, and/or an exceptionally high turnover (beta diversity) among habitats in an area, or a lack of parasite diversity altogether, could be signs that a plethora of natural ecological interactions (e.g., spatial and temporal overlap, trophic relationships, population dynamics, behavior) among the free-living species of the ecosystem are being disrupted by climate-related changes.

15.6 A One Health view on tropical wetlands

One Health and related integrative paradigms (e.g., EcoHealth) call for jointly considering human, animal, and environmental health (Keune et al., 2017). A holistic approach of health at the human–animal-ecosystem nexus is particularly relevant for the science/policy interface regarding wetlands, in view of the diversity of biota, abiotic environments, and ecosystem interfaces they hold. Wetlands are also prime illustrations of the “shared risk” paradigm proposed by Rabinowitz et al. (2008). Rather than regarding animals in nature as mainly a threat to human health in an "us *versus* them" perspective (cf. the above-mentioned association of wetlands with diseases), these authors propose that animals, being exposed to similar risks as humans, are ideal models and sentinels to better understand infectious and environmental hazards. The above-mentioned potential of wetland blood parasites as models for human diseases agents, and of environmental parasitology in wetland conservation, aptly illustrates the relevance of the "shared risk" perspective with regard to parasites in wetlands.

Obviously, a One Health approach should avoid a purely academic and biophysical perspective, and therefore requires inter- and transdisciplinarity to include the vision of, for example, social sciences and of stakeholders in decision-making and practice. This is particularly important in the Global South, where poverty alleviation, health, food provisioning, and water are often strongly intertwined, which of course may heavily impact wetland habitats (Biggs et al., 2018). Implementing One Health research and policy in the Global South will require stepping up capacity building in the monitoring, detection, and identification of parasites and all hosts involved (including vectors) (Keune et al., 2017). In the hope of joining a call for such efforts, this section will showcase how tropical wetland parasitology ties into human and wildlife health.

15.6.1 Aquaculture and agriculture may influence the distribution of tropical wetland parasites and vectors

Agricultural activities heavily impact the health of tropical wetlands wildlife. In the Florida Everglades, there are indications that decreases in water level due to water diversion for agriculture may lower fungal diversity and favor pathogenic plant fungi, although the latter could also act as decomposers (Almeida et al., 2020). Junk and Nunes da Cunha (2018) sum up animal diseases introduced into the Pantanal with horses and cattle. Examples include *Trypanosoma evansi* (spilled over into capybara *Hydrochoerus hydrochaeris* and coati *Nasua nasua*), foot and mouth disease (spilled over into deer), and, more recently, equine infectious anemia virus (a retrovirus) and *Trypanosoma vivax*. Although our focus here is on natural wetlands, disease outbreaks in captivity (e.g., shrimp ponds) and the associated challenges of water quality and wastewater treatment obviously also heavily impact the surrounding ecosystems (De Graaf and Xuan, 1998; Senarath and Visvanathan, 2001) and escapes and cross transmission threaten natural populations. In this context, it is important, in concertation with stakeholders, to monitor native stocks for potential pathogen transmission from aquaculture (e.g., Eastern Research Group, 1998 for the risk of viruses introduced through shrimp culture). Disease-related failures in coastal shrimp farming may lead to aquaculture being moved inland, constituting an indirect environmental impact of shrimp disease on tropical freshwater wetlands (Walker and Mohan, 2009).

Anthropogenic **introduction of aquaculture species** has many devastating consequences, but the cointroduction of parasites and shifts in the parasite fauna of native species is among the least studied of them. This is even the case for well-known invasive alien species like the Nile tilapia, now widespread in various aquatic systems throughout the tropics. This fish is known to have cointroduced various parasite species, some of which spilled over to indigenous fish species, with monoxenous parasites as logical candidates as they only depend on the introduced host (e.g., monogeneans: Jorissen et al., 2020). Because transmission patterns may be conserved throughout a parasite genus, even heteroxenous parasites may be cointroduced as they do not always rely on conspecific hosts. Brooks et al. (2006) illustrate this with the lungfluke *Haematoloechus floedae*. This plagiorchiid digenean originally infects the bullfrog *Rana catesbeiana* in the United States, but occurs in the leopard frogs *R. taylori* and *R.* cf. *forreri* in wet and dry forest in Costa Rica, where introduced bullfrogs no longer occur. Cointroduced parasites may constitute a serious conservation risk in wetlands, as suggested by Pérez-Ponce de León and Aguilar-Aguilar (2019) for the cestode *S. acheilognathi* and the digenean *Centrocestus formosanus* in the Cuatro Ciénegas system in Mexico. Another potentially devastating effect of invasive alien species (IAS) is the amplification of native parasites in nonnative hosts, followed by spill-back to native species. For example, local plant pathogens frequently accumulate in invasive plant species. However, this is not always accompanied by transmission to native plants, as shown by Schroeder et al. (2020) for invasive *Phragmites australis* (Poaceae) in Louisiana (United States) wetlands. In the Everglades, a zoonotic pentastome, *Raillietta orientalis*, introduced with its invasive Burmese python host spilled over to native snakes, whose own pentastomids in turn spilled over to the invasive python, leading to both reptiles boosting the life cycles of all these parasites (Miller et al., 2018, 2020; Walden et al., 2020).

There are also **indirect health effects of the introduction of IAS**. One of the most notorious examples is the water hyacinth, *E. crassipes*. Introduced as a floating ornamental plant, and despite other potential applications (e.g., for bioenergy production), it has strongly contributed to the degradation of (sub)tropical wetlands worldwide. Apart from its direct impact on ecosystem stability, it provides favorable conditions for various mosquito and snail disease vectors, and thus increases the human health risk of wetlands (Malik, 2007; Kriticos and Brunel, 2016). Similarly, zoonotic parasites of introduced species such as the pentastomid of the Burmese python mentioned above can be a public health threat (Mendoza-Roldan et al., 2020).

The unique **heterogeneous physicochemical conditions** in (sub)tropical freshwater wetlands have consequences for invasion biology and community ecology of parasites. Bittencourt et al. (2014) found a higher fish parasite diversity in the main channel than in the floodplain of a tributary of the Amazon system and suggested this difference was related to the dominance of native host fish species in the river proper. Conversely, invasive Nile tilapia had a relatively depauperate parasite fauna that was, however, more species-rich in the floodplain area than in the main river channel. The authors report that one parasite species, the ciliate *Trichodina nobilis*, had spilled over from Nile tilapia to the native cichlid *Aequidens tetramerus*. There was no spill-back to Nile tilapia, which the authors attribute to parasite host-specificity and to the tilapia introduction being less than a decade old. In a South African floodplain, Welicky et al. (2017) reported that a drought caused hypersaline conditions to the extent that the invasive parasitic copepod, *Lernaea cyprinacea* (Cyclopoida, Lernaeidae) became extirpated. The native and near-threatened Mozambique tilapia *O. mossambicus* was entirely cleared of it, whereas predrought prevalence of infection was 100%.

15.6.2 Wildlife and (zoonotic) transmission

Parasitology of traditionally defined wildlife (large, charismatic mammals and birds) is a particularly important aspect of wetland ecosystems that has not received sufficient attention. The potential for zoonotic outbreaks in human populations naturally occupies the interests of many researchers, but wildlife—livestock—human interactions are only becoming more important as human activities alter large-scale ecosystems, changing the ecological context in which natural and human-dominated faunas and floras interact. Some of the most dramatic examples of these events have occurred in African landscapes, such as the interactions of rinderpest, trypanosomiasis, colonialism, and civil unrest (Ford, 2007; Selby et al., 2013). Other, less dramatic examples are occurring around the globe. One of the more fascinating involves the Kafue lechwe.

Lechwe (*Kobus* spp.), along with other aquatic antelopes like the water buck, kob, and nyala, occur in marshy areas and similar wetlands in Africa. Lechwe of South-Central Africa inhabit some of the most iconic wetlands of the world, including the Okavango Delta of Botswana and Bangweulu Wetlands of Zambia. The Kafue lechwe (*Kobus leche kafuensis*) is endemic to the Kafue Flats in Zambia and now listed as Endangered by the IUCN, with perhaps as few as 20,000 individuals remaining from a high around 100,000 in the 1970s when records were first kept (IUCN). Kafue lechwe aggregate in leks during breeding season, are reliably semiaquatic, and feed primarily on emergent grasses in floodplains and wetlands. Lechwe as a group cooccur with many other charismatic megafauna, and they interact with domesticated animals, particularly cattle, when present.

The Kafue Flats were irrevocably altered by the construction of hydroelectric dams on the Kafue river both upstream and downstream of the wetlands themselves in the 1970s. Prior to construction of these dams, other megafauna, such as wildebeests and zebra, were common cohabitants with lechwe, and the area supported an astonishing diversity and density of birds (Sheppe, 1985). Much of the pristine floodplain now stands permanently dry, vegetation has been altered dramatically, and the pattern and scale of primary productivity has been changed in ways detrimental to the Kafue lechwe and other large mammals and birds. Sheppe (1985) links these secondary effects of dam building to the decline in the population size of the lechwe, although other factors, such as pathogens no doubt contribute. For example, bovine tuberculosis (caused by the bacteria *Mycobacterium bovis*) was recorded in 45 individuals among 125 Kafue lechwe causing an estimated annual mortality rate of 14% (Gallagher et al., 1972). On the other hand, others have found little association of general parasite infection and body condition (Munyeme et al., 2010b). The status of these animals as an iconic wildlife species and their interaction with livestock have made them the subject of a number of parasitological and epidemiological studies over decades. Stafford (1991) reviewed the literature on bovine tuberculosis in Kafue lechwe and found between 3% and nearly 100% infection among surveys conducted through the 1970s, 1980s, and early 1990s. This review also lists an impressive number of pathogen species recorded from *K. leche kafuensis* (17 viruses and bacteria detected via serological survey, 17 nematodes, 18 trematodes, 1 cestode, and 7 ectoparasites). Munyeme et al. (2010a) found tuberculosis at prevalence similar to that of Stafford (1991) and Gallagher et al. (1972).

Of further concern is the potential for this wildlife species to be tied up into a network of transmission dynamics that link wild animals to livestock (semisylvatic cycles) and therefore humans (thus leading to domestic life cycles). Kafue lechwe and cattle graze together at certain times of the year, and the potential for disease spread is therefore present. In addition, lechwe are poached, farmed, and otherwise moved around the landscape in ways that can both threaten their own populations and livestock. Brucellosis (caused by the bacterium *Brucella*) is present in both wildlife and cattle in the area (Rottcher, 1978), and transmission to cattle from wildlife has at least some empirical support (Muma et al., 2007). In a summary of our understanding of these two bacterial diseases in lechwe and other wildlife and domesticated livestock, Siamudaala et al. (2005) suggested that the evidence supports lechwe as a sylvatic host for both pathogens and a reservoir of infection for livestock, thus having a key role in moving these pathogens both into and out of populations of livestock. Much like brucellosis in bison and antelope in the United States Yellowstone National Park area, conservation and management decisions regarding wildlife can be influenced by the perception of a threat to local economic interests. Kafue lechwe are certainly economically important (Siamudaala et al., 2005), and conservation and management decisions in the future should synthesize inputs from social, economic, and biological parameters. Increasingly, it is recognized that consideration of diseases and parasites needs to be integral to such decisions.

15.6.3 Water-borne infectious diseases of humans are influenced by habitat disturbance

Wetlands around the world are gathering places of humans and many of the diseases that plague humans (Dale and Connelly, 2012). Tropical wetlands are often implicated at the crossroads of economic development, human health, and environmental degradation. Human history is unfortunately littered with examples of how modifying ecosystems, particularly aquatic ecosystems, resulted in changed epidemiological landscapes that often came with brutal, albeit often predictable, consequences. As seen above with the lechwe example, **dam building** is among the most important of these, both because the activity itself is so widespread and because of the drastic changes dams impose on aquatic systems both upstream and downstream of their location. In the parasitological literature, the archetypal examples of how dams change patterns of human disease involve blood flukes belonging to *Schistosoma*, the etiological agents of schistosomiasis (bilharzia). The life cycles of schistosomes require egg-bearing human excrement (feces or urine, depending on the species) to contaminate surface waters where snail intermediate hosts (also referred to as vector by many) occur. Infective free-living schistosome larvae (cercariae) shed by those snails can infect people percutaneously. Since humans acquire infections by wading in water harboring these cercariae, the intimacy of the ecological interaction between humans, snails, and aquatic ecosystem is governed by myriad of behavioral, socioeconomic, biological, and ecological factors (Lund et al., 2019). The construction of a dam at Diama on the lower reaches of the Senegal River was completed in 1986 to prevent seawater intrusion into the basin. The prevention of seawater intrusion by the dam reduced the salinity of the water, increased its pH to neutral/slightly alkaline, allowed establishment of freshwater aquatic vegetation in the river and its associated canals and flooded areas, all of which provided far more suitable habitat for snails. Prior to the construction of the dam, urinary schistosomiasis (caused by *S. haematobium*) was low and intestinal schistosomiasis (caused by *S. mansoni*) was absent from villages in the lower and mid regions of the basin. Eggs of *S. mansoni* were first recorded from individuals in the area in 1988 (Talla et al., 1990), less than 18 months after the dam was operational. Outbreaks of both diseases have occurred oftentimes since then, resulting in very high prevalence of infection ($>70\%$) of one or both species of schistosomes (Talla et al., 1990; Picquet et al., 1996; Southgate, 1997; Van den Broeck et al., 2015). To make things even worse, a predator of snails (the prawn, *M. vollenhovenii*) was extirpated locally because its migration routes were blocked by the dam (Alkalay et al., 2014). Although Sokolow et al. (2015) demonstrated that restocking prawns could lead to effective reduction in snail populations and prevalence of schistosomiasis in villagers, to this day the legacy of the dam remains since schistosomiasis is still hyperendemic in the area (Lund et al., 2019). This is only one example among many that illustrates the fact that water management projects often result in increased risk of schistosomiasis (Jobin, 1999; Steinmann et al., 2006). Unfortunately, although predictable, such threats to human health are often ignored to the benefit of a potentially enhanced economy (for instance the Diama Dam project was soon followed by the Manantali Dam in Mali).

In general, while land conversion can reduce transmission of water-borne human diseases (e.g., via wetland drainage for agriculture), it has clearly had enormous negative consequences on the environment, wildlife, biodiversity, and human well-being. Rehabilitation and reconstruction of wetlands may help mitigate or reverse this destruction. However, such wetland restoration efforts need to heed the potentially increased disease burden on local populations. **Constructed wetlands** may act as reservoirs, amplifiers, and propagation sites of anthropozoonotic parasites such as diplomonad *Giardia*, coccidian *Cryptosporidium*, or microsporidian *Encephalitozoon* (see Graczyk and Lucy, 2007). Also, the creation of artificial wetlands for **aquaculture or agriculture** can increase vector and host (habitat) availability (Rohr et al., 2019) although adequate management can minimize this risk (Dale and Connelly, 2012). Johansen and Ferreira (2021) report on a Brazilian Amazonian urban environment close to seasonally flooded forest and lined with streams, making it favorable for fish culture. Increased availability of mosquito breeding sites with the advent of fish ponds, in combination with increased human population mobility associated with urban services, led to a considerable increase in malaria incidence. Still other examples include the increased global spread of fish-borne zoonoses, such as opisthorchiasis, as a result of aquaculture production and trade (Sithithaworn et al., 2012), and the connections between fasciolopsiasis in Asia and cultivation of water plants or production of pigs, or between the construction of irrigation infrastructure and outbreaks of fascioliasis in South America and Egypt (Mas-Coma et al., 2007). One other important example of disease amplifier constructed wetlands are rice fields that harbor mosquito vectors of agents of malaria, encephalitis, and filariasis as well as snail vectors of schistosomes (e.g., Appleton and Madsen, 2012 in southern Africa wetlands). Rice fields in the vicinity of natural wetlands may also provide an interface between domesticated and wild water birds, with implications, for instance, on Highly Pathogenic Avian Influenza (Gilbert et al., 2006). However, when managing rice fields in view of disease control, it is important to consider that they are of conservation interest as replacement habitat for wetland fauna after land conversion (Lawler, 2001; Stenert et al., 2009).

Table 15.1 summarizes some human parasitic or infectious diseases that are commonly associated with wetlands. Fig. 15.7 illustrates the life cycle of

TABLE 15.1 Communicable and transmissible diseases of humans associated with wetlands, with etiological agent(s), hosts and/or vectors, geographical distribution, and some details of symptoms and pathology.

Disease	Etiological agent (s)	Hosts and vectors	Distribution	Symptoms/Pathology
Water-borne				
Bacterial diarrheal	*Salmonella* spp.; *Vibrio cholerae; Campylobacter* spp.; *Aeromonas* spp.	NA	Worldwide	Diarrhea; fever; dysentery; gastroenteritis; weakness; septicemia; etc.
Other bacterial	*Mycobacterium ulcerans*	Biting aquatic insects	Circumtropical and subtropical	Skin nodules, plaques, and ulcers; osteitis; deformity.
Viral	Hepatitis A; Hepatitis E; Noroviruses	NA	Worldwide	Fever, fatigue, pain, jaundice, diarrhea, etc.
Protozoal	*Cryptosporidium;* *Giardia;* *Entamoeba*	NA	Worldwide	Diarrhea, dysentery, pain, abscesses, etc.
	Naegleria fowleri	NA	Worldwide	Primary amoebic meningoencephalitis

(*Continued*)

TABLE 15.1 (Continued)

Disease	Etiological agent (s)	Hosts and vectors	Distribution	Symptoms/Pathology
Mosquito-borne				
Malaria	*Plasmodium* spp.	Female anopheline mosquitoes	Circumtropical and subtropical	Paroxysms; anemia; cerebral malaria; hepatosplenomegaly; hemoglobinuria; acidosis; etc.
Rift Valley Fever	Arbovirus	*Aedes* spp.	Sub-Saharan Africa; Arabian peninsula	Fever; pain; ocular lesions; encephalitis; hemorrhagic fever.
West Nile	Arbovirus	*Culex* spp.	Worldwide	Fever; fatigue; encephalitis; meningitis; etc.
Chikungunya	Arbovirus	*Aedes* spp.	Circumtropical and subtropical; some temperate zones	Fever; joint pain; rash; etc.
Dengue	Arbovirus	*Aedes aegyptii*	Circumtropical and subtropical; some temperate zones	Fever; intense pain; rash; etc.

Yellow Fever	Arbovirus	*Aedes* spp.	Central Africa; South American; Panama	Fever; intense headache; pain; fatigue; bleeding; shock; organ failure; etc.
Lymphatic filariasis	*Wuchereria bancrofti; Brugia* spp. (Nematoda)	*Culex* spp.	Circumtropical and subtropical	Lymphoedema; elephantiasis; hydrocele; immune disruption; etc.
Other arthropod-borne				
River Blindness	*Onchocerca volvulus* (Nematoda)	Black flies, *Simulium* spp.	Sub-Saharan Africa; limited in C & S America; Yemen	Skin lesions and nodules; vision changes, including blindness.
Dracunculiasis	*Dracunculus medinensis* (Nematoda)	Copepods, *Cyclops* spp.	Africa	Fever; dizziness; severe skin edema; then abscesses, septic arthritis, tetanus, etc. from complications.
Snail-borne (Trematoda)				
Schistosomiasis	*Schistosoma* spp.	*Bulinus, Biomphalaria, Oncomelania* spp.	Circumtropical and subtropical	Fever; chills; aches; hepatosplenomegaly; bleeding; fibrosis; cancer; etc.
Cercarial dermatitis	Nonhuman schistosomes, mostly	Lymnaeid, physid, planorbid, semisulcospirid snails	Worldwide except for Antarctica	Skin eruption, itching, other skin symptoms; massive infection: fever,

(*Continued*)

TABLE 15.1 (Continued)

Disease	Etiological agent (s)	Hosts and vectors	Distribution	Symptoms/Pathology
	Trichobilharzia spp.			limb swelling, nausea, diarrhea, insomnia.
Fascioliasis	*Fasciola* spp.	*Lymnaea* spp.	Worldwide, or nearly so	Abdominal pain; fever; fibrosis of bile ducts; inflamed gall bladder; etc.
Fasciolopsiasis	*Fasciolopsis buski*	Planorbid snails belonging to *Segmentina*, *Hippeutis*, and *Gyraulus*; humans and pigs as final hosts	Asia	Depending on worm burden: from anemia, eosinophilia, headache, dizziness, gastric pain, and loose stools, to severe epigastric and abdominal pain, diarrhea, bowel obstruction, nausea, acute ileus, anasarca, pronounced eosinophilia and leukocytosis, damaged intestinal mucosa, intestinal and duodenal erosions, ulceration, hemorrhages, abscess, and catarrhal inflammation.
Paragonimiasis	*Paragonimus* spp.	Snail-host varies; Decapod second intermediate host	Circumtropical and subtropical	Abdominal pain; bronchitis-like symptoms; etc.
Clonorchiasis	*Clonorchis* spp.	*Parafossarulus manchouricus*; *Bulinus* spp.; Fish second intermediate host.	Eastern Asia	Fibrosis of bile ducts, bile duct cancer.

Fish-borne (Nematoda)				
Gnathostomiasis	*Gnathostoma* spp.	Freshwater copepod first intermediate host; fish or amphibian second intermediate host; wide range of fish-eating paratenic hosts; mammal definitive host	Asia, Latin America	Erythema, cutaneous larva migrans, may be deleterious or fatal when larvae in vital organs incl. CNS

Based on Barnett et al. (1996), Choi et al. (2004), Horák et al. (2002, 2015), Mas-Coma et al. (2007), Nawa and Nakamura-Uchiyama (2004), Ramirez-Avila et al. (2009), and online resources from the Centers for Disease Control and Prevention (https://www.cdc.gov/). This is only a selection of examples; it is not comprehensive. Additional details on individual diseases are beyond the scope of this treatment.

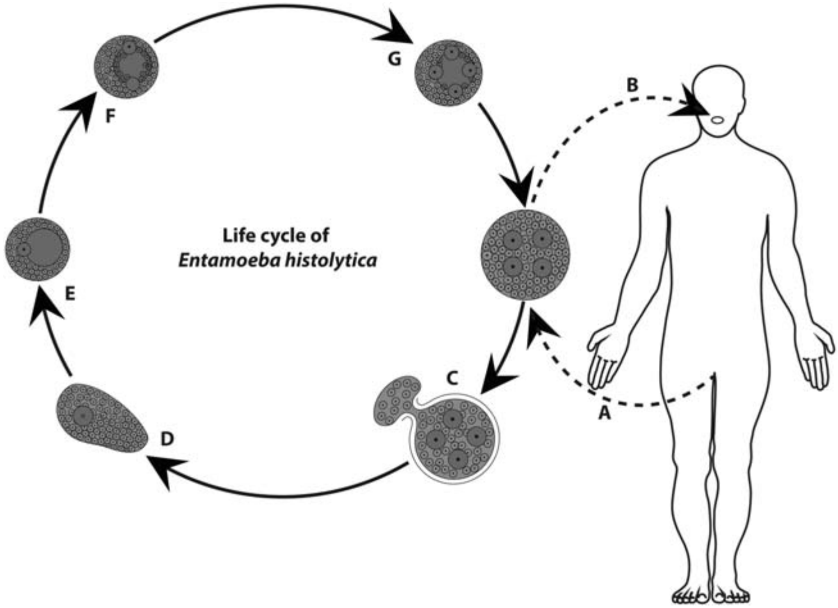

FIGURE 15.7 Life cycle of *Entamoeba histolytica*. (A) Cysts from infected hosts are passed through with feces. (B) Infection occurs via ingestion of mature cysts from contaminated food, water, or hands. (C) Excystation occurs in the small intestine where trophozoites (D) are released, and migrate to the large intestine. (D) Trophozoites multiply by binary fission and infect either intestinal lumen (noninvasive infection), intestinal mucosa (intestinal disease), or blood vessels, reaching other organs such as the liver, brain, and lungs (extra-intestinal disease). (E–G) Trophozoites then undergo encystation eventually forming into infectious cysts ready to be excreted with the hosts feces to repeat the cycle. Images not drawn to scale (Lv et al., 2013). *Adapted from Lv, S., Tian, L.-G., Liu, Q., Qian, M.-B., Fu, Q., Steinmann, P., et al., 2013. Water-related parasitic diseases in China. International Journal of Environmental Research and Public Health 10, 1977–2016.*

a typical amoebozoan human disease agent. Note that chemical and other exposure-mediated diseases are not included here but may be of equal importance when considering human use of wetlands and health. Malan et al. (2009) argued for including disease risk into wetlands management, and organizations such as the Ramsar Convention (a convention on wetlands) have responded to these risks in their recommendations for wetlands research and restoration (Horwitz et al., 2012). There is no question that the relationship between wetlands, public health, and human well-being is complex, probably to an extent that precludes practical, operational specifics as to how best to achieve a balance between the benefits of wetlands and their inherent risks to human health (see Irvine et al., 2022, Chapter 19). However, what is clear is that unintended consequences are nearly universal when humans modify their environments, even in cases where the impetus to do so is environmental restoration. Detailed knowledge of the local life histories of hosts and vectors of human pathogens is needed to be confident in how any given ecosystem change will potentially affect disease transmission and human health. While the need for such research is very clear, the resources to implement it are usually lacking. One perspective to keep in mind though is that mitigating or reversing the course of wetland destruction, for example, through wetlands rehabilitation and reconstruction, can bring back many of the ecosystem goods and services necessary to sustain all life.

15.7 Life cycle reconstruction of water-borne parasites: a lost art?

The interest in a better understanding of the biological world and diseases is what drives the scientific reconstruction of many parasitic life cycles (National Research Council, 1970). This, in turn, has provided researchers, parasitologists, medical doctors, and the general public with an increased knowledge of host−parasite relationships, transmission dynamics, the range and vastly different life stages of certain parasite taxa, the etiology of certain diseases, and how to either prevent or eliminate infection by certain parasites (Vaumourin et al., 2015; Blasco-Costa and Poulin, 2017).

A story behind the myth

A classic story behind the drive of understanding parasite life cycles concerns the fever tree *Vachellia xanthophloea* (Fabaceae). This tree and its green bark caused early European visitors of Africa to falsely associate it with people contracting bad fever in areas where it grows. This was, however, purely coincidental as the swampy and tropical areas where it naturally grows are the ideal breeding grounds for anopheline mosquitoes, the vectors of the malaria agent. And thus a myth began, the fever tree received its name, and a parasitic disease was left blameless, until the fever was eventually linked to the malaria parasite and its mosquito vector.

In the infancy of parasitology research, life cycle reconstruction was the focus of many studies and laid the foundation for research on parasites today, revealing the often complex ways in which they complete their cycles, one stage at a time (Despommier and Karapelou, 1987). The data gathered from a single life cycle are instrumental in understanding the classification, taxonomy, host−parasite relationships, ecology, and diversity of any parasite taxon (Thompson et al., 2005). However, the pressure to publish, the constraints of nowadays more ethical and noninvasive sampling efforts, and the use of newer technologies to answer complex questions have shifted the focus away from classical life cycle elucidation, which is slow, painstaking at times (Pauli et al., 2010;

TABLE 15.2 Summary of field sampling and life cycle elucidation of anuran filarial nematode *Neofoleyellides boerewors* (Netherlands, 2019).

Step 1—Find the target parasite species in situ:
Guttural toads were first screened for the presence of microfilariae in the peripheral blood using blood smears and light microscopy.

Step 2—Monitor host behavior and search for potential vectors:
Once a toad population with a medium-to-high parasite prevalence was identified, it was selected to be monitored for interactions with potential vectors. Monitoring consisted of studying the natural behavior of the toads in their habitat. Individuals were first examined for the presence of hematophagous insects on their bodies. These observations eventually led to the detection of mosquito vectors feeding on certain individual toads.

Step 3—Monitoring vector behavior:
During the initial field observations of these mosquitoes, they were noted to only be found on male toads actively calling. To test that this was not coincidental, calling toads were located at night, systematically checked for the presence of mosquitoes on their bodies, and then watched using an infrared light to not disturb toads or mosquitoes. If toads were reluctant to call, playback-calls were broadcasted and a response call was waited for. Remarkably, once a toad started to call, mosquitoes would almost instantly hone in on the calling individual. Several of these mosquitoes were collected and identified (as two species of *Uranotaenia*: *U. mashonaensis* and *U. montana*) to gain better perspective on their feeding habits, distribution, and general ecology.

Step 4—Plan for data collection and experimental setup:
Based on those field data, we could begin the planning of how to elucidate the life cycle of this parasite, while also being fully prepared to make the most of every opportunity as one needs to be when attempting field-based experiments. One important factor to consider includes time of the year since presence of any hosts involved (and parasites, albeit not in this case since no free-living stages occur) may be restricted by seasonal changes or environmental conditions in general.

Step 5—Return to the field site and experimental setup:
Upon return to the collection site, the first objective was to collect as many toads as possible and screen them to identify the individuals parasitized with microfilariae. These parasitized individuals were placed individually in holding containers and later returned to the sampling site to be used as enticement for collection of feeding mosquitoes. Three different tools were used to collect mosquitoes: (1) A modified portable Center for Disease Control (CDC, USA) mosquito trap fitted with a speaker to play the toads' calls; (2) an aspirator, used directly from propped infected toads enticed to call using playbacks; and (3) a glass tank fixed with a fine mesh funnel and baited with a propped infected toad enticed to call using playbacks.

Step 6—Laboratory phase
Additional mosquitoes collected using the CDC trap were housed in a vivarium and enticed to feed on infected toads using playbacks in the laboratory. Using only infected individuals ensured that all mosquitoes collected after taking a blood meal were most likely infected and could be monitored and successively dissected to track the different phases of development in the mosquito vectors. Detailed notes on larvae

(*Continued*)

TABLE 15.2 (Continued)

stages in the mosquito were made, recording the infection habitat, the route of migration of the various stages, and all were associated with the number of days postfeeding. All developmental stages recovered were examined, measured, and identified according to their morphology and larval classification keys. Lastly, infected toads were dissected to recover and tally all adult nematodes to determine their site of infection and their intensities. Furthermore, for the different stages collected, partial sequences of the 18S rRNA and COI genes were obtained to confirm all stages were conspecific.

Rawat and Meena, 2014; Zemanova, 2020), and at great risk of failure. Furthermore, most of the major parasitic groups, or at least those of medical or economic importance, already have a number of life cycles completed, rendering further work on closely related taxa "unnecessary" from a funding perspective. For example, schistosomes are a very well-studied group of blood flukes due to their involvement in causing human and animal schistosomiasis (Loker and Mkoji, 2005; Brant and Loker, 2013). However, the majority of blood flukes that infect birds, turtles, or fishes are still largely understudied (Brant and Loker, 2013; Power et al., 2020).

Life cycle reconstruction, especially for heteroxenous parasites, requires proper planning, patience, and a solid understanding of the hosts' ecology. The current-day availability of molecular techniques is a considerable advantage. For instance, genetic characterization to explore potential conspecificity of parasite life stages infecting hosts at different levels of a food web reduces reliance on difficult experimental studies. Furthermore, the importance of serendipitous observations made in the field should not be underestimated. A breakdown on the completion of a complex parasite life cycle in a wetland habitat will provide the reader with a better perspective on how life cycles may be elucidated. The study by Netherlands et al. (2020) on the life history of the anuran filarial nematode *Neofoleyellides boerewors*, whose adults are found in the body cavity of the common guttural toad, *S. gutturalis* and two species of mosquito vectors belonging to *Uranotaenia* is used as an example, and summarized in Table 15.2.

In the case of the life history elucidation of *N. boerewors* not only were the different stages of development identified, but also the host-vector/parasite relationships (Fig. 15.8). Field observations of the feeding habits of the mosquito, revealed intriguing findings about host targets and mechanisms these mosquitoes use to locate their preferred hosts. Overall, this particular study contributed to the limited knowledge on the biodiversity, distribution, evolution, and ecology of this group of neglected anuran parasites (Netherlands et al., 2020).

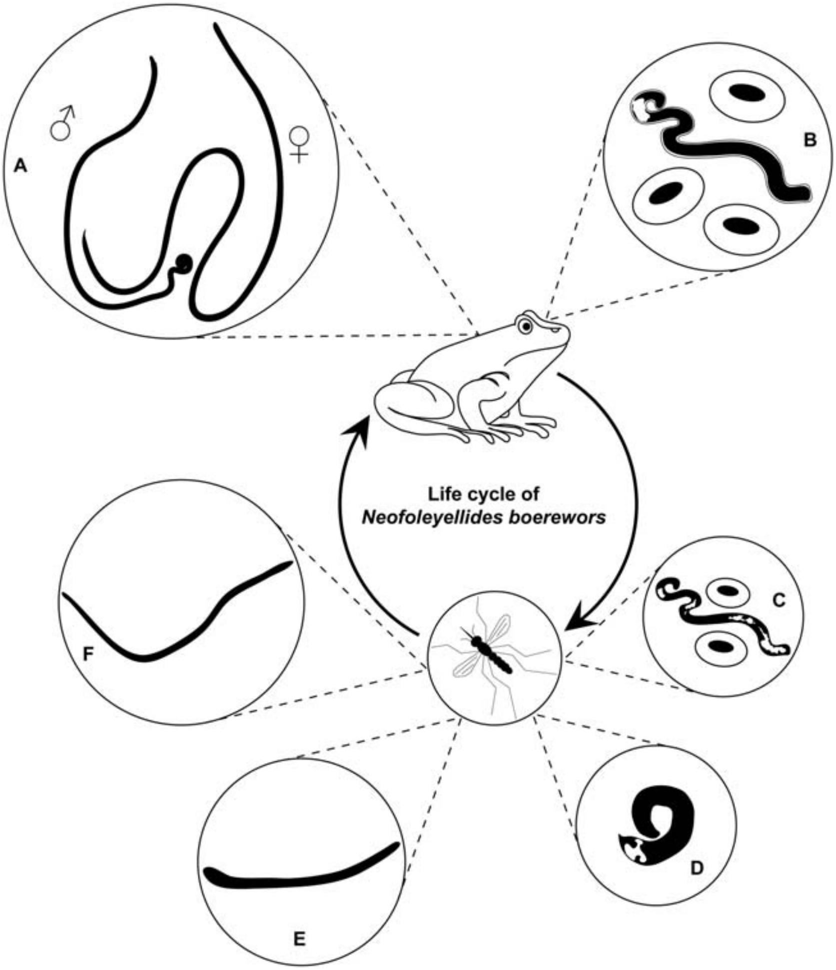

FIGURE 15.8 Graphical representation of the life cycle of *Neofoleyellides boerewors* in its vertebrate frog host and invertebrate mosquito vector. (A) Male and female adult stages. (B) Sheathed microfilaria in the peripheral blood of frog host. (C) Unsheathed microfilaria in the blood meal of the mosquito. (D) Sausage-shaped first-stage larvae. (E) Second-stage larvae, observed from between 6 and 14 days postinfection. (F) Third-stage infective larvae transmitted to new host during next blood meal. Images not drawn to scale. *Adapted from Netherlands, E.C., Svitin, R., Cook, C.A., Smit, N.J., Brendonck, L., Vanhove, M.P.M., et al., 2020. Neofoleyellides boerewors n. gen. n. sp. (Nematoda: Onchocercidae) parasitising common toads and mosquito vectors: morphology, life history, experimental transmission and host−vector interaction in situ. International Journal for Parasitology 50 (3), 177−194.*

Tips for parasite life cycle elucidation in the field:

- Prepare to get your hands dirty and for concentrated effort.
- Be adaptable and patient; it's hard work.
- Learn from other fields of research.
- Know about the biology of the target host.
- Use controls, and verify conspecificity of different life stages using molecular data.
- Be ready for unexpected observations. Don't miss them! Don't underestimate them! Remember: "Chance favours the prepared mind."
- Make sure data gathered are reproducible.
- If possible plan to repeat this cycle in the laboratory and fulfill Koch's postulates.
- If not possible, then try to verify cycles with molecular data.
- Think ethically.

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Chapter 16

Impacts of alien invasive species on large wetlands

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16.1 Introduction

Freshwater ecosystems cover less than 1% of the Earth's surface area but support over 10% of all known species and provide clean water, food, livelihoods, and other ecosystem services to humanity (Darwall et al., 2018). River floodplain systems are considered among the most productive freshwater ecosystems because of periodic inundation of a complex array of lagoons, disconnected river channels, marshes and floodplain grasslands. They are also under immense pressure from a dramatic increase in global consumption of natural resources, which over the last century has led to unsustainable water abstraction, widespread habitat loss and degradation, increased levels of pollution and proliferation of invasive species (Garrick et al., 2017; Irvine et al., 2022, Chapter 19; Wasserman and Dalu, 2022, Chapter 1; Marambanyika et al., 2022, Chapter 22).

Increased globalization, travel and trade has underpinned the unprecedented and relentless rate of translocation of plants and animals around the world (Seebens et al., 2021). This phenomenon results in increasing numbers of introduced nonnative species (i.e., species moved by humans to sites outside their historic range). Species introductions may be unintentional (accidental) or intentional (Gozlan et al., 2010). Examples of unintentional introductions include the movement of aquatic plants, biofouling invertebrates and plankton

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†. Deceased.

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on boats and trailers, in bilge water (Rothlisberger et al., 2010) and within ballast tanks (Bailey, 2015). Another example is the escape of captive organisms from aquaculture. Intentional introductions may be done within a legal framework, such as governmental stocking of fisheries species (Halverson, 2008) or biocontrol agents (Pipalova, 2006) or outside of a legal framework, such as aquarium or pet release (Padilla & Williams, 2004), sportfish release by anglers (Rahel, 2004) or ceremonial release (Magellan, 2019). There is a strong link between human activity and the number and extent of non-native species colonizations (Calderon-Aguilera et al., 2012). Tropical wetlands are often the sites of permanent and temporary habitations, transport routes and sites where natural resources are exploited, as well as sites of agriculture and aquaculture (Ricciardi & MacIsaac, 2010; Wasserman and Dalu, 2022, Chapter 1). The more people rely upon and use the wetlands, the more the systems' vulnerability to invasion by nonnative species increases.

Once introduced, non-native species advance through a series of invasion stages, overcoming abiotic and biotic barriers along the way (Blackburn et al., 2011). Invasion failure can occur at any stage if the species population cannot overcome these barriers. For example, a tropical species may live for a time in a temperate or cold zone but eventually, the abiotic factor of temperature will prove too difficult to surmount and the species will fail to establish. Successful species that disperse and spread are termed invasive. Wetland environments are, by nature, highly stochastic (Catford et al., 2011) and, as a result, many wetland specialist species have life history and physiological traits suited to the vastly changeable environmental dynamics. Successful invasive species often exhibit these same traits which facilitate their persistence and proliferation in novel environments. These include high reproduction rates, the ability to reproduce asexually, high tolerance to environmental stressors and high phenotypic plasticity (Richards et al., 2006). The latter two traits allow these novel species to establish, whereas the former two allow for the rapid increase in their population size (López-van Oosterom et al., 2019).

The majority of introduced species fail to establish and many established species have few noticeable impacts; those that do can cause myriad environmental and socio-economic impacts (Table 16.1). In this case, environmental impact is defined as a measurable change to a native ecosystem as a result, direct or indirect, of a nonnative species (Ricciardi et al., 2013). Non-native invasive species threaten global biodiversity, often by simplifying and homogenizing freshwater communities (Clavero & García-Berthou, 2005). Ecological impacts may be exhibited across a range of biological scales: (1) genetic; (2) individual; (3) population; (4) community; and (5) ecosystem (Crystal-Ornelas & Lockwood, 2020). Impacts of invasive species in tropical wetlands are observed at all organizational scales. As an example of genetic impacts, non-migratory, native mottled ducks *Anas fulvigula* from Mexico through the Gulf of Mexico coast to peninsular Florida suffer from

TABLE 16.1 Common impact mechanisms of alien species in wetland ecosystems.

Mechanism	Description
Competition	The alien taxon competes with native taxa for resources (e.g., food, water, space).
Predation	The alien taxon predates on native taxa.
Hybridization	The alien taxon hybridizes with native taxa.
Transmission of disease	The alien taxon transmits diseases to native taxa.
Poisoning/toxicity	The alien taxon is toxic, allelopathic to plants or allergenic by ingestion, inhalation, or contact to wildlife.
Grazing/herbivory/browsing	Grazing, herbivory, or browsing by the alien taxon.
Chemical impact on ecosystem	The alien taxon causes changes to the chemical characteristics of the native environment (e.g., pH, nutrient, and/or water cycling).
Physical impact on ecosystem	The alien taxon causes changes to the physical characteristics of the native environment (e.g., disturbance or light regimes).
Structural impact on ecosystem	The alien taxon causes changes to the structural biotope characteristics of the native environment (e.g., changes in architecture or complexity).
Indirect impacts through interactions with other species	The alien taxon interacts with other native or alien taxa (e.g., through any mechanism, including pollination, seed dispersal, habitat modification, apparent competition, mesopredator release) facilitating indirect deleterious impacts on native taxa.

In all cases, the impact leads to deleterious impact on one or more native taxa.
Source: Adapted from IUCN EICAT.

hybridization with feral mallards *Anas platyrhynchos* (Avery & Moulton, 2007). Mallards naturally migrate to northern parts of the northern hemisphere to nest, but humans have released numerous feral mallards which are year-round residents. Feral mallards threaten many nonmigratory ducks worldwide with genetic swamping (Kulikova et al., 2005). At the ecosystem level, nutria *Myocastor coypus* graze large quantities of marsh vegetation and tree seedlings, leading to erosion and loss of marsh area as well as interfering with wetlands restoration (Sasser et al., 2018). Nutria introductions occur in wetlands nearly worldwide (Carter & Leonard, 2002).

Impacts can be direct or indirect, often acting through other species or habitat features. Community effects of invasive species are complex, as an impact on one species population may result in trophic cascades. For example, invasive mosquitofish *Gambusia* spp. consume zooplankton and some amphibian larvae, which causes increases in nutrient concentrations that can facilitate phytoplankton blooms as well as increases in some, but not all, amphibian larvae (Preston et al., 2012). Invasion meltdown occurs when biotic interactions of one invasive species aid the establishment and success of another invasive species through competitive interactions as well as facilitative interactions (Simberloff & Von Holle, 1999). The invasive macrophyte, alligator weed *Alternanthera philoxeroides*, indirectly facilitates abundance and persistence of invasive mosquitofish in the Yangzte River by providing overwintering thermal refuges (Xiong et al., 2019). The red swamp crayfish *P. clarkii* increases the propagule pressure of the invasive large flower primrose willow *Ludwigia grandiflora* by cutting the stalks while foraging which releases fragments to spread (Thouvenot et al., 2017).

Impact complexity also results from variation in behavior or species traits. Differences in individual behavior may drive different ecological impacts. For example, cane toads *R. marina* at the invasion front (i.e., at the edges of the population range) have greater endurance than those found in the core of the invasive population allowing them to disperse further and forage more (Llewelyn et al., 2010a). Cane toads also show population-level impacts on native predators, depending on the native species' phylogenetic, behavioral and morphological traits. The fact that cane toads are toxic when consumed, are relatively large-bodied and occur in terrestrial habitats influences which predators are heavily affected. That is, predators with head sizes and foraging behavior suited to consuming cane toads (i.e., in terrestrial habitats) experienced population declines, but predators that foraged in arboreal habitats showed increases in populations (Feit & Letnic, 2015). Conversely, some predators of anurans may have learned (Llewelyn et al., 2010b) or been evolutionarily "pre-adapted" (Llewelyn et al., 2011) to avoid attempting to consume cane toads.

Socio-economic impacts of invasive species are often more difficult to measure, especially as costs also include research, monitoring, and management interventions. Invasive species may confer negative socio-economic impacts from loss of resources and associated livelihoods, system functioning, and ecosystem services (Ricciardi et al., 2013). The well-known example of the Nile perch *Lates niloticus* (Fig. 16.1) introduction into Lake Victoria illustrates a species with both positive and negative socio-economic effects and numerous negative ecological impacts (Aloo et al., 2017). However, in the case of some intentional species introductions, there can be a positive economic or intrinsic value associated with the species (Bacher et al., 2018). The purposeful introduction of butterfly peacock bass *Cichla ocellaris* into south Florida as a sportfish has proven to be socio-

FIGURE 16.1 Despite their negative effects, non-native Nile tilapia *Oreochromis niloticus* can provide valuable ecosystem services such as food production. *Courtesy: Olaf Weyl.*

economically beneficial with little evidence of negative ecological effects (Shafland, 1995, 1999; Shafland et al., 2008). Other species, such as rainbow trout *Oncorhynchus mykiss* used in aquaculture and for sport fishing, may have positive socio-economic benefits but also negative ecological impacts, thus there is a potential for stakeholder conflict (Woodford et al., 2017).

Managing invasive species is constrained by time and budget; identifying the most damaging species is key to prioritizing management (Robertson et al., 2020). Making generalizations is problematic as the realized impacts of invasive species, both ecological and socio-economic, can be highly context-dependent. However, in most cases early and ambitious intervention can prevent significant long-term costs and may be effective across multiple taxonomic groups (Leung et al., 2002).

16.2 Part I: invasive species case studies

Here the focus is on a representative series of case studies using a variety of taxa and ecosystems to illustrate the variety of wetland invasions and the associated challenges and opportunities. Those species that are most widely distributed and/or considered most detrimental (Luque et al., 2014) are used as examples to illustrate the characteristics of invaders, invasion routes, impacts, and management of these species.

16.3 Plants

16.3.1 Water hyacinth *Eichhornia crassipes* (Mart) Solms 1883 and giant salvinia *Salvinia molesta* Mitchell 1972

Water hyacinth and giant salvinia are perennial free-floating plants which have been widely spread through the ornamental trade due to their attractive appearance, as well as unintentionally as hitchhikers to aquaculture. Water hyacinth is native to South America and giant salvinia to south-eastern Brazil; both now have almost pan-tropical distributions (CABI, 2020d; Piedade et al., 2022, Chapter 7). When living they form large mats, which block light and smother submerged native vegetation. Once dead, the huge quantities of decomposing biomass lower dissolved oxygen and pH while increasing carbon dioxide and hydrogen sulfide (Julien et al., 2012). These changes to the waterscape and chemistry induce consequent changes in invertebrate (Oliver, 1993) and fish (Perna et al., 2012) populations from rich native assemblages to depauperate communities.

From a socio-economic perspective, small-scale fisheries are most directly impacted by losses of fish reported in floodplain rivers, such as the Congo and Nile (Gopal, 1987). Loss of access is a further concern (Fig. 16.2) (Harley et al., 1996). In the lower floodplain of the Sepik River in Papua New Guinea, problems of access to subsistence gardens, hunting, and fishing areas and markets were so severe that entire villages that depended on aquatic transportation were abandoned when infestations of giant salvinia limited access (Gewertz, 1983). Floating plants may block irrigation directly (Arp et al., 2017) and in wetland areas where rice is grown, compete and interfere with the crops (Gopal, 1987). Giant salvinia can also increase disease transmission in wetlands as the dense mats are an important host of *Mansonia* spp. mosquitoes which are vectors of West Nile virus, St. Louis encephalitis, Venezuelan equine encephalitis and rural elephantiasis (Lounibos et al., 1990), encephalitis, malaria and dengue fever (Oliver, 1993; Vanhove et al., 2022, Chapter 15). Both plants also harbor snails that transmit schistosomiasis (Plummer, 2005).

Water hyacinth eradication is generally considered impossible once established; however, control is attempted using biological control agents in

FIGURE 16.2 Water hyacinth, pictured here in Lake Victoria, may block access for transport and fishing. *Courtesy: Ian G Cowx.*

combination with herbicides and manual removal (Gutiérrez et al., 1996). A biological control agent, the salvinia weevil *Cyrtobagous salviniae*, has been used successfully to control giant salvinia (Martin et al., 2018).

16.3.2 Melaleuca tree *Melaleuca quinquenervia* (Cav.) S.T. Blake

Melaleuca tree is a semiaquatic member of the Myrtle family. Native to Australia, New Guinea, and the Solomon Islands, melaleuca trees have been introduced to tropical wetlands globally for the purposes of landscaping and soil stabilization (Turner et al., 1997). The species has become invasive in parts of the United States, Puerto Rico, and the Bahamas (Watt et al., 2009). The showy flowers attract a wide range of pollinators, including commercial honey bees *Apis meliffera*. However, wind-dispersed seeds, aggressive growth and lack of specialist herbivores and parasites in their recipient ecosystems have led to vast areas of near monocultures of this tree (upto 12,400 trees per hectare) (Fig. 16.6). It displaces native plant communities, renders habitats unsuitable for many wildlife species, alters fire regimes, changes local water flow patterns and restricts navigation and recreational use of public and private lands (Langeland et al., 2020). In Florida, United States, melaleuca tree stands displace three imperiled species: the Cape sable sparrow *Ammodramus maritimus mirabilis*, wood stork *Mycteria americana* and the Florida panther *Puma concolor coryi*. Humans may be allergic to melaleuca trees and react through physical contact with the tree or by odor sensitivity during the blooming season. Pollen can cause allergic reactions but is dispersed by bees rather than airborne; many cases of pollen allergy are due to the flowers' odor or pollen from other trees. Estimates of the cost of melaleuca trees for South Florida communities exceed US$1 billion including US$30 million in reduced environmental and economic services. Management of these trees became a priority for the Florida Department of Environmental Protection in the 1980s with an allocation of US$1 million annually (Serbesoff-King, 2003). Despite progress on public lands, increasing spread on private lands resulted in no net loss of infested areas within South Florida. Melaleuca tree is the target of most invasive plant management most years in the Everglades National Park (ENP), involving cultural, mechanical, chemical, and biological control (Keller et al., 2007). Current trends are favorable with density approaching the desired conservation state of $<1\%$ cover per km^2 and the declining area of infestation.

16.4 Invertebrates

16.4.1 The golden apple snail *Pomacea canaliculata* (Lamarck, 1822)

The golden apple snail is a mollusc native to Argentina and Uruguay. This yellow-brown snail is medium-sized (35–60 mm in height) with deep channeled whorls and a low rounded shell spire (Hayes et al., 2012). Its broad thermal range (-3°C to 35°C; Seuffert et al., 2010) and high fecundity (average of 4000 eggs per annum; Barnes et al., 2008) have contributed to its invasion success. Introduced to Asia and Hawaii with the intention to provide cheap and accessible protein for rural communities (Lowe et al., 2000), it is currently invasive on all continents besides Antarctica (CABI, 2020a,b,c,d,e).

Golden apple snails primarily consume macrophytes, as well as algae, cyanobacteria, detritus, and animals, often as carrion but not strictly (CABI, 2020a,b,c,d,e). Removal of large quantities of macrophytes through grazing leads to phytoplankton blooms and subsequent turbid water conditions (Carlsson et al., 2004). Direct predatory interactions have caused local declines and extirpations of bryozoan species in Thailand (Wood et al., 2006) and in the Philippines native snail species have been competitively excluded by the golden apple snail (Peña et al., 2017).

A notable crop pest (Wada et al., 2004), the golden apple snail resulted in the cost of rice yield lost to be an estimated US$12.5—17.8 million annually the Philippines (Naylor, 1996). However, the golden apple snail is sometimes integrated into rice paddy fish farming systems or ground into fishmeal for aquaculture feed. It has also been suggested as a weed biocontrol in rice paddies, provided seedlings are transplanted after 21 days when they are too tough for the snails to consume (Joshi, 2007). The golden apple snail is also a known host and vector of multiple pathogens which endanger human health. These include dermatitis-inducing schistosome species, trematode flukes and the rat lungworm *Anglostronglyus cantonensis* which can cause eosinophilic meningitis. There have been increases in angiostrongyliasis as the golden apple snail is regularly consumed raw or not thoroughly cooked (Cowie, 2013).

Removal of the golden apple snail, while challenging, has been achieved through saltwater inundation in rice paddies in Kedah, Malaysia. In most cases, control measures aim to reduce snail numbers below 2 per m^2 (Teo, 2003). Efforts tend to focus on manual removal, often aided by using aggregators such as low-value fruit leaves which attract the snails more than rice. Ducks and fish are used with some success as biocontrol, although ducks may damage rice (Su Sin, 2006) and fish require a minimum depth of water (Wada et al., 1999).

16.4.2 Red swamp crayfish *Procambarus clarkii* (Girard, 1852) and Australian redclaw crayfish *Cherax quadricarinatus* (von Martens, 1868)

While crayfish aquaculture within the animals' native range can be a multimillion dollar industry (FAO, 2020), in many of the introduced, ranges commercial aquaculture ventures have not been as profitable as expected and indeed have had extensive ecological and economic costs (Lodge et al., 2012).

The red swamp crayfish is a cambarid crayfish species native to the southern states of North America and northern Mexico. An established global invader, populations in wetlands include Ramsar sites in Morocco (Rmel Plateau), Kenya (Lake Naivasha), Spain (Ebro Delta), and France

(Camargue wetlands). The Australian redclaw crayfish is a nonburrowing crayfish species native to northern and southeastern Papua New Guinea. Australian redclaw crayfish is being recognized as an emerging global invasive species and is established in Ramsar sites in Zambia (Barotse Floodplain and Kafue Flats), Ndumo Game Reserve (South Africa), Australia (Lake Kununurra), and Jamaica (Black River Lower Morass). Both have optimal thermal ranges above 20°C, however, are capable of surviving air temperatures of a few degrees colder (Westhoff & Rosenberger, 2016).

Crayfish consume across all levels of the food web and deleterious effects are particularly seen for macrophytes, invertebrates (Ephemeroptera and Gastropoda), fish, and amphibians (Twardochleb et al., 2013). Crayfish also harm native freshwater crab species through competitive exclusion; the red swamp crayfish has caused population declines and local extirpations of native crab species in Tanzania, Kenya, and Cyprus (Madzivanzira et al., 2020; Dube et al., 2021, Chapter 11). Red swamp crayfish burrowing and foraging activities can drive trophic cascades via increased bioturbation which releases sediment-bound nutrients (Yamamoto, 2010). Additionally, it is a carrier of crayfish plague *Aphanomyces astaci*, which has caused severe damage to the native and endangered European crayfish species (Svoboda et al., 2017). The invasive temnocephalan, *Diceratocephala boschmai*, has been detected on the Australian redclaw crayfish in the Barotse Floodplain, Kafue Flats, and the Phongolo Floodplain (Madzivanzira et al., 2020). Crayfish have also been implicated in declining fishery performances through scavenging in gillnet catches (Fig. 16.3) (e.g., red swamp crayfish in Lake Naivasha, Kenya, and Australian redclaw crayfish in the Kafue Flats, Zambia). Secondary losses occur through damage to the fishing gear caused by crayfish entanglement (Madzivanzira et al., 2020). Burrowing behavior by red swamp crayfish can cause damage to irrigation infrastructure, which incurs both costs to repair the irrigation canals as well as secondary losses in crop yield due to reduced water delivery (Madzivanzira et al., 2020).

Common methods of crayfish control include mechanical removal, sterile release, physical barriers and biocides (Manfrin et al., 2019). Worryingly, the red swamp crayfish shows harvest-induced trait changes, such as larger body mass and increased boldness, in response to intensive mechanical removal (Závorka et al., 2020). There are currently no management programs or recommended control methods for the Australian redclaw crayfish.

16.5 Vertebrates

16.5.1 Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758)

The native range of Nile tilapia is tropical and subtropical regions of East Africa. This species has been widely distributed for aquaculture and sport fisheries and has established populations in many countries where introduced

FIGURE 16.3 Invasive crayfish predate upon netted fish, consuming or devaluing catches and damaging fishing nets. *Courtesy: Bruce Ellender.*

(CABI, 2020a,b,c,d,e). Nile tilapia is considered highly invasive and feral populations exist in tropical and subtropical regions worldwide (Canonico et al., 2005). Their success has been attributed to aggressive spawning behavior, high levels of parental care, the ability to spawn multiple broods throughout the year and its broad diet (Canonico et al., 2005). In some areas where this species has become established, ecological effects include decreased abundance and extinction of native species resulting from habitat and trophic overlaps and competition for spawning sites (see reviews by Canonico et al., 2005), habitat destruction and water quality changes (Figueredo & Giani, 2005) and hybridization with other *Oreochromis* species (Deines et al., 2014). However, the level of impact Nile tilapia has across all regions is difficult to ascertain. Many impacts in the literature are anecdotal and have not been corroborated by directed research (De Silva et al., 2005, 2006). A directed study of Nile tilapia and common carp *Cyprinus carpio* impacts found increased fish biomass and little effect on native fish communities in wetlands in the Lower Mekong Basin (LMB) (Arthur et al., 2010). This case study illustrates that impacts are often poorly studied even in well-known species and that impacts are context-dependent.

In tropical wetland ecosystems the most devastating impact of Nile tilapia introductions has been via hybridization. In the Lake Victoria basin, hybridization between Nile tilapia and the endemic Victoria tilapia *Oreochromis variabilis* and singida tilapia *Oreochromis esculentus* is thought to have contributed to the ultimate disappearance of these two species from Lake

Victoria, though both species were so overexploited by gillnet fishers that Nile tilapia was introduced to restore a tilapia fishery (Balirwa, 1992; Goudswaard et al., 2002). In southern Africa, hybridization with three spotted tilapia *Oreochromis andersonii* and longfin tilapia *Oreochromis macrochir* threatens these species in the Kafue River (Deines et al., 2014).

Furthermore, Nile tilapia are asymptomatic vectors for the disease epizootic ulcerative syndrome (EUS) caused by the oomycete *Aphanomyces invadans*, which causes epidermal lesions (Fig. 16.4), ultimately resulting in skin erosion and exposure of underlying musculature and ulceration (Lilley and Roberts, 2003). In subSaharan Africa, the first report of *A. invadans* and an associated EUS outbreak was from the Okavango and Zambezi River systems in 2008 (Andrew et al., 2008). This disease infects at least 27 native fish species in the Okavango and upper Zambezi floodplains, although the cause of the outbreak has not been directly linked to Nile tilapia in the latter.

16.5.2 Cane toad *Rhinella marina* (Linnaeus, 1758)

The cane toad is native to South America, Central America, Mexico and southern Texas (CABI, 2020a,b,c,d,e). Cane toads were introduced primarily as biological control agents against crop pests (Hinkley, 1962). Unfortunately, most of the introductions were made into island nations in the Caribbean and Pacific where the toads flourished. They are opportunistic consumers, so while much of their diet is terrestrial arthropods, they have been known to eat other frogs, crabs, birds, and snakes (Shine and Wiens, 2010). Adult cane toads spend more time on land than juveniles but need water bodies to reproduce. Nevertheless, cane toads are unselective and make use of rainforest habitats, small lakes, man-made ponds, drainpipes, and most standing shallow waters. Both adults and tadpoles have a very high tolerance of salinity which allows them to use estuarine habitats. Dispersal occurs through a range of means, such as stowaways in freight and through

FIGURE 16.4 A tigerfish *Hydrocynus vittatus* infected with epizootic ulcerative syndrome (EUS). *Courtesy: Olaf Weyl.*

water currents, but most astounding is through adult cane toads moving around 55 km per year as a result of selection pressure at the invasion front (Philips et al., 2007).

Cane toads have toxic parotoid glands which secrete venom that can be shot up to one meter (Smith & Phillips, 2006). Predatory snakes and lizards that specialize in amphibian prey are vulnerable to poisoning by these toxins. Consequently, declines in predators release other prey species from predation pressure, altering food webs (Shine and Wiens, 2010; Cuthbert et al., 2022, Chapter 17: Food Webs). Many deaths of domestic dogs and cats have also been attributed to cane toad consumption. Some predators learn to avoid cane toads or their eggs and tadpoles. Shovel-nosed catfish *Arius midgleyi* were found to prey on toad eggs, and while some died, mortality was not significant, and the catfish showed an aversion to the eggs the next time they encountered them (Somaweera et al., 2011). Northern quoll *Dasyurus hallucatus*, a small marsupial, is imperiled by attempting to prey upon cane toads. This species has been the subject of experimentation with "toad sausages," a manufactured bait to learn to avoid cane toads. Preliminary experiments suggest that this technique might be a viable tool for large-scale training of wild northern quoll (Indigo et al., 2018). Additionally, this toxin has value as an aphrodisiac, heart rate reducer and as a narcotic and there is interest in its pharmacological potential (Rodríguez et al., 2017).

Preventing invasion and spread is the best management solution. In Australia, public awareness campaigns have resulted in people collecting and removing toads (Taylor and Edwards, 2005) and toads can be excluded from water bodies by incorporating a physical barrier higher than 50 cm. Biological control using viruses and parasites has also been developed to disrupt cane toad breeding cycles and stunt growth (Shanmuganathan et al., 2010; Vanhove et al., 2022, Chapter 15).

16.5.3 Burmese python *Python bivittatus* (Kuhl, 1820)

The Burmese python is a large-bodied (upto 5.4 m) constrictor snake (family Pythonidae) (Fig. 16.6C). This snake is semiaquatic, using watercourses or flooded marsh to disperse across the landscape and levees for sunning and hunting (Hart et al., 2015). Fertilization is internal and females lay upto around 100 eggs (average clutch is 36) that she coils around and tends for 2–3 months (CABI, 2020a,b,c,d,e). Native to Southeast Asia, Burmese pythons were introduced to Florida primarily via illegal pet releases. Additionally, pythons were released when Hurricane Andrew (1992) destroyed a python breeding operation near Homestead, Florida and possibly increased propagule pressure enough to facilitate establishment (Snow et al., 2007). The first nest was discovered in 2006 (Krysko et al., 2011).

Impacts of the Burmese python are primarily linked to predation; its large body size makes a wide range of mammals, birds and reptiles available as food. Pythons are the cause of marked declines (85–100%) in small mammals in the ENP (Dorcas et al., 2012), with the potential to fundamentally alter food webs (Reichert et al., 2017). Further, this snake threatens imperiled species such as the Key Largo woodrat *Neotoma floridana smalli* and the wood stork.

Management of Burmese pythons in Florida has become a priority activity for several state and federal agencies. However, despite considerable efforts, management has failed to prevent spread and reduce abundance. Hunting can be locally effective if pythons are well targeted (Reed & Rodda, 2009) but detection is a particularly difficult problem, with tests showing $<1\%$ detection rates in many cases. Use of trained personnel, tracking dogs, eDNA, tagged "Judas snakes" and other methods have improved detection, though rates are still very low in most cases (Hunter et al., 2015). Burmese pythons are listed as injurious wildlife by the US Fish and Wildlife Service, prohibiting importation of this species and restricting use to permitted activities.

16.6 Part II: invaded tropical wetland ecosystems

In natural systems single species invasions are rare. Included here are three examples from North America, Africa, and Asia to illustrate the ecological consequences of multiple invaders in complex systems, the problems these cause stakeholders impacted by them and the challenges faced by those tasked with managing them.

16.6.1 Greater Everglades Ecosystem, North America

The Greater Everglades Ecosystem (GEE) covers 47,000 km^2 of central and southern Florida, USA. Historically, water from the Kissimmee River flowed into Lake Okeechobee and spilled out through extensive littoral broadleaf marshes south into the famed "River of Grass," a vast (160 km long by 80 km wide), shallow, slow-moving marsh dominated by the sedge, sawgrass *Cladium jamaciense*. Nearer the coast, waters moved through tidal rivers and creeks and mangrove swamps (red mangrove *Rhizophora mangle* and black mangrove *Avicennia germinans*), into Florida Bay, an open estuary and the Ten Thousand Islands, a network of bays, channels and mangrove islands off the Gulf of Mexico. The ecosystem is heavily influenced by hydrology, with expansive waters during the summer/autumn rainy season and remnant waters in sloughs, alligator holes, solution holes, and surficial aquifers within porous limestone late during the spring dry season.

Extensive modification of the region, primarily in the early to mid-20th century, disrupted natural flow patterns both seasonally and spatially. These included channelizing the Kissimmee River, building a levee around Lake Okeechobee, and constructing a complex canal system (1160 km of canals, 1600 km of levees, and 200 water control structures) designed to de-water land for agriculture and development, prevent flooding, and provide dry season water storage for agriculture and urbanization (Fig. 16.5). Frequently these mismatched water delivery magnitude and timing to environmentally sensitive protected areas such as the ENP. Environmental degradation of the ecosystem due to hydrological changes, eutrophication, and invasive species proliferation led to the ongoing Comprehensive Everglades Restoration Project (CERP), the largest and most expensive ecological restoration project ever attempted. Amongst the goals within the CERP are two related to invasive species: (1) protecting the ecosystem from the harmful effects of invasive species through prevention, eradication, containment, and management; and (2) reducing invasive species pathways originating from the modified environments (LoSchiavo et al., 2013).

Southern Florida is a hotspot of species invasions with thousands of established species, including plants, insects, crustaceans, molluscs, fishes, amphibians, reptiles, birds, and mammals (Krysko et al., 2011). Diversity of invasive species is lowest in the northern GEE and increases rapidly south of Lake Okeechobee due to the ability of tropical species to survive in this region. Conversely, native species are a mix of temperate species from the southeastern United States and tropical species from the Caribbean Sea region.

Management occurs throughout the GEE but is most intensive within the ENP. The GEE management priorities focus on plants, reptiles and fish. Most management is directed at early detection and rapid response (EDRR) for new introductions, monitoring for spread of known invaders, and control of long-term, established nonnatives.

Plants receive the bulk of management attention and resources. About 250 species of non-native plants have been established, mainly from

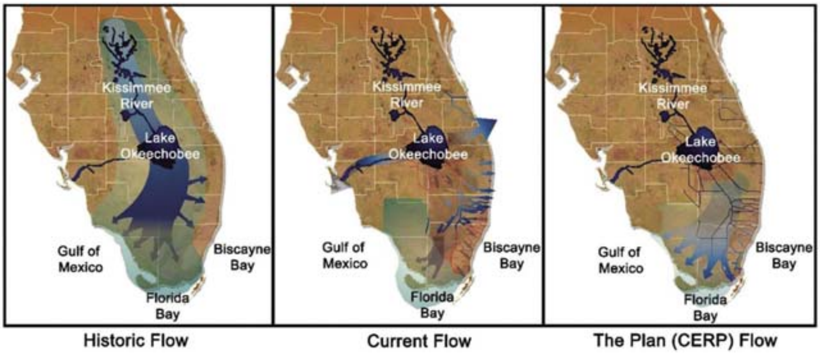

FIGURE 16.5 Historic, current, and future water flow patterns for the Greater Everglades Ecosystem. *Courtesy:* *https://www.evergladesrestoration.gov/content/cerpreports/cerp_2010_rpt_to_public.pdf.*

intentional plantings for soil stabilization and de-watering or from escape of landscape plants. Four species are of highest management priority: melaleuca tree, Australian pine *Casuarina equisetifolia*, old world climbing fern *Lygodium microphyllum* and Brazilian pepper *Schinus terebinthifolius*. Managers use aerial mapping every two years to document percentage of cover and area infested. These data are used to direct control efforts and to evaluate progress toward desired states of conservation. Control includes removals (e.g., mowing, logging, mulching, and hand removal), herbicide treatments (e.g., spraying, stump treatments, and frill-and-girdle), seedbed removal (i.e., soil removal) and biological control (i.e., insects) (Rodgers et al., 2018). Several of these techniques are typically applied in an integrated pest management approach. Melaleuca tree and Australian pine are current success stories, meeting conservation goals and trending downward. However, the area of infestation is expanding for the other two priority species and for invasive plants in general.

Sixty-five species of nonnative reptiles have been observed in or near the GEE. The priority reptiles are Burmese python, other large constrictor snakes and Argentine tegu *Tupinambis merianae*. A wide range of activities are directed at python removal and trapping is used to remove tegus. Management has failed so far to prevent new invasions of reptiles into the ENP and to limit the expansion of Burmese pythons. Of the 17 non-native freshwater fishes in the ENP, the main priorities include African jewelfish *Hemichromis letourneuxi* (Fig. 16.6), Asian swamp eel *Monopterus albus* and bullseye snakehead *Channa marulius*. Most fish species enter the park through canals on the eastern and northern borders where they have escaped aquaculture or, more commonly now, have been released by aquarium hobbyists or live seafood purchasers. Extensive monitoring programs document range expansion and abundance within the ENP and in some adjacent public holdings. Much effort is directed to detect new invasions from the numerous established nonnative fishes in the canal system east of the GEE. Limited control programs using electrofishing removals of Asian swamp eel in the canals were terminated when this species established within the ENP (Shafland et al., 2010).

Although invasive species remain a management priority within the CERP, conflicting demands over water delivery and re-establishing hydrological connectivity facilitate the introduction, establishment, and spread of nonnative taxa. Uneven efforts are clear in the response to invasions of specific taxa, such as the historical emphasis on invasive plants. The large size, complexity, and interconnectivity of the GEE, its long history of anthropogenic disturbances and proximity to invasion sources in adjacent, highly urbanized landscapes make future invasions inevitable. Nevertheless, invasive species management through a variety of agencies and other entities continues to improve in the region. Development of additional tools for risk

FIGURE 16.6 Select invasive species in the Greater Everglades Ecosystem. (A) Melaleuca tree. (B) African jewelfish. (C) Burmese python. *Courtesy: (A) Ken Langeland, University of Florida, (B) Jeffrey E Hill, University of Florida, (C) Florida Fish and Wildlife Conservation Commission.*

assessment, EDRR, control, and eradication are needed to inform and facilitate management.

16.6.2 Kafue Flats, Africa

The Kafue Flats in Zambia is a 6500-km^2 alluvial plain that is located between the Itezhi-Tezhi reservoir and the Kafue Gorge dam on the Kafue River, a principal sub-catchment of the Zambezi River (Fig. 16.7). Home to 77 fishes, >400 birds and 40 large mammal species, the 255-km long and 60-km wide Kafue Flats are one of the most biologically diverse ecosystems in Zambia and provides a source of livelihood to many of the 1.3 million people who live in the area. Activities in the Kafue Flats include small-scale agriculture and the grazing of cattle during the dry season (Mumba & Thompson, 2005). Fishing is important, with about 20 of the 77 fish species being harvested by small-scale fishers mainly using artisanal gear. Tourism is also an important activity on the floodplain, some of which is protected in the Lochinvar National Park where endemic Kafue lechwe *Kobus leche kafuensis* and rare wattled cranes *Bugeranus carunculatus* draw tourists.

Like many tropical floodplain ecosystems, the fish and wildlife biodiversity of the Kafue Flats have been subject to numerous threats (Cowx et al., 2018). After the construction of Itezhi-Tezhi reservoir in 1978, floods that used to extend from between 22 and 60 km from the river channel, now only extend 10–15 km. This decrease in available fish habitat decreased the overall productivity of the system and annual fish production decreased from around 10,000 to 6,000 tonnes (Cowx et al., 2018). Faced with decreasing catches, fishers moved onto smaller meshed nets and more efficient monofilament material (Tweddle et al., 2015). This resulted in a decline of larger, predatory fishes in the system. The concomitant decreasing fish supply drove an increasing interest in aquaculture, which resulted in the escape and subsequent establishment of nonnative Australian redclaw crayfish and Nile tilapia in the Kafue Flats (Deines et al., 2014; Madzivanzira et al., 2020). Nile tilapia have now completely replaced the native three-spot tilapia in the system. Australian redclaw crayfish have become highly abundant in the Kafue Flats

FIGURE 16.7 Kafue landscape. *Courtesy: Bruce Ellender.*

and fishers report that upto 30% of their catch is damaged by crayfish predation.

Introduced via an unknown pathway, water hyacinth became problematic in the mid-1970s, resulting in reduced flows and increased eutrophication. This resulted in the formation of vast mats that covered the entire breadth of the river, not only affecting water quality and disrupting fishing activities, but also blocking the intakes for Lusaka's Municipal water supply and the turbines at the Kafue Gorge hydropower station. Despite several initiatives involving mechanical removal by hand and dredging machine, spraying with glyphosate and 2–4D and biological control with four imported agents, the problem was only resolved in the year 2000s through the reduction of eutrophication via pollution control measures for aquaculture, agriculture and industrial initiatives in the area.

Giant mimosa *Mimosa pigra*, an evergreen semi-aquatic shrub or small tree native to Central and South America, has also invaded the Kafue Flats. First reported on the Kafue River Floodplains in the late 1970s (Mumba & Thompson, 2005), its coverage increased to >2500 hectares by 2003 (Mumba & Thompson, 2005). Giant mimosa is rapidly replacing native grassland vegetation on the floodplain forming dense monospecific stands which result in reduced biomass, species richness, and cover of native plants (Blaser et al., 2014). This has a significant negative impact on biodiversity (Witt et al., 2020), with the invaded habitat containing 50% fewer bird species and the dense stands of giant mimosa shown to smother the shallow littoral breeding habitat of tilapia species (Cowx et al., 2018). People living on the Kafue Flats report that the dense stands of these plants limit their access to croplands, grazing lands and fishing areas (Witt et al., 2020). Biological control of giant mimosa was initiated with the release of the stem boring moth *Carmenta mimosa* in the Kafue River Floodplains in May 2019. However, Witt et al. (2020) suggest that the most appropriate long-term giant mimosa control would be enhanced by the development and implementation of an integrated weed management strategy using a combination of herbicide, clearing and biological control.

16.6.3 Lower Mekong Basin (LMB), Asia

The Mekong River is a transboundary watershed which originates in the Tibetan Plateau and flows through China, Myanmar, Thailand, Lao People's Democratic Republic, Cambodia, and Vietnam. The wetlands associated with the LMB cover around 5 million hectares and are subject to biannual extensive flood pulses which support ecosystem services, biodiversity and productivity throughout the basin (Fig. 16.8). Habitats within the wetland system are dipterocarp forests, riverine forests, and inundated grasslands. About 60 million people rely on the LMB for ecosystem services, such as agriculture (rice paddies) and fisheries (around 120 commercial species) (Mattson, 2006). The LMB is a biodiversity hotspot and the world's most productive inland fishery with around 1500 fish species recorded, many of these endemic (Vidthayanon, 2008). The basin is home to several charismatic megafauna, such as the endangered Mekong giant catfish *Pandasianodon gigas*, giant freshwater sting ray *Himantura chaophraya*, Irrawaddy dolphin *Orcaella brevirostris*, giant ibis *Pseudibis gigantea*, and the Siamese crocodile *Crocodylus siamensis*. Threats to the LMB include development for hydropower and irrigation, overexploitation of fish stocks, rising sea levels and invasive species. There are over 200 large dams (>15 MW) and more than 250 smaller hydropower dams (<15 MW) posing barriers to fish migration and sediment dispersal throughout the floodplains which negatively affects system productivity (Dugan et al., 2010). Population expansion has caused an increase in people reliant upon fisheries, with an increase in fisher numbers and decreases in per fisher catch.

There are 27 known invasive species present in the LMB from a range of taxa including plants, invertebrates, fishes, one reptile and one mammal species. Of the current invaders in the LMB, plant species are the most species-rich invaders (48.1%) followed by fish species (37%). All three invertebrate species (11.1%) are snails and originate from Africa, South America, and North America. The single reptile species (3.7%) is the North American red-eared slider terrapin *Trachemys scripta elegans* and the single mammal species (3.7%) is the South American nutria. The golden apple snail, Mozambique tilapia *Oreochromis mossambicus* and common carp were all introduced as aquaculture species to supply rural areas of the LMB with cheap and accessible protein (Mattson, 2006).

FIGURE 16.8 Lower Mekong Basin landscape with water hyacinth in the foreground. *Courtesy: Ian G Cowx.*

Giant mimosa is a problematic plant in the LMB (Triet et al., 2004). It has high dispersal capacity through its buoyant seed pods and is an ecosystem engineer which converts productive floodplains and pastures into unproductive scrubland. Giant mimosa forms dense thicket and canopy which competitively excludes native plant species but also restricts access to the water body for animals and people (Rijal & Cochard, 2016).

The vast scale of the LMB means that forming cohesive management practices and monitoring across the relevant countries is a serious barrier to invasive species prevention. Across all countries sharing the LMB, the main constraints on management efforts are related to insufficient funding and gaps in capacity development, as well as a lack of data sharing and commonplace legislation on invasive species. However, there are management interventions being implemented at local levels. There is currently no management action for any of the nonnative fish species as a result of their positive socio-economic benefits with regards to supplemental income and protein, although there is a trend toward promotion of native fishes (Mattson, 2006). Biocontrol has been somewhat successful in controlling plant invaders. The parasitic wasp *Brachymeria euploeae* and gall fly *Cecidochares connexa* have been trialed in the LMB to combat a toxic shrub *Chromolaena odorata*. The beetle *Agasicles hygrophila* drastically reduced alligator weed in Thailand. Two weevil species (*Neochetina* spp.) have been used to control water hyacinth in both Thailand and Vietnam. Management of the golden apple snail has been approached through a combination of methods including hand removal, pesticides, water level manipulation and biocontrol with mixed results. In Vietnam, an integrated management system where common carp is used to control apple snail populations in rice paddies has had very positive outcomes where the common carp becomes an extra income source (Joshi, 2007).

16.6.4 Case study comparisons

Three case studies of invaded tropical wetlands in North America, Africa and Asia illustrated a wide range of invaders, impacts and management. Comparisons can lead to better conceptualization of invasive species in tropical wetlands and improve management.

Aquatic and semiaquatic plants were prominent invaders in all three systems. Each system had at least one woody, semiaquatic plant with large ecosystem effects. These effects included conversion of habitat from grass, broadleaf marsh or wet grass habitat, disruption of flow, increased density of habitat (lower quality for many native species and humans) and reduced diversity of habitats. Invasive aquatic plants varied in importance, though all three wetlands were invaded by water hyacinth. All areas had programs to reduce the density of invasive plants, though the magnitude of the programs varied.

Fish invaders were likewise important in all three wetlands, though few management programs were implemented to reduce their abundance, as often there were both benefits as well as costs, demotivating removal. Monitoring programs in the GEE were among the most intensive of the management actions for fish, though some small-scale control efforts were reported. Fish in the Kafue Flats and LMB were considered largely beneficial as a source of protein and income from fishing. Commercial fishing is largely illegal within the GEE, but many view the nonnative fish as beneficial due to their importance in recreational sport and food fish fisheries. Nile tilapia is a species shared by the three wetlands, though their density in the GEE is low compared to the other wetlands.

Invertebrates were prominent in the Kafue Flats and to a lesser extent in the LMB. Few aquatic invertebrates have become invasive in the GEE, though various apple snails *Pomacea* spp. occur in addition to the native Florida apple snail *Pomacea paludosus*. In contrast, apple snails were regarded as invasive in the other two tropical wetlands in addition to crayfish in the Kafue Flats.

The three wetlands differed considerably in a variety of structural and geographic characteristics. The GEE is in the lower half of a large peninsula jutting out into subtropical and tropical seas. The hydrology is heavily altered from its historic flow and it is bounded by dense, urban areas and agricultural zones along the east side (less to the west). Despite ongoing restoration of historic patterns of hydrology, de-watering urban and agricultural lands, flood control and water storage remain priorities. The Kafue Flats wetland is landlocked and located between two dams. Water management has reduced the size of the wetland considerably, dampening the magnitude of seasonal flooding. The LMB covers the extensive channels and waterways of the Lower Mekong River. Numerous hydroelectric projects have altered flow and created barriers to fish movement in this wetland.

Management intensity and monetary inputs differed across the wetlands. The GEE is currently undergoing the largest and most expensive ecological restoration attempted. The wetland lies completely within the USA state of Florida and both federal and state authorities have contributed funds, lands and expertise to the restoration efforts and overall management. Current management activities promote mimicking historic hydrology, reducing eutrophication and removing invasive plants and reptiles. The Kafue Flats are likewise within a single country, Zambia. Management of invasive plants is a priority and has been augmented by reducing eutrophication. Nevertheless, programs are much less extensive here due to budgetary constraints. Unlike the other two, the LMB occupies parts of five countries, complicating management. However, regional management is common.

16.7 Summary

The value and extent of use of tropical wetlands by humans makes them vulnerable to intentional or accident introductions. While invasive species can provide some ecosystem or socio-economic benefits (Vimercati et al., 2020; Irvine et al., 2022, Chapter 19), they often impact upon biodiversity, ecosystem integrity and human health and prosperity. In almost all cases, eradication, once an invader becomes established, is near impossible and control can be prohibitively labor-intensive and costly, especially in low- and middle-income countries. The scale, and often transboundary nature, of tropical wetlands adds further complexity to invasive species management. The need to understand risk, forecast potential invaders, employ effective biosecurity measures and respond rapidly to novel invasions is essential to protect tropical wetlands from the harm these species can cause.

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Chapter 17

Food webs

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17.1 Introduction and overview

The trophic level concept organizes the biotic components of ecosystems into discrete compartments by trophic status (primary production, herbivory, predation). In tropical and subtropical systems (hereafter referred to as tropical), biodiversity within each trophic compartment is typically diverse (see Deemy et al., 2022a, Chapter 6; Piedade et al., 2022, Chapter 7; Dalu et al., 2022, Chapter 8; Brendonck et al., 2022a,b, Chapters 9 and 10; Dube et al., 2022, Chapter 11; Reichard, 2022, Chapter 12; Moraes et al., 2022, Chapter 13; Tarakini et al., 2022, Chapter 14), in turn facilitating food web complexity and cross-ecosystem fluxes or connections. For example, tropical wetland systems harbor high diversities of invertebrates, amphibians and fishes, which provide important foraging environments for birds (Heyer et al., 1975; Frederick et al., 2009; Polačik et al., 2014; Wasserman and Dalu, 2022, Chapter 1). However, in addition to diversity-driven complexity, food webs in tropical wetlands are further complicated by the fluctuating existence of various spatial compartments that can be connected directly via water, or are connected by mobile animals moving between aquatic environments (Winemiller, 2004; Vanschoenwinkel et al., 2011; Layman et al., 2012; Wasserman et al., 2018).

Water level fluctuations during the hydroperiod are a dominant force regulating community dynamics and ecological processes in many tropical freshwater wetlands, particularly in the subtropics (Nhiwatiwa and Dalu, 2017; Wasserman et al., 2018) (Fig. 17.1). The shallow nature of these systems, and their high surface area to volume ratios, make them sensitive to changes in water inputs (Mitsch and Gosselink, 1986; Talling, 2001; Nhiwatiwa and Dalu, 2017). While such changes in water inputs inevitably

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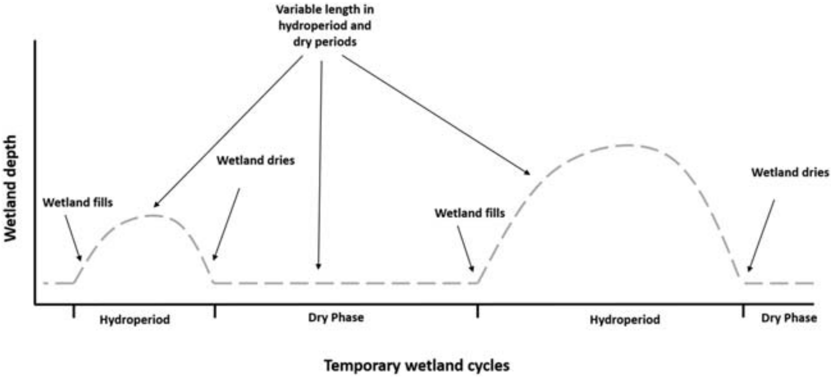

FIGURE 17.1 A hypothetical schematic diagram of temporary wetland cycles between dry phases and wet phases (hydroperiods), highlighting the variable nature of the ecosystems. Hydroperiods refer to periods of inundation when depressions/floodplains hold water. Dry phases represent those periods between the hydroperiods when the floodplains/depressions hold no water. *Modified from Tladi, M., 2021. Bioecology of Large Branchiopods in Central District, Botswana. MSc Thesis. Botswana International University of Science and Technology. 138 pp.*

have implications for physico-chemical water properties, the direct role of fluctuating water is the main driver of environmental heterogeneity, with implications for food web structure and trophic interactions in these environments. Indeed, tropical wetlands are frequently characterized by extremes—both wet and dry periods, driven by marked seasonal variations in temperature and precipitation patterns. Under these conditions, the necessity for rapid growth to facilitate reproduction during short hydroperiods can drive marked trophic interaction strengths among biota. Accordingly, the nature of trophic interactions in these wetlands frequently facilitate high rates of species turnover and potential "boom-bust" dynamics, making these systems important models for testing wider food web and community ecology theories (De Meester et al., 2005).

The wet-dry climate of tropical wetlands, in interaction with microtopography, drives seasonal patterns in food web dynamics. The characteristic hydrograph exhibited by temporary wetlands, isolated ponds, and bottomlands is a result of interactions between seasonal precipitation and fine-scale elevation differences, or microtopography. These elevation patterns can be the result of interactions and feedbacks among plants, sediment, water, and even animal activity (Nhiwatiwa and Dalu, 2017). Populations respond to changes in hydroperiod, water depth, and associated physico-chemical changes with corresponding changes in density, diet, and movement. As a result, food webs in tropical ecosystems are characterized by a high degree of plasticity, omnivory, and complexity. Wetting and drying cycles also impart important links between aquatic and terrestrial realms in wetlands, with consumers often supported by organic matter inputs from upland catchments or adjacent areas (Carpenter et al., 2005). This high connectivity between terrestrial and aquatic environments necessitates quantitative understanding of how both allochthonous and autochthonous nutrient inputs alter food webs.

The primary objective in this chapter is to provide an overview of the structure, diversity, and intensity of trophic interactions in tropical wetland ecosystems. We begin by providing an appraisal of trophic groups and environmental factors which mediate food web dynamics in these systems. We then discuss trophic structure dynamics, distinguishing between endorheic wetlands and those temporarily connected to permanent waters, with emphasis on cross-ecosystem subsidies with permanent water bodies and adjacent terrestrial habitats. Then, a focus on predation is made in these systems. Further, approaches to quantify trophic dynamics are presented, which can be used to rapidly determine interaction strengths, food web structure and resource selectivities to inform wider food web models in wetlands.

17.2 Trophic groups

17.2.1 Aquatic primary production

Freshwater tropical wetlands tend to have high productivity, but are variable depending on factors such as plant types present, tidal energy, flooding, flow rates, soil nutrients, grazing, and toxins. There is a strong relationship between above ground biomass and summer temperatures, and therefore tropical wetlands are generally more productive than those in temperate systems. The flow of energy through any ecosystem starts with sunlight fixation by plants (i.e., phytoplankton, macrophytes) and other autotrophic organisms (i.e., certain bacteria). Thus, phytoplankton and macrophytes principally accumulate energy, forming an important component of aquatic food webs. The development of diverse plant communities within wetland systems often fuels complex food webs that not only sustain microbial communities through large detrital inputs to wetland soils, but also support diverse invertebrate and vertebrate animal communities that utilize these systems in part or for the entirety of their lives (Cherry, 2005).

Wetland productivity has been highlighted to be mostly affected by the flooding degree, duration and periodicity. Water movement in wetlands, through drainage and recharge processes, can promote enhanced productivity by increasing nutrient mineralization (Schlesinger and Bernhardt, 2020). For most freshwater wetlands, the inflow sources such as groundwater and precipitation, and outflows such as evapotranspiration, groundwater and surface flow, tend to change over time, making the hydrology unstable and causing fluctuations resulting in pulsing hydroperiods (Cherry, 2011). Thus, these hydrologic pulses have been shown to alter wetland productivity along a flooding gradient by altering the extent of wetland flood subsidies and stresses (Odum et al., 1995). The flood pulses may also influence the function and structure of wetland ecosystems through their influence on species richness, organic matter accumulation, and nutrient cycling (Odum et al., 1995; Cherry, 2011).

17.2.2 Detritivory and consumers

In wetlands, most of the plant biomass dies and decays and is passed through the detrital food web where the major consumers are bacteria and fungi. This is one component that is the least studied within tropical wetland systems and more studies are needed to better understand detrital food web dynamics. These materials are then consumed by small invertebrate animals, such as worms, copepods, rotifers, and larval stages of benthic invertebrates. The larger benthic invertebrates are often either scavengers (e.g., crabs, snails) or filterers (e.g., mussels, fairy shrimp, and clam shrimp).

Most animal life in wetland systems consumes either phytoplankton directly, or smaller organisms that feed on phytoplankton. Others feed on detritus provided primarily by plant material. Consumers (heterotrophs) obtain their energy by consuming other organisms. Consumers can be plant eaters (herbivores), animal (invertebrate/vertebrate) eaters (predators), scavengers which eat dead animals or detritus (detritivores), or they can eat a variety of these sources (omnivores). Most of the energy within each trophic level is utilized for growth, respiration, reproduction and movement, but much energy is lost as heat.

Macroinvertebrates and zooplankton play important roles in wetland ecosystems as consumers at intermediate trophic levels. They have an important influence on nutrient cycling, material decomposition, translocation, and primary production (Merritt and Cummins, 1996). Detritivores, such as shredding insects and crayfish, can utilize dead plant material as their primary energy source, while others (e.g., snails, worms) help process organic matter for subsequent use by other organisms. Herbivory of phytoplankton by invertebrates and fish, and of plant biomass by some invertebrates, birds, and mammals, is a significant energy source for primary consumers in many wetlands. Secondary production by these primary consumers supports higher trophic levels, including predatory insects, fishes, reptiles, amphibians, birds, and mammals.

17.3 Trophic dynamics

17.3.1 Temporary endorheic wetlands

Temporary wetlands, among the most extreme of aquatic ecosystems, are ideal systems for the depiction of how complex and variable food web dynamics can be within tropical wetlands. These aquatic environments are essentially temporarily available as a habitat for aquatic organisms, with water depth continuously shifting through precipitation and seeping dynamics. This makes for a temporally variable habitat, further complicated by spatial dynamics such as differing distances between isolated temporary wetlands of various shapes and sizes. In addition to complicated metacommunity dynamics between isolated temporary wetlands (see Gálvez et al., 2022, Chapter 18 on these processes), within-system complexities are considerable, driven by phenological processes associated with hydroperiod dynamics.

During dry (non-hydroperiod) phases, areas that get inundated are often overgrown with nonaquatic vegetation. In many instances, this vegetation community is dominated by pioneer species that are capable of survival in disturbed areas (Datry et al., 2018; Wasserman et al., 2022; Dalu et al., 2020). Following inundation as the hydroperiod commences, much of this vegetation dies off, providing detritus within the aquatic environment, which contributes to available nutrients within these systems. Phytoplankton, bacteria and fungi then arise from diapause states in the sediment during early hydroperiod stages, instigating primary productivity activities in these systems—driven primarily by depth dynamics and nutrient availability (see Job et al., 2022, Chapter 2; Deemy et al., 2022b,c, Chapters 3 and 4; Moyo, 2022, Chapter 5 for these processes). The consumer community in temporary wetlands is comprised of "internal" and "external" recruits, with their relative contributions to consumer community structure highly variable over the hydroperiod (Fig. 17.2).

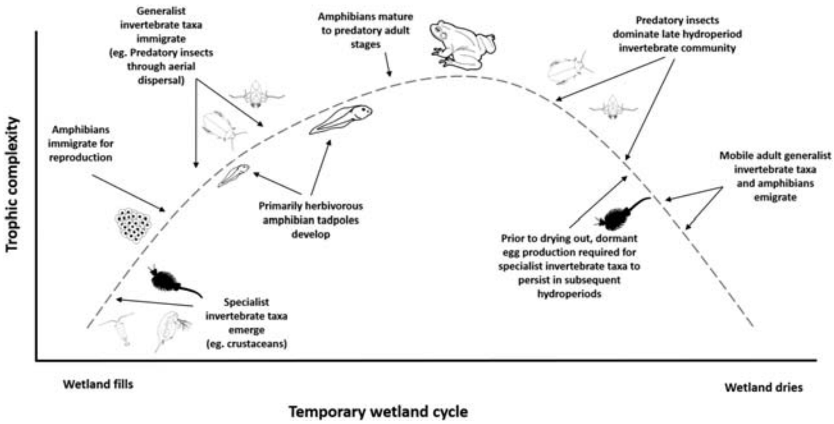

FIGURE 17.2 A hypothetical schematic diagram on temporary wetland consumer trophic complexity development over the course of a hydroperiod. Key consumer groups contributing to complexity dynamics are outlined. *Modified from Tladi, M., 2021. Bioecology of Large Branchiopods in Central District, Botswana. MSc Thesis. Botswana International University of Science and Technology. 138 pp.*

Upon inundation, populations of many specialist taxa are driven by hatching of dormant cysts that are present in the sediment. These "internal recruits" typically comprise the pioneer consumer community within temporary wetlands, most of which feed on primary producers (Dalu et al., 2016; Celewicz et al., 2018). Crustaceans (branchiopods, copepods and ostracods) feature in this community, along with planarians, annelids and molluscs (Bird et al., 2019). Given high levels of primary (phytoplankton) and secondary (specialist metazoans) productivity that rapidly develop in these systems, generalist aquatic invertebrate and vertebrate taxa start to invade these aquatic food patches (O'Neill and Thorp, 2014; Wasserman et al., 2016c; Dalu et al., 2017a). The invertebrate general fauna typically comprise numerous predatory insect species, many of which invade as semiaquatic adults (e.g., Notonectidae and Dyticidae), and some of which lay eggs that rapidly hatch to produce predatory early life stages (e.g., Odonata) (O'Neill and Thorp, 2014; Bird et al., 2019). Vertebrate generalist aquatic taxa that enter these environments are dominated by herpetofauna (amphibians and testudines) (Whiles et al., 2006; Channing and Rödel, 2019), which serve as apex predators in these systems. As the wetlands start to dry out near the end of their hydroperiods, the generalist taxa are typically required to emigrate to survive. Many taxa migrate to permanent water bodies during drier periods when temporary wetlands hold no water. Others, such as some frogs and testudines, may burrow in sediment in or near the wetland. The specialist "internal" recruiting taxa, however, persist locally through the production of cysts (dormant eggs). Viable cysts remain in the sediment over the dry period, ready to hatch in the following hydroperiods (Jocque et al., 2010).

17.3.2 Temporary wetlands connected to permanent water bodies

Temporary wetlands, such as river floodplains and temporary lakes, that are connected to permanent water bodies function in similar ways to the endorheic systems mentioned above, in that fluctuating water levels facilitate environmental heterogeneity and phenological processes. Microtopographic patterns in temporarily inundated areas can facilitate very similar conditions to those of endorheic systems. However, their connection to permanent water usually means that fishes (often a diverse community in tropical regions, see Reichard, 2022, Chapter 12) are included in the food webs. Aquatic reptiles are also more of a major feature in wetlands associated with permanent waters, such as testudines, snakes, and crocodylians (Uzarski et al., 2009). The presence of larger-bodied vertebrate species has implications for "food chain length" in these wetlands, which can make overall food web structure more complex than the smaller endorheic systems. For example, large-bodied fish can assume the role of high trophic levels, while crocodylians feature at the highest levels in aquatic food webs (Bondavalli and Ulanowicz, 1999; Grigg and Kirshner, 2015; Villamarín et al., 2017, 2018).

Crocodylians play a particularly dynamic trophic role in tropical wetlands, given ontogenetic shifts in diet from aquatic and terrestrial invertebrates when young, to fish and even terrestrial vertebrates as they grow (Radloff et al., 2012). However, many taxa that inhabit tropical wetland environments exhibit high levels of trophic flexibility, facilitating their success in these dynamic systems.

A striking example of the complexity of floodplain systems is that of the floodplains on the Zambezi River system in Africa. Taylor et al. (2017) contrasted food web structure in the Upper Zambezi, Kavango and Kwando floodplains, all tributaries of the Zambezi River. While the majority of the fish species encountered in the study were ubiquitous between rivers, there was still evidence that food web structure differed among floodplains. They found that the Upper Zambezi and Kavango River food webs were likely supported by C4 riparian vegetation from the floodplain, whereas the Kwando River food web was likely driven by autochthonous filamentous algae and aquatic macrophytes. These differences were linked to floodplain pulses between the study areas. The Everglades provide another good example of aquatic food web complexity in flooded systems. In the Everglades, a regular microtopographic pattern of ridges (high, marsh dominated) and sloughs (low, inundated, periphyton dominated) occurs. Sloughs exhibit both long and short hydroperiods, and the density of large fish varies with hydroperiod (Chick et al., 2008). As a result, predation pressure on smaller omnivorous fish, and rates of herbivory on epiphytic algae, are also proportional to hydroperiod (Chick et al., 2008). Similarly, during the dry season when floodplain lagoons and waterholes become isolated, invertebrates and fish must shift their diets. Food webs in isolated waterholes are subsidized by allochthonous riverine resources in the wet season, but switch to become supported by autochthonous algal basal resources in the dry season (Pettit et al., 2016; Venarsky et al., 2020).

17.4 Wetlands as attractants and sources of predators

Tropical wetlands are productive environments, with high levels of secondary productivity. As such, these environments make for very good foraging patches for invertebrate and vertebrate predatory species. Many of the semiaquatic insects that make use of wetlands have complex life cycles, the adults of which are predatory. Through flight (e.g., odonates, notonectid hemipterans, dyticid coleopterans), these predators invade wetland environments for feeding and reproductive purposes. At times (e.g., in endorheic systems), invertebrate predator numbers can even reach levels where they dominate those of prey (O'Neill and Thorp, 2014; Wasserman et al., 2018). Other semiaquatic insects (e.g., dipterans) also reproduce in these environments (Bird et al., 2019), with the emerging adults serving as important food sources for terrestrial consumers such as spiders, herpetofauna, bats and birds

(Adler and Courtney, 2019). Given that nearly one-third (46,000 spp.) of all true flies (Diptera) have some affinity with the aquatic environment, the importance of dipterans in ecosystem functioning cannot be overstated (Adler and Courtney, 2019). In this way, aquatic habitats can be a major consumer attractant, even of terrestrial organisms, facilitating cross-ecosystem fluxes of energy.

Consumers with complex life cycles also disperse from aquatic habitats (Knight et al., 2005; McCoy et al., 2009; Semlitsch, 2008). Many insects reproduce in wetland habitats, the adults of which predate on terrestrial organisms (e.g., odonates). Similarly, amphibians participate in multiple levels of the food web, with larval stages feeding on algae and detritus (Whiles et al., 2006; Channing and Rödel, 2019), while the adult amphibians are exclusively predatory, with many taxa (e.g., anurans) feeding primarily in terrestrial habitats (Crump, 2009; Wells, 2010). Given that wetlands are typically embedded within a terrestrial matrix, fluxes of predators from aquatic habitats may have important impacts on the surrounding terrestrial environment, contributing to spatially-structured patterns of herbivore consumption and primary production in receiving environments (Knight et al., 2005; McCoy et al., 2009). As such, wetlands export substantial predation pressure from the aquatic habitat to the surrounding terrestrial landscape. For example, within some parts of the humid tropics, adult amphibians represent the most abundant land vertebrates (Pough, 1980), with many of these predators having originated from wetlands. The implications of adult amphibian export from wetlands to adjacent terrestrial environments, within the context of predation pressure, is, however, poorly reported in the literature. In temperate regions, the transfer of energy and predation pressure between wetlands and receiving terrestrial habitats would be highly seasonal (pulsed), whereas in the "true" tropics, the more consistent abiotic factors would result in a more consistent transfer, and in the subtropics, these processes would be driven primarily by rainfall dynamics.

17.5 How predator–prey interactions shape wetland communities

Predation is a fundamental biotic process that alters the structuring and functioning of ecological communities and is a key driver of evolutionary change (Dayton, 1971; Paine, 1980). Interactions between predators and their prey can result in both direct, lethal changes to prey abundance (i.e., density-mediated effects; Connell, 1972; Paine, 1980; Abrams, 1995), or can manifest in a plethora of indirect, nonlethal effects (i.e., trait-mediated effects; Abrams et al., 1996; Lima, 1998; Peacor and Werner, 2002). In the latter phenomena, predator presence alters key phenotypic traits in prey, including behavior, morphology, and physiology (Lima, 1998; Peacor and Werner, 2002). For example, predator presence can reduce activity rates in prey, in turn negatively affecting foraging (Alexander et al., 2013), or can induce defensive structures that reduce predation rates (Tollrian, 1995).

In aquatic systems, the strength of trait-mediated effects is thought to be as strong as, or stronger, than density-mediated effects, owing to the immediacy and ubiquity of predator chemical cues in water bodies, which can influence entire populations across their life histories (Peacor and Werner, 2001; Trussell et al., 2002, 2004). In turn, the elicitation of such effects can be dependent on eco-evolutionary contexts between predator−prey participants (Barrios-O’Neill et al., 2014; Cuthbert et al., 2018b). Specifically, trait-mediated responses can be contingent on whether predator−prey pairings have shared evolutionary histories, and whether prey can recognize specific cues. The strengths of predatory interactions are also highly context-dependent, driven by a range of biotic and abiotic factors, such as temperature (Englund et al., 2011; Uiterwaal and Delong, 2018), habitat complexity (Barrios-O’Neill et al., 2015), salinity (Cuthbert et al., 2019a), predator−prey body size ratios (Rall et al., 2011; Barrios-O’Neill et al., 2016), predator density (Wasserman et al., 2016a; Sentis and Boukal, 2018), and prey supply (Alexander et al., 2012). These context-dependencies make derivations of empirical interaction strengths challenging to predict, with many effects often interacting to influence community dynamics and population outcomes.

17.6 Predation in temporary wetlands

Temporary wetlands represent excellent model systems to test ecological theory, owing to their relatively small size, rapid succession, accessibility, abundance, high heterogeneity and structural simplicity (De Meester et al., 2005). They also host a diverse array of predators that mediate population structure (Brendonck et al., 2002). Trophic dynamics and community composition in these systems are atypical, differing substantially from permanent freshwaters, such as lakes and reservoirs. That is, because temporary wetlands are internally drained and dry out completely for extended periods of time, community composition spatiotemporally is contingent on dynamics of internal and external recruitment (Brendonck and De Meester, 2003; O’Neill and Thorp, 2014). Wind is a key dispersal mechanism in temporary wetlands during dry periods (Brendonck and Riddoch, 1999; Vanschoenwinkel et al., 2009), as well as ingestion and transportation of eggs by predators (Rogers, 2014, 2015) and adherence to mobile organisms (Vanschoenwinkel et al., 2011). Both predation and demographical constraints associated with pond drying are key structuring processes in these systems.

17.6.1 Temporary wetlands in southern Africa

Austral temporary wetlands are particularly understudied and are at high risk of degradation due to land-use changes, invasive species and pollution (Dalu et al., 2017a; Mabidi et al., 2018). Many temporary wetlands are dredged and deepened to facilitate fish stocking or for water storage purposes in drought-risk areas, in turn, risking the high and often endemic biodiversity of these systems (Bird et al., 2019). Indeed, environmentally protected areas have been shown to foster higher pond biodiversity than those that are degraded anthropogenically (Dube et al., 2020). The trophic structure of temporary wetlands in southern Africa has been recently delineated using stable isotope analyses (Dalu et al., 2016, 2017b, 2017c; de Necker et al., 2020; Box 17.1). These food webs have been found to comprise of three-to-four distinct trophic levels, whereby top predators are notonectids and diving beetles and intermediate trophic groups include zooplankton, tadpoles, macroinvertebrates and mollusks (Dalu et al., 2016). Other studies have also found frogs and killifish to occupy the top trophic level (de Necker et al., 2020). Furthermore, generalist species have been found to typically dominate higher trophic levels, while lower trophic groups are more specialist (Dalu et al., 2016). However, owing to the transient nature of these systems and the aforementioned recruitment dynamics, the length and shape of temporary wetland food webs changes markedly over time (Dalu et al., 2017b; de Necker et al., 2020). Specifically, food webs in the early hydroperiod are highly simplified, with trophic chains lengthening depending on the timing of external predator “invasion.” In turn, basal food resources become more heterogeneous during the hydroperiod initially, before then again decreasing in later stages. Moreover, resource partitioning and specialization can differ both within and between species in temporary wetlands (Dalu et al., 2017c).

Predatory copepods can dominate the upper trophic levels in the early to middle stages of hydroperiod, depending on the phenology of dormant egg hatching events and other colonization dynamics (Wasserman et al., 2016b, 2018). Such predators can also act as regulatory species for abundant crustacean and dipteran groups such as daphnids (Wasserman et al., 2016b) and larval mosquitoes (Cuthbert et al., 2018a), and can show strong prey selectivities (Cuthbert et al., 2020a). Moreover, sex-skewed ratios have been shown to develop empirically in southern African temporary wetlands over time (Wasserman et al., 2018), caused principally by selective predation processes. Furthermore, predation can cause trophic cascades through the elimination of consumer types that impact other organisms in ponds. For example, the high voracity of notonectids has caused periphyton increases through extirpation of grazing taxa (Blaustein, 1998), with “boom-bust” dynamics thus common in temporary wetlands (Wasserman et al., 2018) (e.g., Cladocera, Fig. 17.3).

In the Eastern Cape province of South Africa, Wasserman et al. (2018) found female-biased copepod sex ratios to develop temporally over the hydroperiod, which coincided with notonectid (i.e., higher predator) colonization dynamics. Notonectid colonization can also correspond tightly with intermediate copepod predator declines (Fig. 17.3). Results from that

BOX 17.1 Copepod trophic niche specialization in response to shifts in resource diversity over a temporary wetland hydroperiod (Dalu et al., 2017c).

In Dalu et al. (2017c), a small temporary wetland was sampled over a hydroperiod to test for trophic niche specialization in response to shifting basal resource diversity. Differences in isotopic $\delta^{13}C$ and $\delta^{15}N$ signatures between two closely related copepod species (*Lovenula raynerae* and *Paradiaptomus lamellatus*) and between sexes within these species, in relation to heterogeneity of basal food resources over the course of the pond's hydroperiod, were assessed. The study showed that basal food resource heterogeneity increased over time initially, before decreasing toward the end of the hydroperiod (Image 1), reflective of the expected evolution of trophic complexity for these systems (as in Fig. 17.2). Resource partitioning also varied over the hydroperiod with evidence of intra- and inter-specific specialization in relation to resource availability, whereby increased resource availability facilitated increased trophic specialization (Image 2). This study is one of the few to show that trophic specialization at both the intra- and inter-specific level is likely, as least partly, driven by food resource availability.

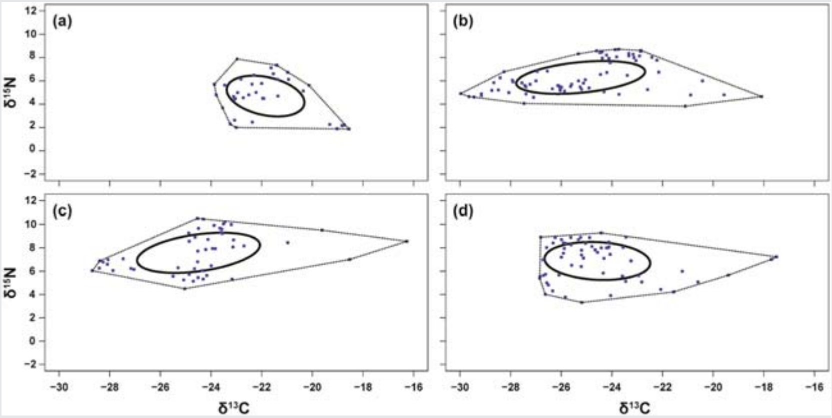

IMAGE 1 Overall trophic diversity ($\delta^{13}C$ and $\delta^{15}N$) of the entire food web over a hydroperiod. The temporary wetland food web was characterized on four consecutive sampling occasions (a = 2 weeks, b = 7 weeks, c = 12 weeks, and d = 16 weeks after inundation). *Adapted from Dalu, T., Wasserman, R.J., Vink, T.J.F., Weyl, O.L.F., 2017c. Sex and species specific isotopic niche specialisation increases with trophic complexity: evidence from an ephemeral pond ecosystem. Scientific Reports 7, 43229.4*

(*Continued*)

BOX 17.1 (Continued)

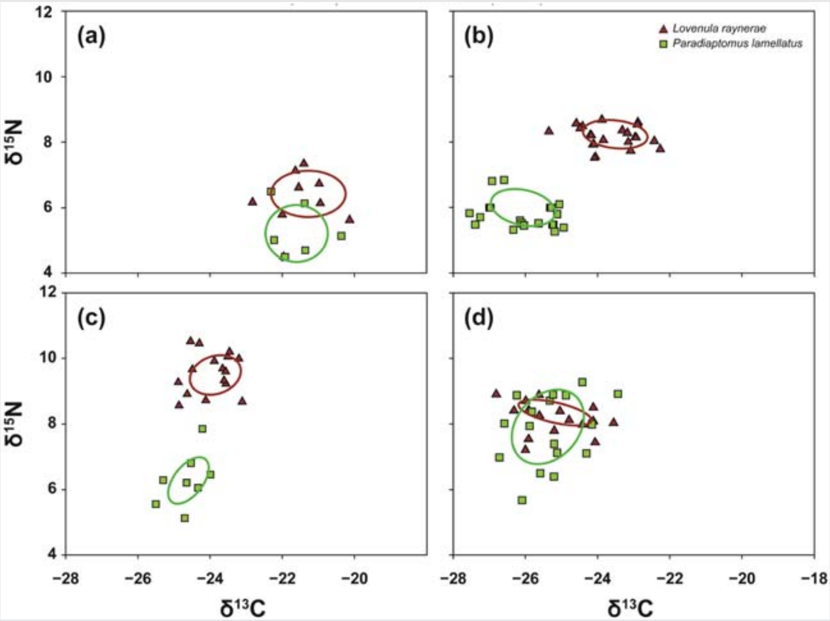

IMAGE 2 Stable Isotope Bayesian Ellipses for male and female *Lovenula raynerae* and *Paradiaptomus lamellatus*, showing increased levels of interspecific and intraspecific (between sexes) specialization in response to increased basal resource heterogeneity (a = 2 weeks, b = 7 weeks, c = 12 weeks, and d = 16 weeks after inundation). *Adapted from Dalu, T., Wasserman, R.J., Vink, T.J.F., Weyl, O.L.F., 2017c. Sex and species specific isotopic niche specialisation increases with trophic complexity: evidence from an ephemeral pond ecosystem. Scientific Reports 7, 43229.*

laboratory study suggested that these patterns were due to selective predation during copepod copulations. Specifically, while female and male copepods were consumed similarly as individuals, as copulating pairs, males were significantly more vulnerable as females orientated males toward predators when at risk, releasing males following their capture. This study concerned predatory *L. raynerae*, the largest species of freshwater copepod in Africa, and possibly globally (Suárez-Morales et al., 2015). Other experimental predation studies have shown gravid females of this species to be significantly more voracious than males, and to be more affected by the presence of habitat structure (Cuthbert et al., 2020b). In other systems, such as temporary rock pools in Botswana, flatworms (turbellarians) and dragonfly juveniles (odonates) have been identified as key predators which influence the

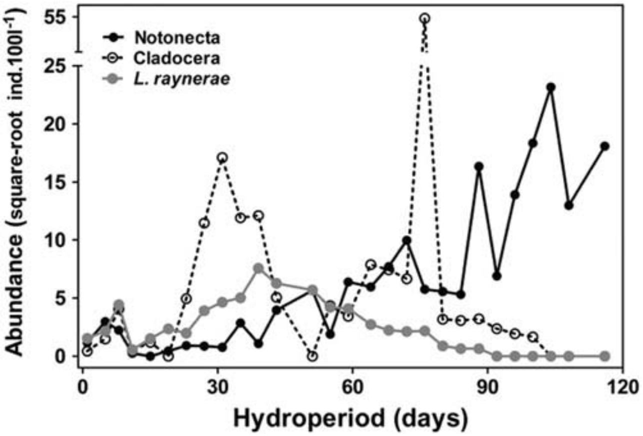

FIGURE 17.3 Abundances of notonectids, cladocerans, and copepods (*Lovenula raynerae*) through a hydroperiod, illustrating boom-bust dynamics among taxa through time. *Adapted from Wasserman, R.J., Weston, M., Weyl, O.L.F., Froneman, P.W., Welch, R.J., Vink, T.J.F., et al., 2018. Sacrificial males: the potential role of copulation and predation in contributing to copepod sex-skewed ratios. Oikos 127, 970–980.*

population dynamics of internally recruited prey groups (e.g., fairy shrimp: anostracans) (De Roeck et al., 2005).

17.6.2 Context-dependencies and trait-mediated effects

The small size and simple structuring of temporary wetlands communities lend these systems to empirical mesocosm experiments. Experimental research has also demonstrated emergent effects of temperature and habitat structure in temporary wetlands ecosystems, whereby the effects of habitat structure on predation by top predators are contingent on levels of warming (Wasserman et al., 2016c). As well as trophic structure, vegetation colonization dynamics are highly variable over the course of the hydroperiods in temporary wetlands, and such habitat structure is known to have a marked effect on trophic interactions in food webs more generally (Barrios-O'Neill et al., 2015). Aquatic plants (i.e., submerged macrophytes) generally colonize later in the hydroperiod and could provide physical refuge for prey. Furthermore, given their shallowness, temperature is known to undulate considerably in these ecosystems (Wasserman et al., 2018). Therefore a suite of abiotic characteristics is known to modulate predation rates in these systems, challenging predictions of trophic dynamics therein. From an applied perspective, recent works in temporary wetlands have highlighted a novel ecosystem service, whereby internally -recruited species are able to contribute to mosquito regulation via predation (Cuthbert et al., 2018a). The primacy of context-dependencies as a mediator of predator effects is thus of great relevance in a public health context. This is especially pertinent in southern Africa, where there are high incidences of several mosquito-borne diseases.

Trait-mediated effects of predators can also be pertinent in temporary aquatic ecosystems. Time stresses associated with temporary wetlands necessitate rapid development—species must reach maturity before the pond dries. As such, morphological phenotypic traits are thought to be more pronounced than behavioral in this respect, so that species can retain foraging intensities even when faced with predation risk (Richter-Boix et al., 2007; but see Schalk, 2016). One key example concerns species' egg banks in substrate, which are reported to employ "bet-hedging" strategies to reduce total recruitment into conditions that are potentially unsuitable. That is, not all eggs hatch during one wet phase, with some remaining dormant to reduce the risk of the pond drying before the population reaches maturity, and to alleviate intraspecific competition (Simovich and Hathaway, 1997; Brendonck et al., 1998). Importantly, these strategies can also be mediated by the presence of predators, with hatching success reduced under predation risk (e.g., De Roeck et al., 2005; Pinceel et al., 2015). In tropical regions of Africa, killifish can additionally be important predators in temporary wetlands, and can bridge hydroperiods through the production of dormant eggs (Watters, 2009). Trait-mediated effects have been demonstrated in annual killifish, whereby higher predators that invade following flood events heighten peak and total fecundity levels, potentially allowing for killifish life stages that can persist until the predation risk has been removed (Grégoir et al., 2017). Conversely, intermediate copepod predation has been shown to be unaffected by invasive fish predatory cues (Cuthbert et al., 2018b), indicating naiveté that could heighten the impacts of higher predators; trait-mediated effects can thus be congruent on shared eco-evolutionary histories (but see Cuthbert et al., 2019b). Overall, the profound presence of both density- and trait-mediated effects in ephemeral wetland ecosystems makes these systems highly dynamic, and exceptional platforms for studying trophic interactions.

17.7 Models and experimental approaches to quantify trophic interactions

17.7.1 Functional responses

A combined use of experimental and statistical modeling approaches is frequently used to quantify the strength of trophic interactions between consumers and resources. From an overall perspective, food webs comprise a network of interacting "nodes," with the strength of these pairwise interactions differing largely. Functional responses are fundamental to the quantification of *per capita* (i.e., individual-level) consumer-resource interaction strengths (Holling, 1959). Definitively, functional responses quantify resource use as a function of resource density and can be applied to any consumer-resource system. That is, all organisms require resources, and thus all organisms exhibit a functional response, from plants, to detritivores, to herbivores, to predators.

Functional responses have been readily applied to quantify interaction strengths in aquatic ecosystems, and especially freshwaters. Both the functional response type and magnitude provide information pertaining to the interaction strength of a consumer. Three types of functional response are typically thought to ensue from consumer-resource interactions (Hassell, 1978) (Fig. 17.4). The type I functional response is linear, whereby resource use increases with resource availability until an immediate plateau:

$$N_e = aN_0T \tag{17.1}$$

where N_e is the initial resource density, α is the attack rate, N_0 is the initial density of prey and T is the time available. This type of functional response is mechanistically restricted to organisms which do not need to "handle" their resources, such as filter feeders (Jeschke et al., 2004). The type II functional response is hyperbolic, characterized by high rates of resource acquisition at low resource densities, which declines until a plateau is reached. Most commonly, Holling's disk equation is classically used for type II functional responses where resources are replaced as they are consumed (Juliano, 2001):

$$N_e = (aN_0T)/(1 + aN_0h) \tag{17.2}$$

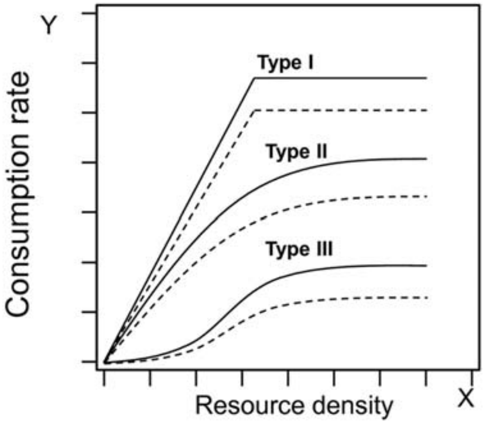

FIGURE 17.4 Three common functional response types, considering resource use as a function of resource density. Within each type, the dashed line illustrates lesser consumer impacts than the solid line. *Adapted from Dick, J.T.A., Laverty, C., Lennon, J.J., Barrios-O'Neill, D., Mensink, P.J., Britton, J.R., et al., 2017. Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. Journal of Applied Ecology 54, 1259–1267.*

where h is the handling time. For situations where resources are not replaced, Rogers' random predator equation is commonly fit instead for type II functional responses (Rogers, 1972):

$$N_e = N_0(1 - exp(a(N_e h - T))) \tag{17.3}$$

Studies have found that use of the random predator equation is suitable even when resources are totally depleted at certain densities (Cuthbert et al., 2020c). In contrast, the type III functional response is sigmoidal, whereby consumption rates are reduced at low resource densities, increase initially as densities grow, before again falling and plateauing as in the type II functional response. Where this functional response is exhibited, Hassel's Type III functional response model can be fit for experimental designs that replace resources following consumption:

$$N_e = (dN + bN^2)/(1 + cN + dNT_h + bN^2T_h) \tag{17.4}$$

where b, c, and d are constants, which can be optimized or removed to aid model fitting. For situations where resources are not replaced, Hassel's Type III functional response model can be modified as follows:

$$N_e = N_0(1 - \exp((d + bN_0)(T_h N_e - T)/(1 + cN_0))) \tag{17.5}$$

Importantly, these functional response types and their parameters can allow for quantification of the strength of feeding interactions, whereby type II functional responses have been typically associated with destabilizing effects for resource populations, and type III functional responses deemed to be more stabilizing (Dick et al., 2014). This is because low-density prey populations are more likely to be extirpated in the case of the type II functional response.

Depending on the functional response model, there are several key parameters that can be used to quantify the strength of feeding interactions. The attack rate (or search coefficient) can be used to deduce the strength of feeding interactions at low resource densities, and thus high attack rates are more likely to destabilize resource populations. Further, the handling time (time taken to capture, subdue and digest) of resources can be used inversely to infer maximum feeding rates, that is, the functional response curve asymptote. Both the attack rates and handling times can be used to infer the potential of consumers to impact upon resources (Cuthbert et al., 2019c) (Fig. 17.5). Furthermore, classically, the consumer functional response has been combined with the consumer numerical response to quantify population-level effects (Solomon, 1949; Holling, 1959). While the functional response quantifies individual effects, the numerical response accounts for population-level changes of a consumer resulting from differences in resource densities, including both predator aggregation and reproduction. The functional response and numerical response product, deemed the total

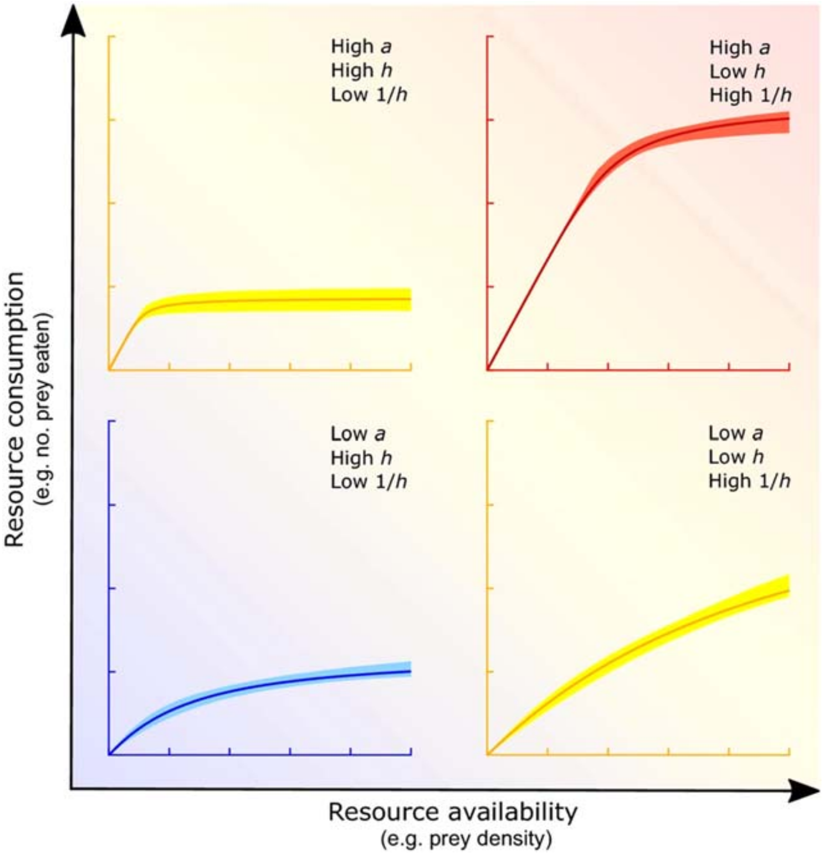

FIGURE 17.5 Functional response "heat map" demonstrating differences in consumer impact based on attack rates (*a*; initial slope of curve) and handling times (*h*; which inversely gives maximum feeding rates, i.e., 1/*h*, curve asymptote). Increasing *per capita* impact is illustrated from bottom-left to top-right. *Adapted from Cuthbert, R.N., Dickey, J.W.E., Coughlan, N.E., Joyce, P.J., Dick, J.T.A. 2019c. The Functional Response Ratio (FRR): advancing comparative metrics for predicting the ecological impacts of invasive alien species. Biological Invasions 21, 2543–2547.*

response, allows for insights of population-level interaction strengths based on the assimilation of individual and population effects. While the numerical response is more difficult to quantify in a laboratory setting, recent advances have sought to use proxies such as consumer abundance or fecundity as a supplement (Dick et al., 2017). Therefore the combination of functional response and numerical response can be used to quantify the offtake rates by consumers in wetlands.

17.7.2 Resource preferences and switching

One further important component of consumer-resource interactions concerns resource preferences. Many consumers are generalists and are thus simultaneously exposed to a range of resource types at varying relative proportions in their environment. Preferences among resource types at different proportions can mediate stability within communities, and data on the diets of consumers can inform understandings of resource partitioning (Shoener, 1971). In particular, consumers may avoid prey which are relatively rare in their environment, and instead preferentially select abundant prey (i.e., "switching"; Murdoch, 1969). This patterning can thus allow rare resources to persist in the environment, allowing for species coexistence, while regulating relatively abundant resources. Such processes can be driven by phenomena such as "predator learning," whereby a "search image" for abundant prey is developed and targeted (Tinbergen, 1960).

As with functional responses, numerous models have been developed to quantify and compare consumer-resource preferences (Manly, 1974; Chesson, 1978, 1983). Model selection can, again, depend on whether resources are replaced as they are consumed during a given experiment. Where replacement occurs, Chesson's index can be used to derive preferences:

$$a = \frac{r_i/n_i}{\sum_{j=1}^{m}(r_j/n_j)} \tag{17.6}$$

where α is the selectivity index for resource type i, n_i is the amount of resource type i available at the start of the experiment, r_i is the amount of resource type i consumed, m the number of resource types, r_j is the amount of resource type j consumed and n_j the amount of resource type j available at the start of the experiment. Conversely, where a given resource is not replaced (i.e., it depletes), the following equation can be applied:

$$a = \frac{\ln((n_{i0} - r_i)/n_{i0})}{\sum_{j=1}^{m}\ln((n_{j0} - r_j)/n_{j0})} \tag{17.7}$$

For both of these selectivity metrics, output values are between 0 and 1, with values closer to 1 indicating increased preference for the focal resource, and $1/n$ indicating null preference. The converse is true for prey avoided (i.e., values closer to 0 are disproportionately avoided).

Experimentally, controlled feeding trials can be used to quantify functional response and prey preferences in aquatic systems, and typically in a laboratory environment. The often simplified structure of ecosystems such as temporary wetlands makes representing natural communities relatively straightforward (De Meester et al., 2005). Broadly, these experiments typically expose consumers, standardized according to body size or another measure, to different densities (for functional responses) or proportions (for resource preferences) of singular or multiple resource types. For aquatic study systems, mesocosms can be used to examine feeding rates toward resources over fixed experimental durations; modeling is typically based on quantifications of resources consumed as a function of initial levels supplied over that time interval (see above equations). This approach additionally allows for comparative examination of other environmental contexts (e.g., temperature, habitat complexity) while controlling for other factors, depending on the specific hypotheses of a study. However, feeding experiments could also be conducted in field-based conditions (Novak, 2010), and this may be particularly practical in small-sized tropical wetlands.

17.7.3 Stable isotopes use in aquatic food webs

Stable isotope analysis provides a powerful and important tool for identifying energy sources which fuel consumers, and enables us to better understand trophic interactions and infer consumer trophic positions (Quezada-Romegialli et al., 2018). The assessment of food web structure cannot be discerned using only short-term, traditional methods (e.g., stomach contents, regurgitates and fecal matter), but can be advanced by employing stable isotope analysis which provides understandings of diet over a longer period of time (Post, 2002). Stable isotopes provide time-integrated information on the material assimilated by organisms, with carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope composition being most commonly used in ecological studies (Cornwell et al., 2006). The $\delta^{13}C$ isotopes change little from primary producer to consumer, hence it reflects consumer diet closely. Whereas, the $d^{15}N$ isotope values are generally high and are mostly used as a trophic position indicator (Post, 2002; Layman et al., 2007). Thus, the use of $\delta^{13}C$ and $\delta^{15}N$ isotope analysis can provide substantial information about different food sources, trophic relationships and energy pathways utilized by aquatic organisms (Jones et al., 1998; Dalu et al., 2017a,b; Jackson et al., 2020). Other elements such as hydrogen (H) and sulfur (S) show little change between trophic levels, and oxygen (O) is mostly used to investigate changes in water temperature. A limited number of studies have been conducted using stable isotopes within tropical wetland systems (e.g., Wantzen et al., 2002; Frings et al., 2014; Dalu et al., 2016; 2017b,c; De Necker et al., 2020).

17.7.3.1 Hypervolumes

Consumer trophic niches are difficult to characterize. However, new tools, such as hypervolume analysis, allow for more definitive quantification (see Newsome et al., 2007; Blonder et al., 2014, 2018; Shipley and Matich, 2020). These can be of great use, particularly within wetland environments, although were initially developed for the marine environment. This new tool has already been applied in assessing the degree of recovery of ecosystem energy flow and success of habitat restoration (see James et al., 2020) and to test for trophic niche partitioning in an adaptive radiation of Hawaiian *Tetragnatha* spiders (see Kennedy et al., 2019) with great success. Therefore, hypervolumes offer useful insights that enable us to understand interactions at many ecological resolutions (i.e., individual, population, community, and ecosystem levels). This approach is based on the conceptual framework of Hutchinson's n-dimensional niche, where n-variables represent multiple axes which define a hypervolume that quantify the role of a species in its environment (Blonder et al., 2014). Depending on the variables included (e.g., abiotic factors, basal resources), hypervolume geometries and locations in n-dimensional space are particularly useful to gain insight into complex ecological processes that depend on multiple drivers, such as energy flow in a food web (Blonder et al., 2014, 2018). However, a variety of intrinsic and extrinsic factors may drive isotopic variability and influence the ultimate geometry of observed hypervolume niche dimensions within the natural environment (see Shipley and Matich, 2020). The hypervolume size varies with the values of the input data (i.e., larger hypervolume = more variation) and can be used to characterize resource use variation in food webs. The overlap between two hypervolumes (i.e., food webs from two different habitats) can be used to determine the similarity between two food webs, because overlap increases as two hypervolumes occupy more of the same n-dimensional space. This approach presents an opportunity for quantification of resource use within tropical wetland ecosystems through the use of stable isotope analysis. These metrics have the potential to be used at the system scale by combining resource use data from multiple species to quantify and compare food web-level resource use among habitats.

17.7.3.2 Best practices for use of stable isotope mixing models

The best practices for using stable isotope mixing models are presented in detail in Philips et al. (2014). For proper implementation of stable isotope mixing models, it is important to note that models can only be as good as the study design and/or data collected (Philips et al., 2014). Clear questions for studies are therefore important and these should be informed by study system knowledge, with strong sampling designs needed to characterize resource and consumer isotope variability at spatiotemporal scales. One of the implicit assumptions of any mixing model is that all the food sources are included, and researchers should thus strive to ensure that this is the case to get the most reliable results. It is also imperative to note that decisions on source grouping or incorporation of concentration-dependence can influence results, and studies should be careful about model output interpretation. Combining some sources to reduce the total number may sometimes lead to more constrained, less diffuse solutions, and should be considered to be an option if the sources examined have isotopically distinct signatures (Gannes et al., 1998; Phillips et al., 2005).

17.7.3.3 Tissue sample collection choices

Bone collagen and fish otoliths provide dietary information that spans an organism's entire life history, while metabolically active tissues have a turnover of days (e.g., liver) or months (e.g., muscle) (Philips et al., 2014). However, sampling of tissues such as bone collagen and otoliths requires the scarification of consumers. When such destructive sampling is not possible or ethical, there are nondestructive options available, such as blood which can be separated into two components: (1) plasma, which rapidly turns over and reflects diet from previous days, depending on the metabolic rate of the study species and (2) red blood cells, which represent diet from the previous few weeks and have a slow turnover. Tissues (i.e., claw, hair, feather) that are metabolically inert after formation offer scope for constructing time series (Philips et al., 2014).

17.7.3.4 Layman community metrics for food web structure analysis

Six community-wide Layman metrics that reflect important aspects of trophic structure are described below. The first four metrics are measures of the total extent of spacing (i.e., community-wide trophic diversity measure) within $\delta^{13}C-\delta^{15}N$ biplot space, and the last two metrics reflect relative species position within a trophic niche space and are also used for estimating the extent of trophic redundancy (see Findley, 1973; Winemiller, 1991; Cornwell et al., 2006; Layman et al., 2007 for details on the underlying theory, mathematics, and methodological considerations). In summary, the following community metrics are described:

1. The $\delta^{15}N$ Range (NR) is the distance between two species with the most enriched (maximum $\delta^{15}N$) and most depleted (minimum $\delta^{15}N$) values, and represents the vertical structure (i.e., trophic levels) within a food web. The organism's trophic position must be calculated in relation to the $\delta^{15}N$ values of a standardized baseline (i.e., normally a primary consumer) and, a larger $\delta^{15}N$ range among consumers suggests more trophic levels and high trophic diversity (Post, 2002; Layman et al., 2007).
2. $\delta^{13}C$ range (CR) is the distance between two species with the most enriched (maximum $\delta^{13}C$) and depleted (minimum $\delta^{13}C$) values. High CR is common in food webs with multiple basal food sources with varying $\delta^{13}C$ values, providing food web base niche diversification.
3. Total area (TA) is the convex hull area of all species in a $\delta^{13}C-\delta^{15}N$ biplot space. Thus, TA is a measure of the total amount of niche space occupied by all organisms, and is a proxy for the total food web trophic diversity. The TA value is influenced by species with extreme positions on either the $\delta^{13}C$ axis, $\delta^{15}N$ axis or both.
4. Mean distance to centroid (CD) is the mean Euclid-distance of each species to the $\delta^{13}C-\delta^{15}N$ centroid, where the centroid is the mean $\delta^{13}C$ and

δ^{15}N value for all food web species. The CD value is important as it provides a measure of the mean degree of food web trophic diversity and also as a function of species spacing degree.

5. Mean nearest neighbor distance (MNND) is the average of the Euclidean distances to each species' nearest neighbor in the δ^{13}C–δ^{15}N biplot space, and thus MNND is a measure of the overall species packing density. For example, food webs with a large species proportion with similar trophic ecologies will exhibit a smaller MNND (i.e., increased trophic redundancy) than a food web in which species are, on average, more divergent in terms of their trophic niche (Layman et al., 2007).
6. Standard deviation of nearest neighbor distance (SDNND) is a measure of the species packing evenness in a δ^{13}C–δ^{15}N biplot space that is less influenced than MNND by sample size. Generally, low SDNND values indicate trophic niches which are evenly distributed.

17.7.3.5 Calculating trophic position using stable isotopes

The calculation of trophic position for one baseline follows standard equations linking ^{15}N enrichment per trophic level and the trophic position of the baseline (e.g., a primary producer or primary consumer). In the case of two baselines, a simple mixing model incorporating $\delta^{13}C$ allows for the differentiation between two distinct nitrogen sources, thus including heterogeneity derived from alternative $\delta^{15}N$ sources (Quezada-Romegialli et al., 2018). Statistical analysis packages integrate three Bayesian models, depending on the baseline number and carbon (C) trophic discrimination factor inclusion. The simplest model is:

$$\delta^{15}N_c = \delta^{15}N_b + \Delta N(TP - \lambda) \tag{17.8}$$

where $\delta^{15}N_c$ and $\delta^{15}N_b$ refer to the consumer and single baseline $\delta^{15}N$ values, respectively, ΔN is the nitrogen (N) trophic discrimination factor, TP is the consumer trophic position, and λ is the baseline trophic position (Vander Zanden et al., 1997).

The dual baseline Bayesian approach includes a mixing model to discriminate among two distinct C and N sources, for example, pelagic versus benthic, and extends the single baseline approach using two equations:

$$\delta^{15}N_c = \Delta N(TP - \lambda) + \alpha\left(\delta^{15}N_{b1} + \delta^{15}N_{b2}\right) - \delta^{15}N_{b2} \tag{17.9}$$

and

$$\delta^{13}C_c = \delta^{13}C_{b1}\alpha + \delta^{13}C_{b2}(1 - \alpha) \tag{17.10}$$

where $\delta^{15}N_{b1}$, $\delta^{13}C_{b1}$, $\delta^{15}N_{b2}$, and $\delta^{13}C_{b2}$ refer to the $\delta^{15}N$ and $\delta^{13}C$ values of baselines 1 and 2, respectively, and α is the N proportion derived from baseline 1 (Post, 2002; Vander Zanden and Rasmussen, 2001). The full model is based on the former, but α includes the carbon trophic discrimination factor:

$$\alpha = \frac{\left[\delta^{13}C_{b2} - \left(\delta^{13}C_c + \Delta C\right)\right]/(TP - \lambda)}{\delta^{13}C_{b2} + \delta^{13}C_{b1}} \tag{17.11}$$

where $\delta^{13}C_c$ is the consumer $\delta^{13}C$ value, and ΔC is the C trophic discrimination factor (see Quezada-Romegialli et al., 2018 for further details).

17.8 Conclusions

Wetland habitats, particularly floodplain areas, represent buffer zones between rivers and adjacent terrestrial systems, and these habitats often support high densities of organic matter and consumers. They provide ideal growth conditions to biota as a result of the resource exchange between aquatic and terrestrial habitats. Further, the wetting and drying phases that often characterize tropical wetlands drive highly dynamic trophic interactions that provide excellent model systems for testing food web and community theory (De Meester et al., 2005). Nevertheless, there remain pervasive knowledge gaps regarding trophic interactions in many types of tropical wetlands, regions and taxonomic groups. In particular, there is a general need for ecologists to transcend from a single-population (i.e., autecological) to a multicommunity perspective of feeding connections (i.e., multitrophic), especially when developing strategies for resource management or conservation. Thus, further research that encapsulates this need is required, such as by approaching the question of connectivity through trophic linkages and subsidies via aquatic organisms at the holistic level of a catchment within tropical wetland systems. For example, freshwater wetland systems are linked to land through a variety of passive and active transfers of plant, animal and human matter. Acknowledging the movement of nutrients and consumers within and among adjacent habitats is critical to our general understanding of trophic dynamics, as the health and sustainability of wetland aquatic food webs can be strongly influenced by these factors. Further studies in wetland ecosystems are also required to unravel how contributions of terrestrial versus aquatic resources, in sustaining secondary production, drive community structuring. Emergent effects associated with ongoing climate change and habitat degradations should additionally be examined in the tropical wetland context.

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Chapter 18

Metacommunity structure and dynamics

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18.1 The metacommunity approach

Biological populations are not isolated systems, as they are linked by interspecific interactions such as competition, mutualism, and/or predation. All these populations of different species living together at the same time and in the same area make up an ecological community (Elton, 1927; Fauth et al., 1996). Community ecology can therefore be defined as the study of patterns and processes in the structure and behavior of these multispecies assemblages (Morin, 2011; Mittelbach and McGill, 2019). One of the main goals of community ecology is understanding species distribution according to their biotic and abiotic environments. But ecological communities are not static elements occupying discrete localities. In fact, local communities are regionally related, so that the habitat patches where they live are embedded in a landscape matrix and interconnected through dispersal events (Fig. 18.1; see Brendonck et al., 2022a,b, Chapters 9 and 10; Dalu et al., 2022, Chapter 8; Piedade et al., 2022, Chapter 7; Reichard, 2022, Chapter 12; Moraes et al., 2022, Chapter 13; Dube et al., 2022, Chapter 11). The niche-assembly perspective in Ecology (Hubbell 2001) considers that species distributions are mostly the result of the range of environmental conditions and resources that organisms can tolerate and their function in the ecosystem (the niche concept; Hutchinson, 1957; Chase and Leibold, 2003). However, this mainstream view usually underestimates other important factors also affecting species distributions. Consequently, modern community ecology

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FIGURE 18.1 Metacommunity system in Okavango delta, Botswana. Aquatic habitats (patches) are surrounded by terrestrial habitat (matrix), but potentially connected between them (bidirectional arrows). Aerial picture taken from a plane in the vicinity of Maun (Southern delta).

considers that species composition in a given locality is the result not only of niche processes but also, and importantly, of dispersal constraints, that is, through spatial filtering of a larger-scale species pool, and of internal dynamics (Belyea and Lancaster, 1999). However, defining the spatial and temporal boundaries of a community may not always be straightforward, and ecological community studies come upon very variable and scale-dependent results (Chave, 2013), so that some authors have even challenged the use of the community concept itself as too artificial (Ricklefs, 2008).

The metacommunity concept was born under the need for a theoretical framework that considered multiple processes at different scales (Leibold and Chase, 2018). A metacommunity consists of a set of communities distributed in ecosystem patches, embedded in a landscape matrix, and potentially connected by dispersal of multiple interacting species (Hanski and Gilpin, 1991; Wilson, 1992). In this way, the metacommunity view stresses the potential connections among communities and highlights the influence of regional-scale processes on diversity and composition at the local scale.

Metacommunity theory shifts the focus from the local to a combination of local and regional processes (Fig. 18.2). Species richness and composition are therefore the result of not only environmental filtering (or species sorting; Leibold et al., 2004) but also of dispersal between patches (Wilson, 1992; Bell, 2000; Hubbell, 2001). In addition, dispersal strategies widely differ among species (Leibold, 2011), and dispersal processes are also affected by the landscape matrix characteristics (Castillo-Escrivà et al., 2017a). The emergence of metacommunity neutral models (Bell, 2000; Hubbell, 2001) demonstrated how empirical patterns of biodiversity (e.g., species-area relationships, rank-abundance diagrams) could be replicated in silico relying on stochastic demographic dynamics and neutral migration processes (considering all species equal regarding their niche and dispersal abilities, hence in the absence of selection and adaptation). Therefore, ever since these theories

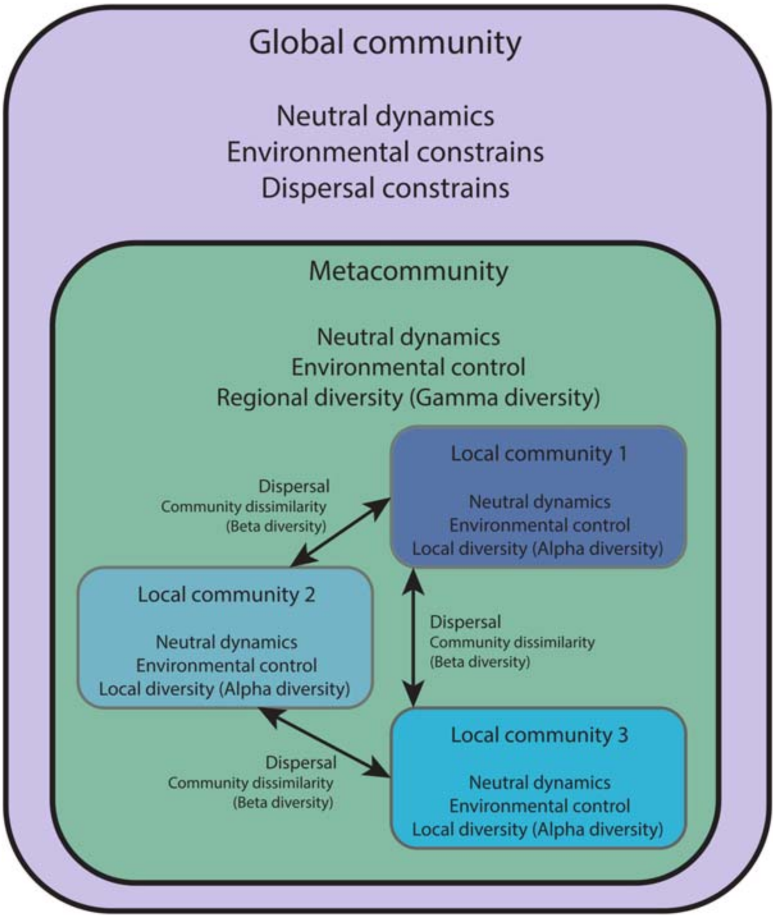

FIGURE 18.2 Schematic diagram of the main ecological processes acting at different scales on metacommunity organization, so as indication of the scale focus of diversity components. Neutral dynamics (ecological drift), environmental control (selection), and dispersal are the main ecological processes structuring metacommunities at different spatial scales. Alpha, beta, and gamma diversities describe different dimensions of metacommunity diversity at the local, between localities and regional scales, respectively. *Based on Vellend, M., 2010. Conceptual synthesis in community ecology. Quarterly Review of Biology 85, 183–206.*

were published, ecological drift and spatial autocorrelation through neutral dispersal had to be considered in null hypotheses when explaining the organization of metacommunities. However, subsequent tests with empirical data suggested that niche-related deterministic processes might dominate over neutral processes, indicating that the niche also needed to be considered in such analyses (Cottenie, 2005).

Under this framework of local communities linked by dispersal processes within a regional metacommunity, both local diversity and regional species pools play a role in understanding small-scale biodiversity patterns. As such, metacommunity theory links the multiscale components of biological diversity (Whittaker, 1972; Magurran and McGill, 2011): alpha diversity, corresponding to local diversity, beta diversity, which quantifies the dissimilarity between local communities, and gamma diversity, with focus on the larger-scale regional diversity (Fig. 18.2).

Along this chapter, we will consider how the three main processes, environmental control, dispersal, and neutral dynamics, structure metacommunities of tropical freshwater wetlands. In addition, we will compare the effects and importance of each of these processes in tropical water bodies, to the more intensely studied temperate wetlands, in relation to their influence on biological diversity. For that purpose, we will provide examples of different groups of organisms and habitat types, as shown by variation partitioning analysis. This analysis allows to disentangle the relative effects on species distribution played by environmental and spatial factors (environmental control and dispersal processes) and the remaining undetermined (partly stochastic or neutral) effects. Finally, we will discuss the implications of metacommunity theory for tropical wetland conservation.

18.2 Processes shaping aquatic metacommunities

There is a considerable body of literature discussing the relative fit of different metacommunity paradigms or archetypes, especially on the role of species sorting against neutral theory (Cottenie, 2005); Gravel et al., 2006; Logue et al., 2011; Brown et al., 2017). This has led to general agreement about the main processes structuring metacommunities, both at small and large spatial, and even temporal scales. Among these processes, those assumed to have a marked influence on metacommunity dynamics in the short term are selection (niche or environmental effects, also known as species sorting), dispersal (spatial effects), and neutral processes, epitomized by ecological drift (demographic stochasticity) (see Vellend, 2010). These are general drivers of metacommunities, including those in aquatic environments. Indeed, the study of freshwater metacommunities, because of their relative isolation in a landscape matrix, has been instrumental for the evaluation and understanding of processes of metacommunity organization in the natural context (Heino et al., 2015; Leibold and Chase, 2018).

18.2.1 Environmental control

The concepts of environmental control, niche-control, species sorting, and habitat filtering, all have very similar meaning and refer to biotic and abiotic factors controlling species establishment and fitness (Lozada-Gobilard et al., 2019). This idea is encapsulated by the more traditional term in the biological (evolutionary) literature of “selection” (Vellend, 2010). In this context, selection infers that environmental tolerance and resource utilization varies among species (Chase and Leibold, 2003). At the local scale, abiotic and biotic factors, such as environmental stress, resource availability, or biological interactions (competition, predation, mutualism) can strongly influence species presence, performance, coexistence, and distribution, and therefore metacommunity structure (see Dalu et al., 2022, Chapter 7; Deemy et al., 2022, Chapter 4). At larger scales, habitat heterogeneity and consequently resource and interaction heterogeneity, allow for the coexistence of more species, increasing regional pools (MacArthur and MacArthur, 1961). This heterogeneity leads to environmental gradients where several species survive with different adaptations.

18.2.1.1 Important environmental factors

Local environmental biotic and abiotic pressures can deterministically filter the species composition within a patch, what is known as species sorting (Leibold et al., 2004). Unlike the major influence of temperature on temperate wetland metacommunities, where seasonal variation exert a strong control, tropical wetland metacommunities seem to be mostly influenced by hydrological cycles (such as the flood pulse), playing a key role on metacommunity assembly (Wantzen et al., 2016). Tropical wetlands can be highly variable, ranging from large river floodplains to small temporary shallow ponds, and including oxbow lakes and coastal freshwater marshes. The hydrological cycle *per se* can strongly influence other environmental variables, for example, light penetration, salinity, nutrient concentration, pH, or organisms dilution, which work as direct environmental filters (Nursuhayati et al., 2013; Sasa et al., 2015). Other relevant drivers are wide variation in oxygen concentration due to high temperatures, high organic matter decomposition rates, and shading by helophytic and floating vegetation (Roldán and Ramírez, 2008). In addition, there are peculiar microhabitats in tropical wetlands that affect ecosystem functioning but are rare in other climates. For example, vegetation architecture is an important influence on aquatic invertebrate community assembly. Some organisms, especially benthic invertebrates, depend on the root systems of floating vegetation such as *Eichornia* spp. and *Polygonum* spp. (Heckman, 1997; Barker et al., 2014; Ohtaka et al., 2014). In contrast, in temperate wetlands, it is mostly the submerged vegetation (such as *Myriophyllum* spp., macroalgae of the family Characeae) which support a high diversity and biomass of invertebrates, from ostracods to insects (Tessier et al., 2004). Nevertheless, De Klerk and Wepener (2011) highlight the high species richness of aquatic macroinvertebrates inhabiting also marginal and emergent vegetation, which are common in either temperate or tropical wetlands. In addition to facilitation, other positive (mutualism) and negative (predation, competition) biotic interactions also affect metacommunity structure, and some studies suggest that they can be even more intense in tropical compared to temperate areas (Andresen et al., 2018).

18.2.1.2 The role of scale and patch variability

The strength and direction of the environmental control on species composition in a metacommunity can vary through space and time. Habitat heterogeneity is expected to positively correlate with the increase in area (Rosenzweig, 1995). Furthermore, environmental fluctuations and cycles can be produced by various time-dependent processes such as climatic seasonality, disturbances, or biotic interactions, including shifts related to phenological and demographic changes. In tropical wetland metacommunities, many local environmental factors that deterministically filter the regional pool of species include salinity, oxygen concentration, light intensity, nutrient availability, or the presence of fish and other predators. These environmental conditions can differ between wetlands in the same region, generating spatial heterogeneity. Even within the same waterbody, the presence of different microhabitats (shallow shorelines, water column, aquatic vegetation, etc.) can lead to increased habitat heterogeneity and ultimately to higher species richness (Gleason et al., 2018). Furthermore, water and nutrient inputs during the rainy season, bird migrations, fires, or seasonal desiccation give rise to temporal changes in environmental conditions, that is, temporal heterogeneity. Therefore temporal changes in niche-control also originate differences in metacommunity structure. As a consequence, one can expect the role of environmental factors and species sorting intensity to vary across time (Rojo et al., 2016; Csercsa et al., 2019; Gálvez et al., 2020). Thus the length of spatial and temporal environmental gradients can lead to intrapatch and interpatch heterogeneity (Questad and Foster, 2008). As a result of intrapatch heterogeneity, alpha diversity may increase, and interpatch heterogeneity leads to higher beta and gamma (regional) diversity (Larkin, 2018). Such patterns have also been observed in tropical wetlands. In a study of sediment bacteria communities from an Indian mangrove forest, Behera et al. (2018) found that interpatch and seasonal heterogeneity, related to changes in environmental conditions (such as monsoon precipitations), drove differences in bacterial species composition. Crossetti et al. (2018) showed how intrapatch heterogeneity did not correlate with phytoplankton community structure in a Brazilian coastal wetland, but seasonal changes lead to strong differences in community composition. Ronchi-Virgolini et al. (2013) also found no intrawetland differences in a bird community of the Paraná River, although it significantly differed between seasons and years. However, Ferreira et al. (2019), working in the Amazon River floodplain, observed a strong influence of intrapatch heterogeneity on species richness and abundance of ardeid birds, suggesting that this heterogeneity provided suitable microhabitats for a variety of species.

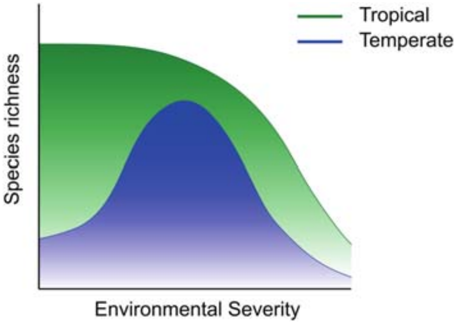

FIGURE 18.3 Expected relationship between environmental severity and species richness, based on terrestrial vegetation studies from Pärtel et al. (2007) and Yang et al. (2015), assuming strong competitive exclusion processes and relatively high dispersal in the temperate setting.

18.2.1.3 The influence of environmental stress on biological diversity

Variation in the intensity of local environmental (abiotic) control has implications for the biological diversity of a metacommunity. When species sorting by the abiotic environment is weak, but competition is strong, diversity can be reduced through exclusion due to the influence of dominant species, as observed in vegetation studies of temperate environments using productivity as a surrogate of severity (Yang et al., 2015; Fig. 18.3). When the intensity of niche-control increases (in a heterogenous way between patches), so do alpha, beta, and gamma diversities, because each patch diverges in environmental conditions, and can therefore support different species. Finally, under severe species sorting effects, only few species are adapted to survive in such harsh environmental conditions, provoking a decay in biological diversity, revealing a unimodal pattern in the diversity—severity relationship. However, this pattern does not seem to hold in tropical vegetation (Pärtel et al., 2007), with a monotonic decrease of species richness with increasing severity (Fig. 18.3). It is still unclear whether or not these relationships of environmental stress with diversity hold in tropical and temperate freshwater ecosystems. Considering the more isolated character of water bodies compared to the terrestrial landscape, the pattern might depend more strongly on connectivity and patch size, influencing, respectively, the arrival of strong competitors and the possibilities of finding refugia by weak ones, and therefore affecting competitive exclusion (Lomolino, 2000).

Extreme environments are also strong environmental filters in tropical aquatic ecosystems. For example, Chakraborty et al. (2011) found that salinity drove important changes in phytoplankton community composition in an Indian estuarine system. Sosa-López et al. (2007) found a negative relationship between fish species richness and salinity in Mexican coastal lagoons. Pinder et al. (2005) showed the same relationship when studying aquatic invertebrates in Australian wetlands. Verschuren et al. (2000) also found this negative relationship in the invertebrate community of a Kenyan shallow lake, but they concluded that this relationship was an indirect effect of changes in microhabitat and resource availability. It is not so clear, however, whether or not reduced environmental stress could produce a reduction in local species richness due to competitive exclusion (Yang et al., 2015), not only in tropical but neither in temperate aquatic communities. For instance, if we consider drought as a stress for aquatic communities, when comparing between permanent and temporary water bodies at a global scale, Antón-Pardo et al. (2019) found reduced species richness in temporary waters, independent of climate and other factors, suggesting a monotonic negative relationship between local diversity and drought stress in fresh waters, not a unimodal one as suggested by Yang et al. (2015).

18.2.2 Dispersal

Dispersal is the key element integrating local communities in a metacommunity framework. Not only does it allow genetic flow between populations from different patches, but it also enables colonization of patches by species. This process is especially important in colonization—competition dynamics, where good colonizers but bad competitors (fugitive species) compete with bad colonizers but good competitors. Fugitive species are able to successfully colonize empty patches but they become locally extinct when a better competitor arrives (Mittelbach and McGill, 2019). Nevertheless, fugitive species can persist at regional scale (Levins and Culver, 1971), and good competitors may not be able to colonize an already occupied patch because of priority effects (discussed in the next section).

18.2.2.1 Dispersal limitation, connectivity, and dispersal surplus

Species distribution can be strongly influenced by dispersal ability, not only by niche-control. As a consequence, species distributions are the result of local environment and regional dispersal limitation. Dispersal limitation depends on organism dispersal ability (e.g., flying vs walking dispersal). For example, some organisms will be more dispersal limited between drainage systems than within the same hydrological basin (Heino et al., 2017). In these riverine ecosystems, dispersal can be influenced by water flow (i.e., downstream passive drift vs upstream active movement; Tonkin et al., 2017). Sometimes it is the own ecosystem traits which limit dispersal. For instance, organisms inhabiting small isolated temporary ponds are expected to be more dispersal limited than those inhabiting well-connected marshlands (Heino et al., 2015).

Once again, this process can be time dependent. For example, seasonal bird migration events can become key dispersal mechanisms at a particular

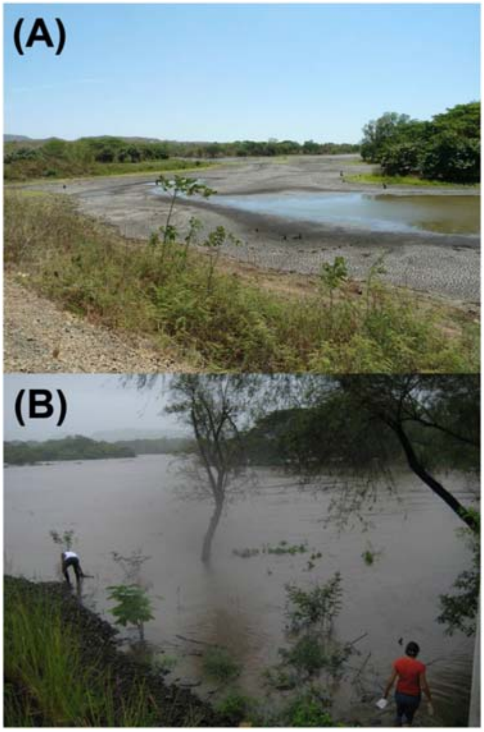

FIGURE 18.4 Connectivity between wetlands is highly influenced by seasonal hydrology. Palermo wetland in Nicaragua during the dry (A) and the rainy (B) seasons.

time for many organisms (Green and Figuerola, 2005; Green et al., 2016; Viana et al., 2016). Waterways are obviously essential for the dispersal of many aquatic organisms, but these can also be temporary. No matter the taxon or the ecosystem, dispersal is strongly influenced by seasonal hydrology. For example, Thomaz et al. (2007) showed that metacommunities in tropical river-floodplain systems are homogenized by patch connections established in rainy seasons. During the flood phase, connectivity between isolated water bodies increases (Fig. 18.4). By the same token, connectivity between tropical water bodies decreases during the dry season (Brasil et al., 2020). Patches become progressively isolated and even wide wetlands can be split into several small ponds, with their communities becoming more environmentally and spatially independent.

With the increased connectivity during the rainy season, and the resulting decrease in dispersal limitation, one might assume that dispersal limitation is not as relevant in tropical wetlands as it is in temperate regions. However, organism dispersal may be limited by strong barriers such as those derived from regional orography. As Janzen (1967) stated, "mountain passes are higher in the tropics." Strong altitudinal climate gradients, in addition to narrow climatic niches, can restrict species dispersal. Myers et al. (2012), when studying plant beta diversity, found support for stronger dispersal limitation in tropical forests than in temperate ones, although the authors suggest this might be related to the rarity of many species in such rich metacommunities.

Dispersal surplus is an opposing process to dispersal limitation. Populations of an organism inhabiting a suboptimal patch can be maintained by migration from a near patch, what is known as source-sink dynamics, or mass effects (Loreau and Mouquet, 1999). These mass effects can lead to increasing species richness, but eventually this overdispersal can produce a metacommunity homogenization. However, disentangling unsuccessful dispersal events related to sink habitats from successful colonization needs from monitoring of populations to acknowledge absence of reproduction of the dispersed individuals in those habitats, a type of study seldom performed in natural aquatic environments. In support of the mass-effects expectations, Brasil et al. (2020) found that during rainy seasons in tropical wetlands, patch connectivity lead to metacommunity homogenization in the phytoplankton from Brazilian riparian lakes. Other instances of mass-effects in aquatic metacommunities may include the migration of amphibians to breeding sites (Sinsch, 1990), floating plants drifting downstream (Gay, 1960), or insect oviposition after massive synchronized emergences such as those produced by mayflies (Sartori and Brittain, 2015).

18.2.2.2 Variation among organisms

Dispersal limitation is considered to differ among organisms and life-cycle strategies (Nathan et al., 2008; Incagnone et al., 2014; Tesson et al., 2015). For instance, plankton dispersal through resting forms must be different from that of active dispersal by amphibians, while birds, with flying abilities, are generally less dispersal limited than fish. In aquatic ecosystems, propagule size and type of dispersal are considered to be key factors for dispersal limitation and therefore metacommunity organization. Some studies in both temperate and tropical regions (De Bie et al., 2012; Padial et al., 2014) found that active dispersers are less influenced by spatial effects than passive dispersers. These works also concluded that propagule size is negatively correlated with dispersal ability in passive dispersers (small propagules can be transported further by wind, water, or animals; Vanschoenwinkel et al., 2008, 2009) and positively in flying active dispersers (bigger animals can fly further). In contrast, fish and amphibians were strongly dispersal limited (De Bie et al., 2012; Padial et al., 2014).

However, such an established pattern between propagule size and type of dispersal has been challenged because of some contradictory results (Astorga et al., 2012; Gálvez et al., 2020). A study in tropical freshwater metacommunities found that the distribution of passively dispersing cladocerans was affected by spatial constraints, even within the same hydrographic basin (Rocha et al., 2017). In addition, Langenheder et al. (2016) found a strong spatial effect in a highly connected bacterial metacommunity. Dias et al. (2016) detected high variability in the role of spatial processes in a zooplankton metacommunity, as did Benito et al. (2018) working on diatoms, whereas Verleyen et al. (2009) found a low influence of dispersal processes on the structure of another diatom metacommunity. In South African rock pools, Vanschoenwinkel et al. (2007) found spatial effects in invertebrates with passive dispersal, but not in active dispersers. Flying active dispersers, such as birds, are important dispersal vectors for microorganisms (Green and Figuerola, 2005; Tesson, 2015; Viana et al., 2016), so that we may expect passive dispersers not to be more strongly limited by spatial barriers compared to birds (although birds could be more efficient, due to their oriented movement toward suitable habitats). It is probable that snapshot surveys, which do not take into account the highly temporal variability of dispersal related with seasonal hydrological cycles, may give rise to misleading results (Rojo et al., 2016; Gálvez et al., 2020). Despite the large variability and apparent disagreement between some studies, all of them remark the importance of dispersal in all taxa, showing how it differs between groups of organisms. This wide variability is summarized in Table 18.1, which will be discussed below.

18.2.2.3 Influence on biological diversity

Dispersal is a key process structuring metacommunities, having a strong influence on their biological diversity. According to metacommunity theory (Fig. 18.5), for a fixed regional species pool, low migration rates imply low local species richness due to dispersal limitation. As migration rates increase, species richness slightly increases, limited by environmental filtering (species sorting). When mass effects overtake the limiting capacity of species sorting, local species richness reaches its peak. Finally, if migration rates are too high, metacommunity is homogenized. Then, dominant species exclude less competitive ones, and species richness declines (Leibold and Chase, 2018). However, we hypothesize that under a relaxation of the competitive exclusion strength or/and allowing certain degree of ecological redundancy in local communities, the reduction in species richness at high dispersal rates ought not to be as sharp as expected from initial simulations (Mouquet and Loreau, 2002). These models, on which Leibold and Chase (2018) figure is based (see Fig. 18.5), assume strong competition and high probability of local extinction when the number of occupied locations is low (Mouquet and Loreau, 2002). So, we suggest that a certain intermediate diversity level above that attained under pure species sorting effects could be maintained with high intensity of dispersal (dashed lines in Fig. 18.5), notwithstanding priority effects, which could also help avoiding or delaying competitive exclusion of less adapted species.

However, not only local species richness, but all diversity components, either alpha, beta, or gamma, are dispersal-dependent in different ways.

TABLE 18.1 **Results of variation partitioning analyses for metacommunities of temperate and tropical wetlands, obtained by different authors for various taxonomic groups.**

Region	Taxon	E|S	S|E	E ∩ S	R	References
Tropical	Bacteria	0–19	0–19	0–16	70–99	Nabout et al. (2009)
Temperate	Bacteria	11–14	2–6	4–6	76–81	Beisner et al. (2006)
Temperate	Bacteria	8–15	1	0	85–90	De Bie et al. (2012)
Temperate	Bacteria	13	10	2	75–77	Langenheder and Ragnarsson (2007)
Temperate	Bacteria	7–16	8–16	1	76	Langenheder et al. (2016)
Tropical	Diatoms	0–13	0–38	0–21	37–97	Benito et al. (2018)
Tropical	Diatoms	12	4	5	77	Gálvez et al. (2020)
Tropical	Diatoms	17–18	6–9	2–4	69–75	Verleyen et al. (2009)
Temperate	Diatoms	7–8	2–3	2–5	84–89	De Bie et al., 2012
Tropical	Phytoplankton	3–10	0–7	0–2	84–92	Brasil et al. (2020)
Tropical	Phytoplankton	4–12	2–6	3–8	77–86	Gálvez et al. (2020)
Tropical	Phytoplankton	20–27	0–7	1–7	66–72	Padial et al. (2014)
Tropical	Phytoplankton	0–13	0–9	n.a.	85–94	Rojo et al. (2016)[a]
Temperate	Phytoplankton	2–7	0–3	1–6	92–94	Beisner et al. (2006)
Temperate	Phytoplankton	7–8	2–3	0–1	90	De Bie et al. (2012)
Temperate	Phytoplankton	27–9	0–6	0–3	73–91	Loewen et al. (2020)
Temperate	Phytoplankton	12	12	2	74	Soininen et al. (2007)[b]

Tropical	Macrophytes	1–4	7–28	0–1	68–90	Padial et al. (2014)
Temperate	Macrophytes	1–16	0–9	2–14	73–93	Alahuhta et al. (2018)
Temperate	Macrophytes	4	6	2	88	De Bie et al. (2012)
Tropical	Rotifera	8	1	9	82	Gálvez et al. (2020)
Tropical	Cladocera	19	0	0	81	Gálvez et al. (2020)
Tropical	Cladocera	31	1	2	68	Rocha et al. (2017)
Temperate	Cladocera	2–6	4	3	87–95	De Bie et al. (2012)
Tropical	Zooplankton	3–11	0–8	0–6	75–95	Brasil et al. (2020)
Tropical	Zooplankton	0–30	0–25	0–15	55–100	Dias et al. (2016)[b]
Tropical	Zooplankton	4–5	1–3	0–1	88–93	Padial et al. (2014)
Temperate	Zooplankton	4–22	0–20	0–6	56–92	Beisner et al. (2006)
Temperate	Zooplankton	4	16	4	76	Soininen et al. (2007)[b]
Tropical	Ostracoda	0–25	1–19	2–11	64–89	De Campos et al. (2018)
Tropical	Ostracoda	13	5	14	68	Gálvez et al. (2020)
Temperate	Ostracoda	22–59	0–17	0–3	41–77	Castillo-Escrivà et al. (2017c)
Temperate	Microcrustaceans	4–44	0–30	7–20	38–56	Gascón et al. (2016)
Tropical	Microcrustaceans	6–19	0–7	0–14	67–77	Gálvez et al. (2020)
Tropical	Macroinvertebrates	1–11	2–15	0–6	69–91	Gálvez et al. (2020)
Tropical	Macroinvertebrates	12–23	0–17	29–54	27–59	Li et al., 2020a
						(*Continued*)

TABLE 18.1 (Continued)

Region	Taxon	E|S	S|E	E ∩ S	R	References
Tropical	Macroinvertebrates	5–41	0–12	0–10	49–90	Li et al., 2020b
Tropical	Macroinvertebrates	6–7	4–12	0–1	79–88	Padial et al. (2014)
Tropical	Macroinvertebrates	5–20	2–15	3–10	60–90	Petsch et al. (2017)[b]
Temperate	Macroinvertebrates	14–22	13–27	9	42–62	Bertin et al. (2014)
Temperate	Macroinvertebrates	2–9	1–8	0–3	86–95	De Bie et al. (2012)
Tropical	Invertebrates	38–47	4–9	0–2	42–57	Vanschoenwinkel et al. (2007)
Tropical	Fish	9–14	7–19	4–19	53–75	Fernandes et al. (2014)
Tropical	Fish	2–7	8–23	1–10	67–76	Padial et al. (2014)
Temperate	Fish	4–8	0–11	0–6	81–83	Beisner et al. (2006)
Temperate	Fish	1	10–11	2	85–87	De Bie et al. (2012)
Temperate	Amphibians	3	11	2	84	De Bie et al. (2012)

We include percentages of variance explained by pure environmental component (E|S), pure spatial component (S|E), and the environment-space overlap (E ∩ S), so as the residuals (R).

[a] *E ∩ S not indicated in original work.*

[b] *Approximated values from graphs due to numeric results not shown in the original work.*

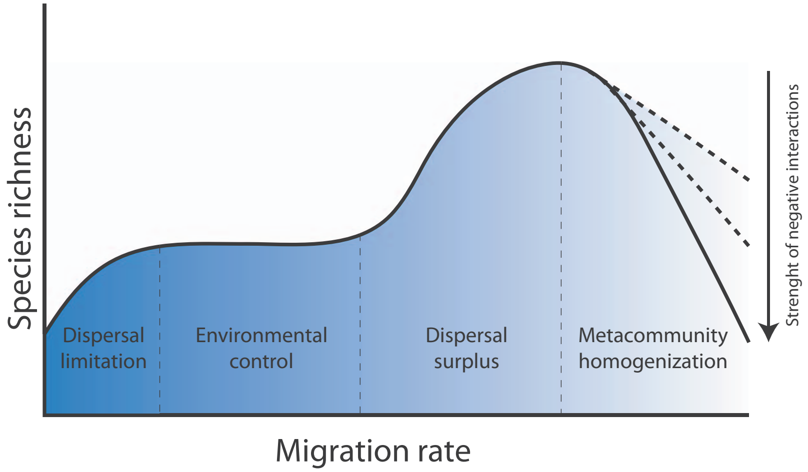

FIGURE 18.5 Theoretical relationship between species richness and migration rate. The rate of biodiversity decay due to metacommunity homogenization might be positively related with the strength of negative interactions and negatively with ecological redundancy (dashed lines). *Based on Leibold, M.A., Chase, J.M., 2018. Metacommunity Ecology. Princeton University Press, Princeton.*

Mouquet and Loreau (2003; Fig. 18.6), using metacommunity simulations (20 communities with restricted capacity and 20 competing species), concluded that, with no dispersal, every patch is occupied by a different species, so that alpha diversity is minimal and gamma and beta diversities are maximal. At intermediate dispersal rates, alpha diversity increases, reaching a peak when the local species composition of each patch includes all components from the regional pool, while beta diversity falls to near zero values. When dispersal increases to maximum values in the models (every individual of every species can go everywhere), alpha diversity is reduced due to negative biotic interactions (competition), and so does gamma diversity due to regional extinctions. Beta diversity continues to be low with small variations, because the same species becomes dominant in every patch. However, as previously suggested in Fig. 18.5, we also consider that if the competitive exclusion effects would be relaxed, we might expect a less sharp decline of local and regional diversity at high dispersal scenarios, although this needs to be tested with further models and empirical data.

The negative relationship between connectivity (i.e., dispersal) and beta diversity is a well-described phenomenon in the literature, also in tropical ecosystems. This correlation has been found in multiple studies and taxonomic groups, including planktonic organisms (Lopes et al., 2014; Brasil et al., 2020) and wetland vegetation (Deane et al., 2017). Regarding alpha diversity, Hartz et al. (2019) showed that well-connected small lakes support higher alpha diversity (species richness) of fish than larger lakes in a set of

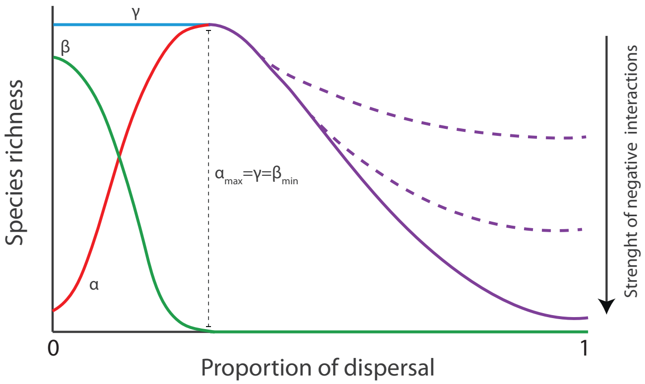

FIGURE 18.6 Theoretical relationship between proportion of dispersal between communities and different components of diversity: Local alpha diversity (red line, α), regional dissimilarity, or beta diversity (green line, β), and regional pool of species, or gamma diversity (blue line, γ). Beta diversity decreases with dispersal. Alpha diversity reaches its peak at intermediate dispersal levels, when $\alpha = \gamma$. At increased dispersal, alpha diversity decreases at the same rate as gamma diversity (purple lines). However, we would expect that at high proportion of dispersal, the decay rate in alpha and gamma diversities might be positively related with the intensity of negative interactions (competitive exclusion) and negatively with ecological redundancy (purple-dashed lines). *Based on Mouquet, N., Loreau, M., 2003. Community patterns in source-sink metacommunities. The American Naturalist 162, 544–557.*

Brazilian coastal wetlands. Bao et al. (2017) also found that vegetation diversity was related to the distance among sampled wetlands: closer wetlands showed higher similarities (lower beta diversities) and higher species richness than more isolated ones, suggesting that dispersal limitation plays a key role in wetland diversity. Similar results were obtained by Bortolini et al. (2014), working on phytoplankton of the Paraná River floodplain. These patterns in alpha and beta diversity were also found by Vanschoenwinkel et al. (2007) in invertebrate communities of South African rock pools. All these results may be representative of the theoretical trends in biological diversities in the first half of Fig. 18.5. However, we found no studies carried out in tropical freshwater ecosystems showing a decay in alpha or gamma diversity at very high dispersal rates (or connectivity). Assuming that connectivity and dispersal rates can be maximal in some ecosystems during the flooding seasons, more effort should be done in order to disentangle if this theoretical expectation proposed by Mouquet and Loreau (2003) is observed from natural patterns, and in tropical wetlands in particular.

18.2.3 Neutral dynamics

The consideration of neutral processes in community ecology has been of paramount importance ever since the early work of Connor and Simberloff (1984), and it has later been also incorporated to metacommunity theory

(Bell, 2000; Hubbell, 2001; Leibold et al., 2004; Leibold and Chase, 2018). Although dispersal-related processes are sometimes included in the neutral perspective (Hubbell, 2001), we have discussed these effects separately in the previous subsection. We separated them not only because of the fundamental influence of dispersal on metacommunity organization, but also because of clear nonneutral effects that can be derived from different adaptations of species to movement, and therefore dispersal (Clobert et al., 2012). In any case, the distribution and coexistence of species, or its lack thereof, can be related to processes other than environmental filtering or dispersal limitation and surplus, including demographic stochasticity and derived ecological drift. In this context, stochasticity does not refer to total randomness but probabilistic and hardly predictable processes, such as birth/death, migration, and speciation/extinction rates (Vellend et al., 2014). Demographic stochasticity can drive changes in metacommunity composition through ecological drift. This ecological drift can be especially important in early stages of ecosystem assembly and through priority effects, leading eventually to differences in the more mature communities (Orrock and Watling, 2010).

18.2.3.1 Historical processes structuring metacommunities

Stochasticity can mask several environmental, spatial, or temporal deterministic processes (Vellend et al., 2014). For example, zooplankton from temporary wetlands will be strongly influenced by apparently stochastic environmental or demographic events. As a consequence, we may wrongly assign to neutral processes some deterministic but difficult to measure environmental effects (Boyce et al., 2006). So, for instance, precipitation intensity could be considered to be stochastic, but it will determine water column depth or organic matter inputs. Also, some organisms will be incorporated from upstream wetlands or displaced downstream from the community during floods, and egg-bank hatching can depend on community structure before desiccation, time-dependent egg-bank deterioration, hatching clues, etc. Colonization rate can also be thought of being stochastic, but it may strongly depend on propagule density or species composition of the potentially colonized patches, so that a colonizing species can be excluded due to priority effects (Vellend et al., 2014).

Nevertheless, demographic stochasticity, especially in small populations or under weak selection, can lead to ecological drift and changes in species richness and composition within and between patches, depending on the spatial scale of this stochasticity (Fukami 2004; Chase, 2007). As a consequence, we can observe species whose distributions or abundances do not respond to niche or dispersal differences, or even find random species coexistence patterns. For example, (Castillo-Escrivà et al., 2017b), while comparing living communities with their corresponding past remains, found that an ostracod metacommunity was highly related to environmental and spatial processes, but its past history (estimated through the paleoassemblage) played a key role too, suggesting that contingent, neutral processes had also structured the recent metacommunity.

Colonization is sometimes considered stochastic. In early stages of the assembly of a community, this stochasticity can have a great influence on future species composition (Fukami, 2015; Rojo, 2020). For example, two similar species of Branchiopoda may play the same ecological function, so that they may compete until one species excludes the other. Thus the colonization by one of these species will fail if the other species is already established in the waterbody. This phenomenon is known as the priority effect, and it can be an essential process when a species colonizes a new patch (Drake, 1991). In early stages of the community (or even in early stages of the hydroperiod in temporary waters), there are also important colonization events of the water column from the egg bank in the sediment (Castillo-Escrivà et al., 2017c). Succession can then progressively lead to differences in interpatch assemblages just because of ecological drift (Segre et al., 2014), sometimes related to stochastic demographic dynamics at the onset, then leading to changes in priority effects and followed by further drift or deterministic processes (selection).

18.3 Assessment of main processes through variation partitioning

18.3.1 The methodological approach

The relevance of these three processes, that is, environmental control (selection), dispersal, and neutral dynamics (ecological drift), in metacommunity organization has received much attention in the scientific literature, but their relative role can be difficult to quantify from empirical data. One of the most used and accepted statistical methods for this purpose is known as variation partitioning analysis (Peres-Neto et al., 2006). Using constrained multivariate ordination methods, this analysis decomposes the variance of observed metacommunity data into different components related to several sets of explanatory variables. As a result, the relative contribution of environmental and spatial variables to the observed variance can be quantified. In this way, variation partitioning analysis can give information about the percentage of species variance explained by pure environmental variables (independent from spatial variables, E|S), purely by spatial variables (independent from environmental variables, S|E), the overlap between environmental and spatial variables (related for instance to spatially structured environmental variables such as climate, $E \cap S$), and the remaining unexplained variance or residuals (Fig. 18.7).

The results of variation partitioning analysis provide information about the role of different processes in metacommunity assembly. The pure

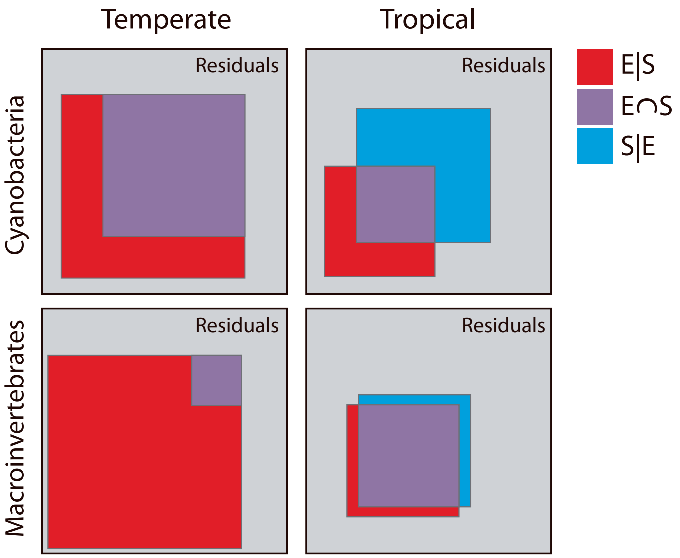

FIGURE 18.7 Diagrams depicting the results of variation partitioning analysis for each of the four metacommunity datasets (2 groups of organisms × 2 geographic settings). For each analysis, the bottom left square (E|S + E ∩ S) is sized to a surface area corresponding to the proportion of metacommunity variance explained by the environmental component (E). The upper right square (S|E + E ∩ S) represents the proportion of metacommunity variance explained by the spatial component (S). Both squares together (E + S) account for the total explained variance of the metacommunity by the explanatory variables. E|S = pure environmental component, independent from space. S|E = pure spatial component, independent from environment. E ∩ S = overlap between environmental and spatial components. Residuals (gray) = unexplained metacommunity variance. The larger square represents the metacommunity total observed variance (both explained or not; E|S, S|E, E ∩ S, and Residuals). See text for further explanations. *Based on unpublished data for variation partitioning of copepods and amphibians from temperate and tropical ponds from Gálvez, Á., Peres-Neto, P.R. Castillo-Escrivà, A., Bonilla, F., Camacho, A., García-Roger, E-M., et al., 2021. Pond metacommunities from bacteria to birds: overall stronger environmental than spatial effects on most taxa and in Mediterranean than in tropical habitats. BioRxiv 2021.03.24.436596*

environmental component is often associated to species sorting (Cottenie 2005), that is, selection or environmental control. The pure spatial component is related to dispersal processes (Cottenie 2005). The overlap between these two components is sometimes assigned to spatialized environment (such as climate, or other environmental variables following a spatial pattern), but cannot readily be disentangled from dispersal processes statistically associated to environmental gradients. Finally, the residuals, or unexplained variance, are usually related to unmeasured environmental variables (both abiotic and abiotic factors), temporal dynamics (short and long-term unknown history of the assemblages), or stochasticity (ecological drift), so that neutral processes are probably essential elements in this component of the variance (Legendre et al., 2009). Historical effects, due to the difficulty of measuring them, have been set aside in many metacommunity studies, unless repeated samples in time are available. However, Castillo-Escrivà et al. (2017b), using remains of individuals previously occupying an ostracod metacommunity, found strong pure temporal (historical) effects when explaining variation in an ostracod metacommunity; this may be related in part to priority effects. More recently, Oliveira et al. (2020) showed that the best predictor of a tropical fish metacommunity was not space or environment but information on its composition in the previous year. Pure temporal effects can also be significant in tropical metacommunities, although environmental and spatial effects are usually stronger (Gálvez et al., 2020).

18.3.2 Environmental versus spatial effects

18.3.2.1 Influence of the spatial scale and the regional species pool

The relative importance of environmental (E) and spatial (S) components provide information about which processes are dominant in shaping metacommunities, from environmental control (i.e., selection, accounted for by E|S) to dispersal (S|E) (Cottenie, 2005). Residuals can be assigned to neutral processes, but also to unknown dispersal effects, or to unmeasured environmental factors. Nevertheless, these three components (S, E, and residuals) are not totally independent from one another. The relationship between dispersal and environmental control (as species sorting) is particularly well studied (Fig. 18.8). In the context of high dispersal (or small spatial extent), we expect a strong influence of the spatial component and a low percentage of explained variation by the environmental component, due to intense mass effects. At an intermediate range of dispersal ability (or an intermediate spatial scale), species sorting is expected to be dominant, as the environmental component dominates over the spatial one because mass effects are no longer relevant, but there is enough dispersal for organisms to arrive to those habitats with the best conditions to which they are fitted. Finally, at large spatial extents, or with low dispersal ability, dispersal limitation has a strong influence shaping metacommunities, and the spatial component dominates again over the environmental effects (Heino et al., 2015).

Environmental and spatial effects, together with the residuals, must account for the total percentage of metacommunity variance observed. For this reason, increased environmental or spatial effects must necessarily imply a decrease in the residual proportion (and vice versa). The size of the regional pool of species (gamma diversity) is relevant in these analyses: when it increases (increasing variation in community composition), then the unexplained variance (residuals) also increases and, as a consequence, the proportions of spatial and environmental explanation decrease (Leibold and Chase, 2018). Thus the

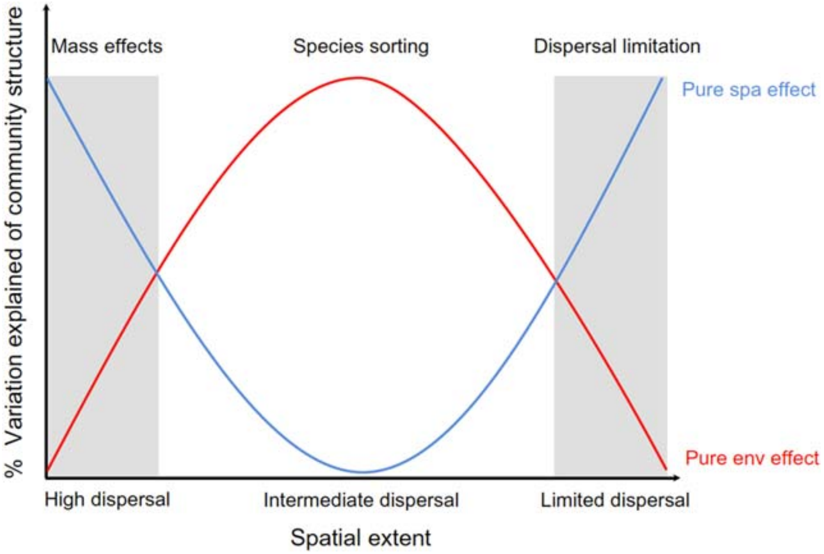

FIGURE 18.8 Hypothetical relationship between spatial extent (and consequently dispersal capabilities) and the percentage of variance explained by pure environmental and spatial effects. The dominance of one or another, according to spatial extent and dispersal limitation, gives information about primary processes structuring metacommunities (dispersal limitation, species sorting, and dispersal surplus or mass effects). *From Heino, J., Melo, A.S., Siqueira, R., Soininen, J., Valanko, S., Bini, L.M., 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. Freshwater Biology 60, 845–869.*

regional pool of species should also be taken into account when comparing variation partitioning among different metacommunities.

18.3.2.2 Tropical versus temperate metacommunities

All the patterns in metacommunity ecology, although gathered from studies mostly carried out at intermediate latitudes, are also relevant to metacommunities in tropical wetlands (see Wasserman and Dalu, 2022, Chapter 1). However, there is a scarcity of information regarding the relative role of space and environment in structuring aquatic tropical metacommunities, although some differences have been observed (or can be predicted) between tropical and temperate wetlands. Before disentangling the relevance of these processes, we would like to note some important differences between these two types of aquatic ecosystems. Climatic seasonality is an important dynamic factor driving major environmental changes of water bodies. In temperate regions, it implies changes in precipitation through time but also wide fluctuations in temperature and light intensity, whereas the climatic seasonality in tropical areas produces changes mostly in precipitations rather than insolation or temperature (Coen, 1983). As a consequence, the hydroregime and the amount of water inflow, rather than temperature variation, will strongly shape tropical aquatic ecosystems, and this temporal dynamic becomes crucial when analyzing tropical metacommunities (Rojo et al., 2016; Brasil et al., 2020).

Considering the large temperature variations in temperate wetlands, we might expect a higher temporal variability of the relative role of environmental versus spatial factors than in tropical ones, but the large hydrological effects of the flood pulse in tropical wetlands might strongly affect connectivity and therefore counteract the reduced temperature variation effects. The direct comparison between temperate and tropical ponds (Gálvez et al., 2021; Fig. 18.7) shows the expected prevalence of environmental control in temperate water bodies, and slightly higher dominance of spatial control in tropical ones, for several groups of organisms, but the differences are minimal.

The large environmental gradients (at least regarding temperature fluctuations) present in temperate regions are expected to produce stronger species filtering effects than in tropical wetlands. However, other influential environmental factors can also widely affect tropical water bodies, including dissolved oxygen concentration, water transparency, pH, or salt and nutrient concentrations (Roldán and Ramírez, 2008; Bleich et al., 2009). One remarkable element that gives rise to large differences between tropical and temperate wetlands is the abundance and species richness of floating vegetation in the former, so that many organisms are adapted to microhabitats associated with these macrophytes or use them as basic substrate or refuge (Wantzen et al., 2016). Environmental control is therefore common also in tropical wetlands (Table 18.1). For example, Rojo et al. (2016) found a significant influence of electric conductivity (a surrogate for salt content), dissolved oxygen concentration, macrophyte cover, and water transparency shaping phytoplankton metacommunities. Similarly, De Campos et al. (2018) found ostracod species distribution in a tropical floodplain metacommunity to be significantly affected by dissolved oxygen concentration, salt content, macrophyte species richness, pH, and water temperature. Additionally, Brasil et al. (2020) found a significant influence of salt content, water transparency, pH, and water temperature on plankton assemblages, but not of dissolved oxygen concentration. Also Rocha et al. (2017) observed significant effects of dissolved oxygen concentration, pH, water temperature, electrical conductivity, and water transparency, among others, on macrophyte-associated cladocerans. Therefore important limnological variables, such as dissolved oxygen and salt content, seem to strongly influence metacommunity structure in tropical water bodies.

Despite the importance of temporal dynamics (Magurran and Henderson, 2010; Castillo-Escrivà et al., 2020), snapshot surveys dominate the literature on variation partitioning in aquatic metacommunities. Studies including temporal changes and focused on tropical wetlands are even scarcer. However, whenever seasonal variability is considered, the importance of connectivity during rainy seasons due to flood pulses is often highlighted (Wantzen et al., 2016), although some contradictory results have also been obtained. Thomaz et al. (2007) found an increased similarity between communities of floodplain systems during rainy seasons, and Brasil et al. (2020), studying multiple wetlands from close river basins, found pure spatial effects to have less influence during the rainy season in a floodplain phytoplankton metacommunity. In contrast, Rojo et al. (2016), studying phytoplankton metacommunities from Mesoamerican wetlands, found just the opposite, a dominant spatial effect on phytoplankton from temporary tropical wetlands during the rainy season. They suggested a lag between sampling and homogenization, so that spatial patterning would have been produced earlier due to isolated hatching. Nonetheless, all of these contributions (Thomaz et al., 2007; Rojo et al., 2016; Brasil et al., 2020) agreed on the heterogenization of local communities after isolation during the dry season, quantified as an increase of pure environmental effects (stronger selection and consequently species sorting) in variation partitioning analyses.

18.3.2.3 Differences according to dispersal ability

As previously discussed, De Bie et al. (2012), according to results on variation partitioning analyses of temperate ponds, proposed the idea that good dispersers are more environmentally controlled than bad dispersers, which are more spatially controlled. They assumed that propagule size and dispersal type (active or passive) are key traits for dispersal, so that active dispersers with larger propagules should disperse better than those with small propagules, while in passive dispersers, those with small propagules would have higher dispersal capabilities. However, few works besides Padial et al. (2014) have found similar results in tropical wetland metacommunities. When Dias et al. (2016) studied zooplankton during rainy and dry seasons for two consecutive hydrological years, they obtained dissimilar results between years. Nevertheless, they clearly found species sorting controlling zooplankton metacommunities of small organisms (amoebae and rotifers), and a significant spatial influence in crustaceans (cladocerans and copepods). This is somehow expected assuming the (controversial) idea of increased dispersal ability of smaller organisms with passive dispersal (De Bie et al., 2012). However, Brasil et al. (2020) found significant spatial effects even in small-bodied zooplankton during the dry season, in agreement with Thomaz et al. (2007), but no pure spatial effects in larger-bodied zooplankton, contrary to the findings of Dias et al. (2016). The idea that spatial processes may affect the structure of metacommunities of all taxonomic groups, no matter their body size (and their supposedly related dispersal ability), was supported by De Campos et al. (2018), who found no differences between crawling and swimming tropical ostracods, and even lower pure spatial effects in larger-bodied species.

As for nonflying active dispersers, all authors agree on the important role of the spatial component, due to dispersal limitation. When studying amphibian beta diversity in the Pantanal, Moreira et al. (2017) found spatial variables significantly driving differences between communities (during the rainy season), suggesting dispersal processes such as mass effects may play an important role in amphibian metacommunity structure. In addition, interwetland landscape can also influence amphibian metacommunity (Gray et al., 2004). As observed by Rojo et al. (2016) for phytoplankton, Fernandes et al. (2013) found stronger spatial effects during the rainy season and higher environmental effects during the dry season for fish metacommunities from tropical floodplains.

All these studies agree on the key role of hydrology and dispersal processes on tropical wetland metacommunity structure, increasing connectivity and dispersal rates during rainy seasons. However, there is no clear pattern for the relative role of space and environment in structuring wetland metacommunities (other than spatial scale effects), but both processes, species sorting and dispersal, seem to be essential (Soininen et al., 2007; Declerck et al., 2011; Gascón et al., 2016; Alahuhta et al., 2018).

18.3.3 Unexplained variation and further limitations

Due to the larger regional pool of species in the tropics, we may expect a higher percentage of unexplained variation when analyzing tropical wetland metacommunities (Leibold and Chase, 2018). Therefore a higher relative influence of neutral, stochastic processes (so as probably also unmeasured biotic interactions) can be predicted for tropical systems. Indeed, residuals usually represent high percentages of the total variation, with wide differences among organisms, in tropical metacommunities: 70%–99% (mostly around 90%) for bacteria (Nabout et al., 2009), 85%–94% for phytoplankton (Rojo et al., 2016), 75%–95% for zooplankton (Brasil et al., 2020), c.70% for cladocerans (Rocha et al., 2017), 70%–90% for ostracods (De Campos et al., 2018), 30%–90% for macroinvertebrates (Li et al., 2020a), or 50%–75% for fish (Fernandes et al., 2014). In a multitaxon approach, Padial et al. (2014) found residuals ranging from approximately 60% in phytoplankton, to more than 90% in zooplankton. Gálvez et al. (2020), in another multitaxon study including temporal dynamics in neotropical ponds, found 67%–91% of residuals. In temperate aquatic metacommunities, which have been studied more intensely and for a longer period of time, nonconcordant results have been recorded. For example, a multitaxon study by Beisner et al. (2006) showed residuals ranging from 60% in zooplankton to 90% in phytoplankton, while residuals in De Bie et al. (2012) were always higher than 83%. There is a lack of comparative studies using the same methodology in similar spatial scales across biogeographic regions, so it is difficult to find a pattern in the residuals. Nevertheless, some studies show lower percentages of residuals in temperate metacommunities compared to those found in tropical metacommunities: 75% in bacteria (Langenheder and Ragnarsson, 2007), 73%–91% in phytoplankton (Loewen et al., 2020), 38%–56% in microcrustaceans (Gascón et al., 2016), or 42%–54% in macroinvertebrates (Bertin et al., 2014). More examples of variation partitioning analyses from temperate and tropical regions are compared in Table 18.1.

It is difficult to establish general patterns on how relevant are environmental, spatial, and neutral processes, due to disparate results between studies in similar ecosystems, even working within unique biogeographic regions and taking into account ecological traits such as dispersal mode. However, in spite of the big fluctuations in results observed in metacommunities of even the same organism group and biogeographic region, it seems that environmental processes dominate over spatial processes (see Table 18.1). Can we then expect that all species in the same ecological guild are equally affected by niche, dispersal, and neutral processes? Not all species appear in the same frequencies and abundances. Actually, some species, known as core species, appear in high abundances and frequencies, and this commonness is related to their permanence in time. Satellite or rare species are more prone to extinction and their persistence over time is more dependent on dispersal and drift (Gaston, 1994; Magurran and Henderson, 2003). These rare satellite or transient species are not always detected in snapshot surveys. As a consequence, they will probably inflate the residual proportion in variation partitioning analyses. In tropical ecosystems, we could expect a higher number of satellite species and, in addition to the above-mentioned higher species richness, residuals would then represent a higher proportion than in temperate ecosystems.

In conclusion, environmental control, dispersal, and drift together contribute to metacommunity organization. Even though there are no defined general patterns related to the influence of these processes among organisms, it seems clear that local habitat characteristics and hydrology play a key role in structuring metacommunities in tropical wetlands. Hydrology has an important influence on dispersal and environmental processes, inducing deep changes in interwetland connectivity and regional environmental heterogeneity. As a consequence, not only dispersal rate but also local environmental variables experience wide temporal changes, producing marked differences between rainy and dry seasons.

18.4 Conservation implications

One of the outcomes of metacommunity ecology most relevant to conservation biology is the remarkable role of dispersal on metacommunity structure (see Bredin et al., 2022, Chapter 19). However, despite this relevance of dispersal and connectivity, we must not forget that local and regional environments are also essential elements for metacommunity conservation practice.

Thus once local environments are properly preserved or restored, a successful management of protected areas must consider connectivity between patches at larger scales through regional environment management (Amezaga et al., 2002). In a wetland context, this connectivity needs to be more or less explicit according to the organism group. Some organisms, such as plankton, with high dispersal ability, will probably not suffer much dispersal limitation from human impacts. Birds, except for large geographical barriers, are not expected to be highly spatially limited. However, for many freshwater fish species, connectivity loss is a worldwide major threat (Gido et al., 2015); but also connectivity gained through artificial corridors or human transport may allow invasive predators or competitors to colonize new basins and reduce native populations (Clavero and García-Berthou, 2005; see Pegg et al., 2021, Chapter 16). In organisms with amphibian lifestyles, such as amphibians and many aquatic insects, they will not need such an explicit connection as fish do, but their dispersal capabilities will strongly depend on interpatch terrestrial habitat conditions (Ribeiro et al., 2019).

There is a trade-off between increasing and reducing connectivity for conservation. *A priori*, some degree of connectivity is necessary to prevent local stochastic extinctions, allowing patch colonization. However, despite maintaining connectivity between patches is an important element in metacommunity management, we should not forget the potential for habitat homogenization driven by too high dispersal rates (Mouquet and Loreau, 2003). In addition, high connectivity can be a concerning issue when effective competitors, predators, and pathogens, either native or invasive, could be a threat to some species of conservation concern. When an invasive species is established, increasing connectivity between patches can lead to higher migration and colonization of connected patches, producing a short-term increase in alpha diversity, but a long-term biodiversity loss (Crooks and Suarez, 2006). As shown by Harding et al. (2012), increased migration in host-pathogen metapopulations can produce regional host extinction due to the spread of the pathogen. Finally, connectivity is necessary to properly preserve metapopulations of several species, but we must not forget that habitat fragmentation and isolation is also a source of speciation (e.g., in freshwater fish, Dias et al., 2013), and isolation is necessary for effective conservation of these species. Indeed, fragmentation *per se* does not seem to be as detrimental to biodiversity as formerly thought; habitat destruction and the reduction of undisturbed habitat area is the most negative outcome of the ongoing fragmentation of natural environments (Fahrig, 2017).

In the current and future humanized world, where habitat loss is one of the major threats to biodiversity, artificial wetlands, such as rice fields, could be important elements in maintaining wetland area (even if disturbed), connecting more natural wetlands of high conservation value, and as transition or buffer ecosystems between terrestrial and aquatic habitats. Rice fields can therefore host species that are at risk due to human development and urbanization. For example, Holzer et al. (2017) found that Vietnamese rice paddies are refugia for many amphibians, which were being displaced by rapid human urbanization and habitat alteration. Nevertheless, although rice fields can be an interesting option in metacommunity management of tropical wetlands in an anthropized landscape, we must take into account that rice fields can also facilitate naturalization of exotic species, in temperate regions and elsewhere (Valls et al., 2014; Smith et al., 2018).

Conservation science has traditionally focused on preserving patches with high species richness or unique organisms, as opposed to patches with high similarity (in other words, protecting those patches with the highest alpha and beta diversity). However, under the metacommunity framework, Economo (2011) highlighted that the persistence of species at large spatial scales is an important element for regional biodiversity conservation. When removing a low-dissimilar patch, cascade effects could drive to extinctions at the remaining metacommunity. Consequently, Economo (2011) suggests that increasing the number of protected (and connected) areas is more important in the long term than protecting a small number of patches with high diversity representation.

In certain cases, especially regarding conservation of species with particular ecological needs, a metapopulation rather than a metacommunity approach might also be effective. For example, conservation of large mammals suffering from habitat fragmentation needs a large-scale management that is not necessary in conservation of organisms such as micromammals or insects (Elmhagen and Angerbjörn, 2001). In this metapopulation framework, patch size, dispersal, and connectivity are essential (as they are in metacommunity ecology), giving rise to different metapopulation models with direct implications on management and conservation (Hanski and Gyllenberg, 1993). However, provided that knowledge on interacting species with the species of interest is available, we believe that a metacommunity approach to conservation of such key species is more integrative and can better deal with interactions that might become unexpected when not included in single-species metapopulation models.

In conclusion, the conservation implications of metacommunity theory can be summarized in five statements proposed by Bengtsson (2009): (1) Control local environment via management; (2) landscape management and not only local management; (3) keep regional environmental heterogeneity; (4) increase regional connectivity avoiding landscape homogenization; and (5) keep disturbance regimes close to natural. However, there is a lack of general knowledge about direct and explicit implications of metacommunity ecology in conservation biology, and most of its proposals are purely theoretical. Nevertheless, metacommunity theory offers an excellent framework to forthcoming applied studies which integrate local and regional processes, hopefully also including temporal processes, and giving rise to new approaches in environmental management and conservation.

18.5 Conclusions

Even though metacommunity ecology is still in its infancy, its theoretical assumptions and predictions are highly relevant to the study of aquatic ecosystems. An increasing number of studies on tropical wetlands show that environmental control has a strong influence on metacommunity structure. In addition, dispersal limitation and dispersal surplus, which can be readily studied in tropical freshwater bodies such as river floodplains during rainy and dry seasons, also have a crucial effect on metacommunity homogenization and heterogenization and therefore on beta diversity. Different studies using variation partitioning analysis suggest a major role for neutral processes, even higher than in temperate regions, suggesting that stochasticity is fundamental for tropical metacommunity assembly. Finally, metacommunity theory can have interesting implications for wetland conservation; by confirming the importance of local environmental management and also by proving the significance of regional management and the essential role of dispersal for metacommunity conservation.

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Section 3

Monitoring, conservation and management

Chapter 19

Vegetated wetlands: from ecology to conservation management

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19.1 Introduction

The heterogeneity of wetlands globally has evoked a range of descriptions and classifications. These encompass shallow permanent lakes, palustrine, riverine, lacustrine marshy areas, forested areas that are permanently wet or periodically flooded, ephemeral and endorheic water bodies, floodplains that can alternate between wet and dry phases, montane bogs, and a variety of coastal habitats from lagoons to mangroves (see Wasserman and Dalu, 2022, Chapter 1). These ranges of habitat types are populated by an even more diverse array of species, whose presence is influenced by natural features of climate and biogeography and, increasingly, effects of human disturbance and pressures. The resulting mosaic of wetland habitats makes for extraordinarily interesting ecology, but associated difficulties for policy and management. In the tropics these aspects can be further amplified by limits in knowledge of wetland form and function, and frequently a deficit of policy and resources for conservation management. Linking ecology to conservation management of tropical wetlands requires, therefore, the cognizance and appreciation of scales from species autecology to global policy goals and their instruments.

A long evolutionary history has promoted high species diversity in tropical ecosystems to exploit available ecological niches (Gaston, 2000), with

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many lakes, rivers, and floodplains rich in endemic species. While the understanding of ecological function of tropical wetlands has expanded considerably in the last 50 years, there remain many knowledge gaps on species distribution, community ecology, ecosystem function, and conservation biology compared with terrestrial systems (Darwall et al., 2011; Tisseuil et al., 2013). Assumptions of ecology based on traditions of theory and practice developed in temperate ecosystems cannot be assumed to be simply transferred to tropical ones. For many tropical wetlands, basic inventory of habitats and species remain rudimentary, and their diversity has hindered basic description of wetland types. This makes defining and communicating management goals all the more difficult (Junk et al., 2014).

Much work remains to be done for understanding the ecology of tropical wetlands, such as species interactions and energy transfer. For many tropical wetlands, and in contrast to, especially, many high latitude northern temperate ones, seasonal hydrology and especially flood pulses, are of major importance for their form and function. Seasonal inundation of floodplains and ephemeral lakes support high primary and secondary production of both obligate aquatic species and terrestrial species relying on that production. This high productivity has wide implications for ecosystem function and stability, affecting both the capacity to resist pressures and providing resilience to ecosystem change. Transitional hydrological zones (or ecotones) often support high species richness resulting from changing hydrological gradients. In core areas of wetlands, subject to a more constant environment, biodiversity can be comparatively reduced compared with the surrounding transitional or terrestrial landscapes (Piedade et al., 2022, Chapter 7; Job and Sieben, 2022, Chapter 2).

Limits on the extent of knowledge of tropical wetlands apply also to social−ecological dimensions and their links with conservation management (Dowie, 2009; Sarkar and Montoya, 2011). The link between people and wetlands, as outlined in the Ramsar 2008 Changwon Declaration (Ramsar Convention Secretariat, 2010a), is often more critical for local livelihoods in the tropics than in many temperate zones. The character of many tropical wetlands, comprising a mosaic of natural and human-managed habitats across water-terrestrial transitions (Box 19.1), has profound effects on their management and conservation.

BOX 19.1 Proposed definition of wetlands of Brazil (Junk et al., 2014).

Wetlands are ecosystems at the interface between aquatic and terrestrial environments; they may be continental or coastal, natural or artificial, permanently or periodically inundated by shallow water or consist of waterlogged soils. Their waters may be fresh, or highly or mildly saline. Wetlands are home to specific plant and animal communities adapted to their hydrological dynamics.

Seasonal wetland-terrestrial transitions support multiple livelihoods and are of immense ecological value for species life cycles and ecosystem processes. Wetlands are now broadly understood as socio-ecological systems (Berkes and Folke, 1998), requiring considerations of ecology and management from a perspective that integrates human use and value with biogeochemical processes and habitat description. This approach recognizes the many ecosystem services wetlands provide (Millennium Ecosystem Assessment, 2005; Russi et al., 2013) and the interactions that occur between ecological and social processes (Kumar et al., 2020).

Wetlands provide four commonly recognized socio-ecological services, summarized as:

Provisioning services: At the local level, human communities across the tropics rely directly on provisioning services from wetlands for fish, wildfowl and other wildlife, construction material, thatch, mats and furniture, medicinal plants, crafts and paper making (dating back to ancient Egypt, and the etymon for the word paper), and fuel from burning e.g., papyrus stems. Wetlands are naturally a source of water supporting livelihoods, water for domestic purposes, and navigation. Many wetlands act as important nursery grounds for commercial or artisanal fish stocks. The fringes of wetlands, or seasonally inundated wetlands, are used for both intensive and traditional extensive stock grazing and growing crops, often mixed together (Arias-Hidalgo et al., 2013; Wood et al., 2013).

Regulating services: Regulating services provided by wetlands include wastewater purification, recharging aquifers, water storage, stream-flow regulation, and flood mitigation. Permanent wet tropical wetlands provide evaporative cooling of regional importance for climate patterns (Taylor et al., 2018).

Cultural services: Cultural services include ecotourism, knowledge and understanding of ecology and biogeochemistry, and spiritual importance and relaxation (Maltby and Acreman, 2011).

Support services: The so-called supporting services (Millennium Ecosystem Assessment, 2005) are mainly through providing habitat and processes such as nutrient recycling, and are closely intertwined with the other services. Views on support services can overlap with those on regulating services.

In Africa, the steady decline of papyrus swamps, for example, has negative effects on ecosystem regulating services (Uwimana et al., 2018), biodiversity (Maclean et al., 2014), and a range of provisioning services affecting local livelihoods in many ways (van Dam et al., 2014). Modifications of floodplains can disrupt ecosystem energy flows and provisioning services with effects far beyond the floodplain itself (Junk, 2007; Taylor et al., 2006). A direct physical loss of wetland by human encroachment of formal or informal settlements can enhance flooding of both settlement and downstream areas. Infestation of alien plants and animals can have a dramatic effect on a range of ecosystem services (Cook et al., 1996; Horgan et al., 2014; Shanungu, 2009).

Despite providing so many benefits, tropical wetlands are, however, often perceived to be of low value, and even as detrimental for agriculture or human settlement. In contrast to such ideas, there are increasing examples where conversions of wetlands and floodplain habitat increases risk of, potentially catastrophic, impact on humans (Falkenmark et al., 2007; Gunnell et al., 2019). The benefits of wetlands for conservation and human well-being are well recognized (Russi et al., 2013). The total value of all wetlands was recently valued at US$ 47.44 trillion, and of swamps and marshes at US$ 6.5 trillion a year (Davidson et al., 2019b). While estimating value in purely economic terms can miss important cultural and existence value, there is no doubt the ecosystem services wetlands provide are of immense benefit to human well-being and of direct use for millions of people (Xu et al., 2020). Nevertheless, a utilitarian view of wetlands as service providers does not automatically align with their conservation. Good wetland management takes account of both wetland ecosystem services and the broader dimension of habitats and species protection. Achieving that balance has been difficult. Despite widespread governmental agreement on protecting water resources, the decline in extent and quality of inland waters is of major global concern (Davidson et al., 2020; Tickner et al., 2020). The steady loss of extent and quality of wetlands diminish ecosystem service provision.

This chapter describes a number of important considerations for the conservation and management of tropical wetlands. To illustrate key principles we have focused primarily on tropical marshes and their floodplains. Section 19.2 provides an introduction to the tropical wetland resource, the Ramsar Convention as the primary international policy for the protection of wetlands, and the Sustainable Development Goals (SDGs) (https://sdgs.un.org) [and Convention of Biological Diversity (CBD) (https://www.cbd.int)] that integrate wetland monitoring in holistic frameworks, together with the character of wetlands. Section 19.3 introduces the challenges and methods used for the delineation of wetlands, and in Section 19.4, those methods related to the assessment of wetland structure and response to human pressures. Section 19.5 introduces recommended approaches to wetland management, whereas Section 19.6 takes a step back to consider the reality of management under variable availability of financial and human resources, and using three African wetlands to illustrate some key points. Section 19.7 provides a summary and considerations for the future.

19.2 Tropical wetland resources

19.2.1 Ramsar Convention

The international Convention on Wetlands (www.ramsar.org), commonly known as The Ramsar Convention dates from 1971, and currently has 171 signatories, each of whom commits to wetland protection and the principle of "wise use of wetlands" (Box 19.2). Each signatory that is a Member State is required to have designated at least one wetland of international importance within its territory.

Subsequent international agreements on protection of wetlands have been afforded through a range of international agreements and conventions (Davidson, 2018). Many countries, including those in the tropics, have national legislation or specific wetland policies (Bonells, 2018; Finlayson and Gardner, 2018). It is important, however, to recognize both the importance and limitations of international and national policies for wetland protection. The Ramsar Convention has raised the profile of the importance of wetlands, with a permanent secretariat producing extensive guidance on the wise use of wetlands. The Ramsar Convention connects with other international policy aspirations, but each member state is responsible for developing their own national policies for wetland conservation. In the European Union this is guided by legally binding regional law agreed across Member States, such as Directive (92/43/EEC) on Conservation of Natural Habitats and of Wild Fauna and Flora, and its interaction with the Water Framework Directive (WFD; 2000/60/EC) (Irvine, 2009).

Throughout this chapter, we draw on the Ramsar Convention and its guidance as an international benchmark for the protection and management of wetlands. However, sites designated under the Ramsar Convention comprise a very small proportion of the total wetland resource in the tropics. While Ramsar guidance is a very important resource for conservation and management, the opportunities to apply that in many tropical wetlands remain limited. Indeed, apart from some notable exceptions, wetlands are in practice poorly protected in many tropical countries. Finlayson (2012) reported that less than 50% of signatories to the Ramsar Convention have developed National Wetland Policies and/or reported activities agreed to in the Ramsar Strategic planning. Overall, the loss and degradation of wetlands accelerated between 2010 and 2017, including Ramsar sites (Davidson et al., 2020). The situation is made worse in that data on habitat extent and distribution of species in tropical vegetated wetlands are often sparse or unknown, even in Ramsar sites and those non-Ramsar sites recognized as Key Biodiversity Areas (KBAs) (Garcia-Moreno et al., 2014).

BOX 19.2 Definition of wise use of wetlands.

Wise use of wetlands is the maintenance of their ecological character, achieved through the implementation of ecosystem approaches, within the context of sustainable development.

http://www.ramsar.org/handbooks4/

From the start, the Ramsar Convention was constrained by both the generality of wetland definition and the voluntary nature of protection. The Ramsar Convention's definition of wetlands (Article 1) is as "areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres." This breadth of definition has hampered the conservation of wetland resources in general, and particularly vegetated wetlands that transverse open-waters to terrestrial zones. The seasonally fluctuating terrestrial—aquatic nature of many wetlands has inhibited adoption of a holistic view of wetlands, for both policy and conservation management (Dickens, 2003; Sullivan and Fisher, 2011). One effect of this is that the transitional zones are very often treated as terrestrial habitats that are periodically wet rather than distinctive wetland-associated habitats, or habitats in their own right. Junk et al. (2014) captured the problem well with "The fact that most inland wetlands are subject to extended dry periods implies the risk that developers and politicians regard these areas as permanently dry habitats in which natural flooding is not considered an inherent attribute of the system, but rather a catastrophic event that must be avoided or controlled." Similarly, effects of land use changes upstream of wetlands are often viewed as external pressures rather than as an inherent feature of wetland conservation and management.

19.2.2 Wetlands in other international conventions

While the home of international wetland management is undeniably within Ramsar, wetlands also find prominence in several other key policy instruments:

1. The Agenda 2030 on Sustainable Development, the United Nations (UN) initiative that includes SDG 6.6.1 "percentage of change in water-related ecosystems extent over time," and SDG 15.2.1 which seeks to establish protection for wetland biodiversity as well as other ecosystems.
2. The Convention on Biological Diversity (CBD) and its Aichi Targets, included many aspects of wetland monitoring and management. This is in the process of being replaced by a new framework of targets and indicators for monitoring.

19.2.3 Overview of the character of tropical vegetated wetlands

A number of wetland typologies and classification schemes have been developed that can be applied to tropical vegetated wetlands (Brinson, 1993; Cowardin et al., 1979; Finlayson, 2018; Mitsch and Gosselink, 2015; Semeniuk and Semeniuk, 1995; Tiner, 2009). Others have also been developed for specific tropical regions or that can be applied to tropical wetlands

(Araújo et al., 2002; Gopal and Sah, 1995; Junk et al., 2011, 2014; Ollis et al., 2015; Ricaurte et al., 2019). Many wetland habitats are dependent to a greater or lesser extent on groundwater, that include wetland riparian vegetation along streams and where groundwater rises to the surface as springs (Eamus et al., 2016). An overview of tropical wetland hydrology and soils is provided by Deemy et al. (2022, Chapter 3). Often, habitat types form mosaics of surface growing plants rooted in wetland soils or floating mats, emergent semiaquatic species, shallow water species, and permanent or seasonal pools. They are often dissected by permanent, seasonal, or ephemeral rivers. Across the tropics, similar habitats might occur within different ecosystem types. For vegetated wetlands, classifications to guide management and policy needs should account for both ecosystem type and, nested within that, habitat type. An example of such an ecosystem type would be papyrus-dominated wetland. An example of habitat type would be shallow floating vegetation.

The Ramsar Classification System of wetlands (Finlayson, 2018) lists 42 different types, which reflect the very broad approach of the Convention. The very general vegetated wetland descriptions do not however distinguish between tropical and temperate climates. There is recognition of the connectivity with floodplains, but not a focus on them. For non-montane inland natural and semi-natural tropical vegetated and wetlands, the Ramsar list of 42 is reduced to six types (Table 19.1). An additional type applicable to tropical vegetated wetlands is “seasonally flooded agricultural land” that includes “intensively managed or grazed wet meadow or pasture.” In many tropical wetlands these areas, subject to a range of management intensities, are important for changing seasonal patterns of use. When intensively managed, however, they can sever ecological and hydrological connectivity within the wetlands’ contributing catchment and with downstream impact on these processes.

The focus of this chapter is on (1) inland tropical wetlands characterized by permanent or seasonally water-dependent vegetation, lacking tree cover, and commonly recognized as vegetated or marsh-like. This includes wetlands that fringe larger rivers and lakes, but not the lakes or rivers themselves; and (2) floodplains that connect to permanently wet areas. The principles of many aspects described in the rest of the chapter also apply to other categories of vegetated wetlands. Confusion in the use of terms abound. A swamp is mostly considered as a wetland with extensive tree growth, as is common throughout the Amazon basin. A marsh is commonly viewed as a wetland dominated by herbaceous vegetation, or tall growing plants such as rush (Juncaceae) and sedge (Cyperaceae) or grasses (Poaceae). Throughout Africa, wetlands dominated by the sedge *Cyperus papyrus* are commonly referred to as papyrus swamps,

The Ramsar typology and classification scheme that covers inland vegetated wetlands is based on quite general vegetation character and hydrology.

TABLE 19.1 Ramsar classification of natural and seminatural inland vegetated wetland types.

Ramsar wetland type code	Description of wetland type
Tp	Permanent freshwater marshes/pools; ponds (below 8 ha), marshes and swamps on inorganic soils; with emergent vegetation water-logged for at least most of the growing season.
Ts	Seasonal/intermittent freshwater marshes/pools on inorganic soil; includes sloughs, potholes, seasonally flooded meadows, sedge marshes.
U	Nonforested peatlands; includes shrub or open bogs, swamps, fens
W	Shrub-dominated wetlands; shrub swamps, shrub-dominated freshwater marsh, shrub carr, alder thicket; on inorganic soils.
Xf	Freshwater, tree-dominated wetlands; includes freshwater swamp forest, seasonally flooded forest, wooded swamps; on inorganic soils
Xp	Forested peatlands; peat; swamp forest.

In the wetland classification scheme proposed for Brazil by Junk et al. (2014), a second hierarchical scheme for inland vegetated wetlands is based on whether water levels are stable or not, with a number of tertiary levels separated by emergent vegetation properties or amplitude and predictability of water level. Junk et al. (2014) were clear in their recommendation that wetland classification schemes are needed for specific regions (e.g., Junk, 2012; Nunes da Cunha and Junk, 2011). The scheme proposed for Brazilian wetlands includes specific types of dominant vegetation or even the floodplain of a particular river. The overarching structure of Junk et al. (2014) is, however, flexible to accommodate use in other regions as it can include other wetland types in the third tier of the typology.

Seasonal flooding characterizes many very extensive wetland systems throughout South America and Africa. These systems are subject to high-amplitude seasonal rainfall interspaced with dry periods, with predicable consequences for soil structure and chemistry. The inclusion of floodplains as wetlands, however, illustrates the difficulties in geographical demarcation. Areas that flood periodically range from short-lived flooding events with variable volumes of surface water present for short amounts of time, to areas of land that are flooded seasonally and take on clear and recognizable aquatic character, often for many months (Junk et al., 2014). In large wetland systems such as the Amazon and Abras de Mantequilla of Ecuador, flood waters can be many meters deep (Arias-Hidalgo et al., 2013; Junk et al., 2014). In the Okavango, the flood waters reach the seasonal wetlands in the midst of the dry season, many months after the annual rainfall in the Angolan highlands to the north. Seasonal flooding can fill shallow depressions including salt pans, whose peaks of biological production make them of critical importance for, especially, migratory species (McCulloch et al., 2003).

The ecological importance of pulsing of water into wetlands, and inundation of surrounding land that drive life-cycle responses for plants and animals (Junk et al., 2014; McClain and Naiman, 2008) is of key importance for conservation and management, and also is a key provider of ecosystem services to multitudes of small-scale farmers who grow crops on the receding floodwaters, which fertilize and replenish their land (O'Brien et al., 2020). Lower lying savannah areas and floodplains provide vital seasonal grazing for wild and domestic herbivores (Fynn et al., 2015) and transitional zones for human vegetable cultivation (Wood et al., 2013). Higher ground within the seasonally flooded areas can provide a refuge for plants and animals (Junk et al., 2014). These phenomena highlight the need for the inclusion of landscape features and distinct habitat zones into local classification and management (Fisher et al., 2001).

Vegetation provides habitat structure and, largely, the emergent properties of a marsh. In permanent marshes, high biological production and low oxygen in sediment can restrict decomposition of plant debris. This contrasts with the high rates of carbon oxidation in periodic dry and savanna habitats (Junk et al., 2014). A consequence of this for soil structure, and hence agricultural land use, is the transition from predominantly dry soils with low organic content in floodplains to permanently wet soils with higher organic content.

The Ramsar description of lowland tropical marshes lying on mineral soils is, therefore, a very relative descriptor, and a distinction from peatlands, as the buildup of organic matter depends on the balance between accumulation and mineralization of organic matter in the litter layer. High accumulation of organic matter can promote seral succession toward terrestrialization, although the character of many tropical wetlands is maintained by regular disturbance such as flooding, natural grazing, and human management such as harvest of vegetation (Hes and van Dam, 2019) and fire that affects ground litter and growth of vegetation (Giesen, 2018; McGregor et al., 2010). Ecosystem engineers such as hippopotamuses and other grazers can open up areas, maintaining structural and species diversity. Other biotic disturbance includes removal of keystone species through harvesting. External physical disturbance such as reduction of water input or transitional zone flooding from, for example, upstream dams or irrigation schemes can reduce or eliminate hydroperiods, with predictable consequences on wetland character. This, in turn, can lead to opportunities for invasive species affecting wetland vegetation structure, and water balance (Setterfield et al., 2013). Given the range of ecological processes that can so profoundly affect wetland character, it is easy to appreciate the challenges of classification indicated above, and the implication for conservation and management. Already, and more so into the future, human-moderated climatic cycles from global warming will generally lead to greater amplitude of extremes of floods and drought (Moomaw et al., 2018). Wetland conservation and management require not only the understanding of how hydrology affects wetland ecology, but reliable measurements of wetland extent. It also requires a better appreciation of the role that wetlands play in management of catchments as a whole, through their contribution via water runoff regulation, infiltration to groundwater, river baseflow augmentation, etc., but also through the many other services they provide through, for example, biodiversity, carbon storage, and nutrient cycling. The diversity and range of contributions present a particular problem for the mapping of wetlands in landscape and conservation planning, but is of critical importance for management.

19.3 Delineating tropical wetlands

The need for integrated spatial planning for wetland conservation is well recognized (Nel et al., 2009; Reis et al., 2017). It requires placing the wetland in the context of connectivity with the wider catchment, and the drivers and pressures that come from that (Maltby and Acreman, 2011). Many tropical wetlands are poorly defined (Junk et al., 2014). Geographical boundaries remain largely confined to administrative ones or some average or nominal wetland extent. Variable seasonality of wetlands makes definition of boundaries inherently difficult, attracting a variety of methods and opinions (Amler et al., 2015; Giesen, 2018).

Delineation of vegetated wetlands uses a combination of biophysical properties, catchment hydrology and geospatial data (UN Environment, 2018). Over the last 20 years, access to Earth Observation (EO) has increased the opportunities for global mapping of wetlands (Dube et al., 2022b, Chapter 21; Rebelo et al., 2018; Weise et al., 2020). Developments in technical resolution and analysis of spectral images, collected at more frequent regular intervals, have improved accuracy of extent of wetlands, and even some aspects of habitat structure and ecosystem function (van Deventer et al., 2016). Satellites provide 10- or 8-day periodicity of coverage of most of the Earth's land areas, much of which is available for download free of charge. Satellite options that are available for SDG 6.6.1 monitoring of the *spatial extent of water-related ecosystems*, are shown in Table 19.2 (Dickens et al., 2017). For swamps, marshes and forested wetlands, a 10–30 m resolution is available from ESA Sentinel 1 and 2, LandSat (all), ALOS PALSAR 1 and 2, although challenges remain in distinguishing seasonal from permanent wetland. Combining images from different sources provides better-than-weekly coverage at moderate resolution.

TABLE 19.2 **Current space agencies and satellites that provide images applicable to water-related ecosystem.**

Satellite sensors	Sources
ALOS PALSAR, ALOS-2 PALSAR 2, AVHRR, Envisat, ERS-2/SAR, Ikonos, IRS, JERS-1 SAR, Landsat, MODIS, QuickBird, Radarsat, Sentinel (several), Spot, WorldView	https://earthdata.nasa.gov/ http://reverb.echo.nasa.gov/reverb (NASA) https://lpdaac.usgs.gov/ http://www.satimagingcorp.com/gallery/more-imagery/spot-5/ (SPOT) http://en.alos-pasco.com/ (ALOS PALSAR) https://sentinel.esa.int/ (Sentinel) http://scihub.Copernicus.eu/dhus/#/home (ESA Copernicus) https://worldview.earthdata.nasa.gov/ (WorldView) https://www.asf.alaska.edu/sar-data/jers-1/ (JERS-1 SAR)

Source: Modified from Dickens, C., Rebelo, L., Nhamo, L., 2017. Guideline and indicators for Target 6.6 of the SDGs: change in the extent of water-related ecosystems over time. Report by the International Water Management Institute. CGIAR Research Program on Water, Land and Ecosystems (WLE).

Current accuracy of coverage by EO for vegetated inland wetlands does not, however, match that of open water or mangrove swamps (e.g., http://mangrovewatch.org.au/). A number of projects are developing methods to address this gap. While EO has been applied to many tropical wetlands through individual projects (e.g., Ndayisaba et al., 2017), consolidated data sets for wetland extent do not yet exist. Central to resolving this, and to make EOs more accessible for wetland conservation, are two initiatives, the GEO-Wetlands knowledge hub (https://geowetlands.org/) and the Global Wetland Outlook (https://www.global-wetland-outlook.ramsar.org/). These can help attain SDG indicator 6.6.1 "percentage of change in water-related ecosystems extent over time" (Box 19.3). The ambition is to establish a Global Wetland Community of Practice (GEO-Wetlands CoP) and a Global Wetlands Observing System (GWOS). Further developments of EO for vegetated wetlands are in progress, advancing the delineation of wetlands with more explicit incorporation of the hydro-ecological cycle within catchment and aquifer boundaries (Malak et al., 2019). This will also require a more standardized approach to wetland classification, illustrated by the work that has been done in South America by Junk and colleagues.

Building a portfolio of EO for tropical vegetated wetland assessment through GEO-Wetlands is done through collaboration and combined efforts, with recent tropical case studies including mapping of wetlands through the Globwetland Africa project (http://globwetland-africa.org/). This, for

BOX 19.3 Wetlands and Sustainable Development Goal (SDG) Indicator 6.6.1.

Target 6.6: By 2020, protect and restore water-related ecosystems, including mountains, forests, wetlands, rivers, aquifers, and lakes.

Indicator 6.6.1: Change in the extent of water-related ecosystems over time

The official repository of the indicator method is https://www.sdg6monitoring.org/ whereas up-to-date metadata and ongoing developments is https://unstats.un.org/sdgs/metadata/

One subcomponent of the 6.6.1 indicator is spatial extent of vegetated wetlands which include swamps, fens, peatlands, marshes, paddies, and mangroves. Artificial wetlands such as paddies and flood recession agriculture are disaggregated in order to prevent spurious conclusions. Guidance on assessment of wetland extent using an online app https://www.sdg661.app/productsmethods remains under development, with advances taking place at a rapid pace. For vegetated wetlands, a global baseline was established for 2016–18. The data are freely available and the method summarized at https://files.habitatseven.com/unwater/Measuring-wetland-area.pdf

Data from Sentinel 1 & 2 and Landsat 8, used to predict wetland extent, has a reported 70% level of accuracy, which will improve with method development. The 6.6.1 indicator sets out to use 2017 as the reference date against which to measure change, but there are aspirations to take this back to 2000, recognizing that there will still be a massive underestimate of previous wetland loss. Where possible, efforts at least at a country level should estimate a more historical wetland extent.

example, has produced a baseline wetland inventory map for Uganda based on Sentinel 1 and Sentinel 2 satellite data for 2016 and 2017. The potential to use these data hubs to build up a comprehensive global inventory of wetlands is enormous. For example, among many initiatives, in tropical Africa, the Nile Basin Initiative (https://nilebasin.org/) has recently produced an inventory and maps for important and transboundary wetlands of the basin (https://www.hydroc.de/nbi-nteap-wetlands-inventory-and-mapping-in-the-nile-basin/). The project DeMo-Wetlands (https://www.zfl.uni-bonn.de/research/projects/demo-wetlands) has worked to develop automated satellite-based wetlands detection and monitoring, with examples from Rwanda. For the extensive floodplains of the Inner Niger Delta (IND), extent of flooding related to rainfall has been assessed using EO (Normandin et al., 2018; Ogilvie et al., 2015). Similar developments are in progress in other parts of the tropics (e.g., Kandus et al., 2018; Mcinnes et al., 2016).

There are, however, limitations in developing capacity for the processing large data sets, available expertise in remote sensing technology and applying the methodology for local regional use. The approach adopted by the UN through the SDG Agenda is to provide a ready-mapped wetland extent to all countries who have merely to verify the information. This removes the onus on all countries to produce their own maps. While EO is increasingly important for wetland inventory, it does not obviate the need for local mapping and groundtruth validation, local monitoring, and studies that assess local wetland change and response to pressures (Rebelo et al., 2018). Even with improved resolution of EO, a high proportion of smaller wetlands may not be detected (UN Environment, 2018). For management and conservation, local assessment remains critical, which can be supported by rapid assessment techniques for geomorphology and habitat structure (Lidzhegu et al., 2020; Macfarlane et al., 2020).

19.4 Assessing wetland status, structure, and function

19.4.1 Pressures and impacts

Management and conservation of wetlands is based on the understanding of wetland type and the habitats therein. Human pressures affect wetlands and habitats in various ways. Assessing those impacts requires comparison with what is considered as minimal impact, which can profoundly affect perceptions of habitat quality (Irvine, 2012). Identifying an ecological baseline can, however, be difficult (Stoddard et al., 2006). For vegetated wetlands, often with multiple and stochastic effects affecting wetland character, the description of a true reference condition can seem elusive (Beuel et al., 2016). This can be accentuated in the tropics, where fundamental processes have, overall, been far less studied than in temperate zones. The progress on classification schemes described above for Brazil and other parts of South America, has not been as developed in Africa, Asia, or Oceania. Nevertheless, if status of a wetland is to be assessed, this requires a judgment on condition and character, and is *de facto* gauged against an estimation of intactness. It should be clear whether a baseline is really an estimate of preimpact or whether we excuse changes that may have taken place over recent decades. Recognizing that “reference conditions are not static, but vary naturally over time” Sustento Development Service (2016) suggested use of “reference wetlands” for long-term monitoring and assessment of how features may change naturally over time. There are many factors that make this decision complex. There may be little empirical data describing the original state of an ecosystem, and the perception of change may be obscured by human memory. It is, therefore, necessary to be mindful of the mental trap of “shifting baselines” (Humphries and Winemiller, 2009) to guard against unintentionally viewing degraded habitat as management targets.

A further consideration is the very relevance of historical baselines when so much is changing in the Anthropocene, and when new thinking is needed to accommodate large-scale shifts in climate patterns and other dramatic-induced human changes in Earth systems (Kopf et al., 2015). This would mean that:

Project relevant natural condition = True natural condition−climate change-induced changes

This is an unfortunate but perhaps pragmatic approach that deliberately overlooks a human impact that appears beyond our ability to manage. Whatever the approach adopted, it is recommended that options for reference condition are described in any management plan, and where there is uncertainty a description of site condition that is viewed as "sustainable" can be developed as a target for management. The use of *natura*l (no impact) or *historical reference* (using available data from before developments), is recommended, but it may be necessary to consider reference condition from the commencement of monitoring, or by construction of a theoretical reference condition based on wetland natural-like functions. This can be done by using local expert judgment and also by consultation with indigenous people who may have longer memory of natural conditions (Brinson and Rheinhardt, 1996; Kotze et al., 2020; Peh et al., 2013). Using comparative assessment across a regional network of sites can, however, place a particular wetland in a relative ranking of quality among sites.

Making a judgment of how pressures and impacts on a habitat changes ecological quality requires a framework of habitat structure and knowledge of the plants and animals that use those habitats. The geology, topographic position, and climatic conditions under which a wetland was formed and is now located largely determine the ecological setting (Ellery et al., 2008). As such, wetland features, including vegetation which typically plays a central role, can vary considerably in response to the core interrelated drivers of hydrology, geomorphology, and water quality (i.e., physical and chemical attributes) (Macfarlane et al., 2020). A range of approaches can be used to describe local habitats that incorporate, separately or as a mix, features of hydrology, geomorphology, water quality, and vegetation structure. This can be supported with simple conceptual models describing hydrological, chemical, and biotic drivers of habitat structure (Keith et al., 2020).

Observed responses of animals to environmental pressures led to the development of faunal biotic indices to estimate ecosystem quality [e.g., Index of biotic integrity (Karr, 1981)]. A large number of ecological assessment methods have been developed, but seldom have these methods been specifically developed for tropical freshwater habitats, and less so for tropical marshes. In this section, we present how an evaluation of the hydrogeomorphology can be used as a foundation to assess quality of tropical marshes, and a brief overview of the use of bioindicators.

19.4.2 Hydrogeomorphic types

Hydrology and geomorphology can be used to identify similar hydrogeomorphic units (HGMUs) based on geomorphology, water source, and hydrodynamics (Brinson, 1993). The HGMUs can be linked, forming transitional features along hydrological gradients, or separate and distinct surface features. These are commonly connected by subsurface water flow. A relatively simple suite of observations can determine the form and extent of HGMUs in any wetland, and how they are affected by anthropogenic impact.

The application of HGMUs (Fig. 19.1) for wetland management has probably been most notably applied by the WET-Health (Macfarlane et al., 2020) and WET-EcoServices (Kotze et al., 2020) techniques developed over two decades for South African wetlands (Macfarlane et al., 2020), and incorporated into the South African Wetland Classification System (SAWCS) (Ollis et al., 2013, 2015). It provides a foundation for assessment of ecological quality and ecosystem services provided by, particularly, floodplains, marshes, and herbaceous dominated wetlands (Kotze et al., 2020). The WET-Health is designed to be a fairly rapid assessment method, combining satellite-based mapping with fairly straightforward observations and measurements in the field. It has also been tested and applied in East and Central African wetlands (Behn et al., 2018; Beuel et al., 2016).

Brief descriptions of the wetland HGMUs described by Ollis et al. (2013) are given below and elaborated further in the original report (see also Job

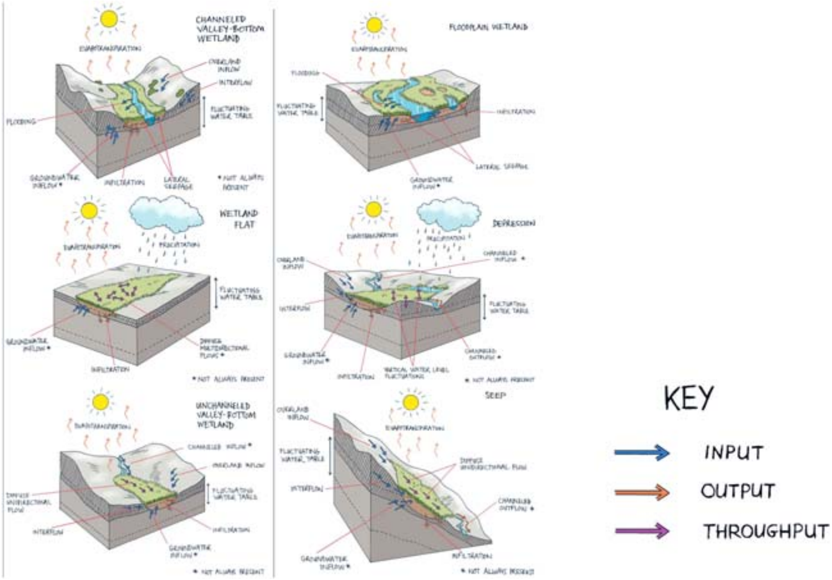

FIGURE 19.1 Representation of types of hydrogeomorphic units (HGMUs) in inland wetlands. *Reproduced from Ollis, D.J., Snaddon, C.D., Job, N.M., Mbona, N., 2013. Classification system for wetlands and other aquatic ecosystems in South Africa. User manual: inland systems. SANBI Biodiversity Series 22. Pretoria. Drawing by Chip Snaddon, in which SANBI retains full copyright.*

and Sieben, 2022, Chapter 2). These do not necessarily correspond to HGMUs described throughout the literature, as authors tend to assess things relatively at individual sites such that locally described HGMUs may differ from each other, but without adherence to any internationally recognized classification, or to use subcategories of wetland type to distinguish local features (Maltby, 2009).

- Channeled Valley-Bottom Wetland: a mostly flat area located along a valley floor with a river channel running through it, and with an absence of characteristic floodplain features. Dominant water inputs are from the river channel flowing through the wetland, either as surface flow resulting from flooding or as lateral seepage, and/or from adjacent valley-side slopes.
- Floodplain Wetland: an area on the mostly flat or gently sloping land adjacent to and formed by an alluvial river channel, under present climate and sediment load. It is subject to periodic inundation by overtopping of the channel bank. Floodplain wetlands generally occur on a plain and are typically characterized by a suite of geomorphological features associated with river-derived depositional processes.
- Wetland Flat: a level or near-level wetland area that is not fed by water from a river channel. Elevation contours are not evident around the edge of a wetland flat, which are characterized by dominance of vertical water movements associated with precipitation, groundwater inflow, infiltration, and evapotranspiration. Horizontal water movements within these wetlands, if present, are multidirectional, due to the lack of any significant change in gradient within the wetland.
- Depression: an inland aquatic ecosystem with closed (or near-closed) elevation contours, which increases in depth from the perimeter to a central area of greatest depth, and within which water typically accumulates. If flat bottomed, they are often referred to as “pans.”
- Unchanneled Valley-Bottom Wetland: a mostly flat wetland area located along a valley floor without a river channel running through it. It is characterized by its position on a valley floor, an absence of distinct channel banks, and the prevalence of diffuse flows. Water inputs are typically from an upstream channel and seepage from adjacent valley side-slopes.
- Seep: a wetland area located on gently to steeply sloping land and dominated by colluvial (i.e., gravity-driven), unidirectional movement of water and material downslope. Seeps are often located on the side-slopes of a valley but they do not, typically, extend onto a valley floor.

Under the South African Water Act 36 of 1998, wetlands are defined as: “land which is transitional between terrestrial and aquatic systems where the water table is usually at or near the surface, or the land is periodically covered with shallow water, and which land in normal circumstances supports or would support vegetation typically adapted to life in saturated soil.” The

SAWCS (Ollis et al., 2013, 2015) has adopted the HGMU approach. This can serve as a good model for the development of wetland classification across much of the tropics. In South Africa, Resource Quality Objectives (RQOs) are determined according to a balance between user and ecological requirements of significant wetland resources, with the intention of balancing the protection and development of wetland resources. Through a process of evidence-rich consultation, local targets or objectives are set in keeping with the local ecosystem and user situation. The key principle is that only when managers have clear, generally numerical objectives, will they be in a position to manage the wetlands and will protection of resources become a reality (Bredin et al., 2019). Key factors also included are: the assessment of supply and demand of wetland ecosystem services to determine significant wetland resources from a user perspective; the assessment of land cover within wetland resources and a zone of influence to determine condition of the resource for the purposes of setting and implementing RQOs.

19.4.3 Vegetation structure and bioindicators

The interactions of local hydrology, soil chemistry, climate, and human management can very much affect perceptions of quality of a vegetated wetland. The traditional classification of plant communities and their character using a phytosociological approach (Braun-Blanquet, 1932) identified similarities within plant communities based on total species composition and diagnostic species (Dengler et al., 2008). This reflects the variety of undelaying causative factors, but not a measure of habitat quality or response to human pressures *per se*. Assessment of quality requires some *a priori* view of gradients from natural communities to those altered by some impact, such as nutrient additions that can shift dominance to a few competitively superior plant species (Wilson and Tilman, 1993). A scheme of indicator scores associating plants to nitrogen and other environmental gradients developed by Ellenberg (1988) for Central Europe has been used in other regions, but with variable success (Hill et al., 2000; Miller et al., 2006; Shipley et al., 2017).

Single or a limited number of taxa may only be useful as indicators for specific aspects of the environment and over limited scales. Assessment schemes based on biotic communities can require analysis of large and geographically relevant "training sets" of data, and are increasingly reliant on multivariate techniques of analysis. The necessary training sets are generally lacking for tropical wetlands. Even fairly simple keys for floristic indicators and community assessment remain limited for many regions. In tropical Africa, there have been a few attempts to use existing schemes or develop new metrics to assess wetland quality (Behn et al., 2018; Beuel et al., 2016; Moges et al., 2016). This has included using socio-economic attributes in vegetated wetland classification. In the absence of regionally specific and robust assessment methods, there is inevitably reliance on schemes developed elsewhere. Assessment techniques using geomorphology and habitat structure developed for margins of lakes rivers and riparian zones (Raven et al., 1998; Rothrock et al., 2008; Rowan et al., 2006) are, however, amenable for adaptation for use in the tropics. Availing of such knowledge transfer is normal to guide management and conservation, developing more locally specific schemes over time. See also recent reviews on use of bioindicators for monitoring in tropical wetlands by Dalu et al. (2022, Chapter 8), Dube et al. (2022a, Chapter 11), and Greenfield (2022, Chapter 20).

The value of applying and adapting a technique such as WET-Health (MacFarlane et al., 2020) for tropical habitats is that it is rooted in a functional approach, and so less dependent on species identification or plant growth forms. Species can also be grouped into broad categories such as "graminoids," "succulents," "trees," or "annuals" (Sieben et al., 2014). A simplified approach can be particularly useful when comparing a site over time. In vegetated wetlands where distinct zonation of vegetation occurs, shifts in patterns of zonation can indicate habitat changes and can be detected by EO (Schmidtlein et al., 2012). For tropical wetlands in general, there is, nevertheless, a strong need for identifying indicator species or vegetation traits that are useful to assess changes in habitat structure (Junk et al., 2014).

The reliability of any indicator is, however, subject to varying degrees of uncertainty that affect the confidence in their use. Jackson et al. (2000) suggested that indicators should be:

1. Conceptually relevant in providing information on ecological condition;
2. Feasible for inclusion in long-term monitoring programs;
3. Robust in distinguishing extrinsic/irrelevant factors from a true environmental signal; and
4. Able to provide results that are clearly understood and accepted by scientists, policy makers, and stakeholders.

These guiding principles have been used for a variety of bioassessment techniques for surface waters (Dixon and Chiswell, 1996; Karr and Chu, 1999). Many bioassessment techniques may have limited application for tropical vegetated wetlands for a variety of reasons. Natural features of marshes play a role in this. Chemical variables such as dissolved organic matter (DOM), oxygen, pH, and conductivity of standing or flowing waters in a marsh often take on a so-called dystrophic character, dominated by microbial ecological pathways. This can be observed by water in marshes being often highly colored.

With the exception of the macrophyte community, sampling and measuring biological elements in the pools and channels of vegetated wetlands are confronted with the very difficult challenge of taking samples that could provide a meaningful pressure-impact signal. The substrata of pools, lake margins, and channels in vegetated wetlands typically consist of loose sediment, and supports life adapted to low oxygen. This overrides signals from, for example, nutrients or other chemical pollutants. Particular response of some organisms to, for example, heavy metals entering a vegetated wetland, as occurs downstream of mining areas, are also subject to attenuation depending on the ambient environment such as redox conditions (Eggleton and Thomas, 2004).

Pollutant transport and loads are dependent on hydrological pathways and residence time. Emissions of pollutants to marshes are likely adsorbed, or otherwise immobilized in a similar way as in constructed wetlands (Mitsch et al., 2008). Inundation of polluted surface waters into a marsh can, however, change the character of the vegetation. Apart from within a narrow riparian zone, subsurface hydrological pathways from a water body into a marsh are likely insufficient to affect the character of marsh vegetation.

Where a stream runs through a vegetated wetland with sufficient energy to expose gravelly substrata, then bioassessment techniques using invertebrates (Resh and Jackson, 1993) could potentially be part of a monitoring strategy. The South African Scoring System (SASS) (Dickens and Graham, 2002) for river invertebrates has been used, with minor modifications, to assess water quality in tropical African countries (Chikodzi et al., 2017; Tafangenyasha and Dube, 2008). Adopting or developing bioassessment techniques in tropical vegetated wetlands has an added potential if they can use taxa groups that are relatively simple to identify and easy to sample. Two such groups are the Odonata, comprising dragonflies and damselflies (Simaika and Samways, 2011; Stephenson et al., 2020) and birds (Bino et al., 2014; de Deus et al., 2020; Galib et al., 2018; Maclean et al., 2014).

19.5 Wetland management

19.5.1 Monitoring and management cycles

Across the tropics, multiple external and local drivers affect the ecological health of wetlands (van Asselen et al., 2013). These lead most notably to local pressures of changes in hydrology, pollutant loads, encroachment, habitat destruction, and invasive species, or affect land use in the catchment that has an impact on the wetland. Pressures often occur in combination. At very local scales, incremental increase of pressures across much of the tropics often results from food production relating to subsistence grazing, cropping and settlements. Drivers at larger scales can relate to, for example, demands from mineral or sand extraction, but most commonly to regional and/or international demands for food and other agricultural commodities. This can result in pressures on a wetland resulting from a decision made by actors far removed from the wetland itself. In many tropical zones, food security policies, degradation of agricultural land, or deficits in supply of water or nutrients have prompted policies that actively convert marshes to cropland (e.g., MINAGRI, 2009). Addressing drivers and pressures to protect and restore wetlands can be addressed at both policy and locally managed scales.

Guidance on the management of wetlands is available from a large range of sources, from specific sites to national policies and international information platforms, notably the International Union for the Conservation of Nature (IUCN), Wetlands International, World Wide Fund for Nature (WWF), and the Ramsar Secretariat. The latter has produced a series of handbooks that provide a "toolkit" for the conservation and wise use of wetlands (Ramsar Convention Secretariat, 2010a). To date there are 20 handbooks for guidance available for download at www.ramsar.org/resources/the-handbooks. The Handbook on Managing wetlands (Ramsar Convention Secretariat, 2010b) provides a detailed framework for applying best practice to wetland management, with the basics, based on an early version, is summarized in Fig. 19.2.

Fundamental components of wetland management described by Rebelo et al. (2018) are:

> *Wetland assessment*: the identification of the status of, and threats to, wetlands as a basis for the collection of more specific information through monitoring activities; and
>
> *Wetland monitoring*: the collection of specific information for management purposes in response to hypotheses derived from assessment activities, and the use of these monitoring results for implementing management. The collection of time-series information that is not hypothesis-driven for wetland assessment is appropriately termed "surveillance" rather than monitoring.

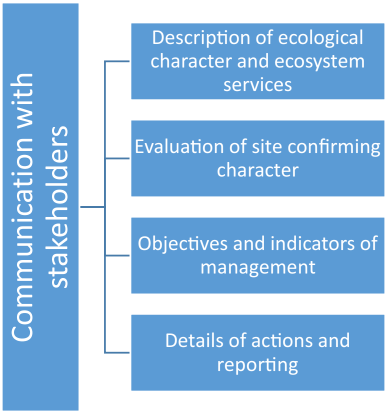

FIGURE 19.2 Overview of management planning. *Adapted from Chatterjee, A., Phillips, B., Stroud, D.A., 2008. Wetland Management Planning. A Guide for Site Managers. WWF, Wetlands International, IUCN, Ramsar Convention, Gland, Switzerland.*

Whether or not the term surveillance can in practice be considered separate from monitoring poses some difficulties, as even the most rudimentary checking on wetland condition is a type of monitoring, with presumably even vaguely formulated objectives. At least clarifying the meaning of the terms in any management plan, and documenting the objectives the plan, would seem necessary to provide meaning to on-the-ground activities.

Advanced conceptualization of management involves placing a wetland in the context of the catchment (Kingsford et al., 2011), making use of an adaptive management approach (i.e., learning by doing) as outlined in Fig. 19.3. There is general consensus of the benefits of using both "expert" and "local" knowledge to develop objectives for management, and for these to be agreed with local stakeholders and compatible with local and national policies. This improves legitimacy. The concept of adaptive management is necessary for a comprehensive wetland management plan, where the so-called "critical path" incorporates stakeholder engagement, together with policy, to assess the present and reference conditions, to set objectives, to incorporate wetlands into management plans, to monitor and reflect and finally to be willing to adjust if the outcome is not as intended. This allows for learning through experience, and responding to changes that affect the ecological character of the wetland. See also Fig. 19.2 in Kingsford et al. (2021) for a conceptual framework for adaptive management and links with assessing ecological character through research and monitoring.

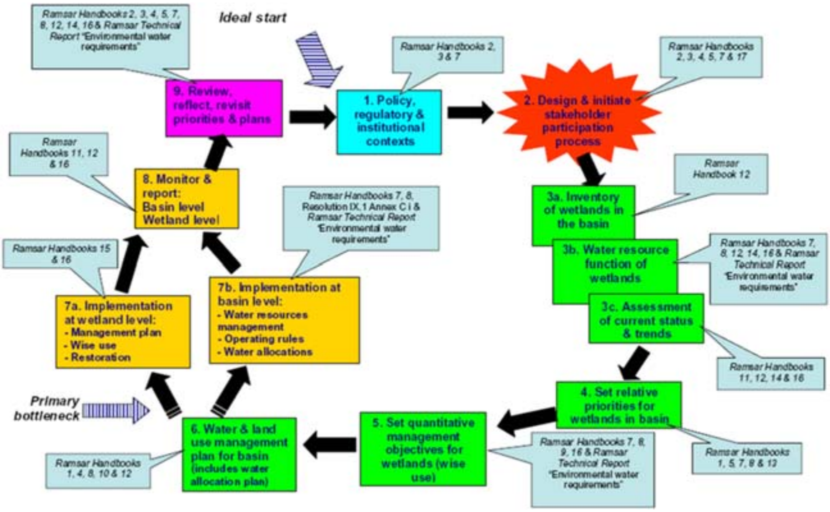

FIGURE 19.3 Generic version of the "Critical Path" approach (from www.ramsar.org Ramsar 2005 Resolution IX.1 Annex C i). *Adapted by Ramsar from Dickens (2003).*

19.5.2 Environmental flows for wetland management

The need for adaptive management in the face of increasing pressures on water resources has led to the development of decision-making processes that explicitly recognize the mutual dependence of people and the environment. This has been prominent in assessment of minimal river flows for sustainable development and right of water for people and environment. Linking human and environmental needs for water is the foundation of the concept of environmental flows (e-flows) that aim to maintain healthy rivers and the ecosystems services they provide (Bunn and Arthington, 2002; Poff et al., 2010). The concept of e-flows has more recently been applied to vegetated wetlands and floodplains (Rountree et al., 2013; Salinas-Rodríguez et al., 2018).

Implementation of environmental flows is increasingly recognized as an important approach to management and also restoration of rivers, and this includes floodplain wetlands. The globally accepted standard definition today is "*Environmental flows describe the quantity, timing, and quality of freshwater flows and levels necessary to sustain aquatic ecosystems which, in turn, support human cultures, economies, sustainable livelihoods, and wellbeing*" (Arthington et al., 2018).

Alteration of water flow and water quality represent some of humanity's greatest pressures on aquatic ecosystems, and thus management of these two pressures represents an important means to protecting and restoring wetlands and, especially, floodplain ecosystems. Determination of the quantity and quality of water that is required to sustain an ecosystem is a complex issue, with the need for crucial elements of natural variability to be maintained. Numerous approaches exist for this determination, ranging from simple desktop methods (e.g., Hughes and Hannart, 2003) to holistic approaches that include detailed consideration of important ecosystem components as well as the livelihoods associated with them. Initial methods such as the *Building Block Methodology* (King et al., 2000) clearly and intuitively illustrated the essence of these assessments but did not have much capacity to evaluate scenarios and livelihood impacts. They are now superseded by more comprehensive models or frameworks such as the *Ecological Limits of Hydrologic Alteration* (ELOHA) (Poff et al., 2010), DRIFT (King et al., 2004), and PROBFLO (O'Brien et al., 2018).

While most e-flow assessments focus on rivers, water allocations for wetlands are developing in, for example, Mexico with the "Mexican law for the determination of environmental flow" and "National Water Reserve Programme" (Salinas-Rodríguez et al., 2018), and in South Africa (Rountree et al., 2013). While river e-flow assessments are driven by stream-flow discharge, the same principles applied to wetlands are based on water levels /depths. It is in floodplains, however, where river and wetland ecosystems really intersect, and where e-flows can play an immediate role in management of wetland ecosystems by linking river discharge to duration and extent of flooding of the floodplain. Two examples are the determination done on the Pongola Floodplain using the DRIFT model (Brown et al., 2018) and for the Inner Niger Delta (IND) in north Africa (Dickens et al., 2020; O'Brien et al., 2020). The PROBFLO model (O'Brien et al., 2018) used in the IND study, makes the connection between the sources of stress on water availability (e.g., dams, water abstractions), the resulting stress, and through impacts on the ecosystem and risks to provision of benefits to the ecosystem and people relying on it (Fig. 19.4).

The determination of e-flows to support wetland management requires engagement with stakeholders to provide a thorough assessment of potential impact on livelihoods and stakeholders response to that. Consultation should be transparent and should include key sector interests to ensure equitable delivery of flow-related ecosystem services. This can be further supported by application of appropriate economic valuation (Russi et al., 2013) that supports trade-off analyses.

19.5.2.1 *Case study—Inner Niger Delta*

A recent study on the IND, one of the world's iconic floodplain wetland ecosystems (Fig. 19.5), determined the e-flows necessary to maintain the floodplain in a sustainable condition (Dickens et al., 2020). The IND is an inland floodplain system lying in Mali in north Africa, 400 km long and 100 km

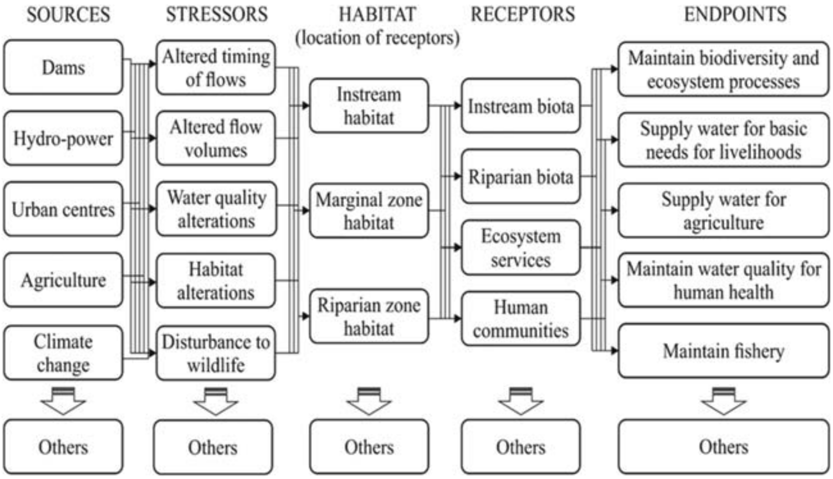

FIGURE 19.4 Example of a conceptual model from the PROBFLO model which describes causal risk relationships between sources, stressors, habitats, effects, and impacts to Endpoints. *Reproduced from O'Brien, G.C., Dickens, C., Hines, E., Wepener, V., Stassen, R., Quayle, L., et al., 2018. A regional-scale ecological risk framework for environmental flow evaluations. Hydrology and Health System Sciences 22, 957–975.*

wide. The Niger River and other tributaries rise in Guinea, travel through the IND, and then exit on a long journey through largely desert to enter the sea at the Niger Delta in Nigeria.

The IND floodplain is home to nearly 2 million people and some 5 million livestock, who live with enormous variability of water levels in an arid terrain. The annual IND flood can increase water levels by 4 m, with the land drying rapidly once the water recedes. The receding water provides many benefits, adding agriculture to the substantial benefits derived from fisheries in the deeper water. However, large-scale irrigation projects already in progress upstream are inevitably a risk for maintaining stream flow.

The e-flow study was carried out with minimal data because of security issues that prevented field surveys from taking place, but it was still possible to determine the e-flow albeit at a lower level of confidence. The estimation was that some 58% of the natural total annual flow was required to maintain the IND in a condition where it would continue to be a sustainable ecosystem providing benefits to people. The distribution of flows over the hydrological year (Fig. 19.6), illustrates the natural reference flows, the Present Day flows (PRS1) and the e-flows (EFA), highlighting that while there appear to be abundant flows during the wet season, during the dry season the bulk of the baseflows need to be available to maintain the floodplain through provision of minimal aquatic habitats. Under any future developments,

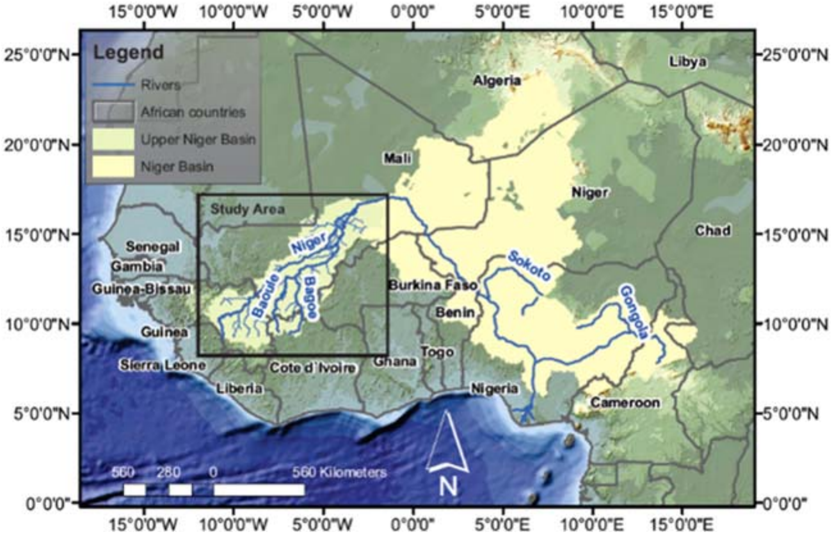

FIGURE 19.5 Location of the Inner Niger Delta. *Reproduced from Dickens, C., O'Brien, G., Stassen, R., Eriyagama, N., Kleynhans, M., Rowntree, K., et al., 2020. E-Flows for the Upper Niger River and Inner Niger Delta: synthesis report V2. International Water Management Institute for Wetlands International. CGIAR Research Program on Water, Land and Ecosystems (WLE).*

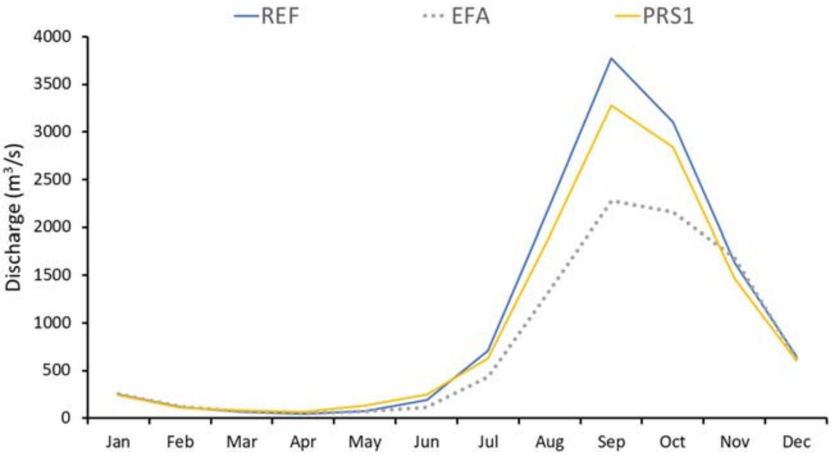

FIGURE 19.6 Distribution of flows entering the Inner Niger Delta, illustrating the natural reference flow, the present-day flows (PRES1) and the e-flow recommendation (EFA). Hydrological record was 38 years from 1961 to 1998. *Reproduced from Dickens, C., O'Brien, G., Stassen, R., Eriyagama, N., Kleynhans, M., Rowntree, K., et al., 2020. E-Flows for the Upper Niger River and Inner Niger Delta: synthesis report V2. International Water Management Institute for Wetlands International. CGIAR Research Program on Water, Land and Ecosystems (WLE).*

upstream dams would be required to add flow to the downstream river to maintain a sustainable floodplain. The challenge with this investigation, however, was the absence of prior decision making in policy that would have established the required extent of flooding as an objective for management. Such an objective would need to be related to the human population size and its requirements, balanced with what the ecosystem requires to be sustained. Such an objective would have assisted setting the e-flow to ensure the flood extent objectives were attainable, together with the many other objectives that were provided for.

19.6 Grasping reality

19.6.1 Resources for management

Management of ecosystems inevitably involves making decision about contested resources, to achieve some stated or tacitly recognized state. In wetlands this typically involves a number of staklehoders with different interests, and often varying degreees of influence. Prevailing norms provide a basis to judge the value of decisions made. Transparent involvement of stakeholders reduces the risk of narrow interests dominating and for a better possiblity of sustainable and equitable decisions making. Evidence-informed decisions clearly support more sustainable management (Adams and Sandbrook, 2013).

Many countries in the tropics have desire and even well-developed policies for the protection and management of wetlands (Bonells, 2018). Marambanyika et al. (2022, Chapter 22) provide an overview of policies and approaches in southern Africa, and Uganda even has a government department dedicated to the management of wetland resources (Mafabi, 2018). Nevertheless, effective management on the ground can remain elusive, and many beautifully written management plans are not, or are only partially, implemented, or not supported by sufficient political will, with the result that the benefits of wetlands are not mainstreamed (Russi et al., 2013). The adaptive management framework outlined in Fig. 19.3 and advocated by, for example, Kingsford et al. (2021) provides a state-of-the art approach. Such a level of detail is, however, often not done for most tropical wetlands. Management of wetlands in the global south is often severely limited of resources (Irvine et al., 2016), while at the same time facing increased pressure that lead to their loss and degradation. Protecting and restoring them is of major importance for global conservation and for the good of the societies that rely on them.

Where pressures are low and where management of the wetland is through local custom and institutionalized traditions, such as by the Lozi in the World Heritage Site of the Barotse Floodplains in Zambia (Estrada-Carmona et al., 2020), or where a site is generally inaccessible, formal management is hardly needed. In such cases, surveillance monitoring using EO can be sufficient although it does come with the risk that unobserved cryptic changes to, for example, water quality degradation or invasion by aliens is occurring. Unfortunately even areas that a few years ago where considered remote are now subject to high rates of encroachment and habitat destruction.

Active management is needed where there are ongoing or known potential threats that need to be tackled by actions. Establishing causal relationships between pressures and impact within wetland type, and having a known (preferably documented) process of response to hydrological change and human pressures is a key element of management (Soranno et al., 2010). Management goals, at whatever level is possible, are typically set to prevent degradation and loss, or guide restoration. Many tropical wetlands, including Ramsar sites (see below), lack effective management planning, with a high need for better reporting using relevant indicators (Kingsford et al., 2021). Where monitoring does occur, this should assess the success of management activities toward objectives, and guide policy, planning and interventions. For many important wetland sites, planning and monitoring remain a key gap.

At its most basic, wetland management planning includes a site description, information on ecosystem services provided by, and the pressures on, the wetland. This creates a documented understanding of the structure and functioning of the wetland. When resources are very limited, building information is often opportunistic, and gathered from local interest groups or small research projects. Even basic EO supports identification of wetland extent and likely internal and proximate pressures. Identifying direct pressures on tropical swamps and marshes requires a review of activities going in within the wetland itself, and those from outside the immediate boundary of the wetland that can affect wetland character. While detailed studies are needed to quantify impact of pressures, this scale of input is only available for very few tropical wetlands. The understanding of processes and wetland functions, nevertheless, provide a rich but generally underused resource, to guide management in similar situations where detailed information may be missing. Useful information on pressures and their potential impact can be gathered with use of modest resources through local knowledge and, increasingly, citizen monitoring. In any particular situation, it should be possible to identify a realistic availability of "low," "medium," and "high" capacity for wetland management. Where possible, the use of *appropriate* rapid assessment techniques can greatly aid management. As an example, the WET-EcoServices (Kotze et al., 2020) technique has been used to guide rehabilitation of the Gikondo Wetlands in the city of Kigali (World Bank, 2020) and is an example of an approach that may be appropriate for low budget situations. An assessment of ecosystem services highlighted the gap between current supply and demand for each of 16 ecosystem services, and hence provided potential management targets (Fig. 19.7) as well as motivation for local or national authorities.

19.6.2 Prioritizing where and what to manage

Throughout the tropics, designated Ramsar sites might be considered to represent the priority for protection and management of wetlands, but this presents a risk that deflects from the efforts that need to be directed to the protection and management of the overall wetland resource. A focus on a few nominally and typically isolated protected areas could even inadvertently be a factor in the loss and degradation of other sites (Irvine, 2015). In addition to managing Ramsar sites, each signatory to the Convention also undertakes to make wise use of all wetlands in their territory, which translates to maintaining the ecological character of all wetlands (Finlayson et al., 2011). While designated Ramsar sites may represent the crème de la crème of wetlands, the strength of legal protection even for these may be limited. In general, designation of legally protected wetland or mixed habitat sites has occurred to a much lower extent than for terrestrial habitats (Lovejoy, 2006; Nel et al., 2009). Critics of the protected area paradigm point to the lack of inclusion of local communities, or worse, social exclusion (Adams and Hutton, 2007). As support of human livelihoods is a central theme of the Ramsar Wise Use of Wetlands concept and a specific element of the 2010 Aichi targets under the Convention of Biological Diversity, the extent that

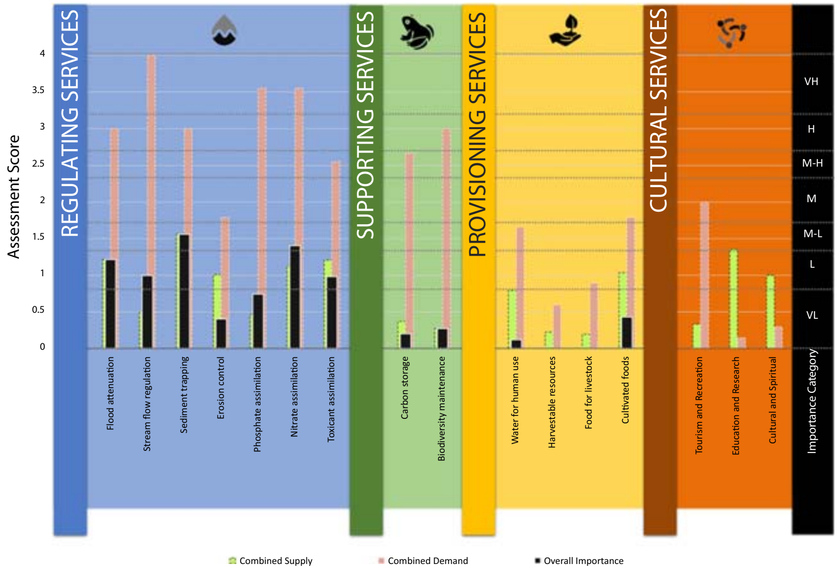

FIGURE 19.7 A summary of the Gikondo Wetland's functionality assessment results from the WET-EcoServices tool. *Diagram courtesy Douglas Macfarlane.*

this applies to protected wetlands is uncertain. Only a small percentage of inland seasonally flooded wetlands lie within protected areas, and the extent of these in the tropics is lower than in temperate regions (Reis et al., 2017).

In Africa between the tropics of Cancer and Capricorn (23°26′11.8″N to 23°26′11.8″S) a search within the Ramsar website (https://rsis.ramsar.org/; 13th September 2020) found 118 Ramsar sites that included the descriptor *Tp* for "permanent freshwater marshes/pools" (Table 19.1). Some of these sites occur within national parks, biosphere reserves, or World Heritage sites. Of the 118 sites, 48 entries on the Ramsar platform indicated that management plans existed, of which six appeared to have no, or very small amount of habitat that could be really considered as a freshwater marsh. Of these remaining 42 sites, the descriptions on the website suggested that for 22 sites, no update of reporting had been submitted to the Ramsar Secretariat since 2000. A similar search for tropical Asia, suggested seven sites meeting the description of *Tp* had submitted management plans. For tropical Latin America, Caribbean and Mexico this was 40 sites, and for Oceania seven sites, of which three are in Northern Australia.

The information gathered through this exercise aligns with the analysis and observations that many designated Ramsar sites do not have the extent of management and planning needed for their protection (Davidson et al., 2019a; Finlayson, 2012; Kingsford et al., 2021). The lack of information on the Ramsar website, does not necessarily, however, mean that up-to-date management plans do not exist. An example is the Lake Nabugabo Wetlands

System Ramsar Site in Uganda. A comprehensive management plan has been produced to cover 2017–27, which at the time of writing was freely available for download from https://www.climatelinks.org/resources/lake-nabugabo-wetlands-system-ramsar-site-management-plan. The plan contains an informative description of the site, its administrative setting with roles and responsibilities of stakeholders, time-bounded management objectives with indicative costs, and frameworks for implementation and monitoring. This plan was developed through funding by the USAID development program *Planning for Resilience in East Africa through Policy, Adaptation, Research, and Economic Development* (PREPARED), and "defines the optimal desired future state and is intended to serve as a clear guide for making choices to sustainably manage the ecosystem." The Lake Nabugabo management plan identifies many issues and suggested actions by named parties. Making the plan involved extensive stakeholder consultations and the site has high tourist potential. Monitoring recommendations are focused, however, on the progress of activities, not the state of the ecosystem.

Total estimated costs of the Lake Nabugabo plan over a proposed 10-year implementation period, and guided by 10 lead implanting partners, are in the order of US$ 2.3 million. The extent that the plan will be implemented effectively will depend on mobilization of local and external financing. That a donor has invested in the development of the plan illustrates the desire to support conservation, livelihoods, and development. Bennun (2001), in reviewing the needs and possibilities for monitoring for the Ramsar site Lake Navaisha in Kenya, was of the view that "an inflow of resources from wealthier countries will always be necessary to maintain biological diversity in the tropics." At a meta-level this is likely a simple reality. But reliance on donor support, usually involving short-term interventions, is uncertain for longer-term plans. More important site such as Lake Nabugabo is how local institutions can drive the ambitions of the plan, and be sufficiently adaptable and opportunistic in working toward its goals as resources allow. This can usefully include greater attention to local stewardship arrangements and partnerships with industry, including adoption of a circular economy approach in situations such as Lake Navaisha, with its locally important horticulture.

This raises the significant challenge of resourcing and setting priorities for wetland management, and the monitoring that supports it. This is also not only about designated sites, which may also have specific conservation objectives, but for the safeguard of ecosystem services for all wetlands. Relying on the protection of a very few chosen special sites, they be designated as Ramsar or through some other policy or program, is an ineffective way to maintain the wetland resource in the tropics. By and large the policy framework is in place for governments to provide some sort of protective status to wetlands, both through the Ramsar Convention—with the obligation of signatories to maintain the ecological character of all wetlands, or through stronger national legislation, programs, and policies. Creating the enabling environment and avoiding policy contradictions is a major challenge. This is well demonstrated by how policies for food security can conflict with those of wetland protection. Aligning policies across different government ministries and their agencies is necessary if wetlands in the tropics are to be protected and sustained for their ecosystem services. It is usual that the power (and budgets) of agriculture and industrial-focused ministries far exceed those charged with protecting the environment.

The undervaluing of wetlands and their essential role in catchment processes, also provides important opportunities. Recent economic assessments of global wetland resources, as well as natural capital in general, provide very completing political and policy arguments for better ecosystem protection (Costanza et al., 2014; Davidson et al., 2019b; Russi et al., 2013). While redirecting powerful government ministries and the lobbies that support them is undoubtedly a challenge, the evidence to support that is on hand, while it is the effective communication strategies that seem to lag behind (Darwall et al., 2018; Tickner et al., 2020).

19.6.3 Scales of management

Across tropical vegetated wetlands lies a range of management possibilities and administrative status. There are a minority of sites with designated boundaries and formal protections, but which may or may not have well-formulated management plans or resources for management. The majority of sites will fall outside any formal structure, but there may be good understanding of the pertinent issues. Others will lack even basic documented information of a site description and wetland use. Administrative responsibility for site protection can span, at often nested scales, from Government Departments to local District Councils.

Given this range of possibilities, it can be easy to conclude that the familiar adage “you can’t manage what you don’t measure” has little relevance for tropical swamps and marshes. The problem can, however, be seen from a different perspective following the Indo-Chinese saying: “when you don’t have what you want, you make do with what you have.” The extent that resources can be mobilized to guide management (as, e.g., outlined in Fig. 19.3) provides for a gradient of management possibilities. For most tropical wetlands, the ideal of the adaptive management cycle, with periodic evaluation to guide new directions may be constrained by a lack of long-term funding and underdeveloped institutional structures. This does not mean that ambitions for top quality management should be discarded, but unrealistic aspirations bring little benefit.

What can be achieved at the policy level is closely linked to advocacy and political will. It occurs at international, regional, and local levels. It involves creation of partnerships and effective communication channels, especially involving sectors and influential individuals who may not yet appreciate the real value of wetlands. Tools of the trade include short well-informed communication material such as information sheets and policy briefs. Personal dialogue across all scales of stakeholders from political leaders to local communities is often essential. Local and international alliances, including those who may provide resources, are highly beneficial. An essential component is building a national and local skills base, and the formal and informal institutional structure to support that. This means that personnel embedded in government structures develop the skills and competencies that can support wetland conservation and management on the ground. All scales of management, from institutional to operations at a particular site, can benefit from administrative and wetland management capacity development (Gevers et al., 2016; Logan et al., 2020). Where possible, these are linked to Communication, Education and Public Awareness (CEPA) Programmes (Ramsar Convention Secretariat, 2010c) that can be tailor made for local stakeholders.

For the many thousands of smaller sites, forming network of wetlands, the social-ecological reality of tropical wetland use inevitably involves community engagement, and varying degrees of traditional practices affecting common-pool resources and land tenure. Linking traditional knowledge with an evidence-informed approach is an important component of management (Adams and Sandbrook, 2013). Many communities that depend on tropical wetlands live in or close to poverty. Considering how management alleviates poverty and preserves the conservation importance of wetlands remains an urgent need. Being explicit in this can also help connect the formal and informal institutions involved (Cleaver, 2002). Unfortunately it is not always the case that managing for conservation leads to poverty alleviation (Roe et al., 2013). Better understanding of the link between conservation and human social structure is a critical area to guide effective interventions that benefit both people and ecosystems (Alessa et al., 2009; Dowie, 2009).

Furthermore, although it is a compelling argument that local resources should be managed by local communities, the community-based participatory model can reveal other problems of governance and accountability (Etiegni et al., 2017; Lane and Corbett, 2005). Like all interventions, conservation strategies require effective, transparent, and multiscale governance, and a range of appropriate skills and competencies. Communities may even decide that their interests are best served by converting a wetland to another use, but such a decision needs to be weighed against the perspectives of downstream users and even users at a regional and global level. To complement the case of the Lake Nabugabo Wetland described above, two additional case studies from the African Great Lakes region are illuminating (see below):

19.6.3.1 The Ombeyi wetlands, Kenya

A government subsidized rice-growing scheme in the Nyando wetlands on the shores of Lake Victoria near the town of Kisumu in Kenya motivated

FIGURE 19.8 Conversions of papyrus wetland to rice farming at, top images, Nyando (0°11′–0°19′S, 34°47′–34°57′E) and, bottom image, Ombeyi (00°6′40″S–00°10′00″S, 34°51′00″E–34°56′40″) wetlands, Kenya.

nearby communities of the village of Ombeyi to embark on their own conversions of papyrus swamp (Fig. 19.8). Customary use of the wetlands lies with groups of families who own land through inheritance (Osoro et al., 2019). Conversion of the papyrus swamp to rice paddies therefore, needed agreement among family groups for each patch of wetland. Local hydrology meant that drainage for the conversions had to proceed from the periphery to the center of the wetland. While many community members appreciated the traditional value of the wetland, and its use for papyrus harvesting for some community members, collective action favored the potential of income from rice over traditional use. Grander notions of regulating or cultural services, or the loss of livelihood of the papyrus harvesters, were either not considered or viewed as a reasonable trade-off. In a visit to the site by the lead author of this chapter, there did not appear to be any oversight of the conversions by any governmental authority. The wetland conversion appeared wholly decided and enacted by the local community.

19.6.3.2 Namatala Wetland, Uganda

This case study shows how the pressures on a wetland may mount gradually, and although ostensibly protected, the wetland can be lost piece-meal. The Namatala Wetland (Fig. 19.9) lies along approximately 30 km of the Namatala River of the Lake Kyoga Basin, north of Lake Victoria. Land use spans intact papyrus swamp to mixed agriculture. The basin is densely populated, and the wetland surface water inputs include polluted discharges from the town of Mbale and wastewater stabilization ponds. The wetland has no specific designation, but

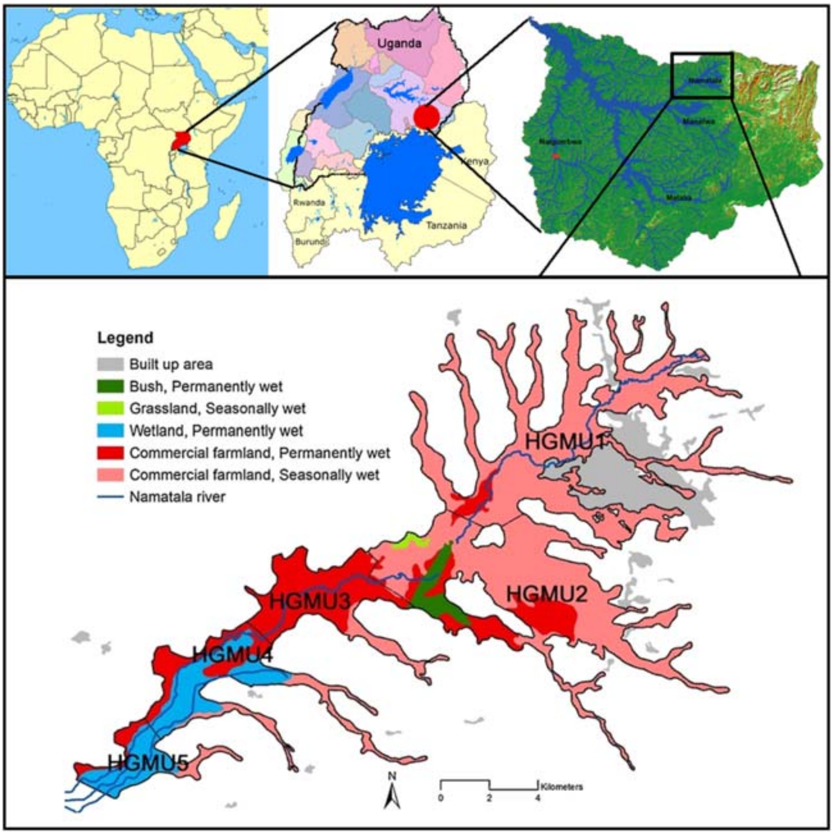

FIGURE 19.9 Lower image: Map of Namatala Wetland created on the basis of land use, with outline of the hydrogeomorphic units (HGMUs). The Namatala River flows from the northeast to the southwest, through a land use transition from the upper wetland (dominated by agricultural land use) to the lower wetland (dominated by original wetland vegetation). Situation of wetland provided in top images. *Reproduced from Namaalwa, S., van Dam, A.A., Funk, A., Ajie, G.S., Kaggwa, R.C., 2013. A characterization of the drivers, pressures, ecosystem functions and services of Namatala wetland, Uganda. Environmental Science and Policy 34, 44–57. Map river basins top middle: https://www.mdpi.com/2073-4441/11/9/1805/htm#. Topographic map top right: https://link.springer.com/chapter/10.1007/978-3-030-12974-3_10. Map Africa: Wikimedia commons.*

like all wetlands in Uganda falls under the National Wetlands and Policy programme (NWP) formally adopted in 1994 (Mafabi, 2018). The wetland has been subject to ongoing degradation for at least three decades, but has also been the site of a detailed research program (Namaalwa et al., 2020; Zsuffa et al., 2014). This included working with key stakeholder groups identified as water managers, resource users, political leaders, environmental groups, civil society, and community service agents in agreeing management options and potential solutions to stemming the loss of wetland ecosystem services. The well-known Drivers, Pressures, State, Impact, Response (DPSIR) model of decision support (Smeets and Weterings, 1999) guided the diagnosis for management of the wetland (Fig. 19.10).

In the Namatala Wetland, land use in the wider catchment and agriculture in the wetland has led to a loss of nutrient and sediment retention function in

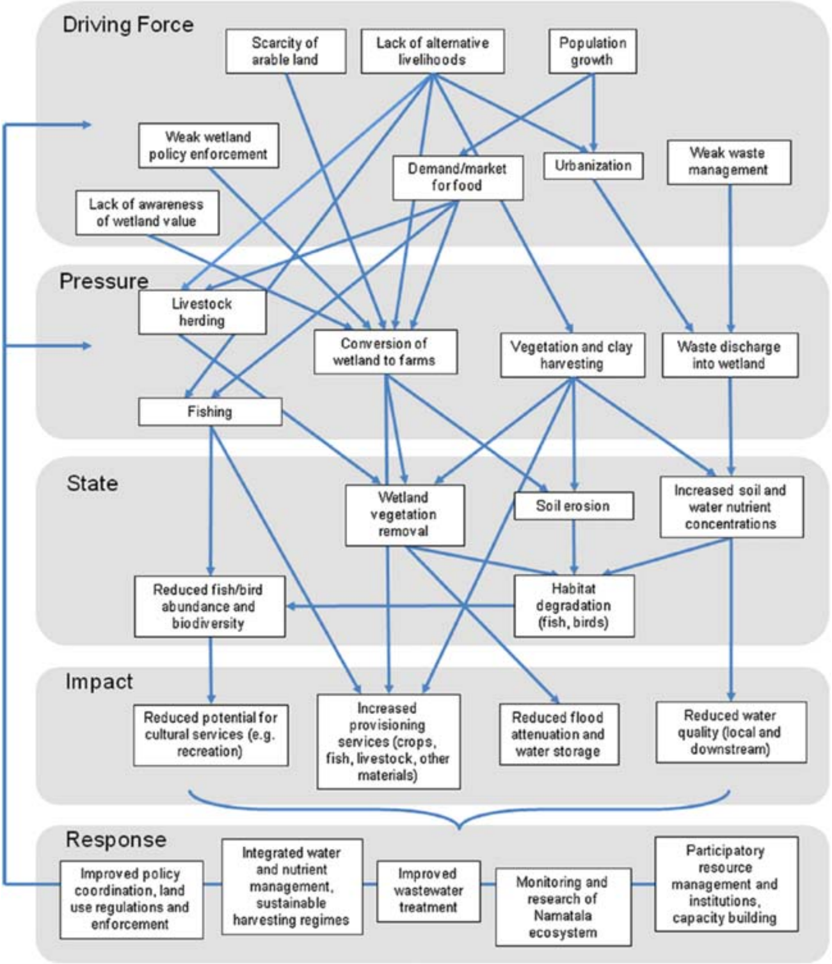

FIGURE 19.10 A driver–pressure–state–impact–response framework for the Namatala Wetland based on analysis by stakeholders of actual and potential issues. *Reproduced from Namaalwa, S., van Dam, A.A., Funk, A., Ajie, G.S., Kaggwa, R.C., 2013. A characterization of the drivers, pressures, ecosystem functions and services of Namatala wetland, Uganda. Environmental Science and Policy 34, 44–57; Zsuffa, I., van Dam, A.A., Kaggwa, R.C., Namaalwa, S., Mahieu, M., Cools, J., et al., 2014. Towards decision support-based integrated management planning of papyrus wetlands: a case study from Uganda. Wetlands Ecology and Management 22, 199–213.*

the agricultural zones of the wetland, and increased water discharge during months with highest rainfall (Namaalwa et al., 2020). Farming in the upper part of the wetland has completely changed the ecological character, which is now largely disconnected from the river. The wetland was divided into five locally distinguishable areas based on hydrology and vegetation structure HGMUs running from upstream main channel and seasonally wet zones (HGMU 1), through increasing drained floodplain agriculture (HGMUs 2, 3, and 4), each with characteristic vegetation, to permanently wet zones dominated by emergent vegetation (Namaalwa et al., 2013). In the lower part of the wetland, HGMU 3 exports sediment and nutrients, whereas HGMUs 4 and 5 retain them. Taken as whole, the wetland has retained ecological regulatory function in terms of sediment and nutrient mobility in the Kyoga Basin, however, these functions can diminish with further changes in the catchment and wetland. The research in the Namatala Wetland led to recommendations with stakeholders to provide: sustainable agriculture in the upper part of the wetland; papyrus buffer strips along Namatala River; more sustainable land use in the lower part of the wetland; papyrus buffer zones at the waste-water discharge points; and managed harvesting regimes for the papyrus.

While the management response to these recommendations has been limited, and the pressure in the wetland continues, detailed work from sites such as the Namatala Wetland improves understanding of wetland functions and ecosystem regulating services. The detailed information that fed into the DPSIR model for the Namatala Wetland cannot occur at many sites across the tropics, as very few have been the subject of detailed research. Nevertheless, it does indicate where problems and solutions may lie in sites where only rudimentary information gathering has occurred.

Sites that have had the benefit of detailed research on ecological processes, often lack any formal management and/or only rudimentary or negligible management planning. These often need to also work through very local administrative structures, inevitably lacking resources. Effective management in such circumstances can benefit through demonstration to local authorities and stakeholders the benefit of ecosystem services and the economic cost of their loss (Russi et al., 2013). In the case of Namatala Wetland, any management response is essentially through land use planning and improved waste water management. On the other hand, research activities can lead to longer-term monitoring (Bennun, 2001), although retaining the funding and political interest for that can be difficult.

In the longer term, sustainable resource management will need to increasingly include citizens and stakeholders in the co-design of management, conservation, and monitoring (Dumakude and Graham, 2017). Assessment of wetland health by local stakeholders (citizen science) can be a valuable resource, and a useful means to involve communities in the protection and management of local wetlands. Very often there can be local expertise in plant and animal identifications and natural history. Traditional knowledge remains a rich resource, and more modern pursuits such as bird watching is common, and of increasing local interest in tropical countries. Guidance and motivation to be involved in citizen monitoring is, however, crucial. When involving the necessary quality control, collected data can contribute to national assessment and reporting of the state of a country's wetlands. This is all part of the much needed building of capacity across institutional; scales and embracing a longer-term vision for the maintenance of ecosystem services of wetlands, and the means to achieve that.

19.7 Conclusions: learning from the past and influencing the future

As pressures on the world's ecosystems increase, so to do the ecosystem services that they provide diminish. Tropical wetlands of all types directly provide food for millions of people. Vegetated wetlands are additionally important for a range of provisioning services, and for crucial regulating services that include carbon sequestration, flood control, and water purification. Conversion of wetlands to other uses such as for more intensive food supply relying on land drainage, or human settlements are human choices that trade natural capital for economic capital. Consequences on social capital can be positive or negative depending on scale and who benefits and who does not. The effects of human pressures on biodiversity have reached a crisis point, leading to well-founded views that we are now witness to the sixth mass extinction of life (Chapin et al., 2000; de Vos et al., 2015) and live in a world so dominated by human activities that merits the definition of a new epoch, the Anthropocene (Waters et al., 2016).

The global policy response to the loss of biodiversity and those ecosystems that support it has so far failed to meet the challenge. For wetlands, the Ramsar Convention provides a foundation of global commitment for their conservation, but overall it has not been shown to have had a sufficiently widespread effect for anything like the required scale of wetland conservation, or to fulfill its moto of "wise use of wetlands." Only a few countries with tropical wetlands have a strong policy framework for wetland protection, and most a general reliance on donor funds for management. As such, the wider resource of wetlands remains very susceptible to human pressures and impacts, often driven by national policies to meet economic or food security objectives, or subject to other pressures arisising from drivers far from the wetland itself. In many countries, the obligations to the Ramsar Convention appears no more than a token effort in so far as the translation to action on the ground can be demonstrated. In reality, the vast majority of wetlands in the tropics fall outside any formal protection. Many countries seem to struggle with even making agreed payments to support core activities of the Ramsar Secretriat or their national focal points, who gather at the periodic Convention of the Parties (COPs) where decisions are made by consensus. The permanent Secretariat manages advisory committees and various outreach products, available at www.ramsar.org. The apparent disconnect with tangible action on the ground reflects a number of factors including political commitment and the flexibility inherent in how a party implements the Convention (Gardner, 2018). While in some countries the Ramsar Convention can play an important role in influencing domestic legal decisions, in many countries it either has a limited role or, in the messy world of policy, hard to discern. This does not negate the positive role that the Ramsar Convention has made to management planning and guidance to governments, or its role in supporting other Conventions and international intiatives. A comprehensive overview of bodiversity-related Conventions and intiatives, and their interactions, relevant to wetlands is provided by Davidson (2018).

Like the Ramsar Convention, the Convention on Biological Diversity (CBD) is a multilateral environmental agreement (see Laltaika, 2022, Chapter 23). The CBD was established at the UN Conference on Environment and Development (the Rio "Earth Summit") in 1992. The CBD has 193 parties, and from members of the UN, only Andorra, South Sudan, United States, and the Vatican are not signatories. The CBD works closely with Ramsar, to such as extent that implementation of the Ramsar Convention is also that of the CBD, and the guidance Handbooks of Ramsar provides guidance for the CBD (Coates, 2018). The so-called Aichi Biodiversity targets of the CBD, adopted in 2010 and including safeguard and restoration of essential ecosystems, were formally incorporated into global commitments of the UN SDGs (www.https://sdgs.un.org). The SDGs 6.6 and 15 include a halting of the decline of aquatic biodiversity by 2020. This has not been realized, and perhaps never could be without a transformation of the way that ecosystems are actually valued in decision making. The future requires a different and more holistic approach to the management of water resources, a greater focus on systems thinking and a broader enagagement across sectors and society at large (Darwall et al., 2018; Tickner et al., 2020; van Rees et al., 2020). Given the urgency for the protection of tropical wetlands and safeguarding their biodiversity and ecosystem services, these initiatives also stand little chance of success if they are only driven by the global north. Successful conservation and management of tropical wetlands will also not occur if imposed only from above, at either national or international levels.

A key component of managing wetlands is to understand the ecological dynamics and how these interact with the availability of ecosystem services and benefits to people. There is a clear need to maintain and reinstate the functions of wetland resources in order to ensure that the *per capita* ecosystem service levels provided by wetlands keep pace with a developing population and its growing demands on the resource base. While significant progress has been made in enhancing our understanding of wetlands, and how to assess them, further work is required to translate that understanding for management of key wetland resources of water quantity or flow regime, water quality, geomorphology, and biodiversity; and how those resources are used within sustainable limits. This can be greatly supported by use of straightforward biophysical and ecosystem service assessment (Kotze et al., 2020; Macfarlane et al., 2020), but also necessitates meaningful participatory processes and local capacity development. It requires asking critical questions, and building local inventory, assessment, and monitoring across useful spatial and temporal scales.

Tropical vegetated wetlands and floodplains typically comprise multiple habitat types, and heterogeneity, often over small scales. They tend to be highly productive systems supporting numerous ecological processes, often dependent on hydrological interconnectivity, especially during periods of flood. Understanding these dynamics and ecosystem functions more fully and how this supports wetland classification is an important area for further research that can benefit particularly from the flexible and hydrologically based approach developed by Junk et al. (2014). This requires thinking about wetlands in the broader sphere of the catchment, what that implies for sustainable use of land and wetlands, and how that relates to current views of development (Russi et al., 2013). These are ambitious needs. Development of wetland-protected area networks can play an important role in that, but of itself is not sufficient as an effective strategy of wetland conservation or provision of wetland services to society. Effective wetland protection can only be realized through partnerships between top-down government mandates and bottom-up stakeholder involvement. Across the tropics, a mid-tier of local authorities and their interactions with NGOs provides for an essential link between national ambitions and local needs.

For most tropical vegetated wetlands, adopting an approach of what can be realistically achieved within the inevitable financial and capacity limits is probably the greatest challenge in conserving habitats and their ecosystem services. Building local management into regional and national frameworks for maintaining a spectrum of ecosystem or provisioning and regulating services provides the basis for sustainability. Smaller community-based management could be supported with the knowledge and experience of larger, perhaps government, managed sites and benefit from further exploration and use of local traditional knowledge. It can benefit from local stewardship, market-based schemes, and environmentally focused enterprises supporting the agency of local communities for environmental stewardship (Buechler and Hanson, 2005; Engel et al., 2008; Sullivan et al., 2018). Such a strategy is multipronged, and what works in one place may not be the case in another. It crucially, however, involves development of knowledge and, often, training to recognize and manage the services that wetlands can provide at scales ranging from government to local communities, and the capacity development needed for that. This broader approach will be achieved as much in the conference hall and the civic office as through activities in the wetlands themselves. Skill development of local communities to manage wetlands for the benefits they provide raises opportunities for community monitoring, which offers a realistic means for better protection and management in the long term. This can be guided by use and locally relevant development of techniques for rapid assessment of ecosystem sevices (Kotze et al., 2020; Peh et al., 2013). Community-based partnerships with government and international organizations can greatly support local development needs, but requires particular competencies that are effective across a spectrum of stakeholders and interested parties and, therefore, requiring attention to cultural and institutional change and education (Finlayson et al., 2017). This can be a messy and uncertain strategy, but one that liberates local wetland managers from a need to have sophisticated management planning. For many wetlands, the perfect can be the enemy of the good.

Superimposed on the challenges of current wetland conservation and management is the specter of climate change. Climate change affects wetland ecosystem functions and the sevices they provide. The consequence of an increase in mean Earth temperatures from Green House Gas (GHG) emissions are already evident, with greater variability in climate and greater frequency of extreme events, notably droughts, floods, and fire. Predictions for the future are that these events will also vary significantly across the tropics affecting surface and groundwater hydrology, biogeochemical cycles, evapotranspiration, and species distributions and their interactions, and respective feedbacks (Junk et al., 2013). For many vegetated wetlands, and those who depend on them, climate change will likely magnify impacts from existing pressures. It is recognized that wetlands are particularly susceptible to climate change (Capon et al., 2013). Vegetated wetlands can also provide resistance to impacts of climate change through maintaining regulating ecosystem services that include flood storage, buffering storm damage, filtering pollutants and sediment from runoff, groundwater recharge and water supply during drought, provision of wildlife refuges and corridors and regulating microclimate and cooling effect of wetlands (Junk et al., 2013; Moomaw et al., 2018). The extent that climate change affects plant and animal communities of vegetated wetlands will depend largely on the extent that wet-dry cycles change, and the vulnerability of species, especially those at the edge of their geographical range. Openings for exotic invaders are likely to increase. Droughts increase the potential for destructive fires.

Globally, limiting GHG emmisions to avoid an average temperature rise below 2°C as set out in Paris Climate Agreement (United Nations, 2015) requires a net sequestration of atmospheric carbon. The role that tropical wetlands can play in that remains an insufficiently explored policy goal, but provides an opportunity for wetland conservation, the maintenance and extension of wetlands in the landscape, and for raising wetland conservation up the political agenda (Finlayson et al., 2017; Moomaw et al., 2018). This can support activities at local scales, where wetland conservation in practice occurs.

Given the urgency of the task, there is a need to engage politically in communicating the importance of wetlands for the benefits they provide at local, national and global scales and thus to mainstream wetland valuation into the body politic. Ultimately, the loss of freshwater life and mitigation of climate change is a political issue that involves land use and economic policies. The politics affect whether or not there is an enabling environment to effect wetland conservation or wetland destruction. This is no longer a nuanced debate on the merits of nature conservation, but how the maintenance of wetlands and other natural systems are essential for human life and well-being.

Dedication

This chapter is dedicated to Paul Mafabi, who dedicated his career with the Environmental Affairs of the Ugandan Ministry of Water and Environment, making a difference and promoting the wise use of wetlands.

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Chapter 20

Introduction to wetland monitoring

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20.1 Introduction

Freshwater ecosystems including wetlands are increasingly being placed under pressure due to human interventions. Increasing human populations and associated developments are threating wetlands with respect to wetland removal, influencing the quantity and quality of water (Deemy et al., 2022a, Chapter 4), and hydrology (Deemy et al., 2022b, Chapter 3). These impacts affect wetland function and biological communities that rely on these habitats for survival. The damage of natural wetlands receiving industrial effluent inflows affects biological attributes, such as biodiversity or taxonomic richness, trophic interactions and structure, community structure, and individual organisms (Batzias and Siontorou, 2008; Cuthbert et al., 2022, Chapter 17; Gálvez et al., 2022, Chapter 18). It is for this reason that the monitoring of wetland abiotic and biotic components is vital. This chapter will examine wetland monitoring, what bioindicators are and discuss some of the suitable bioindicator organisms.

Due to the increased rate of development taking place on a global scale, wetland associated waterbodies are continually under threat from pollution, overabstraction, and infilling (Wasserman and Dalu, 2022, Chapter 1). The assessment of these systems over time is therefore essential to manage them. The monitoring of wetlands on a broad scale is essential to assess and evaluate the efficacy of restoration and rehabilitation programs on both a temporal and spatial scale (Cooper et al., 2018). The increase of effluent discharge entering freshwater systems degrades these systems affecting their functionality. A number of approaches have been developed to assess environmental condition in these highly complex systems, be it aquatic or semiaquatic in nature (e.g., Courtemanch et al., 1989; Davis and Simon, 1995; Dziock et al., 2006; Henle et al., 2006; Overesch et al., 2007; Rinklebe et al., 2007).

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One of the main aims of monitoring is to analyze environmental relationships with an eye on model development for predicting the future impacts on hydrological regimes and biodiversity. Standardized monitoring programs therefore provide the necessary data to allow environmental managers to make informed decisions on the best mitigation measures to implement for the sustainable utilization and conservation of the aquatic resources (Jain et al., 2016). The type of monitoring program employed is largely determined on the purpose of monitoring, the system to be monitored, and on what scale the monitoring is taking place. Artiola and Brusseau (2019) assert that developing a monitoring program to indicate extent and effect requires careful consideration on being able to identify the purpose of the monitoring program is and the approaches to be followed defining the number of samples, type, and measurements necessary.

The monitoring of wetlands has its own positive and negative aspects. The primary consideration in monitoring program development is to determine the purpose of the program. This provides insight into the resolution required by the program, the depth at which the monitoring program is intended to assess, and the duration of monitoring. If you are trying to assess the exact impacts of a particular industry, mining activity or development in the system and the extent downstream the impacts are felt, then a chemical monitoring program coupled with passive biomonitoring may be required. For the purposes of this chapter chemical monitoring involves the collection and analysis of both biotic and abiotic samples and analyzing them for the presence of potential contaminants (van Der Oost et al., 2003). Passive monitoring relies on the use of indigenous organisms to assess the integrity of the ecosystem in question (Goldberg, 1975). If you are trying to assess catchment or subcatchment integrity then a combined biological, hydrological, and habitat monitoring program may be better suited. Wetland monitoring is particularly difficult due to the complex nature of wetland areas. Characterizing the wetland type is particularly important as this will indicate the habitat types one would expect to find and therefore guide the choice of bioindicator organism selected.

20.1.1 What is wetland monitoring?

Wetland monitoring can be described as the assessment of the biotic and abiotic components within a wetland to assess the current integrity of the system in question. Environmental monitoring and by association wetland monitoring is a series of observations pertaining to changes that occur in the environment (Artiola and Brusseau, 2019). This assessment assists interested and affected parties in making management decisions for improving the current health of the wetland in question. Wetland monitoring can be split into a number of categories, with each category having its positive and negative points but the type of monitoring conducted essentially is driven by what

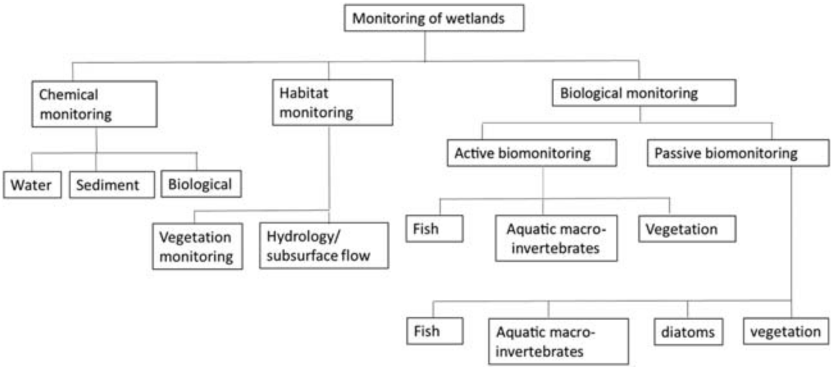

FIGURE 20.1 Diagram indicating the different types of monitoring.

you are trying to achieve during the process. Monitoring can be either active or passive and chemical or biological in nature. Fig. 20.1 presents a diagrammatic view indicating the different types of monitoring.

20.1.2 Chemical monitoring

Chemical monitoring involves a process of collecting either abiotic (water or sediment) or biotic (flora or fauna) tissue samples and analyzing for the presence of metals, nutrients, pesticides, and pharmaceuticals (van der Oost et al., 2003). Many of these contaminants are emerging and rarely included in traditional monitoring programs. Emerging contaminants are defined as naturally occurring or synthetically produced substances that have the potential to enter and effect the natural environment (Daverey et al., 2020). Chemical monitoring in water provides a snapshot of water quality at the time of sampling within a system but cannot provide a time-integrated indication of events taking place within the wetland (Jones et al., 2015, De Baat et al., 2019). Chemical analysis of sediments provides a better idea of what is happening in the system on a temporal scale as wetlands act as a sink and chemicals bound to the sediment will settle in the wetland. Sediment analysis therefore can provide a contamination profile of the wetland if core samples are analyzed. Physicochemical analysis does however not provide insights into the health status of the living organisms that inhabit the system (Van der Oost et al., 2003). Sampling flora and fauna for chemical tissue analysis provides an indication of the accumulation of toxicants by the organisms in the system. The chemical analysis of the tissues can provide an indication of the concentrations accumulated by the organism and how the chemicals may be passed on through the food chain but they do not provide an indication on the health status of the organisms (van der Oost et al., 2003). Biomarker analysis discussed later in the chapter proves an indication of the health status of the organisms inhabiting the ecosystem. An example of where chemical monitoring was successfully employed to understand sediment characterization and heavy metal speciation is in the Ramsar-accredited Deepor Beel tropical wetland, Indo-Burmese province, India. Sediment samples were characterized according to sediment texture, bulk density, particle density, and water holding capacity. Spatial and temporal variation in carbon content, organic content, and heavy metal content were also assessed. The study revealed that heavy metal concentrations were highest during the premonsoon while nutrients and organic content were highest during the monsoon season. Metal content also revealed the impacts of anthropogenic activities on a spatial scale (Kalita et al., 2019).

20.1.3 Habitat monitoring

Habitat monitoring is conducted to assess the integrity or health of a system from an ecosystem function point of view. Assessing the hydrology and subsurface flows within the ecosystem can provide an indication of wetland degradation due to overabstraction of water in the surrounding catchment, anthropogenic effects on stream connectivity affecting the timing and quantity of flow within the wetland, inundation period, and amount of habitat available for organisms to inhabit. Methods for assessing wetlands have been developed covering a range of complexities (Dube et al., 2022a,b, see Chapter 21). Some monitoring methods only focus on stressor indicators, while others focus on biological interactions taking place within the wetland. Kotze et al. (2012) developed the WET-Health methodology for assessing wetlands in South Africa. Due to the lack of baseline data available at the time, the WET-Health methods focused on stressor indicators with less focus placed on the response indicators. The response of vegetation within the wetland system was however included. The WET-Health methodology focused on examining the degree of change within three components and relating them back to a reference condition. These three components were the: hydrology, geomorphology, and vegetation. The hydrology, geomorphology (Deemy et al., 2022b, Chapter 3), and vegetation (Piedade et al., 2022, Chapter 7) are all assessed individually (to prevent double counting) although the interrelated nature of the components is recognized. The interlinked nature of the components stems from the fact that if you affect the geomorphology within a system, you will affect the hydrology and vice versa. These two components will then have a marked effect on the vegetation (see also Piedade et al., 2022, Chapter 7). While conducting the hydrological assessment quantity, frequency and flow patterns are assessed. The geomorphology assesses sediment inputs and outputs as well as the geomorphic indicators of sedimentation. The vegetation component examines the relative abundances of the functional plant groups. The standardized method that is provided by the WET-Health methodology prescribes what factors need to be assessed and provides information and supporting rationale behind the scoring system to follow, but it does allow for some well-motivated adjustment. The scientific rationale behind the development of the WET-Health system is sound and stands upto third-party review.

The WET-health has been used in other African countries, that is, Beuel et al. (2016) found that the WET-health monitoring program was beneficial in assessing a number of wetlands in East Africa. The study assessed four East African sites in Kampala (Uganda); Kigali (Rwanda); Ifakara (Tanzania); and Rumuruti (Kenya). The WET-Health program was adapted as the original protocol as it had not been used on large wetland systems. The modifications adopted to the WET-Health protocol, primarily to the randomization of assessment unit selection and impact score determination made it possible to successfully describe the degree of wetland disturbances in the East African wetlands.

20.1.4 Passive monitoring

Passive monitoring is a process where organisms, both flora and fauna are sampled and assessed to provide an indication of the biological integrity and diversity within the system (Ronci et al., 2016). These organisms can provide data on various hierarchical levels of organization. Data can be obtained on a subcellular level, tissue level, organismal level, population level, community level, or ecosystem level. These different hierarchical levels therefore provide a holistic view of the integrity/health of the system but on a time-integrated scale. Buah-Kwofie et al. (2018) reported on the bioaccumulation and health risks of pesticides in fish tissues from the iSimangaliso Wetland Park. The iSimangaliso Wetland Park is a global biodiversity hotspot and world heritage site. The site is also used by local communities for subsistence fishing. Indigenous fish species were sampled from the site and analyzed for organochlorine pesticides (OCPs). The study revealed high OCPs levels and these high levels indicated potential human health risks for local residents consuming the fish and the potential for bioaccumulation of these pesticides along the food chain.

20.1.5 Passive sampling devices

There has been some research into the use of passive sampling devices for monitoring purposes. This involves using nonbiological technologies, such as the artificial mussel or semipermeable membrane devices, developed for use in marine systems, to mimic accumulation of biologically available contaminants (Wu et al., 2007). Dahms-Verster et al. (2018) tested the use of artificial mussels in the Nyl River floodplain to assess biologically available metal concentrations along the pollution gradient on a seasonal basis. Artificial mussels were deployed at seven sites along the course of the upper Klein Nyl River leading into the Nyl River Floodplain to assess metal bioavailability. The artificial mussels were collected after a 4-week deployment and the accumulated metals were determined using Inductively Coupled Plasma Optical Emission Spectroscopy (ICP OEs) and Inductively Coupled Plasma Mass Spectroscopy (ICP-Ms) analysis. Metal concentrations were compared to water metal concentrations collected at the time of deployment and retrieval. The results indicated that metal contamination was occurring in the system and that artificial mussels are an alternative to using biological samples when conducting a time-integrated analysis of metal concentrations in a system. The study did however conclude that spot water sampling was also required to provide some background metal levels to base comparisons on. Passive sampling devices do have a couple of pros and cons with the biggest drawback being that they are prone to tampering by local communities. Passive sampling devices can also not replace a bioindicator organism but can provide an indication of the trends of metal accumulation within a system. This is because they do not metabolize or sequester the metals so the metal concentrations accumulated by bioindicator organisms will differ from those accumulated by the passive sampling device.

20.1.6 Active biomonitoring

Active biomonitoring is a process where control/unexposed test organisms either flora or fauna from a known source are translocated into a new system to quantify their biochemical, physiological, and/or organismal responses for the purpose of water quality monitoring (De Kock and Kramer, 1994; Smolders et al., 2003; Birungi et al., 2007). This is especially important in assessing contamination of a water body from wastewater treatment plants (Cazenave et al., 2014; McGovarin et al., 2018; Pérez et al., 2018). The advantage of active biomonitoring is that organisms that are not present in the system as a result of anthropogenic activity can be used to assess the study site (Oikari, 2006). These organisms are left in situ for a known period, that is, weeks or months, and then sampled to assess the effect the system has on the organism over that time period. This type of monitoring also provides a time-integrated assessment of the effects of the system on the organism. The organisms are usually placed in cages so that they are easily sampled after the specified exposure period. Apart from the standardization of exposure time, variables such as size, age, sex, number of individuals, distance from contaminant source and predation can be controlled (Oikari, 2006). In selecting the test organism the researcher/principle investigator must make sure that the selected test organism poses no immediate threat to the system. The organisms should be native to the system to prevent the addition of invasive species exacerbating issues within the system. Organisms should also have been quarantined correctly and treated for pathogens so as to prevent the addition of parasites and diseases into the receiving body of water. The exposed organisms can then be collected for various studies including metal accumulation, pesticide and microplastic analysis or physiological and histological stress assessments with the aid of biomarker analysis (Oikari, 2006; Catteau et al., 2020).

20.1.7 Bioindicator organisms and biomonitoring

The use of bioindicators has been advocated since the 1950s (Holt and Miller, 2010) with the development of the Sapronian index by Kolkwitz (1950). Although the use of bioindicators has taken time to gain traction the first biotic indices used for monitoring aquatic systems were developed by Armitage et al. (1983) [i.e., Biological Monitoring Working Party (BMWP)] and De Pauw and Vanhooren (1983) (i.e., Belgian Biotic Index). Since then biomonitoring indices for the rapid assessment of aquatic environments assessing effects of environmental change have become more common (Cairns and Pratt, 1993).

A "bioindicator" is the collective term used to refer to all sources of biological and abiotic interactions within an environment that indicate change (Parmar et al., 2016). They are used to assess the impacts of environmental change in relation to the natural system, assess the synergistic and antagonistic effects of pollutants on an organism, and provide early warnings of potential negative impacts (Parmar et al., 2016). Deviations from the natural condition can either be as a result of global climate change, habitat alterations, or the effects of anthropogenic activities (Parmar et al., 2016). Holt and Miller (2010) further include biological processes, species, and community structure as bioindicators.

20.1.8 What makes good bioindicator species/model bioindicator species?

According to Batzias and Siontorou (2008), the most effective means of assessing wetland pollution burden is to directly assess representative biological components within the wetland supported by chemical and physical data. Interpreting data collected does however require an in-depth, detailed background knowledge of the biological components, which allows for the assigning of sensitivity ratings (Cortelezzi et al., 2020). The selection of a suitable bioindicator or sentinel species is however key in developing an effective monitoring program. The following characteristics are important in selecting the correct bioindicator organism. Bioindicator species should be sensitive to ecosystem change as a result of environmental change and the presence of pollutants with a distinct reaction along a pollution gradient. These effects can manifest with biodiversity alterations, effects on the community structure or sublethal effects (biochemical responses on the organisms), and their presence or absence from the ecosystem (Walsh, 1978; Peterson, 1986; Gerhardt, 2002; Holt and Miller, 2010; Parmar et al., 2016).

Bioindicator organisms should also be easily identifiable, widely distributed; have a well-documented life stage history and biology; reasonably sedentary; the ability to provide an early warning signal; provide a key function within the ecosystem; and have a predictable, homogeneous response to contaminants (Hilty and Merenlender, 2000; Goodsell et al., 2009; Li et al., 2010, 2019).

20.1.9 Fish

Fish have been used as a successful bioindicator as they are in constant contact with their changing environment (see Reichard, 2022, Chapter 12). They also allow for native species to be assessed, which is important as the native species have acclimated to the prevailing environmental conditions (van der Oost et al., 2003). The sensitivity of fish shows that human-based activities make it possible to assess changes throughout the different trophic levels. The socioeconomic, esthetic, and recreational value added by fish within a system adds importance to using fish as a bioindicator (Cooper et al., 2018). The use of fish in biomonitoring can be conducted on various levels. First, the presence or absence of different species from the natural/reference species lists can indicate effects on population size, community structure, and functional role played by the different species inhabiting the system. These changes in population structure can provide insights into the abiotic factors affecting the fish such as water quality, habitat alteration, changes in hydrology and sedimentation, and climate change (Plafkin et al., 1989; Phillips and Rainbow, 1993; Jain et al., 2010). The effects on the fish diversity within the system under study are a relatively cheap and easy assessment that highlights hotspots where more in-depth attention is needed (Naigaga et al., 2011). Second, tissues from the organisms can be used for bioaccumulation studies to assess if the fish are safe for human consumption, which is an important aspect in regions where subsistence fishing is important (Joanna, 2006; Khatri and Tyagi, 2015). Contamination of waterbodies and subsequently the fish that live in them could have economic effects affecting inland fisheries and regional food production. Finally, the tissues from the fish can be assessed on a subcellular level which provides an indication of the physiological stress the fish are under, which could act as an early warning signal within the system under study (Cooper et al., 2018).

Although fish assessments in the various forms provide valuable insights into wetland health, they do pose some difficulties. Catching of fish for diversity assessments in wetland areas is often difficult to conduct due to sampling difficulties. The standard sampling methods for catching fish, be it via gill nets or seine nets, are often not very successful due to the types of habitat present. Low conductivity within the water can hamper the use of electro-narcosis and so the use of baited traps and fyke nets is often the best way to sample in wetland areas. The use of underwater video may provide a noninvasive way for assessing fish diversity within wetland habitats.

Fish have been successfully used to assess the effects of environmental pollution in wetlands. A case study by Naigaga et al. (2011) indicated that the different sensitivities of fish were helpful in assessing the effects of anthropogenic activities in the Lake Victoria wetlands in Uganda. The study highlighted how societal activities around four urban wetlands, with the associated decrease in water quality negatively affected fish community structure. These negative effects were shown in decreased abundance and species richness. The data obtained allowed for informed decision making for conservation planning and sustainable use of the fisheries found within the different wetlands.

Fish have also shown their value as a bioindicator during active biomonitoring studies. Birungi et al. (2007) successfully used fish in active biomonitoring of the Nakivubo wetland in Uganda. Nile tilapia (*Oreochromis niloticus*) were placed in cages for 6 weeks and then assessed to determine the accumulation of selected heavy metals. Fish were collected every 2 weeks from the caged organisms and gill, liver, and muscle tissue were excised. Water samples and physicochemical parameters were collected on a weekly basis. The water and tissue samples were then analyzed for metal content using atom absorption spectrophotometry to determine zinc, copper, chromium, and manganese content. The study found that analyzing the fish tissues and water indicated an integrated accumulation response highlighting the overall effect of the contamination in the fish (Birungi et al., 2007). *Clarias gariepinus* and *Oreochromis mossambicus* have also proven themselves as suitable bioindicator species during bioaccumulation assessments conducted in the Nyl River floodplain (Musa et al., 2017).

20.1.10 Biomarker analysis

Biomarker analysis has gained traction in the field of ecotoxicology over past few decades. This is because a suite of biomarkers can provide a quantitative functional measure of bioindicator species to environmental stressor exposure. These measures can then be related back to anthropogenic activities (Adams et al., 2001). A number of tools have been developed to link chemical inflows and biological responses of exposed organisms. A suite of biomarkers has been developed to define the observed changes within organisms quantifying a measurable change within the exposed individuals. These biomarkers range from the molecular to individual level and from behavioral to biochemical responses (Van der Oost et al., 2003). Biomarkers can also be used to assess a system with regard to ecosystem structure and function by looking at the physiological responses of a range of species. The stress responses provide an estimation of the severity if physiological stress affecting species and allow for species sensitivity comparisons (den Besten, 1998).

Biomarker analysis can therefore assist in acting as an early warning sign for change that can occur further along the different levels of biological organization (Wepener et al., 2005, Jiri et al., 2018). The biomarkers can be split into three groups, being biomarkers of exposure, biomarkers of effect, and biomarkers of susceptibility (Chambers et al., 2002). The most common biomarkers used are those of exposure and effect. Biomarkers of exposure indicate that an individual has been exposed to a toxicant, either metal or organic in nature (Dahms-Verster et al., 2020). The biomarkers of effect indicate the physiological response undergone in the individual to mitigate the oxidative stress induced in the individual during exposure (Volschenk et al., 2019). This approach is particularly useful in assessing the impacts of environmental change from point sources of pollution (Sanchez et al., 2013) and, subsequently in assessing any mitigation measures that may have been implemented for water quality improvement.

20.1.11 Aquatic macroinvertebrates

The use of aquatic invertebrates is common when selecting a bioindicator (see Dube et al., 2022a,b, Chapter 11; Brendonck et al., 2022a,b, Chapters 9 and 10). They have been used since the early 1900s. One of the first biomonitoring tools developed, the Saprobian index, used the presence or absence of aquatic macroinvertebrates to assess water quality affected by organic waste contamination. They are a particularly powerful indicator of water catchment integrity. The use of aquatic macroinvertebrates has been well studied in lotic systems. They are the bioindicator of choice in many countries with the use of tools such as the South African Scoring System Version 5 (SASS5), from South Africa, Stream Invertebrate Grade Number – Average Level (SIGNAL) from Australia and the BMWP from the United Kingdom. The SASS5 monitoring protocol was adapted from the BMWP to suit South African conditions (Dickens and Graham, 2002). The aquatic macroinvertebrates are a popular choice for bioindicator as they are easy to sample, relatively easy to identify in situ with the naked eye, have limited mobility, relatively quick recolonization times, frequently live for more than a year, and an excellent indicator of integrating ecological condition (Plafkin et al., 1989; Khatri and Tyagi, 2015; Dube et al., 2022a,b, Chapter 11). Aquatic invertebrates are regarded as one of the most important organism groups for wetland bioassessments, even though the functional ecological roles in wetlands are not well understood (Bird, 2010). The comparative lack of understanding on the functional role of aquatic macroinvertebrates within wetlands requires future research. Indices developed around the use of aquatic macroinvertebrates are usually centered on diversity or community composition, abundance, and species richness. The aquatic macroinvertebrates can further be used to assess accumulation of metals and other contaminants making them important in assessing movement of chemicals through the trophic levels (Rainbow, 2002; Karimi and Folt, 2006; Fletcher et al., 2019).

Although the aquatic macroinvertebrates are important in assessing water quality in wetlands, community structure is also influenced by biotope characteristics present. Wetlands generally have less biotopes than lotic (riverine) systems and, therefore monitoring indices need to be modified or developed for use in wetlands. Due to the high degree of variability in wetland types these indices generally need to be regional specific (Bird et al., 2014). Habitat preference by aquatic macroinvertebrates in wetlands is primarily affected by the vegetation (Bird et al., 2014), with an increase in vegetation complexity causing an increase in aquatic macroinvertebrate species abundance and richness (Bird et al., 2014). Gebrehiwot et al. (2017) have also indicated the functional feeding groups (FFGs) and feeding interactions can also be used as a robust indicator of ecosystem interactions. During their study in the Gilbe Gibe catchment, Ethiopia, the researchers used stable carbon and nitrogen isotopes from macroinvertebrates to assess the effects of pollution on feeding interactions. Function feeding type metrics and aquatic macroinvertebrate diversity indices indicated a decline in ecological integrity in urban-impacted riverine sites and a substantial recovery in wetlands downstream. The study confirmed the importance of assessing FFGs and feeding interactions in water quality monitoring.

Chironomidae have proven successful as bioindicators with studies being conducted on the relative sensitivities of the different chironomidae species. A study by Cortelezzi et al. (2020) indicated that Chironomidae at subfamily level provide a suitable resolution for determining ecological trends along an environmental gradient. The family Chironomidae has also been successfully used by Dahms et al. (2020) as a suitable bioindicator for microplastic contamination in freshwater ecosystems with the potential for use in wetlands.

The dragonfly biotic index (DBI) is a biomonitoring tool that has been developed as a means of assessing wetland integrity. The index's success in determining aquatic health of rivers and wetlands is based on the low diversity of adult dragonflies, their relatively large size, and ease of identification. Dragonfly taxonomy has been well researched, which aids in the ease of identification (Simaika and Samways, 2008, 2011; Vorster et al., 2020). The index provides a way of assessing riverine and wetland integrity without having to enter the water and allows for direct comparisons of scores from adjacent wetlands and streams (Samways and Simaika, 2016). The DBI works on the premise that sites with similar ecological conditions will have a similar species diversity. The DBI is calculated as the sum of three subcategories. These subcategories are geographical distribution, IUCN status, and sensitivity to habitat change. Field sampling revolves about determining the species that are at the selected sites with species recorded from observation and identification. Scores ranging from 0 to 3 are then assigned in each subcategory providing a score between 0 and 9 for each species observed. These scores are then summed for all the species recorded during sampling providing you with a total DBI site score. The higher the DBI score, the better the ecological condition. The DBI/site can then be calculated by dividing the DBI score found at the sampling site by the number of species identified. This system is a robust monitoring system that has great potential for assessing wetlands (Samways and Simaika, 2016).

The DBI has successfully been used to determine the ecological status of the iSimangaliso Wetland Park by Hart et al. (2014). During the study 50 sites were selected and the odanata species present were determined and total dissolved solids (TDS) in water was determined. The total DBI and DBI score/site were calculated. The DBI scores were then compared to other studies conducted around South Africa and areas of conservation importance within the iSimangaliso Wetland Park were identified.

Research has conflicting reports on which vegetated biotopes provide better habitat for aquatic macroinvertebrate diversity and are therefore better to sample. Researchers generally agree that vegetated biotopes are better than open water biotopes (nonvegetated) indicating a higher diversity and abundance (Bird et al., 2014), although Olson et al. (1995) noted exceptions to this. De Klerk and Wepener (2011) reported higher richness and diversity in marginal and emergent vegetation from endorheic pans from Mpumalanga Province in South Africa whereas a number of researchers are of the opinion that the complex architecture of submerged vegetation provides more suitable habitat to support a larger diversity and abundance of aquatic macroinvertebrates (Bird et al., 2014).

20.1.12 Community structure assessments

The assessment of wetland integrity usually revolves around assessing macroinvertebrate species diversity, abundance, and richness although one should not shy away from assessing FFGs or diversity within specific families. Community structure has successfully been used by Baker and Greenfield (2019) to assess the anthropogenic impacts affecting the Nyl River Floodplain in the Limpopo Province, South Africa. During the study, aquatic macroinvertebrates were sampled from available biotopes within the Nyl River and the wetland floodplain areas to monitor the effects for various activities on a spatial and temporal scale. The biota was collected and identified to its lowest taxonomic level and then through the use of multivariate statistics spatial and temporal trends were determined. The study indicated that the macroinvertebrate community structure had shifted from the reference condition. This aquatic macroinvertebrate community structure shift occurred as a result of human intervention both in the form of water quality deterioration and habitat alterations.

20.1.13 Diatoms

Diatoms are ubiquitous and are found in all aquatic biotypes. Each species has its own specific water quality requirements and they respond quickly to changing environmental and water quality conditions as a result of either natural processes or anthropogenic activities (Gell et al., 2002; Dalu and Froneman, 2016; Dalu et al., 2022, Chapter 8). The siliceous makeup of diatoms is also advantageous to their use as a bioindicator as it allows for monitoring of past and present environmental conditions and aquatic pollution (Kock et al., 2019). Diatoms have also been used to assess temporary wetlands using a functional-based approach (Riato et al., 2017). The unicellular algae are a reliable way of monitoring a water system such as a wetland which provides a robust data set that indicates water quality. Diatom monitoring cannot give you the exact contaminants that are affecting the water but can provide an indication of how the water quality has changed providing a relatively accurate indication of system integrity. Diatom taxonomy is relatively well researched and sensitivities to various water parameters are well known. Variations in water depth, timing of inundation, seasonal flow rates, and habitat availability and alteration make the use of fish and aquatic macroinvertebrates as bioindicators is often problematic. Diatoms however are not constrained by these factors and this makes them ideal bioindicator organisms for the monitoring of wetlands (Pandey et al., 2017). Sensitivity to organic matter and nutrient loading as well as a well-defined relationship between community assemblage and environmental change enhances their suitability as a bioindicator organism.

There is an increasing use of diatoms to assess and monitor wetlands in South Africa with a number of papers being published. A few of these are cited as case studies below. Research done by Musa and Greenfield (2018) used diatom indices to categorize impacts and recovery of the Nyl River floodplain, Limpopo Province, South Africa. During the study, the trophic diatom index (TDI), specific pollution sensitivity index (SPI), percentage pollution tolerance index (%PTI), and generic diatom index (GDI) were used to assess the effects of sewage effluents on the Nyl River floodplain. Seasonal sampling was conducted along a longitudinal section of the Klein Nyl River. The results from the different indices indicated that the sampling sites above the town of Modimolle had good water quality with an increase in organic matter, originating from the sewage treatment works, downstream. Decreasing TDI scores and %PT scores determined in the wetland sites indicated that the system was recovering and that the wetland was performing its purification process sufficiently.

Riato et al. (2018) reported on preliminary findings using diatom community assemblages to assess the effects of acid mine drainage, as a result of coal mining, in depressional wetlands in Mpumalanga. In the study, the researchers developed a Diatom-based multimetric index that accounted for natural variability in depressional wetlands used for acid mine drainage (AMD) storage (Riato et al., 2018). Epiphytic diatom community assemblages indicated a strong ecological response to AMD pollution that offered a viable alternative to more common but less effective biological monitoring using vegetation and aquatic macroinvertebrates. Kock et al. (2019) reported on how diatoms were successfully used to determine the ecological status of Lake Sibiya, a Ramsar-accredited wetland in Kwa-Zulu Natal, South Africa. Four diatom indices were used to calculate a final integrity score. Through the determination of the GDI, SPI, the %PTI, and TDI a final ecological status was determined. The diatom index scores coupled with water quality data indicated seasonal variation in diatom community assemblages. These three studies indicate that diatoms can effectively be used in monitoring wetland systems providing data not only on the diatom community composition and species diversity, but also with regard to ecosystem function and water quality.

20.2 Concluding remarks

Monitoring of wetland systems forms an important part of management, conservation, and restoration practices in general (Irvine et al., 2022, Chapter 19; Marambanyika et al., 2022, Chapter 22). Each of the monitoring tools developed have their pros and cons. A "silver bullet" with regard to one monitoring tool providing a definitive answer to the ecological integrity of a wetland does not exist. Due to the complex nature of wetlands, variability in wetland characteristics, habitat, seasonality, and biota that inhabit them a suite of monitoring tools should be applied. Biomonitoring in general provides an indication of ecosystem integrity but will not tell you the exact cause of the contamination. This can only be done with chemical analysis. Biomonitoring however can provide important information regarding a wetland's ability to provide goods and services and inform if the generally more laborious and expensive chemical monitoring is required. The selection of bioindicator organism is reliant on the intended purpose of the monitoring. Monitoring programs should evolve and if the data generated is insufficient and changes to programs should be made with adaptive management being key.

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Chapter 21

GIS and remote sensing analytics: assessment and monitoring

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21.1 General introduction

Tropical wetlands are among the most productive ecosystems on earth, providing unique and significant ecological, socio-economic, as well as cultural goods and services (Brendonck et al., 2022, Chapter 9; Cuthbert et al., 2022, Chapter 17; Klemas, 2013; Kotze et al., 2008; Lamsal et al., 2015; Walter and Mondal, 2019; Wasserman and Dalu, 2022, Chapter 1; Irvine et al., 2022, Chapter 19, Marambanyika et al., 2022, Chapter 22). For example, these ecosystems provide a vital role as they maintain numerous natural cycles, including water, carbon, and nitrogen cycles, besides supporting a wide range of flora and fauna (Guo et al., 2017; Perennou et al., 2018; Deemy et al., 2022, Chapter 6; Moyo, 2022, Chapter 5). Tropical wetlands also store considerable amount of carbon (Meng et al., 2016; Parker et al., 2018; Moyo, 2022, Chapter 5), which is important in mitigating global warming. In addition, these wetlands protect interior areas from degradation by providing a barrier to wind and waves, which dissipate energy from harmful activities, such as storm surges, hurricanes, and tsunamis, as well as providing a buffer for marine ecosystems against terrestrial sedimentation and pollutants (Kolka et al., 2016). Additionally, tropical wetlands provide a range of services to society globally, among them include the purification and replacing water, food, and valuable grazing lands for wildlife and livestock (Kingsford et al., 2016; Osland and Middleton, 2018; Job et al., 2022, Chapter 2; Marambanyika et al., 2022, Chapter 22).

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Although tropical wetlands play an important role in maintaining and providing critical ecosystems goods and services, they are however, currently faced with a considerable number of threats, which are increasingly becoming a major concern (Murdiyarso, 2012; Laltaika, 2022, Chapter 23). Literature has shown that there is a massive threat, destruction, and loss of tropical wetland worldwide (Smardon, 2014; Davidson, 2014). It is estimated that 64% of the wetlands have been lost globally, since 1900 (Davidson, 2014). These loses have been primarily attributed to unsustainable human activities, as well as natural phenomena, such as climate change and frequent droughts (Masese et al., 2012; Lamsal et al., 2015). The study by Masese et al. (2012) identified the lack of awareness, appropriate frameworks, and guidelines for wetland conservation and management among the root causes of wetland loses. Human threats to wetlands range from water pollution, land cover transformation (Masese et al., 2012), drainage for agriculture, and introduction of alien species (Klemas, 2013; Lamsal et al., 2015; Walter and Mondal, 2019). The aforementioned human activities in association with climate change and droughts, affect tropical wetlands, particularly water quality and species diversity among others (Masese et al., 2012). These significant modifications, destruction, and loss of wetlands alter fundamental ecological, socio-economic, and cultural values and goods provided by these wetlands (Masese et al., 2012). Thus routine assessment and monitoring of these natural resources is required to understand and mitigate the impacts.

There are different techniques that have been developed and used to assess and monitor natural resources including wetlands. Among these techniques are GIS and remote sensing; machine learning techniques, which have recently ince gained popularity bcause of their spatial explicit nature and the provision of repeated measures across various spatial scales (Kumar et al., 2015; Guo et al., 2017). For example, GIS and remote sensing have been used to assess the distribution and extent of wetlands (Wu, 2018; Nhamo et al., 2017), as well as monitoring wetland water quality, productivity patterns, and species diversity (Klemas, 2013). These studies have reported the effectiveness and efficiency of these techniques in monitoring wetlands at large geographical areas (Guo et al., 2017). Moreover, according to Guo et al. (2017) and Hardy et al. (2020), remote sensing has been the most valuable tool to acquire spatial and temporal information about wetland characteristics and their resources. However, despite the potential of using remote sensing and GIS in wetlands assessment and monitoring, there are some considerable shortcomings associated with some of the widely used or accessible remotely sensed data. These shortcomings include limited spectral and spatial resolutions, for detailed extraction of wetlands characteristics, which results in limited information about their status considering their inherent complexity (Walter and Mondal, 2019). In this regard, this chapter covers the importance and progress of GIS and remote sensing application in tropical wetland assessment and monitoring, with particular emphasis on water quality, plant species diversity, wetlands inundation or flood modeling, as well as the impacts of land cover transformation. Further, different GIS and remote sensing methodologies available for wetland monitoring and assessment are summarized, drawing lessons and insights from work conducted elsewhere across the world. In addition, challenges associated with the application of GIS and remote sensing in tropical wetlands monitoring and assessment as well as trade-offs between spatial data acquisition costs, availability, accuracy, and applicability in data scarce environments of Southern Africa. The study further reports on the critical knowledge gaps and possible future research directions in tropical wetland monitoring and assessment, as well as highlighting the role of new computing techniques such as artificial intelligence (AI) and cloud-based computing.

21.2 Livelihoods and ecohydrological benefits of tropical wetlands

It is well documented and established that tropical wetlands provide several ecological, economic, and social goods and services, as well as cultural values that sustain human livelihoods (Kotze et al., 2008; Lamsal et al., 2015; Slagter et al., 2020). The main ecosystem services provided by these wetlands to sustain human livelihood include water supply, water purification, fiber, food, climate regulation, flood regulation, coastal protection, tourism, and other recreational opportunities (Lamsal et al., 2015; Langan et al., 2019; Slagter et al., 2020). For example, Lamsal et al. (2015) indicated that International Union for Conservation of Nature (1998) reported that more than 21 ethnic communities have been listed as dependent on wetland systems. Similarly, Lannas and Turpie (2009) found that 65% of rural communities depend on the wetland for grazing livestock, hunting, and cultivation to sustain their livelihoods in Letseng-la-Letsie area of Lesotho. In a different study, Grundling (2013) found that Tsonga people of the Tembe tribe in Kwa-Zulu Natal, South Africa almost entirely depend on the land and wetland for their survival. In water-limited environments of Southern Africa, the vital ecosystem services provided by tropical wetlands are water supply and purification (Parks et al., 2019). For example, in South Africa, millions of people depend on wetlands for agriculture, which support and sustain their livelihoods (Lannas and Turpie, 2009; McCartney et al., 2010). In confirmation, the study by Lannas and Turpie (2009) reported that some of the communities in Mfuleni in South Africa practice agriculture on the wetland itself. This clearly underlines the relevance of tropical wetland systems in sustaining rural livelihoods especially in areas were droughts are more prevalent and rainfall is erratic.

Besides, tropical wetlands also shelter a wide range of fauna and flora, thereby maintaining species biodiversity. For example, the study by Slagter et al. (2020) has indicated the significance of the St Lucia wetland in harboring various birds and aquatic species in South Africa. Although, wetland resources play an important role in the livelihood of the poor, particularly in developing countries, their provision of services is declining gradually (Lannas and Turpie, 2009; McCartney et al., 2010; Guo et al., 2017). As such, they contribute to the national gross domestic product through tourism, which is the case places like the Nylsvlei Wetland in Limpopo and St Lucia in KwaZulu Natal in South Africa, Okavango in Botswana, Manjinji in Chiredzi, Zimbabwe. This therefore emphasizes the need to continuously monitor and assess the state of these wetlands for their conservation and sustainability in the provision of goods and services.

21.3 Traditional tropical wetland monitoring and assessment techniques

Wetland assessment and monitoring methods vary with time and space. The most accurate approach for assessing wetland extent, species diversity and water quality is the field-based approach (see Piedade et al., 2022, Chapter 7; Dalu et al., 2022, Chapter 8, Dube et al., 2022, Chapter 11; Greenfield, 2022, Chapter 20). Ground-based approaches include the use of qualitative data (Mandishona and Knight, 2019), global positioning system, biological assessment (Fennessy et al., 2002), and taxonomical approaches to map, determine species coverage, services offered, and management practices. For example, taxonomical information and the visual estimation of species percentage cover have been used in species discrimination for floristic mapping (Adam et al., 2010). These methods have been used successfully to identify common wetlands species, coverage, and water quality, as well as to distinguish environmental stressors such as drought, excessive siltation, and other types of human disturbance (Fennessy et al., 2002).

However, although the traditional approaches provide the most accurate data for assessing wetlands and identifying species, they are associated with some challenges. For example, literature on plant species responses to specific stressors is limited (Fennessy et al., 2002). This is critical, especially considering that the rate at which wetlands are being altered, by natural and anthropogenic factors, over time, and space. In addition, sampling techniques for some assemblages, such as submerged species, maybe difficult to conduct; it is possible to omit or mistakenly sample a group of species that could provide strong signals on the condition of a site (Fennessy et al., 2002).

In addition, the traditional techniques require more time, they are labor intensive, expensive, limited to small, specific, and accessible areas (Adam et al., 2010). This makes them difficult to implement in remote and inaccessible areas, as well as in covering large areas monitoring of wetlands. This might result in several species assemblages being masked out (Fennessy et al., 2002). These challenges are most apparent for tropical wetlands, where resources for extensive field work are limited. Consequently, improvements in technology and reductions in cost make remote sensing systems attractive for wetland assessment and monitoring (Klemas, 2013), which is more attentive and proficient (Adam et al., 2010). In agreement, the study by Nhamo et al. (2017) further emphasized that wetlands can only be well managed if their spatial location and extent are accurately and continuously documented.

21.4 Geospatial applications in tropical wetland monitoring and assessment

Remote sensing coupled with GIS modeling and analyses technologies has been used successfully for mapping and monitoring wetlands using different datasets (Herold et al., 2012; Wu, 2018; Whyte et al., 2018). Traditionally, aerial color photography has been used to map emergent and submerged wetlands (Harvey and Hill, 2001; Klemas, 2013; Scarpace et al., 1981; Ritchie et al., 2003). For example, the study by Scarpace et al. (1981) assessed the potential of using aerial imagery to map wetland in Sheboygan Marsh of Wisconsin. The study attained high accuracies (above 90%) in mapping wetland. In addition, the study emphasized that aerial imagery is an operational method for monitoring wetlands, for detailed information. Similarly, Harvey and Hill (2001) used aerial imagery to map tropical freshwater swamp vegetation in Australia, with an overall accuracy of 89%. Although the use of aerial imagery produces accurate results, these are hardly available, in most tropical areas, due to their high acquisition cost and they are therefore limited to particular areas and specific periods. In this regard, they are difficult to use for continuous monitoring of tropical wetlands, especially in expansive and remote areas such as Southern Africa where resources remain a major impediment.

On the other hand, spaceborne satellite remote sensing with repetitive coverage provide data for tropical wetlands monitoring. The availability of satellites provide a better alternative data source for tropical wetlands mapping and monitoring. In addition, satellite data have the capability of detecting and providing reliable spatial environmental indicators for quantitative estimates of wetland conditions and trends, over large areas (Klemas, 2013; Guo et al., 2017). In this regard, the majority of studies have been using satellite remote sensing data to quantify wetland vegetation, water quality, and aboveground biomass, which plays an important role in determining wetland productivity and quality.

The potential of remotely sensed data to provide spatial and continuous data over large areas is critical in characterizing wetlands, which are spatially complex and temporally quite variable. For example, Becker et al. (2005) highlighted the significance of hyperspectral imagery for detecting and distinguishing vegetation spectral properties from narrow spectral bands. In a different study, Klemas (2013) added that the application of the newly advanced satellites, with fine spatial or spectral resolution provides more information on wetland ecosystem health, biological productivity, and habitat quality. In addition, Chasmer et al. (2020) provides an overview on the remote sensing of wetlands mapping. The study concluded that high spatial resolution datasets, with pixel size of less than or equal to 10 m are the most appropriate for detecting and mapping wetlands.

To date, different studies have been conducted using different remote sensing data in mapping wetlands (Rapinel et al., 2015; Guo et al., 2017; Ritchie et al., 2003). For example, the study by Rapinel et al. (2015) indicated the potential of Landsat 8 OLI in mapping riparian vegetation, with 85.9% overall accuracy in Atlantic coastal marshes of France. Remote sensing data also enables the use of combined spectral bands or indices, which enhance wetlands vegetation monitoring, biodiversity assessment, and water quality. According to Guo et al. (2017) and Dong et al. (2014), vegetation indices derived from remote sensing platforms like moderate resolution imaging spectroradiometer (MODIS) and Landsat provide spectral information to derive various vegetation indices. Different vegetation indices were developed since the emergency of remote sensing and are continuously developed to facilitate vegetation monitoring in complex ecosystems, such as wetlands. For example, the Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI), have been successfully used to detect changes in wetland cover and extent. NDVI is one of the long serving vegetation indices used for monitoring the growth condition of wetland plant species using different remotely sensed data. For instance, the study by Mwita et al. (2013) used Landsat ETM + combined spectral bands to map different wetlands in Kenya and Tanzania. The study reported the potential of multispectral Landsat, field survey, and GIS in delineating and mapping small wetlands.

21.5 Trade-offs between costs and availability of remote sensing data for tropical wetland monitoring

Remote sensing data cost and availability determine the success of mapping, assessing, and monitoring wetlands or their different components. Different sensors are available to provide data at varying resolutions and cost. It is therefore essential to cautiously choose the platform and sensors when dealing with wetlands to improve our understanding of their changes. Recent developments in satellite remote sensing offer new and unique opportunities to cost-effectively and timely monitor wetland status and changes. For example, there are some freely available satellite sensors such as Landsat 8 and Sentinel 2 data which have been used accurately in mapping natural resources including wetlands. The availability of Landsat 8 with improved spectral and radiometric resolutions, compared to its predecessors also enables the improved monitoring of wetlands. However, the available low-cost satellite sensors are associated with some pitfalls, as compared to commercial satellite sensors. For instance, Landsat has a medium spatial resolution of 30 m, making it difficult to be applied on a small and spatially heterogenous or complex wetlands (Pape, 2006). The advances in remote sensing which led to the launch of Sentinel 2, however, opened a new opportunity for the monitoring of tropical wetlands at better or advanced temporal, spatial, and spectral resolutions. Sentinel 2 offers data which is better than those offered by the freely available sensors in terms of spectral and spatial coverage. For example, it is the only free sensor that offers data with the red edge, which is only available in commercial satellites. In addition, its 10 m spatial resolution enhances a better spatial monitoring of wetlands—a previously challenging task in data scarce environments.

On the other hand, commercial satellite sensors like the QuickBird, IKONOS, and Worldview are available at high spatial resolution of less than 5 m. These offer spatial explicit datasets at high resolution than the freely available sensors, making them more appropriate for monitoring wetlands, including species diversity, aboveground biomass estimation, and change detection (Silva et al., 2008). However, these datasets are associated with high acquisition cost, which makes it difficult for their application within the tropics for wetland monitoring. In this regard, few wetlands will be considered for monitoring. Similarly, seasonal or continuous monitoring becomes a challenge using these datasets, especially for resource constrained countries in the tropics.

21.6 Available approaches and techniques of wetland monitoring using remote sensing data

In remote sensing, there are a variety of algorithms available for assessing wetlands, including water quality, species diversity, or coverage, which can be applied, depending on the focus of the study. There are two common classification algorithms for detecting wetlands and identifying species distribution using remotely sensed data. These are supervised and unsupervised classification (Al-doski et al., 2013; Whyte et al., 2018). Supervised digital image classification techniques are based on the availability of predefined class samples, which are used to classify the area of interest. On the other hand, unsupervised classifications are based on the classifier to assign spectrally similar pixels into clusters, without prior knowledge or predefined samples; the use only specifies the number of clusters (Liu, 2005). Furthermore, in supervised classification, different algorithms are available and the maximum likelihood is the most widely used. The maximum likelihood procedure determines the value of one or more parameters for a given statistic, which makes the known likelihood distribution a maximum (Ahmad and Quegan, 2012). On the other hand, available common types of unsupervised classification including the K-means and Iterative Self-Organizing Data Analysis Technique (ISODATA) (Al-doski et al., 2013).

The choice of the classification algorithm also has the influence on the output due to their advantages and disadvantages. Thus it was found that another classification technique or algorithm called object-based image analysis can provide more accurate classification results. Object-based image analysis and it takes both the advantages of the supervised classification and unsupervised classification techniques (Al-doski et al., 2013). Furthermore, Whyte et al. (2018) and Dronova (2015) based on a review of 73% studies reported that the algorithm improves wetland classifications by 31% when compared to pixel-based methods. However, according to Mas et al. (2014) the application of object-based image analysis in wetland mapping is lower when compared to other disciplines namely; agriculture and urban infrastructure.

More advanced machine learning algorithms have been developed for classification using remote sensing. A review by Chasmer et al. (2020) found that the use of advanced machine learning algorithms provide the most accurate results in classifying wetlands using remote sensing data for boreal and global wetlands. Some of the commonly and successfully used machine learning algorithms in wetland monitoring and assessment include the support vector machine and random forest. These algorithms have been reported to be robust, associated with enhanced modeling capabilities, overcome challenges associated with small sample sizes, and dimensionality issues related to hyperspectral data (Amani et al., 2017; Walter and Mondal, 2019). These advanced algorithms are therefore gaining popularity for classification of wetlands. For instance, Amani et al. (2017) successfully used an object-based random forest algorithm to classify wetlands in the Gros Morne, Canada, with overall classification accuracy of 84%, and a Kappa Coefficient of 0.77. Similarly, the study by Walter and Mondal (2019) in Delaware in United States recently reported the potential of combining Landsat 8 and Sentinel 1 Synthetic Aperture Radar (SAR) data with advanced random forest in classifying wetland. The study produced high overall accuracy of 93.7%.

In addition, different algorithms are also available for wetland biophysical characterization such as water quality, vegetation quantity (aboveground biomass), and quality (e.g., nitrogen) assessment, using remotely sensed data. The availability of these linear regression algorithms varies from the simple linear regression to more advanced machine learning regression methods. Generally, empirical relationships between spectral reflectance from remote sensing and associated water quality parameters are established and these have been established since the emergence of satellite remote sensing around the 1970s (Ritchie et al., 2003).

21.7 Strengths and limitations of applying GIS and remote sensing in tropical wetlands

Remote sensing has been used widely in assessing and monitoring wetlands (Orimoloye et al., 2019). Most of the studies focused on the land-use and land-cover mapping of wetlands (Hardy et al., 2020), wetland vegetation (Adam et al., 2010), and their hydrological regimes (Lefebvre et al., 2019; Walter and Mondal, 2019). GIS enables the analysis and integration of various spatial data (e.g., topography, remotely sensed, land use and land cover, etc.) for enhanced tropical wetland monitoring. For example, the availability of different analytical and modeling tools in GIS offers the ability to characterize tropical wetlands, including their vulnerability to environmental changes (e.g., climate and topography), as well as linking their degradation to anthropogenic influence. In agreement, the review by Wu (2018) indicated that the use of GIS and remote sensing facilitates the identification and delineation of wetlands by integrating or overlaying the different wetland indicators, such as vegetation, topography, soil, and hydrological layers within a GIS environment. For example, Walter and Mondal (2019) used the Moran's I and Getis-Ord Gi* hotspot analysis tools to detect wetland water stress. The potential of GIS to integrate remotely sensed data and other spatial data layers allow for better monitoring or identification of potential wetlands. Recently, the study by Elias and Chand (2019) reported that the use of GIS is a valuable approach in easing the study and assessment of complex ecosystems associated by intricate ecological processes; wetlands as one of the complex ecosystems can therefore benefit from this approach.

Similarly, advances in sensor design and data analysis techniques make remote sensing application attractive for monitoring wetland changes over time. Wetlands have limited accessibility and hazardous conditions (Silva et al., 2008). The characteristics or conditions of wetlands make the use of remote sensing data and other ancillary data integrated in GIS invaluable to monitor these ecosystems, as the use of ground surveys becomes challenging (Silva et al., 2008).

The application of GIS and remote sensing in tropical wetlands monitoring is limited due to considerable challenges associated with the spatial data and the nature of the wetlands. Wetlands are complex ecosystems characterized by spatial and temporal heterogeneity; this makes it difficult for their successful monitoring. The integration of various datasets in monitoring wetlands can also be a challenging task. Different spatial datasets exhibit different acquisition period, spatial reference, and format; this makes it difficult to integrate them without considerable loss of information, for example, through format conversion and spatial compatibility preprocessing. In this regard, the application of different spatial datasets may result in different challenges in assessing wetlands.

In addition, most of the studies which focused on the use of remotely sensed data have indicated low spatial resolution as one of the challenges encountered in wetland studies, resulting in too many mixed pixels, especially when using medium (e.g., Landsat at 30 m) and coarse (MODIS at 1000 m) spatial resolutions data. For example, Walter and Mondal (2019) emphasized that the use of Landsat in areas characterized by dense foliage is problematic, especially when estimating aboveground biomass. The sensor experiences saturation problems in areas with dense vegetation, making it difficult to characterize vegetation biophysical characteristic. Similarly, spectral mixing is also another challenge associated with the use of Landsat, this becomes critical when performing classification at species level or when characterizing species diversity for wetlands ecosystems. The study further recommended the use integration of Landsat and radar data to improve the estimation of vegetation biomass and species identification. In addition, complexity of image processing of hyperspectral data has been recognized as another challenging issue in characterizing the spectral response of wetlands vegetation. Similarly, the tremendous volume of hyperspectral image data demands the use of specific software packages, large data storage capacity, and extended processing time (Klemas, 2013). These have hindered the application of remote sensing in some parts of tropical wetlands hence the need to explore different image manipulation techniques.

21.8 Remote sensing data fusion for improved tropical wetlands monitoring

Emerging studies within the remote sensing of natural resources have indicated the potential of remote sensing data fusion for enhanced monitoring, over space and time. In particular, remote sensing data fusion is becoming one of the critical approaches for improved vegetation monitoring in complex ecosystems and this provides a new opportunity for monitoring of tropical wetlands.

Recently, a couple of studies have reported the potential of remote sensing data fusion for characterizing wetlands vegetation. According to Walter and Mondal (2019), recent literature indicates that the integration of radar (e.g., Sentinel 1) and optical (e.g., Landsat) data provides improved accuracy when classifying wetlands. These studies have been conducted across various wetland ecosystems across the globe (Walter and Mondal, 2019; Amani et al., 2019; Guo et al., 2017; Mizuochi et al., 2018; Mahdavi et al., 2018). For example, the study by Mizuochi et al. (2018) reported the potential of using passive and active microwave datasets based on the random forest method to characterize the extent of wetland in India. In addition, Slagter et al. (2020) assessed the potential of Sentinel 1 and Sentinel 2 data using random forest for wetland mapping and characterization in South Africa. The study found high accuracies associated with the use of combined datasets, when compared to the use of either dataset in as independent model input data. Consequently, the emergence of new generation sensors, with better resolutions, advances in machine learning algorithms, and data fusion offers unique opportunities for improved monitoring of tropical wetlands, in a cost-effective manner and over time. This is most important in tropical regions, where the acquisition of high-resolution data for large area monitoring is a challenge.

21.9 Future research directions for the remote sensing of tropical wetlands

Advances in spatial data acquisition and modeling techniques open a new way for better monitoring of tropical wetlands. Future tropical wetland studies need to embrace recently launched sensors for improved wetlands monitoring. Emergency and advances in new generation remote sensing have opened a new dimension for tropical wetlands monitoring. This include the availability of improved satellite data from Landsat 8 OLI and Sentinel, which are readily accessible and have been recently used for wetland monitoring (Lefebvre et al., 2019; Walter and Mondal, 2019; Sánchez-Espinosa and Schröder, 2019). These studies have reported the potential of Sentinel 2 and Landsat in classifying land use-land cover for tropical wetlands. Walter and Mondal (2019) used Landsat 8 with Sentinel 1 SAR data to characterize wetland stress. In agreement, Sánchez-Espinosa and Schröder (2019) outlined the advantages of higher spatial and temporal resolutions of Sentinel 2 as a powerful data source for monitoring wetlands. These included the potential of the spatial resolution of Sentinel 2 to detect small features of the wetlands, compared to the Landsat 8. In addition, its higher spectral resolution within the red edge managed to distinguish different vegetation types, whereas its high temporal resolution increased the possibility of obtaining cloud-free images. The study used both Landsat 8 and Sentinel 2 to map Mediterranean wetlands, using pixel and object-based classification methods. Their findings indicate that Sentinel 2 provide better wetland classification results, when compared to Landsat 8 satellite data.

In addition, the new generation commercial data sources also present an alternative for monitoring tropical wetlands, due to their affordability and high spatial resolution (i.e., less than 5 m). These include the Quickbird, IKONOS, GeoEye, and WorldView; which provide data at high spatial resolutions, which is required for a detailed characterization of complex landscapes, including tropical wetlands. A review by Klemas (2013) highlighted that the new generation sensors with fine spatial resolutions, between 1 and 4 m, with narrow spectral bands provide means for more accurate detection ofthe changes in wetlands extent, vegetation status, and productivity. These inhrerent sensors' spatial resolution characteteristics enhance the extraction of various wetland components. In addition, they the have the red edge band, which has been reported to be effective in extracting detailed information about vegetation biochemical characteristics. This unique ability is critical in vegetation mapping as it enhances wetland vegetation discrimination, mapping, as well as in estimating productivity and quality. Various studies have so far used these different high spatial resolution datasets to characterize wetland vegetation, productivity, and quality (Silva et al., 2008; Mutanga et al., 2012). For example, Mutanga et al. (2012) estimated wetland biomass in South Africa, using Worldview 2 and the random forest advanced machine learning algorithm. Although these datasets provide high spatial and spectral resolutions data, it is difficult to use them for continuous monitoring, due to acquisition costs. In addition, they are usually acquired or more appropriate for small geographical coverage (e.g., 16 km swath width for Worldview 2 and 11 km for IKONOS), which limits their application for wetlands covering large geographical areas or even in assessing the influence of external factors such as anthropogenic activities. Similarly, for large geographical areas application, multiple image scenes will be acquired when using high spatial resolution dataset. This results in scene differences due to differences in acquisition time and dates, sun and view angles, as well as atmospheric conditions (Silva et al., 2008).

More recently, the advanced Google Earth Engine (GEE) has been recognized as an outstanding and novel approach for tropical wetlands monitoring, with machine learning algorithms. GEE is an integrated cloud-based geospatial platform for the processing of remote sensing data (Liu et al., 2020; Walter and Mondal, 2019). The cloud-based platform provides accessibility to ready-to-use remotely sensed data, such as Landsat and Sentinel, as well as their classification using advanced machine learning for large geographical areas (Hu and Dong, 2018). Similarly, the study by Walter and Mondal (2019) indicated that the GEE platform provides access to advanced machine learning methods, such as support vector machine, random forest and classification and regression trees. These advanced machine learning algorithms are known to be associated with improved image classification accuracies. In addition, GEE results can be easily reproduced, since the platform is freely accessible, with freely accessible remotely sensed data. In addition, the GEE resolves computer intensive challenges which are usually associated with the use of large remotely sensed data, especially when using time series data (Gxokwe et al., 2020). Consequently, different studies (Alonso et al., 2016; Hardy et al., 2020; Hird et al., 2017; Amani et al., 2019) have adopted this approach in mapping wetlands; and it is gaining momentum. For example, the study by Amani et al. (2019) highlighted that the successful applications of the GEE platform in wetlands mapping in Canada, using different remote sensing data. In a different study, Hird et al. (2017) estimated the probability of wetlands occurrence in Alberta using Landsat 8 satellite data. Similarly, Amani et al. (2019) focused on provincial wetland mapping using multitemporal Landsat 8 data (2016 - 2018) and the random forest algorithm. The study successfully mapped wetlands over time, with high overall accuracies above 70% and user's and producer's accuracies above 60%, respectively, for the different provinces in Canada.

In addition, the development of unmanned aerial vehicles (UAVs) or drones as a new platform for the remote acquisition of data presents an opportunity for improved periodic monitoring of tropical wetlands (Ma et al., 2016). These systems are flexible when implementing, or acquiring near real-time aerial imagery at low cost, without the influence of clouds as well as at high spatial and temporal resolutions (Jensen et al., 2011; Ma et al., 2016). This is more appropriate for continuous monitoring and assessment of different tropical wetland characteristics such as vegetation diversity and productivity. Furthermore, during data acquisition, spectral curves for each pixel are acquired; this is mostly important for the detection and better characterization of the target. The UAVs have been identified to have more advantages, when compared to the freely available and commercial multispectral datasets (Ma et al., 2016). These include their flexibility and the high spatial resolution; making them more valuable and more attractive for the remote sensing of wetland ecosystems.

21.10 Conclusions

GIS and remote sensing applications in tropical wetlands monitoring and assessment have gained considerable traction over the years. However, the use of medium to coarse resolution multispectral satellite images has been overwhelming and the results have been viewed with reservations as the accuracies are moderately low. Although the multispectral satellite data seem to be critical in monitoring and assessing tropical wetlands, broad spectral and spatial characteristics compromise their inherent ability to detect subtle wetland information as they are prone to spectral mixing and spectral saturation in cases where there is high biomass. Although high-resolution data such as hyperspectral and other commercial multispectral datasets provide promising opportunities for tropical wetland monitoring, limitations linked to their footprint and the lack of temporal coverage as well as acquisition costs have hampered their applicability, especially in data-limited environments. However, the advent of high-resolution multispectral data, for example, Sentinel 2 with strategically positioned spectral bands and high temporal coverage provides unique opportunities for tropical wetland monitoring—a previously challenging task with broadband sensors like Landsat and MODIS. Further, the advancements in computer-based processing, AUVs, and AI techniques have the potential to further improve the monitoring and assessment of tropical wetlands across various scales of application.

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Chapter 22

Institutional, policy, and legal nexus and implications

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22.1 Introduction

Wetlands are one of the most biologically productive ecosystems in the world. Research estimates indicate that coastal and inland wetland areas occupy more than 12.1 million km^2 (Davidson et al., 2018; Ramsar Convention Secretariat, 2018). This includes areas that are permanently (54%) and seasonally inundated (46%) (Ramsar Convention Secretariat, 2018). In sub-Saharan Africa, wetlands cover about 7% of the total surface area, with freshwater marshes and floodplains being the most extensive types (Rebelo et al., 2010). Although wetlands occur within all the major river basins of sub-Saharan Africa, areal representation and the spatial distribution of the different wetland types vary greatly (Mitchell, 2012; Wasserman and Dalu, 2022, Chapter 1; Job and Sieben, 2022, Chapter 2). In Southern Africa, wetland types at basin scale include floodplains, swamps, marshes, pans, dambos, estuaries, and lakes (Musasa and Marambanyika, 2020; Ollis et al., 2018; Zambia Ministry of Lands and Natural Resources, 2018).

Wetland ecosystem services have economic and biodiversity value that far outweighs many terrestrial ecosystems (Irvine et al., 2022, Chapter 19; Laltaika, 2022, Chapter 23; Ramsar Convention Secretariat, 2018). The estimated global economic value of wetland goods is US$70 billion a year (Mitsch et al., 2015). The services delivered by wetlands globally have been arguably valued approximately US$14 trillion annually (Ramsar Convention Secretariat, 2018). Wetland ecosystems provide goods and services vital for the sustenance of livelihoods mainly through agriculture and fishing (Dodds et al., 2013; Junk et al., 2013; Mosepele et al., 2009; Pantshwa and Buschke, 2019; Rebelo et al., 2010; Schuyt, 2005). However, natural wetlands are declining in extent and quality (Davidson et al., 2018; Dixon et al., 2016;

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Gardner et al., 2015; Junk et al., 2013; Matamanda et al., 2018) at a rate three times the rate of forest loss (Ramsar Convention Secretariat, 2018). For instance, between 1970 and 2015, inland and coastal wetlands globally, declined by approximately 35% (Ramsar Convention Secretariat, 2018).

The trend of wetland degradation tends to increase where communities are more dependent on this natural resource (Marambanyika and Beckedahl, 2016a; Rebelo et al., 2010; Rivers and Moore, 2012). For instance, in developing countries such as Zimbabwe, 84% of wetlands are degraded due to high community dependence on wetland ecosystem services (Musasa and Marambanyika, 2020). Wetland degradation and loss in developing countries is mainly attributed to pollution, water abstraction, cultivation, livestock grazing, invasion by invasive species, and unsustainable exploitation due to utilization pressure driven by population growth, poverty, and the weaknesses of existing governance systems (Marambanyika and Beckedahl, 2016a; Mosepele et al., 2009; Phethi and Gumbo, 2019; Zambia Ministry of Lands and Natural Resources, 2018).

Wetland use, management, and conservation are governed by legislation and policies (Clare et al., 2011; Dale et al., 2014). Many countries are developing wetland policies to protect fragile ecosystems mainly threatened by human processes (Clare et al., 2011; Dale et al., 2014; Mandishona and Knight, 2019; Marambanyika and Beckedahl, 2016b). Several studies have noted that the absence of policy generally compromises wetland protection especially where users do not engage in self-imposed sustainable practices (Clare et al., 2011; Dale et al., 2014; Maconachie et al., 2009; Matamanda et al., 2018). However, the degree of influence of wetland policy and legislation on wetland protection tend to vary (Adekola et al., 2012; Kotze and Malan, 2010; Mbereko et al., 2015; Turpie, 2010; Yeboah-Assiamah et al., 2017). For example, in Zambia wetlands are better managed due to the presence of a wetland policy backed by legislation (Zambia Ministry of Lands and Natural Resources, 2018), compared to countries such as South Africa where there is no standalone policy (Dini and Everard, 2016).

Legislation, defined as a set of rules instituted by national governments and international bodies to regulate wetland use, management, and protection (Yeboah-Assiamah et al., 2017) has been increasing over the past five decades (Dale et al., 2014; Island Press, 2007; Marambanyika and Beckedahl, 2016b; Ramsar Convention Secretariat, 2018). Meanwhile, a wetland policy, generally defined as the overall plan of action embracing the general goals and acceptable procedures that need to be followed to guide wetland use and management (Yeboah-Assiamah et al., 2017), has been changing the world over in response to societal values, economy, and wetland conditions (Clare et al., 2011; Dini and Everard, 2016; Frenken and Mharapara, 2002; Mwitwa et al., 2018; Phethi and Gumbo, 2019). The changes in policy and legislation is also linked to the existing institutions that formally or informally implement natural resources protection rules, norms, and strategies (Marambanyika and Beckedahl, 2016b; Yeboah-Assiamah et al., 2017).

Good wetland governance also lies within the effectiveness of participating institutions (Yeboah-Assiamah et al., 2017). Chuma et al. (2008) defined institutions as social arrangements that shape and regulate human behavior, have some degree of permanency and purpose, and transcend individual human lives and intentions. The institutions can be formal, having the status of constitutional clauses and laws that are guaranteed and sanctioned at multiple levels largely by public agencies, or informal, having socially shared rules, usually unwritten, that are created, communicated, and enforced outside of officially sanctioned channels (Yeboah-Assiamah et al., 2017). It is through these formal and informal institutions that rules governing natural resources' use, control, and management are shaped (Maconachie et al., 2009; Marambanyika and Beckedahl, 2016b; Yeboah-Assiamah et al., 2017). These institutions can be broadly grouped as state and nonstate actors. The mandates of these actors are sometimes divided between conservation and improving livelihood options, which in turn results in contradictory roles that may undermine wetlands protection (Bethune and Ruppel, 2007; Darkoh and Mbaiwa, 2014; Dini and Everard, 2016; Zambia Ministry of Lands and Natural Resources, 2018).

While studies such as those conducted by Stokstad (2008), Clare et al. (2011), Dale et al. (2014), and South Africa Department of Environmental Affairs (2019) have shown that laws and policies instituted by the state actors have not been very effective in maintaining wetland area and function. However, few studies have been conducted to examine why regulatory compliance has been so poor in most of African countries (Adekola et al., 2012; Frenken and Mharapara, 2002). For instance, Madzudzo et al. (2013) noted that wetland governance arrangements for countries within the Zambezi River Basin are important variables that affect conservation initiatives implemented. This demonstrates that periodic evaluation of policy, legal, and institutional outcomes is essential to determine barriers, unintended outcomes, or unsuccessful aspects of the governance structure in each area (Bethune and Ruppel, 2007; Clare and Creed 2014; Dale et al., 2014; Mwale, 2018; Rebelo et al., 2010).

To date, several studies have been focusing on understanding the biophysical components of wetlands using different methods, including modeling and remote sensing (Adam et al., 2010; Mutanga et al., 2012; Rivers and Moore, 2012). However, effective policy and management for wise use of wetlands also require proper understanding of the drivers of wetland change and degradation. This could help addressing the root causes of wetland loss and degradation (Ramsar Convention Secretariat, 2018) since, effective governance at local, national, and regional levels is a key factor for reversing tropical wetland losses and degradation (Chuma et al., 2008). It is, however, unfortunate to note that there is a dearth of literature on the nexus between policy, legislation, and institutional arrangements and associated implications on wetland management at regional or basin scale. Strengthening of wetland governance strategies will undoubtedly contribute toward the attainment of Sustainable Development Goal (SDG) 14 (life below water) and SDG 15 (life on land), meant to promote wise use of wetlands, from a Ramsar convention perspective.

It is against this background that the chapter focuses on institutional, policy, and legal nexus and implications on tropical wetlands management and conservation in selected Southern African countries, namely, Botswana, Namibia, South Africa, Zambia, and Zimbabwe. These five countries were selected because they are located in the same transboundary river basins such as Okavango, Limpopo, and Zambezi. Moreover, data for these countries were easily accessible for a comprehensive literature review. Kotze (2010, 2011) also indicated that the wetlands in these countries generally exhibit similar hydrogeomorphic characteristics. The chapter examines wetland use patterns, variations in spatial and temporal arrangements in terms of policies, legal setups, and the differences in the composition of multiple stakeholders involved in wetland utilization and conservation as well as the shortcomings and enforcement challenges of wetland policies and legislation.

22.2 Overview of wetland utilization patterns in selected Southern African countries

The functions and uses of wetlands in Southern Africa can be divided into ecological, socio-economic, and cultural (Finlayson and Pollard, 2009; McCartney et al., 2010; Turpie et al., 2010). In this chapter, ecological functions refer to those that are natural and independent of human manipulation, whereas the socio-economic functions refer to uses of wetlands that contribute to the economic well-being of local communities and the nations. Local communities obtain cultural services which are nonmaterial benefits from wetlands. These include opportunities for spiritual development, recreation, tours for academic incursions, and bequest values from appreciation of biodiversity (Turpie et al., 2010; Xu et al., 2020). The utilization of tropical wetlands in transboundary basins of Southern Africa is widespread and is primarily determined by the location, nature, and type of the wetland (Bethune and Ruppel, 2007; Kotze and Malan, 2010).

Tropical freshwater wetlands are rich in biodiversity and provide habitat to a wide range of birds and mammal species (Darkoh and Mbaiwa, 2014; Mmopelwa and Blignaut, 2006). For example, the Okavango Delta in Botswana provides habitat for diverse species of plants, arachnids (spiders and mites) and herbivores. In South Africa, the GaMampa Wetland provides habitat for several species such as carmine bee-eater (*Merops nubicoides*) (Adekola et al., 2012). In Zambia, wetlands support high concentrations of birds and mammals (Mitchell, 2012; Zambia Ministry of Lands and Natural Resources, 2018). Half the global population of the wattled crane is found mostly on the Kafue Flats, Liuwa Plains and Busanga Swamps (Chabwela and Haller, 2010). The Driefontein Wetland in Zimbabwe, also provides habitat and forage for the wattled crane, gray-crowned crane and secretary bird (Chirara, 2011; Fakarayi et al., 2015, 2016).

In the Zambezi basin the net monthly value for material collected from wetlands averaged between US$23 and US$159 which clearly demonstrates the importance of services derived from wetlands (Adekola et al., 2012). McCartney et al. (2011) and Adekola et al. (2012) observed that average annual cash income obtained from sale of sedge bundles and mats in the GaMampa Wetland in South Africa amounted to US$7728. Edible plant collection is also one of the most important provisioning services obtained from wetlands. In the GaMampa this is particularly done in summer (November to March) when abundance is high and later dried for future use during dry spells (Adekola et al., 2012). It is therefore clear that with this extent of benefits, there is need for wise use and management of wetlands in Southern Africa so that they continue to provide services.

Crop cultivation has emerged as the main land-use pattern in tropical wetlands of Southern Africa (Finlayson and Pollard, 2009; McCartney et al., 2010; Phethi and Gumbo, 2019), contributing to their degradation as well (Adekola et al., 2012; McCartney et al., 2010; Marambanyika and Beckedahl, 2016c). In general, agricultural activities in wetlands of Southern Africa contribute 6%–67% of the total wetland value (McCartney et al., 2010). In South Africa, farmers take advantage of the favorable moist wetland conditions to grow cereal and horticultural crops such as maize and vegetables (Adekola et al., 2012; Phethi and Gumbo, 2019), a practice also widely reported in Zimbabwean wetlands (Madebwe and Madebwe, 2005; Musasa and Marambanyika, 2020; Ndiweni and Gwate, 2013). In Zambia, crop cultivation is conducted throughout the year with rice and maize being the major crops in dambos (Chabwela and Haller, 2010).

Wetlands also support livestock grazing since they provide pastures and water (Finlayson and Pollard, 2009). In Zambia's Lukanga Swamp, livestock grazing has emerged as a major land-use pattern (Mapedza et al., 2012). This pattern is also widespread in Botswana, Namibia, South Africa, and Zimbabwe (Kotze 2010; Musasa and Marambanyika, 2020; Ruppel and Ruppel-Schlichting, 2016). However, overgrazing exerts pressure on the vegetation species composition, diversity and richness, especially in areas with sweet pastures (Kotze 2010; Musasa and Marambanyika, 2020). Communal dambos, have been converted from diverse areas of good grazing to communities dominated by low forage grass, such as the *Eragrostis* species and other ruderal weeds (Marambanyika et al., 2016).

Wetlands also harbor a rich diversity of fishes, making fishing one of the cornerstone activities for socio-economic development in the Southern African region (Bruton and Jackson, 2010; Reichard, 2022, Chapter 12).

The most important wetlands used for commercial fishing in Southern Africa include the Chobe Swamps in north eastern Namibia and the Kafue

Flats, the Busanga Swamps on the Lunga River, Barotse Floodplains in Zambia (Chabwela and Haller, 2010; Mitchell, 2012). Fishing in the Kafue Flats is mainly done by the young and economically active groups as a livelihood option (Timberlake, 2000).

Wetlands across Southern Africa have many cultural values (Zambia Ministry of Lands and Natural Resources, 2018), making their protection important to the local communities. Local communities in Botswana, Namibia, South Africa, Zambia, and Zimbabwe obtain nonmaterial benefits from wetlands through spiritual development, recreation, tours for academic incursions and bequest values from appreciation of biodiversity (Darkoh and Mbaiwa, 2014; Kotze, 2013; Ndhlovu, 2012; Swanepoel and Barnard, 2007; Turpie et al., 2010). Wetlands in Zimbabwe are recognized as sacred sites where rain making and other ceremonies are conducted (Marambanyika et al., 2012) and this is presumed to be the case across other Southern African countries.

22.3 Drivers of wetland degradation in selected Southern Africa

Wetlands are sensitive ecosystems that are being degraded at alarming rates in the Southern African countries region (Darkoh and Mbaiwa, 2014; Mapedza et al., 2012; Musasa and Marambanyika, 2020; Phethi and Gumbo, 2019; Swanepoel and Barnard, 2007). The drivers to wetland degradation in Southern Africa may be divided into indirect and direct drivers. Direct drivers which refer to natural or human-induced causes of biophysical changes at a local to regional scale (Van Asselen et al., 2013) include land-use change, pollution, sedimentation, crop cultivation, water abstraction, sand mining, vegetation species harvesting, construction of buildings and pavements, and invasion by alien plant species (Ramsar Convention Secretariat, 2018). Indirect drivers which are processes in society that create the direct drivers include droughts as well as pests and diseases on wetlands plants (Musasa and Marambanyika, 2020; Pantshwa and Buschke, 2019; Royimani et al., 2019; Seutloali et al., 2018; Zambia Ministry of Lands and Natural Resources, 2018). Most of the direct causes of wetland degradation and loss can be controlled or abated using well-articulated policies and well coordination of various stakeholders or institutions (Madzudzo et al., 2013).

In Southern Africa, wetland agriculture has been the major culprit-driving wetlands degradation (Swanepoel and Barnard, 2007). For example, commercial agriculture that is carried out in south of Limpopo province in Tzaneen area and north of Mpumalanga province in Leroro area for sugar cane and tree plantation, causes disappearance of some wetlands hence loss of essential ecosystem services (Phethi and Gumbo, 2019). Livestock grazing in the Okavango Delta in Botswana, GaMampa Wetland in South Africa, Kafue Flats of Zambia and Intunjambili Wetland in Zimbabwe has been contributing to wetland degradation (Chabwela and Haller, 2010; Chuma et al., 2008; Darkoh and Mbaiwa, 2014; McCartney et al., 2010). In the Intunjambili and Makhitha Wetlands in the Limpopo basin, local farmers disregard the local policies as they allow cattle to graze. In the Kafue Flats cattle grazing within the wetland fringes also presents problems to the wetland state. In some cases, regardless of what the local policies enforced by both formal and informal institutions state, the local communities destroy fence in order to allow their cattle to graze on the protected wetland (Marambanyika et al., 2012). This again is sometimes attributed to poor and weak policy as well as the poorly coordinated fragmented laws and lack of other sources of livelihoods for the affected communities (Mitchell, 2012). Therefore, synergies between factors at interplay, which influence policy and legislation governing wetland use and conservation need to be strengthened, if their sustainable use is to be achieved.

In Southern Africa, common factors that contribute to wetland degradation include; population growth, rising poverty, and poor economic performance (Mitchell, 2012; Zambia Ministry of Lands and Natural Resources, 2018). In the ephemeral wetlands of central north Namibia, rapid population growth has increased pressure on the resources including wetlands. It is expected that as populations grow the pressure on wetlands is also likely to increase (McCartney et al., 2010). Population pressure also exposes wetland ecosystems to different activities such as land and sea-based mining activities, which threaten the existence of wetlands resulting in the loss of essential ecosystem services (Chabwela and Haller, 2010; Namibia Ministry of Environment and Tourism, 2014; Phethi and Gumbo, 2019). Therefore, there is a need to understand how population pressure on wetland management and conservation is being regulated from a policy, legal, and institutional perspective.

Considering that Southern Africa is a water scarce region (receiving a mean of approximately 400 mm/yr) desertification and drought are key drivers of wetland degradation and loss (Krugmann, 2000). With climate change set to lead to increased rainfall variability and instances of extreme events, the threat to wetland ecosystems and species diversity is increasing and requires coordinated action (Namibia Ministry of Environment and Tourism, 2004). Wetlands largely depend on water levels, hence changes in climatic conditions is likely to influence their structure and functioning. Erwin (2009, p. 71) notes that, “wetlands are affected through alterations in hydrological regimes” posed by climate change. Therefore, the impact of climate change and droughts on wetland hydrology and vegetation is being witnessed not only in Namibia, but in Botswana, South Africa, Zambia, and Zimbabwe (Dallas and Rivers-Moore, 2014; Magadza, 1994).

Over abstraction of surface and groundwater also poses a threat to the existence of wetlands as this leads to the loss of water sources and riparian vegetation (Darkoh and Mbaiwa, 2014; Mosepele et al., 2009). The environmental water needs for wetlands in Southern Africa's river basins have been threatened by over abstraction. Over abstraction from the Okavango River in Namibia has severe transboundary impacts on the unique ecosystems that make up the Okavango Delta in Botswana (Ashton, 2003; Shaw et al., 2004). The abstraction of water from the Okavango River in Namibia results in significant changes in the vegetation of floodplains downstream (Ashton, 2003; Mitchell, 2012). Changes in water levels as a result of over abstraction also affected the habitat for aquatic animals in the Okavango Delta (Darkoh and Mbaiwa, 2014).

Changes in water flow regimes caused by the construction of canals, dams, and weirs for water storage and supply for hydropower plants reduce and alter the timing, extent, and frequency of flows that sustain wetlands (Pantshwa and Buschke, 2019; Ramsar Convention Secretariat, 2018). One essential activity that has often been viewed as being economically more viable than ecosystem protection is dam construction (Mitchell, 2012). Research estimates indicate that Africa has more than 1000 dams, of which more than 60% are in South Africa and Zimbabwe (Rebelo et al., 2010; Rivers and Moore, 2012). Water impoundments disrupt wetland ecosystems in several ways. For example, the new hydropower Batoka Dam results in regulation of flow below the dam and the downstream area no longer has the seasonal variability it used to experience (Mitchell, 2012; Rebelo et al., 2010). The same was observed for the negative impacts on Okavango communities living downstream in Botswana as a result of water abstractions upstream in Namibia (Darkoh and Mbaiwa, 2014; Mizlow et al., 2009).

Invasive alien species, both plants and animals, are widespread in aquatic systems in Southern Africa and are a serious threat to aquatic biodiversity (Mitchell, 2012). The most common alien invasive species in the Okavango delta in Botswana include *Salvinia molesta*, *Pistia stratiotes*, and *Eichhornia crassipes* (Kurugundla et al., 2016). In Namibia *P. stratoides* is common whereas South Africa wetlands are dominated by *E. crassipes*, *Hypnea musciformis*, *Pinus roxburghii* (Bethune et al., 2004; Mitchell, 2012). On the floodplains of the lower Zambezi River and on the Kafue Flats (Zambia) the indigenous woody plant *Dichrostachys cinerea* is encroaching onto the floodplain together with the invasive alien species *Mimosa pigra* (Mitchell, 2012). In Zimbabwe common invasive species that are problematic in wetlands include *Lantana camara*, *Eragrostis spp.*, and *E. crassipes*. These species are a threat as plants may also choke river channels, reducing the volume of water available for wetland vegetation (Matavire et al., 2015; Mitchell, 2012; Sibanda et al., 2016; Pegg et al., 2022, Chapter 16: Impacts of Alien Invasive Species on Large Wetlands).

In Botswana dense weed infestations harbor vectors such as the species of mosquitoes that transmit encephalitis, dengue fever, malaria, and cholera (Kurugundla et al., 2016; Vanhove et al., 2022, Chapter 15). Compared to other weeds, *E. crassipes* in countries such as Namibia, South Africa, and

Zimbabwe causes significant increase in water loss due to transpiration (Bethune and Ruppel, 2007; Environmental Management Agency (EMA), 2015; Mitchell, 2012]. Unsustainable land management practices result in encroachment by invader species and the disappearance of perennial grasses in countries such as Namibia and Zimbabwe (Musasa and Marambanyika, 2020; Namibia Ministry of Environment and Tourism, 2014).

Another significant cause of wetland degradation and loss is mainly due to the expansion of urban settlements. In KwaZulu-Natal, South Africa, wetlands are cleared to pave way for road construction and industrial sites (Phethi and Gumbo, 2019). They are sometimes drained and turned into settlement in order to pave way for the increasing population (Mandishona and Knight, 2019; Phethi and Gumbo, 2019; Schuyt, 2005). Research estimates show that between 35% and 65% of South Africa's wetlands have already been lost or severely degraded (South Africa Department of Environmental Affairs, 2019). In South Africa, only 11% of wetland ecosystem types are well protected, with 71% not protected at all despite efforts being made to prevent degradation of these ecosystems (South Africa Department of Environmental Affairs, 2019). About half of Zambia's 150,520 km^2 wetlands have been degraded and in need of restoration due to high rates of urbanization (Chabwela and Haller, 2010). The same problem has been reported in Zimbabwe (Government of Zimbabwe, 2015; Musasa and Marambanyika, 2020). Of all the catchments in Zimbabwe, Manyame has the most severely degraded wetlands due to its proximity to urban areas (35%) [Environmental Management Agency (EMA), 2015; Government of Zimbabwe, 2015]. From the above reports, it is clear that wetland degradation is largely related to human wetland use.

The competition for resources and land-use conflicts in the Okavango Delta partially reflect that the area has experienced increase in population and influx of different land users in the last few decades (Darkoh and Mbaiwa, 2014). Lack of land reform and improperly coordinated land-use policies form part and parcel of the problems facing land-use and environmental sustainability in the Okavango Delta (Darkoh and Mbaiwa, 2009). The Okavango Delta has a history of poorly coordinated developments, with investments in infrastructure or facilities sometimes out of sync with the spatial development requirements; hence land-use conflicts continue to escalate (Darkoh and Mbaiwa, 2014). Wetland conservation, therefore, depends on the effectiveness of governance systems that influence peoples' behavior to achieve their wise use (Materu et al., 2018).

22.4 Transdisciplinary wetland monitoring and assessment

Given the growing levels of catchment degradation occurring, it is critical that a higher-level approach be taken to assess wetland ecological conditions (Kotze, 2011; Dalu et al., 2022, Chapter 8; Greenfield, 2022, Chapter 20;

Dalu et al., 2021, Chapter 21). However, wetland assessments generally continue to be undertaken mainly at the scale of individual wetlands, with costs and logistics preventing optimal condition assessments of all known wetlands (Mitchell, 2012; Rivers and Moore, 2012). Therefore, wetland assessments may need to be undertaken at regional basin scale in order to ensure the effective protection of all wetland types that may be interconnected.

To date, extensive research conducted in Southern Africa's wetlands has mainly focused on specific components such as vegetation, hydrology and soils (Dube and Chitiga, 2011; Milzow et al., 2009; Ramberg et al., 2006). All these studies are fragmented and do not provide a comprehensive understanding of the condition of the wetlands considering the ever-changing land uses and interconnectedness of wetlands at regional basin scale. While such studies could serve as good starting points for researchers who want to learn about wetland use and management, spatial and temporal variations in wetland use patterns and related governance systems are not well understood. Evaluation of the overall condition of wetlands using a holistic approach that integrates socio-economic and ecological aspects is critical, since the degree of sensitivity to anthropogenic interventions is still largely unknown in most developing countries (Kotze, 2013; Mtambanengwe, 2006; Musasa and Marambanyika, 2020).

Various approaches applied in wetland monitoring and assessment in southern Africa include remote sensing, Geographic Information Systems (GIS) and in-situ measurements (Dube et al., 2022, Chapter 21; Phethi and Gumbo, 2019; Rebelo et al., 2010). Mitchell (2012) used remote sensing techniques to monitor the proliferation of alien invasive species in Botswana, Namibia, and Zambia. Phethi and Gumbo (2019) used remote sensing to monitor wetland use changes in Makhitha Wetland, South Africa given the ability of the technique to cover extensive areas. Increasing land-use and land cover changes were attributed to land clearance for cultivation and construction. In Zimbabwe, remote sensing has been applied, for example, Marambanyika et al. (2016), explored human impacts on wetland components such as vegetation, hydrology, and soils. Fakarayi et al. (2015) also applied Landsat imagery to assess land-use/cover changes in the Driefontein Wetlands and observed that land-use has been changing gradually, as evidenced by loss of grasslands, water, and increased bare land. Remote sensing enables researchers to reduce costs associated with conducting surveys at the same time saving time.

GIS techniques were applied by Rebelo et al. (2010) in river basins of Southern Africa to monitor and assess wetland conditions. The study mapped wetland distribution, extent covered, and the human activities to determine their impacts on wetland ecological components. Rivers and Moore (2012) explored wetland conditions in Southern Africa and mapped degraded areas using GIS on a spatial and temporal basis (see also Dube et al., 2022, Chapter 21). The above-mentioned study showed that when wetlands are lost or degraded, they will not be able to provide a wide range of services to support human livelihoods. Darkoh and Mbaiwa (2014) applied in-situ field methods to explore the nexus between human activities and environmental threats in the Okavango Delta, Botswana to inform meaningful planning to reverse the increasing trend of wetland loss. In Namibia, these methods were explored by Bethune et al. (2004), to understand how proliferation of invasive species affected water retention and quality. In-situ field methods were used to determine human activities (grazing, ploughing, and burning) which threaten wetland conditions in South Africa (Pantshwa and Buschke, 2019).

The assessment of agricultural practices in wetlands using such frameworks is important, as some cultivation systems have been observed to damage wetland ecosystems (Marambanyika et al., 2016; Mbereko et al., 2007). Moreover, in light of increasing donor-funded programs in wetlands aimed at reducing poverty (SDG 2) and safeguarding water supplies for crops in the context of erratic rainfall, it is important to explore how human practices and governance systems influence wetland conditions especially in areas where factors affecting the wetlands are poorly understood (Marambanyika et al., 2016).

22.5 Wetland management approaches in Southern Africa

22.5.1 Wetland policies in selected Southern African countries

Wetland use and management are cross-cutting issues and tend to vary from one wetland type to the other depending on the hydrogeomorphic characteristics. Developing a wetland policy can be an important paradigm shift in recognizing wetland problems and how to counteract them (Bethune and Ruppel, 2007). Botswana does not have a wetland policy to protect wetlands from the increasing environmental threats attributed to human activities (Table 22.1; Darkoh and Mbaiwa, 2014). The lack of a clear policy that addresses wetland issues implies that the coordination of wetland protection efforts is weak. This was confirmed by Darkoh and Mbaiwa (2009) who observed poor coordination of institutional policies on land-use in the Okavango delta.

Namibia has a Draft Wetlands Policy (2004) set to provide a platform for the conservation and wise use of national and shared international wetlands (Bethune and Ruppel, 2007; Namibia Ministry of Environment and Tourism, 2004). Namibia adopted the water policy as a guideline to develop the draft wetland policy (Bethune and Ruppel, 2007; Namibia Ministry of Environment and Tourism, 2004). The draft wetland policy further calls for the need for sectoral coordination between all stakeholders involved in the use and management of wetlands. However, its implementation and effectiveness have not been realized since the policy has not been promulgated for close to two decades.

TABLE 22.1 Policy positions in selected countries in Southern Africa.

Country	Policy status and year enunciated	Current implications	References
Botswana	National wetland policy not available yet	Poor coordination of wetland protection efforts Lack of synergy between institutions and wetland laws	Darkoh and Mbaiwa, (2009, 2014)
Namibia	Draft Wetland Policy 2004	Poor and weak sectoral coordination between all stakeholders involved in the use and management of wetlands Failure to recognize wetland problems and how to counteract them	Bethune and Ruppel (2007); Namibia Ministry of Environment and Tourism (2004, 2014)
South Africa	Sectoral policy	Poor implementation of laws, rooted largely in insufficient resources and capacity, as well as weaknesses in the structures and practices of cooperative government	Dini and Everard (2016)
Zambia	Wetland Policy 2018	Clear framework to coordinate multisectoral participation in wetland resources management and conservation	Mwitwa et al. (2018); Zambia Ministry of Lands and Natural Resources (2018)
Zimbabwe	Draft Wetland Policy 2020	Poor sectoral coordination and implementation of wetland laws since the policy has not been enunciated	Zimbabwe Ministry of Environment, Climate, Tourism and Hospitality Industry (2020a, 2020b)

Being cognizant of the value and threatened status of its wetlands, South Africa has included wetlands in the national agenda. To this end, South Africa did not come up with a standalone wetland policy but instead, incorporated objectives relating to wetland conservation and wise use into sectoral policies including covering the environment, agriculture, biodiversity, and water sectors (Dini and Everard, 2016). Mainstreaming of wetlands into those sectors was perceived to have a high potential to positively impact wetlands management since one-size fits all approach was considered ineffective, as the impact of different sectors on wetlands considerably vary (Dini and Everard, 2016). The sectoral approach is expected therefore to mainstream wetland management strategies. However, the sectoral approach has brought discord in wetland management since it removes a central focused oversight role in wetland protection, hence wetlands degradation continues unabated in the country (Kotze, 2010; Phethi and Gumbo, 2019). When policies are established it is expected that they provide a conducive framework for implementers and communities for effective operationalization which is lacking in the current sectoral policies in South Africa. The effective conservation of wetlands in South Africa can therefore be attained if wetlands are viewed as a resource that requires harmonized protection approach, the situation lacking in the current sectoral approach. Sectoral policies have also meant limited participation of local communities, yet they are the custodians of the natural resources including wetlands.

In Zambia, a wetland policy was developed in 2018 to coordinate wetland management by various stakeholders (Table 22.1; Mwitwa et al., 2018). The National Wetland Policy seeks to address issues relating to wetland degradation by promoting a coordinated approach to wetland conservation and management. Through the policy it is expected that wetlands contribute more to sustainable development of the nation. Zambia's wetland policy is implemented through stakeholder collaboration including ministries, environmental agency, water authority, traditional leaders, civil society organizations, private sector, and local communities (Mwale, 2018). Though the wetland policy is fairly new, 2 years old, it is already promising to improve wetland management in Zambia.

Zimbabwe has a draft national wetland policy (Zimbabwe Ministry of Environment, Climate, Tourism and Hospitality Industry, 2020a, 2020b). The proposed National Wetlands Policy aims to guide wetlands management to become incorporated in development planning by the Government, private sector, development partners, traditional leaders, communities, and individuals. This will enhance sectoral coordination in wetlands management, currently fragmented and sometimes conflicting (Frenken and Mharapara, 2002; Marambanyika and Beckedahl, 2016b). The other distinctive feature of this policy is that it will enhance capacity building within relevant institutions involved in the management of wetlands. The implementation of the policy will be supported by Wetlands Management Guidelines with clearly laid down procedures on wetland identification, step-by-step procedures for the implementation of suitable development projects, including wetland restoration and creation (Zimbabwe Ministry of Environment, Climate, Tourism and Hospitality Industry, 2020a, 2020b). Therefore if the wetland policy and guidelines are to be implemented, Zimbabwe is likely to improve wetlands management currently under severe threat.

To the best of our knowledge, there is no regional wetlands policy meant to assist in the management and conservation of wetlands at regional scale in Southern Africa. Instead, there is a regional water policy, which does not wholly address wetland conservation and management issues. Given that most of the selected Southern African countries, except Zambia, have no comprehensive national wetland policies, lack of a clear regional wetland policy therefore exposes wetlands to multiple management systems that are either complementary or contradictory. This has potential to create lack of cohesion in transboundary coordination of efforts. Therefore, wetland management policies should be harmonized to ensure sustainable use at regional basin scale. However, the regional policy framework should have clear enforcement guidelines considering that the countries tend to ignore such policies just to protect their own territorial interests (Frenken and Mharapara, 2002).

22.5.2 Legal frameworks guiding wetland protection in selected Southern African countries

In Southern Africa, wetland loss and degradation has provoked wider thinking which has resulted in formulation of legislation. In Botswana, there are fragmented pieces of environmental legislation guiding wetland protection (Darkoh and Mbaiwa, 2014; Fink, 2000). This creates an ineffective and expensive administrative system with overlaps. A good example of this fragmentation and lack of coordination is found in the Agricultural Resources Act of 1972 (Fink, 2000; Table 22.2). This Act gives the Agricultural Resources Board jurisdiction over soil, water, and vegetation. As such, this Board has the jurisdiction to regulate parts of the environment that are also administered by other government departments, including the Department of Water. In Botswana, wetlands are regulated by not less than 20 different laws, each with their own enforcing authority (Darkoh and Mbaiwa, 2014), hence disharmony in wetland conservation and management. Therefore, Mosepele et al. (2018) revealed that there is a need for a harmonized legislative framework to ensure wetlands sustainability on Botswana.

The conservation of the natural environment and ecosystems is a constitutional imperative in Namibia (Namibia Ministry of Environment and Tourism, 2014; Table 22.2). In terms of Article 95 (l) the national constitution implores the state to ensure sustainable management of biodiversity by taking measures to promote and maintain the welfare of the people including the maintenance of ecosystems. Namibia recognizes the critical importance of the transboundary management of natural resources, which is guided by Southern African Development Community (SADC) protocols on tourism, fisheries, watercourses, and forestry (Bethune and Ruppel, 2007; Namibia Ministry of Environment and Tourism, 2014). This is further promoted in the National Biodiversity Strategic Action Plan (NBSAP), particularly regarding

TABLE 22.2 Legislation guiding wetland protection in selected countries in Sothern Africa.

Country	Legislation	Implications	References
Botswana	Agricultural Resources Act (1972), National Conservation Strategy (1990), Water Act (1971)	Fragmented pieces of environmental legislation, ineffective and expensive administrative system with overlaps	Fink (2000), Darkoh and Mbaiwa (2014)
Namibia	Article 95 (l) the national constitution, The Environmental Management Act (2007), Water Act (1966), and Water Resources Management Act (2004, 2013)	Poor implementation and lack of coordinated monitoring and enforcement of the legal provisions	Namibia Ministry of Environment and Tourism (2014), Ruppel and Ruppel-Schlichting (2016)
South Africa	Conservation of Agricultural Resources Act (1983), National Environmental Management Act (1998), the National Water Act (1998), Protected Areas Act (2003), and Biodiversity Act (2004)	Poor implementation as a result of the weaknesses in the structures and practices of cooperative government	Swanepoel and Barnard (2007), Dini and Everard (2016), South Africa Department of Environmental Affairs (2019)
Zambia	Environmental Management Act (2011)	Lack of harmony on what the law says may create confusion	Bethune and Ruppel (2007), Zambia Ministry of Lands and Natural Resources (2018)
Zimbabwe	Environmental Management Act (Chapter 20:27), Statutory Instrument 7 (2007), Section 73 of the Constitution of Zimbabwe Amendment (No. 20) Act (2013)	Weaker penalties undermining enforcement of the legal provisions	EMA Act (2003), Marambanyika and Beckedahl (2016b), Matenga (2019), Mandishona and Knight (2019)

the improved management of the transboundary river commissions such as Okavango Water Course Commission (OKACOM) (Bethune and Ruppel, 2007). The Environmental Management Act (2007), Water Act (1966), and Water Resources Management Act (2004, 2013) are some of the key laws meant to regulate wetlands management and conservation (Ruppel and Ruppel-Schlichting, 2016). Effective implementation of the laws is set to be improved by sectoral coordination in the Draft Wetlands Policy.

In South Africa, the management and conservation of wetlands is covered in Section 24 of the Constitution (South Africa Department of Environmental Affairs, 2019). Several sectoral laws such as the Conservation of Agricultural Resources Act (1983), the National Environmental Management Act (1998), the National Water Act (1998), the Protected Areas Act (2003), and the Biodiversity Act (2004) are used to protect the wetlands (Dini and Everard, 2016). Regulation 7 (3) of the Conservation of Agricultural Resources Act provides guidelines for the sustainable utilization of wetlands as it reiterates that no land user shall drain or cultivate a wetland without permission of the Executive Officer. The major shortcoming of the fragmented legislation is poor implementation as a result of the weaknesses in the structures and practices of cooperative government (Dini and Everard, 2016; Swanepoel and Barnard, 2007).

In Zambia, the Environmental Management Act (2011), Section 25 provides for the declaration of a wetland as an ecologically sensitive area imposing limitations on development in or around wetlands (Bethune and Ruppel, 2007). The Act further prohibits reclaiming or draining, disturbing a wetland by drilling or tunneling in a manner that has, or is likely to have, an adverse impact on the wetland or adversely affect the ecosystem. It also prohibits introduction of exotic animals or plants (Zambia Ministry of Lands and Natural Resources, 2018).

In Zimbabwe, the wetland management is regulated under the Environmental Management Act (Chapter 20:27), Statutory Instrument 7 of 2007. Section 113 of the Environmental Management Act (EMA Act) (Chapter 20:27) gives the Minister of Environment powers to declare any wetland to be an ecologically sensitive area and may impose limitations (EMA, 2003; Matenga, 2019). However, the EMA Act does not give the EMA adequate powers to stop the proliferation of illegal activities that are detrimental to the environment, due to weaker penalties (Mandishona and Knight, 2019). Although the EMA Act is the main environmental law that supersedes other laws that regulate wetland management; it tries to minimize wetland regulation discord.

In general, most Southern African countries have many laws that have a national scope in as far as wetland management and conservation is concerned. Only Namibia has tried to embrace a regional scope as shown in the Draft Wetlands Policy. Although in some instances as in the case of Zambia and Zimbabwe, the framework environmental laws exist, many laws focusing on wetlands continue to threaten the existence of wetlands at regional basin scale. This is attributed to fragmentation and/or lack of stiff penalties as provided in the promulgated laws (Mandishona and Knight, 2019; Mitchell, 2012). This calls for national governments to explore the feasibility of establishing national wetland laws that can be possibly harmonized at regional level.

22.5.3 Institutional arrangement

In the selected Southern African countries, there is involvement of many institutions in wetlands management. In Botswana, Namibia, South Africa, Zambia, and Zimbabwe wetlands management is done by ministries, government departments (environment, water, forestry, and wildlife), local authorities, civil society organizations, traditional leaders, and local people (Darkoh and Mbaiwa, 2009, 2014; Dini and Everard, 2016; Madzudzo et al., 2013; Marambanyika and Beckedahl, 2016b; Ruppel and Ruppel-Schlichting, 2016). In general, these institutions have different priorities and objectives that cause conflicts. This situation presents challenges in the effective wetland management as there is a disconnection between water authorities and wetland utilization and conservation agencies (Darkoh and Mbaiwa, 2009, 2014; Marambanyika and Beckedahl, 2016b).

Like any other country, the effectiveness of local authorities such as Rural District Councils (RDCs) is marred by confusion which emanates from overlapping roles with other central government departments (Fink, 2000; Marambanyika and Beckedahl, 2016b). In Botswana, Namibia, and Zambia, wetland management falls under the jurisdiction of several state institutions with no heterogeneous mandates (Fink, 2000; Mwale, 2018; Namibia Ministry of Environment and Tourism, 2014). These institutions do not pull in one direction. For example, in Botswana, Namibia, and Zimbabwe, the mandate of government departments, nongovernmental organizations (NGOs), traditional leaders, and RDCs is torn between wetland conservation and improving human livelihood, thus conflicts of interest emerge resulting in unsustainable use (Darkoh and Mbaiwa, 2009; Fink, 2000; Marambanyika and Beckedahl, 2016b; Namibia Ministry of Environment and Tourism, 2014).

In South Africa, several statutory institutions including those covering environment, agriculture, biodiversity, and water are involved in wetland use and management alongside traditional structures (Dini and Everard, 2016). The major shortcoming of involving several institutions is the lack of conservation accountability due to divergent and overlapping roles compounded by poor practices of the cooperative government. Therefore, the multifaceted and cross-cutting nature of wetlands require strengthening of what the South African Constitution terms “cooperative government,” involving a wide range of sectors at multiple levels of governance (Dini and Everard, 2016). For instance, in order to deal with the reality of overlaps and sometimes conflicting sectoral policy mandates in the water sector, different responsible institutions jointly developed a set of cross-sector policy objectives for conserving South Africa's freshwater biodiversity (South Africa Department of Environmental Affairs, 2019). This approach should be adopted to improve wetlands management under the current sectoral system used in South Africa.

In Zambia, nonstate institutions such as NGOs often use their financial muscle to influence wetland use and conservation. NGOs are often at loggerheads with local authorities who in turn monitor their activities and end up giving them stiff penalties (Mwale, 2018). This has also been reported in Zimbabwe especially in cases where NGOs deviate from permitted conditions of operation (Marambanyika and Beckedahl, 2016b). In some cases, NGOs provide farming inputs in the form of seeds and this in turn, motivates local communities to extend crop cultivation in sensitive areas much to the dismay of government departments such as EMA which seeks to ensure conservation of these ecosystems (Marambanyika and Beckedahl, 2016b). To this end, divergent institutional motives create confusion as local communities are likely to engage in crop cultivation in wetland fringes by taking advantage of misunderstandings between these institutions thus compromising wetland use and management (Dini and Everard, 2016; Namibia Ministry of Environment and Tourism, 2014).

Research institutions have an omnipotent role in providing guidelines for sustainable wetland use and conservation (Chuma et al., 2008; Darkoh and Mbaiwa, 2014). Research institutions are either private or public, but their main goal is to provide support to existing formal and informal institutions and legal arrangements through research and innovation (Kotze, 2013; Mbereko et al., 2015; Turpie et al., 2010). In Southern African countries, academic institutions are also assisting in raising awareness on wetland conservation based on empirical evidence. For example, in Zimbabwe, Mharapara (1995) designed a method to ensure sustainable cultivation in wetlands (Marambanyika et al., 2016). This method typically known as "ngwarati" has been used to conserve wetlands from increasing farming threats in countries such as Zimbabwe (Mharapara, 1995). Several researches in the wetland discourse have been conducted in Southern Africa with the support from private institutions such as Waternet as well as local universities (Chuma et al., 2008). From the presentation in the previous sections, there are many poorly coordinated institutions, including government departments, NGOs, research and academic institutions, traditional leaders, are involved in wetlands management.

22.6 Implications of the nexus between wetland policy, legal, and institutional arrangements

The coordination of activities within a community is essential for the management of wetland resources (Mbereko et al., 2007, 2015). In this respect, the formation of institutional and legal frameworks that governs management is imperative (Mbereko et al., 2007). In Southern Africa, the involvement of many institutions in the implementation of the legislation, more often brings management discord, resulting in wetland degradation (Darkoh and Mbaiwa, 2014; Dini and Everard, 2016; Marambanyika and Beckedahl, 2016b; Zambia Ministry of Lands and Natural Resources, 2018). The different state and nonstate institutions involved in wetland management are well supported by pieces of legislation that promotes, in many instances, their divergent mandates, to the detriment of wetland conservation (Darkoh and Mbaiwa, 2014; Dini and Everard 2016; Marambanyika and Beckedahl, 2016b; Ruppel and Ruppel-Schlichting, 2016; Zambia Ministry of Lands and Natural Resources, 2018). Therefore, if tropical freshwater wetlands are to be well conserved, there is need to ensure complementarity between the various stakeholders implementing different legislation. Zambia has addressed this discord by developing a national wetland policy (Zambia Ministry of Lands and Natural Resources, 2018). Therefore, other countries without national wetland policies should expedite their crafting and ensure that they are synchronized at regional level in order to ensure effective wetland protection at basin scale, given the interconnectedness of these natural systems.

Despite having a regional water policy, the absence of a regional wetland policy has resulted in uncoordinated actions in as far as wetland conservation and management is concerned. Policies are inconsistent owing to the notable discord in government concerning the regularization of wetland use such as cultivation (Matenga, 2019). This has meant that local communities illegally occupy wetland areas some of which are Ramsar Sites, thus complicating the attainment of national obligations as enshrined in the wise use guidelines (Murungweni, 2013).

In Southern Africa, wetlands found on communal land are common-pool resources (Mbereko et al., 2007; Pantshwa and Buschke, 2019). This exposes these resources to the tragedy of the commons (Ostrom et al., 1994), whereby rural communities in an attempt to maximize the benefits derived thereof do not take into cognizance the full costs associated with their activities (Pantshwa and Buschke, 2019). In common-pool resources, it is difficult to prohibit or exclude users of a resource once it has been made available for exploitation to sustain human livelihood (Pantshwa and Buschke, 2019). Several studies have revealed that in a common shared resource system, individual users may have conflicting interests and through their collective action may become an opposing force to the common good of all the users as the common resource can be exhausted (van Laerhoven and Ostrom 2007). Such power dynamics may threaten the sustainable use of the common-pool resources (Bodin and Crona, 2009; Matenga, 2019). One solution is collective choice rules where users of wetlands design and enforce their own rules on how to share the resources (Pantshwa and Buschke, 2019). However, this solution only works where community members who rely on wetlands are also the ones damaging the wetlands.

22.7 Shortcomings and enforcement challenges of wetland policies and legislation

Fragile as they are, wetlands are seldom explicitly covered at national level in other existing natural resource management policies (Bethune et al., 2005; Mwale, 2018). It is imperative that wetland management policies and regulations put in place consider the impacts of surrounding countries that share the same river basin (Fink, 2000; Mwitwa et al., 2018). In the selected Southern African countries, implementation and enforcement of wetland policies and legislation is hindered by conflicting interpretations of provisions of the law and policies, inadequate financing toward wetland conservation, political interference, lack of awareness on the rationale and existence of laws governing wetland conservation and competing interests between riparian nations (Dini and Everard, 2016; Frenken and Mharapara, 2002; Mwale, 2018; Ruppel and Ruppel-Schlichting, 2016; Zambia Ministry of Lands and Natural Resources, 2018).

22.7.1 Conflicting interpretations of provisions of the law and policies

Conflicting interpretations of provisions of the law and policies presents challenges in Southern Africa (Fink, 2000; Marambanyika and Beckedahl, 2016a). In Botswana, there is contradictory dissemination of the provisions of wetland laws by government agencies (Darkoh and Mbaiwa, 2014). In countries such as Namibia and Zimbabwe, officers from the same agency may either encourage or forbid wetland activities (Bethune et al., 2004; Marambanyika et al., 2012), hence confusing local people's conservation initiatives. In South Africa, fragmented and sectoral policies that focus on wetland use and management has brought disharmony between many institutions and local stakeholders involved in wetland use (South Africa Department of Environmental Affairs, 2019). This means that law enforcement by statutory bodies should be taken into consideration through an approach that encourages citizens' participation in decision making and implementation.

22.7.2 Inadequate financing to wetland management and institutional incapacitation

Inadequate financing to wetland management as well as incapacitation through human resource skills and other valuable resources also hinder wetland policy and legislation implementation in the selected Southern African countries (Dini and Everard, 2016; Marambanyika and Beckedahl, 2016b). In many instances, for example, in Namibia, Zambia, and Zimbabwe, wetland laws are not respected due to lack of effective monitoring and weak enforcement of applicable legal provisions by the formal institutions, mainly government agencies (Marambanyika and Beckedahl, 2016b; Mwale, 2018; Ruppel and Ruppel-Schlichting, 2016). In countries such as Namibia and Zambia, poor enforcement of the law has been attributed to lack of adequate funding to recruit the people with the required expertise (Chabwela and Haller, 2010; Mwale, 2018). In Zimbabwe, lack of monitoring and weak enforcement of the law is a result of lack of funding which is tied to lack of political will to support the initiatives (Marambanyika and Beckedahl, 2016b). Therefore, encroachment into fragile wetland sensitive areas continues despite having a raft of pieces of legislation. In order to improve policy implementation and enforcement mechanisms, well-resourced institutions should be established backed by government support.

22.7.3 Political interference

In Southern Africa, political interference has resulted in the belittling of wetland law. In some cases, political leaders pursued populist policies to win the hearts of the electorate thereby condoning illegal use of the resource (Mandishona and Knight, 2019; Marambanyika and Beckedahl, 2016b). Politicians sometimes persuade regulatory officers to ignore illegal wetland activities with impunity, thereby threatening wetland ecosystems. The prime effect of such a scenario is wetland use without permits. In countries such as Zimbabwe and South Africa, politics has weakened the capacity of the responsible institutions to enforce legal stipulations where political ambitions were under threat (Adekola et al., 2012; Marambanyika and Beckedahl, 2016b). In the Kafue Flats of Zambia many farmers joined local leaders in unsustainable exploitation as they feared losing farming space in the wetlands (Chabwela and Haller, 2010). Politics should not be allowed to interfere with the implementation of measures aimed at conserving wetlands in Southern Africa.

22.7.4 Lack of awareness on the rationale and existence of laws

Lack of awareness on the rationale and existence of laws governing wetland conservation in Southern Africa is a major constraint toward the implementation of policies and legislation (Marambanyika and Beckedahl, 2016a). This is true in countries such as South Africa (Dini and Everard, 2016) and Zimbabwe where there is a disjuncture between the legal provisions and practical implementation. This brings the question; does legislation remain only in theory yet sound wetland management lies within practical applicability? To this end, for as long as there is limited understanding of the law by the local communities, enforcement will remain a challenge.

22.7.5 Poor coordination and non-compliance

Enforcement and compliance are key components to the success of any wetland regulatory program (Dini and Everard, 2016; Frenken and Mharapara, 2002). The focus of enforcement action is on preventing "front-end" violations that is, ensuring that wetlands are not filled without first securing a government permit or approval. In Botswana and Namibia, environmental legislation and its administration are plagued by poor organization and rampant noncompliance (Fink, 2000). It can be noted that, despite persistent noncompliance, little has been done to effectively enforce the environmental laws (Fink, 2000; Marambanyika and Beckedahl, 2016a). One of the most heralded reasons cited is that authorities with the mandate to enforce legislation are more concerned with promoting national and local development. In Zambia and Zimbabwe, history has shown that when faced with a choice between resource conservation and development, enforcing authorities tend to choose the latter (Chabwela and Haller, 2010; Mandishona and Knight, 2019).

22.7.6 Competing interests

The other noticeable drawback toward wetland policy implementation at regional scale in southern Africa is that all nations have their own interests (Frenken and Mharapara, 2002). This, further coupled with conflicting laws on transboundary resource use creates constraints. One such case is the Zambezi River Basin where Zambia manages a fish ban in Lake Kariba, but to the contrary Zimbabwe conducts fishing activities throughout the season (Frenken and Mharapara, 2002; Mitchell, 2012). Therefore, the efficacy of management strategies put in place becomes questionable considering the conflicts of interests between riparian nations.

22.8 A framework to strengthen institutional arrangements and environment

Wetland conservation and management requires a clear policy, well-coordinated institutional arrangements and a harmonized legal framework whereby roles and responsibilities of implementing and enforcing mechanisms are clearly stated. This is important to avoid overlapping and/or contradicting roles as wetland stakeholders may pull in different directions. In this chapter, we propose that a wetland governance approach that allows continuous review of the implications of the wetland law, policy, and institutions on wetland conservation be established (Fig. 22.1).

Wetland governance should take into cognizance institutions that regulate wetland use and access. These institutions can be grouped as state actors (government departments) and nonstate actors (wetland committees,

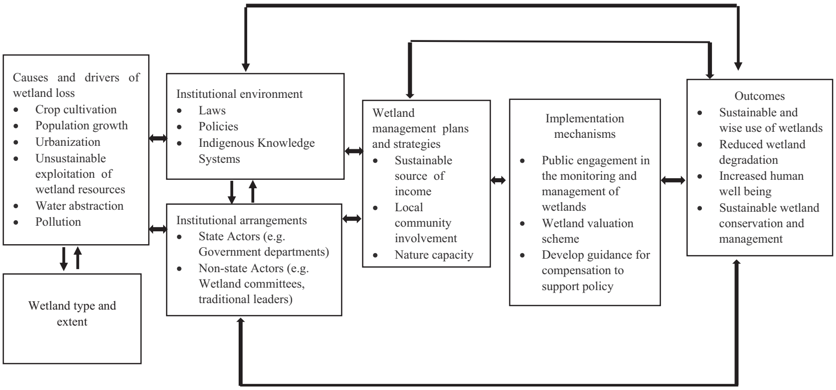

FIGURE 22.1 A proposed wetland governance framework to enhance the management of wetland.

traditional leaders). Both institutional arrangements and environments influence each other as changes in one attribute may in turn affect the other component, and that has a bearing on the strategies that can be adopted and the intended outcomes of wetland management.

It is worth to note the legal and policy framework in each country is shaped by the drivers of wetland degradation and loss peculiar to each country. Therefore, the established institutions influence the provisions of the legal framework and the enforcement mechanisms. On the other hand, the laws influence the establishment of appropriate institutional arrangements, normally statutory bodies. The policy framework will explain how different institutions should be coordinated within the confines of the law and in the interest of wetland conservation.

After establishing the relevant institutions, policy and the law, this will help to define the plans and strategies for the protection of wetlands. The wetland management plans and strategies should necessitate a sustainable source of income for the local people who should be part of the institutional arrangements. The local people normally are the custodians of the natural resources. Clare et al. (2011) stated that countries with a wetland management plan understand their resources and relevant actions are put in place. Therefore, comprehensive land-use planning that identifies high priority wetlands would allow land managers, developers, and individual landholders to make more informed decisions about land-use and gives them the ability to weigh the potential benefits and costs associated with any development especially in wetlands.

A key strength of the proposed framework is that all the listed components are complementary and emphasize on local participation. Previous studies have shown that wetland management plans and strategies work well where there is local community participation (Clare and Creed, 2014;

Marambanyika et al., 2012; Pantshwa and Buschke, 2019). Involving local people in wetland use planning and management brings a sense of ownership. This results in balancing of the human needs and the natural resource base, hence sustainable utilization of wetland resources (Mandishona and Knight, 2019). Indigenous knowledge systems are also instrumental in the determination of suitable wetland use policies, laws and institutions that balance socio-economic and ecological benefits thereby reducing wetland degradation (Fig. 22.1).

Periodic wetland valuation schemes will also assist communities to understand the magnitude and extent of benefits derived from the wetlands, a factor which motivates wetland protection. Normally, the changing value of wetlands is not monitored so that appropriate institutional environment and arrangements are maintained (Turpie et al., 2010; Ndhlovu, 2012; Marambanyika and Beckedahl, 2016c). This will in turn undermine sustainable wetland management initiatives.

In general, Ramsar sites, transboundary as well as local wetlands lack management plans. Where they exist, the implementation mechanisms are weak. To this end, the necessary policy and legal framework to support the proposed framework should be put in place and resources for its operations and monitoring made available. This can be further strengthened by integrating GIS and remote sensing technologies in wetland monitoring to improve decision making that enhances sustainable wetland utilization. Adoption of the proposed framework will assist to create an environment that promotes SDGs as it shows the link between institutional arrangements and institutional environments in shaping the wetland management plans and strategies which determine the intended outcome. If a regional wetland policy is to be developed, it should recognize national and wetland scale institutional arrangements, policies, laws, and livelihood options in a way that does not compromise wetland conservation.

22.9 Conclusions and recommendations

The chapter assessed literature on the implications of institutional, legal, and policy nexus on wetlands management and conservation in selected countries in Southern Africa. Tropical freshwater wetlands in Botswana, Namibia, South Africa, Zambia, and Zimbabwe are largely threatened by anthropogenic activities due to poor policing of wetland use and management strategies, resulting in the loss of essential ecosystem services. Wetland degradation and loss is largely a result of the absence of national wetland policies, fragmented national laws and discord within national institutional arrangements, a situation that has been compromising effective coordination and implementation of management and conservation initiatives. Instead of institutions pulling in one direction through collaborative actions, there is no connection between development agendas and environmental protection, as absence of wetland policies, except for Zambia, result in poor coordination of wetland conservation initiatives. Although national laws that focus on wetland protection exist, their enforcement has been weak. This is attributed to overlaps in many environmental laws that exist in one country, poor funding of statutory institutions responsible for wetland protection enforcement and lack of policies that complements the existing fragmented laws. The study recommends the harmonization of laws that govern wetland protection, establishment of national wetland policies that are synchronized at regional level and the strengthening of institutions specifically focusing on wetland management.

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Chapter 23

Indigenous peoples′ participation and the management of wetlands in Africa: a review of the Ramsar Convention

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23.1 Introduction

The procedural right to participation has recently surged in importance as a central component of the new international legal paradigm of sustainable development. Yet the text of the Ramsar Convention is silent about the safeguard, laying emphasis instead, on state sovereignty, resulting in state-centric or top-down decision-making approach, "without, prima facie, any regard for the impact on the ground" (Sellheim, 2018; Irvine et al., 2021, Chapter 19; Marambanyika et al., 2022, Chapter 21). Sellheim (2018) attributes the Convention's lack of "socio-economic" inclination to the prevailing conditions at the time of its crafting, and cites all international conservation agreements negotiated during the 1970s, such as the World Heritage Convention (WHC), the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), the Agreement on Conservation of Polar Bear (ACPB), and the Convention of Migratory Species of Wild Animals (CMS) to be similarly worded. However, a paucity of literature exists examining the procedural right to participation in relation to Africa's indigenous peoples and local communities when it comes to the designation and management of Wetlands of International Importance or Ramsar Sites. The significance of this line of inquiry hinges partly in the fact that Africa's indigenous peoples and local communities depend on land and natural resources that are fast-shrinking due to climate change and its impacts as well as population growth (Jegede, 2016). Compounding this, while some

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African countries such as the Central African Republic and Congo Brazzaville recognize indigenous peoples within their borders, most Southern African countries such as Tanzania and Botswana do not. The indigenous peoples' rubric is an emerging international law norm aimed at protecting communities on the margin. Adherence to the right to participation is therefore contextually important in Africa for two reasons: firstly, "the level of poverty and local reliance on the continent's natural resources" and secondly "laws and institutions in many African countries are a reflection of the colonial past, fifty years after [the attainment] of independence" (Laltaika, 2013).

While the Ramsar Convention has recently developed processes and mechanisms that ensure effective participation of nonstate actors including indigenous peoples and local communities in the management and conservation processes, the processes and mechanisms are not legally binding as a matter of international law (Wasserman and Dalu, 2022, Chapter 1). Consequently, given the asymmetrical relationships between States on the one hand and indigenous peoples and local communities on the other, the state-centric nature of the convention's contents with emphasis on state sovereignty, will continue to define State actions at the domestic level.

This chapter seeks to examine implications of the Ramsar Convention's silence on the procedural right to participation in the light of indigenous peoples and local communities' rights in Africa. It aims at shading a new light on the understanding of the importance in the African context, of embedding the right to participation in the designation and management of Ramsar sites in the Ramsar Convention as opposed to including them in legally nonbinding documents that elude indigenous peoples' capacity to engage with their governments (Ramar, 2018).

23.2 The Convention on Wetlands of International Importance especially as Waterfowls Habitat (the Ramsar Convention)

Wetlands play crucial roles in hydrology and ecology (Brendonck et al., 2022, Chapters 9 and 10; Cuthbert et al., 2022, Chapter 17; Dalu et al., 2022, Chapter 8; Deemy et al., 2022, Chapter 3). Their functions include water storage, stream flow regulation, flood attenuation, and water purification. Other roles relate to nutrient assimilation and sediment accretion (Begg, 1990) and provision of habitats for a wide variety of animal and plant species. However, despite the unquestionable importance, wetlands have historically been destroyed for being regarded as "wastelands" (Begg, 1990). Prior to the coming to force of the Ramsar Convention, wetlands were also considered barriers to development and breeding grounds for disease vectors such as mosquitos. In addition to historic factors, contemporary threats to wetlands include "accelerated drainage, land reclamation, pollution, and overexploitation of wetland species" (Navid, 1989) undoubtedly due to increase in population resulting in fast-urbanization and conversion of wetlands into farmlands.

Against the background above, it is not surprising that the international community comprising independent states, decided to come up with a Convention for wetlands conservation, albeit motivated by a slightly different objective, namely to provide habitat for birds. Over the years however, the focus of the Convention has been widened to encompass "all aspects of wetland conservation and "wise use" (Odidi, 1999). Reflecting a normative paradigm shift in international conservation discourses from specie protection to habitat protection, the Ramsar Convention has been described as "the first modern multilateral treaty aiming to conserve natural resources on a global scale" (Matthews, 1993). It is thus unquestionably "the first international agreement that puts the wider biosphere under protection," because it normatively integrates resource users as part of its conservation strategy" as opposed to promoting a protectionist-"no-use"- approach to the area it seeks to protect" (Sellheim, 2018). Understandably, the Ramsar Convention, although binding on state parties as a matter of international law, "is less ambitious and more realistic" meaning its spirit is "to help states achieve mutually beneficial outcomes" by encouraging rather than requiring international cooperation (Bodansky, 2010).

Named after a city in Iran where it was concluded in 1971, the Convention came into force in 1975, and according to Mathews, it is "a wide treaty which restrains the countries joining it from the unthinking, selfish exploitation of their sovereign natural patrimony" (Bodansky, 2010). Based on official updates available in the secretariat's website, 171 countries are Contracting Parties, meaning they have signed and/or ratified Convention until the time of writing (https://www.ramsar.org/sites/default/files/documents/library/annotated_contracting_parties_list_e.pdf). In turn, the official website indicates further that the contracting parties have designated 2392 wetlands of international importance, covering a total of 253,898,668 hectares. However, the website does not provide disaggregated data, making it hard to know in specific terms, the amount of land in Africa forming Wetlands of International Importance and designated as such.

The convention has its roots in a general original consensus that wetlands constitute a resource of economic, cultural, scientific and recreational value and that their loss would be irreparable (https://www.ramsar.org/sites/default/files/documents/library/annotated_contracting_parties_list_e.pdf). Also agreed was the fact that due to their transnational seasonal migrations, waterfowl should be regarded as an international resource whose effective conservation requires international cooperation. This is in line with, and may have been a precursor to a growing body of international environmental law norms evidenced by state practice and general principles, which lay emphasis on the need for States to cooperate when it comes to addressing pollution problems.

For example, Principle 24 of the Stockholm Declaration 1972 noted that "international matters concerning the protection and improvement of the environment should be handled in a co-operative spirit," whereas Principle 7 of the Rio Declaration 1992 emphasized that "states shall co-operate in a spirit of global partnership to conserve, protect and restore the health and integrity of the Earth's system."

Commenting on the importance of international cooperation in conserving wetlands, Daniel Navid (Secretary General of the Ramsar Convention Bureau-as he then was), states:

> *In most cases, it is not possible for one country alone to take steps required to conserve wetland habitat and wetland species, and hence cooperation among States is a necessity for effective wetland conservation. The health of wetland habitat is dependent upon the quality and quantity of their water supply. Wetlands are affected by human impacts upon, for example, streams and rivers, which can occur at considerable distance from the wetland area, and in many cases, beyond national borders. Wetlands are also seriously degraded by transboundary air and water pollution. Finally, . . .much of the wetland fauna are migratory species whose conservation and management mandates international cooperation (Navid, 1989).*

The convention upholds the principle of state permanent sovereignty over natural resources (PSNR principle). The PSNR principle is a "fundamental international law principle allowing post-colonial states to assert full sovereignty over 'sovereign rights' found within the limits of their jurisdictions" (Pereira and Gough, 2013). Developing countries still cherish the principle as a right reserved to states, allowing them sovereignty over the management and distribution of natural resources within their jurisdictions. The Ramsar convention's alignment to this principle avoids offending the international law principle of State sovereignty, which was described in the Palmas Arbitration to mean "the right to exercise therein [i.e. within the territory of a state], to the exclusion of any other State, the functions of a sovereign." However, recent developments in the field of environmental law suggest that this principle is not absolute. Kidd and Cowling for example, emphasize that "States effectively surrendered their sovereignty over their wild animals when they became parties to the CITES [Convention on the International Trade in Endangered Species of Wild Fauna and Flora] and decisions that are in the interest of the global conservation of wild animals should hold sway over regional or domestic interests" (Kidd and Cowling, 2003). The objective of the convention, which is "predicated upon the promotion of international cooperation and as such has avoided the confrontation which has marked certain subsequent international conservation agreements," (Navid, 1989) evidences the convention's overall alignment to the principle.

The Ramsar Convention further stipulates that governments are responsible for protection of the "listed" and "unlisted" wetlands. See also Principle 2 of the Rio Declaration on the Environment and Development which provides that: "States have, in accordance with the Chatter of the United Nations and the principles of International Law, the sovereign right to exploit their own resources pursuant to their own environmental policies and the responsibilities to ensure that activities within their jurisdiction or control do not cause damage to the environment of other States or of areas beyond the limits of national jurisdiction. Accordingly, while the Convention permits a State party to limit the boundaries of a nature reserve containing wetlands due to national interests, it further proposes that the State in question compensates as far as possible for any loss of wetland resource, while simultaneously creating additional nature reserve in the same area or elsewhere [see Article 4(2), supra note 64]. This flexibility is well aligned to the principle of permanent sovereignty over natural resources. In principle, there is nothing inherently odd in upholding the principle of permanent sovereignty over natural resources and promoting state sovereignty. However, overextension of the latter may clash with contemporary normative international standards recognizing rights of nonstate actors such as local communities, specifically indigenous peoples. This is particularly likely to happen in Africa where most countries do not recognize rights of indigenous peoples (ACHPR and IWGIA, 2005). In the part that follows, this chapter highlights the right to participation in connection to indigenous peoples and local communities.

The use of the two terminologies namely indigenous peoples and local communities in this book chapter does not diminish the fact that under international law, indigenous peoples are treated as distinct subjects with rights and are recognized in many jurisdictions. In the part that follows, this chapter focuses on the procedural right to public participation and the right of indigenous peoples and local communities.

23.3 The right to public participation

The concept of public participation has long been a question of great interest in a wide spectrum of fields. In the field of Development Studies, for example, public participation and representation are considered to constitute pivotal benchmarks for "ensuring that [development] is not just an economic project, but also contains important political and psychological-social dimension" (Hopper, 2012). Further, public participation in the field in question is "at the heart of contemporary development debates," bringing to the limelight "issues about power, self-determination, empowerment and the purpose of development." In the Law and Development domain, public participation is a key indicator of the move to the domain's "third wave," which calls into question the viability of the neoliberal legal and policy frameworks in improving local conditions (Trubek and Santos, 2006).

In the discipline of Human Rights, the right to public participation is well articulated in various regional and international instruments (Laltaika, 2013). They include the Universal Declaration of Human Rights (see Article 21 of the Universal Declaration of Human Rights, 1948), the International Covenant on Civil and Political Rights (see Article 25 of the International Covenant on Civil and Political Rights), and the International Covenant on Economic, Social and Cultural Rights [see Article 13 (1) of the International Covenant on Economic, Social and Cultural Rights]. The following factors have been highlighted to be causes for the public participation "explosion": "democratization trends since 1989; adoption of the new legal paradigm of "sustainable development"; international environmental movement; human rights regime; organization of indigenous peoples and local communities and technology, particularly the information exchange capabilities of the internet (Pring, 2001).

Recent developments in the field of human rights have heightened the need to assess the contextual applicability of the right to participation for communities on the margin, given apparent power imbalances and information asymmetries underlying their interactions with other actors such as State governments and transnational corporations. Accordingly, the United Nations Declaration on the Rights of Indigenous Peoples (UNDRIP) encompasses the right to Free, Prior and Informed Consent (FPIC) [see article 32(2), http://www.un.org/esa/socdev/unpfii/documents/DRIPS_en.pdf] as an extended version of the right to public participation when applied to indigenous peoples. Article 32(2) provides for example that "States shall consult and cooperate in good faith with the indigenous peoples concerned through their own representative institutions in order to obtain their free and informed consent prior to the approval of any project affecting their lands and territories and other resources, particularly in connection to the development, utilization or exploitation of mineral, water, or other resources. In the next section, this chapter embarks on the concept of indigenous peoples in Africa and their rights in relation to the establishment and management of Wetlands of International Importance.

23.4 Recognition of indigenous peoples in Africa and the right to effective participation

23.4.1 Background

The rubric of "indigenous peoples" has emerged as a powerful platform in the international human rights regime (Wiessner, 1999), aimed at addressing systemic marginalization, subjugation, and exclusion of culturally distinct populations within modern or post-Westphalia Nation States (Anaya, 2013). In response to the steadfast struggles for recognition by representatives of the claimant communities (Miranda, 2010), the United Nations has established specific institutional mechanisms including the UN Permanent Forum on Indigenous Issues, the UN Special Rapporteur on the Rights of Indigenous Peoples and the UN Mechanism on the Rights of Indigenous Peoples (Kluwer, 2009) to protect and promote indigenous peoples rights (Laltaika, 2012). In addition, the UN has spearheaded development of normative standards that are embodied in the UN Declaration on the Rights of Indigenous Peoples, the jurisprudence of the UN treaty monitoring bodies and the International Labor Organization (ILO) Convention 169 (Anaya, 2013). These normative standards are relevant to States' recognition, promotion and protection of human rights of the communities under review. Central to the rubric's discussions in Africa has for many years been the rubric's contextual applicability (Hitchcock and Vinding, 2004a,b), arguably due to the continent's demographic arrangements, largely comprising original inhabitants, unlike settler countries such as Canada, Australia, New Zealand and the USA, whose settler populations outnumber that of original inhabitants. This explains why some countries like Tanzania put forward a counter-argument that "All Tanzanians of African decent are indigenous to Tanzania."

Specifically, African governments (see Titanji, 2009) have raised questions on the usefulness of the concept; and raised concerns that its application in Africa is likely to generate divisions, deepen ethnic tensions, and consequently cause "political instability, secessions, and threats to the territorial integrity of the African States" (Barume, 2009). Simultaneously, the continent's communities that perceive themselves to be on the margins continued to self-identify as indigenous peoples, and robustly engaged various supra-national justice institutions in an effort to vocalize their disadvantaged positions (Dahl, 2009). Comprising majorly hunter-gatherers and some groups of nomadic pastoralists (Bojosi and Wachira, 2006), these communities associate their marginality to their distinct livelihoods that are at variance with their countries' development priorities (Dahl, 2009).

While controversy remains to date (Ndahinda, 2011), the rubric gained strong prominence when the African Commission on Human and Peoples Rights (see Rudman, 2016); the continent's intergovernmental organization charged with promotion and protection of human rights, issued a signature report indicating that the rubric is applicable in the continent (ACHPR and IWGIA, 2005). Whereas most governments still insist that all their citizens are indigenous to Africa (Hitchcock and Vinding, 2004a,b), the concept is slowly gaining recognition in the continent. Ratification by the Central African Republic of the ILO Convention 169 (Laltaika, 2012), and Congo Brazzaville's enactment of a specific law recognizing the country's indigenous people (Laltaika, 2012) attest to the positive developments. Another positive signal relates to most African countries voting in favor of the UN Declaration on the Rights of Indigenous Peoples, dubbed "the most comprehensive and advanced of international instruments dealing with indigenous peoples rights" (Charters and Stavenhagen, 2009), when the UN General Assembly adopted it in 2007 (Hitchcock and Vinding, 2004a,b).

Based on the backdrop above, while most governments uphold a position that their respective citizens are all indigenous to Africa (Hitchcock and Vinding, 2004a,b) (to imply that there are no indigenous peoples in those countries), there is a steadily growing acceptance by some ministries in the same governments. Significantly, ministries in charge of environment and natural resources appreciate the centrality of recognition and implementation of indigenous peoples' rights as indicated in National Reports on the implementation of the convention on biological diversity (United Republic of Tanzania, 2014). This blurs monolithic claims on non-recognition of indigenous peoples in the continent. Accordingly, understanding the complexities of the subject in Africa beyond consideration of regional justice institutions' deliberations or explicit reference to indigenous peoples in the countries' constitutional and legal frameworks, is vitally important in order to appreciate progress made and enduring challenges. But the question still remains: who are indigenous peoples in Africa and what rights do they have? The next subpart addresses this question with reference to the work of the African Commission on Human and Peoples Rights.

23.4.2 The African Charter and the work of the African Commission

The African Charter on Human and Peoples Rights (OAU, 1981), also known as the Banjul Charter, establishes the African Commission on Human and Peoples Rights (the commission) and tasks it to supervise the Charter's implementation. According to Article 30 of the Charter, the Commission's task is to "... promote human and peoples' rights and ensure their protection in Africa" (see Article 30, Supra).

To perform these dual mandates, namely human rights promotion and protection, the commission ascertains whether state parties to the charter comply with their obligations. The commission does this via a communications procedure as well as through consideration of initial and periodic reports that state parties are required to submit. Parallel to this, the commission generates public awareness through research and information visits.

It is in line with its African Charter-based mandates that the Commission has engaged in discussions on the human rights situation of indigenous peoples who constitute one of the most vulnerable groups in the continent. This engagement sprung from recognition by the Commission that "the protection and promotion of human rights of the most disadvantaged, marginalized and excluded groups in the continent is a major concern," as well as a realization that "the African Charter on Human and Peoples Rights must form the framework for the promotion and protection of indigenous peoples rights" (ACHPR and IWGIA, 2005).

The commission's recognition provided space for indigenous communities who from 2001 onwards, consistently participated in the commission's biannual ordinary sessions. Through participation, indigenous peoples have been able to vocalize strong testimonies touching on the gross human right violations to which they are victims, in relation to their vulnerability as distinct populations compared to the mainstream-dominant communities (ACHPR and IWGIA, 2005). Indigenous peoples' requests as discerned in their statements to the commission have mainly centered on recognition, respect, and protection of their human rights on equal footing with other African communities. As stated in the report, indigenous peoples' requests to their nation states relate to "the right to survive as peoples, and to have a say in their own future, based on their own culture, identity, hopes, and visions." In order to advance and coordinate the discussions, the commission in 2001 formed a working group on the right of indigenous populations/communities. The "Resolution on the Rights of Indigenous Populations/Communities in Africa" passed during the commissions' 28th ordinary session, established the working group. In terms of its composition, the working group comprises members of the commission as well as expert representatives of indigenous communities as well as independent experts.

In line with the above mandate, the Working Group issued a report, which is considered as the Commission's "official conceptualization of, and framework for, the issue of human rights of indigenous populations." In addition, the report is generally regarded as "a highly important instrument for the advancement of indigenous populations' human rights situations." As envisaged during its adoption, the report has facilitated constructive dialogue between the Commission and member states and has served as a platform for the commission's activities on promotion and protection of human rights of indigenous populations.

23.4.3 Contents of the report of the Africa Commission's Working Group of Experts

The Working Group in consultation with human rights experts and communities formulated a groundbreaking report that the Commission adopted in November 2003. Formulation and adoption of the report soon became the Commission's landmark achievement in the area of indigenous peoples' rights in the continent.

Touching on the thorny issues of the definition of indigenous peoples the African Commission's report holds that reference to the term "indigenous peoples" in the African context "should put less emphasis on the early definitions focusing on aboriginality." Aboriginality in this context refers to "who was the first occupier of a given land or territory" (Laltaika, 2012).

In reaching this conclusion, the African Commission shed light on the fact that based on aboriginality or first-occupancy most African communities are indigenous to Africa. The report therefore warns about both the difficulty and the futility of engaging in aboriginality debates in Africa.

In the alternative, the report proposes engagement in "the more recent approaches" which include "self-definition as indigenous and distinctly different from other groups within a state." In line with the African Commission's proposal, which emphasizes the primacy of identification, Korir and Shepherd maintain that [self-identification] is both crucial in identifying and recognizing right-holders is emblematic of the general conceptualization of human rights norms:

> *Self-identification should neither detract from the validity of the term nor be seen as an empty mantra. One could argue that self-identification is in fact rooted in the autonomy of the self, the liberal personhood upon which human rights are vested. In fact we should hold the view that self-identification, as opposed to narrower, inaccurate definition, provides flexibility in its application to the highly varied contexts within which indigenous groups exist globally (Sing'Oei and Shepherd, 2010: ACHPR and IWGIA, 2005).*

Other defining characteristics proposed by the Commission for identifying indigenous peoples include "special attachment to and use of traditional land in a manner that the ancestral land and territory is considered to be fundamentally important for the communities' collective physical and cultural survival as peoples." Another feature is the continued subjection to discrimination, marginalization, subjugation, and exclusion based on [the fact that] these peoples have different cultures, ways of life or modes of production than the national hegemonic and dominant model" (ACHPR and IWGIA, 2005).

In view of the above, the report provides that the indigenous rubric as applied in the African context, is a concept for analyzing structural relationships of inequality that have persisted after liberation from colonial dominance" (ACHPR and IWGIA, 2005). Based on the defining characteristics proposed, juxtaposed with the real situations of indigenous peoples in the continent, it is therefore fair to hold that the indigenous rubric in Africa does not constitute new rights, but rather represents "a bold and creative attempt at interpreting traditional human rights norms through the lens of historically excluded and marginalized groups" (Sing'Oei and Shepherd, 2010). In short, the report summarizes the overall characteristics of the groups that self-identify as indigenous as being the following:

1. Their cultures and ways of life differ considerably from the dominant society and their cultures are under threat, in some cases to the extent of extinction.
2. The survival of their particular way of life depends on access and rights to their traditional land and the natural resources thereon.
3. They suffer from discrimination as they are being regarded as less developed and less advanced than other more dominant sectors of the community.

4. They often live in inaccessible regions, often geographically isolated and suffer from various forms of marginalization, both socially and politically.
5. They are subject to domination and exploitation within national political and economic structures that are commonly designed to reflect interests and activities of the national majority.

The next part of this chapter examines the Commission's articulation of the right through a communication filed by an indigenous community from the Republic of Kenya.

23.4.4 Judicial articulation of the presence of indigenous peoples in Africa

In addition to forming the Working Group of Experts and issuing the groundbreaking report discussed above, the Commission has recently issued a landmark decision emanating from the filing of a communication by the Endorois Community from Kenya. According to Dr. Jeremie Gilbert, the Commission's ruling "casts new light on the rights of indigenous peoples in Africa" (Gilbert, 2011). This is because the communication "provided the African Commission with an ideal case to elaborate and clarify the group rights provision of the charter" (Sing'Oei and Shepherd, 2010).

By way of background, the Endorois is a community native to Lake Bogoria area, within Kenya's rift valley Province, comprising approximately 400 families. The community is a subgroup of the larger Kalenjin speaking ethnic group that practice pastoralism as a predominant livelihood system. In 1974 and in the absence of consultation, the Government of Kenya converted the community's ancestral land into a wildlife reserve. The government promised to pay compensation but failed to honor the pledge. In contrast, it denied the community access to pasturelands while at the same time arbitrarily harassing and intimidating community leaders (Sing'Oei and Shepherd, 2010).

Dissatisfied, the community unsuccessfully channeled their grievances through various levels of the Kenyan judiciary. This prompted the community to file a communication before the African Commission Seeking a formal declaration that by evicting them from their ancestral land, the Kenyan government violated their rights that the African Charter protects. In addition, the community prayed for restitution of their ancestral land, insisting that their culture and religion depend on access to the land forming the subject of the claim. In line with a need for tenure security, the Endorois community prayed further that their land be demarcated and a collective title issued to the name of the community.

In addition, the community prayed for monetary compensation as recompense for the unlawful and forced evictions. The African Commission ruled on merits, upholding all the Endorois community's prayers for relief. More importantly, the commission made unprecedented advancements in the jurisprudence on indigenous peoples' rights in the continent. Among other things, the Commission recognized the nexus between access to land and natural resources and cultural rights. It further reiterated that the term "indigenous peoples" does not create a special class of citizens, but addresses "present-day injustices and inequalities" (see the Endorois decision, p. 149).

23.5 Implications of not recognizing indigenous peoples in relation to the establishment and management of Ramsar wetlands in Africa

Recognition of a community as indigenous peoples carries significant juridical weight under international law, requiring adoption of interpretive methodologies that enhance the cultural integrity of indigenous peoples and their ability and continued existence as distinct peoples (Ahren, 2009). Specifically, its implication call for compatibility to the promotion of indigenous peoples in question's "autonomy or self-government" over their "internal and local affairs"; (UNDRIP, Article 18) and appreciation of the centrality of the intrinsic connection or special relationship the community in question attaches to lands, territories, and resources as a prerequisite for the preservation of their culture (Ahren, 2009).

Similarly, recognition of a community's indigenous status under international law carries an obligation on the part of States to ensure that the indigenous peoples in question have a say in all decisions affecting them. For example, Article 18 of the UN Declaration on the Rights of Indigenous Peoples provides, "Indigenous peoples have the right to participate in decision-making in matters that would affect their rights through representatives chosen by themselves in accordance with their own procedures, as well as to maintain and develop their own indigenous decision-making institutions" (see UNDRIP, Article 18). This level of participatory engagement requirement elevates the threshold of the right to consultation more broadly defined, to meet the standards of FPIC [see UNDRIP Articles 32 (2), and 19; Inter-America Court on Human Rights, 2007]. While there is no universally agreed procedure for conducting FPIC, the principles of meaningful consultation more broadly require *good faith* especially due to the asymmetrical relationship between indigenous communities and States.

As indicated above, most African countries do not recognize indigenous peoples' rights within their borders. Compounding this, indigenous peoples are communities on the margin that cannot engage states using nonbiding documents. Accordingly, relaying on nonbinding documents, backed up by state-centric approach of the convention, puts indigenous peoples at a disadvantaged position. Significantly, the state-centric nature of the Ramsar Convention may encourage State that do not willingly recognize indigenous peoples to implement top-down designation and management of Wetlands of International Importance in total disregard of the principle of FPIC. This in turn is potentially detrimental to indigenous communities.

23.6 Conclusion and recommendations

This study posits that the Ramsar Convention came into force as an international legal instrument aimed at addressing an important challenge, namely destruction of Wetlands of International Importance. However, at the time the convention was concluded, international law was largely state-centric, giving primacy to state sovereignty. Consequently, the Ramsar Convention does not mention even in passing, the need for the involvement of local communities or indigenous peoples in the establishment and management of wetlands. Emerging norms of international law recognize the centrality of procedural environmental rights such as the right to public participation, access to justice and the right to information as being hallmarks of good governance.

Accordingly, whereas the original goal of the convention was to conserve wetlands as migratory species' habitats and that it is understandably not a human rights instrument, the Ramsar Convention cannot be detached from contemporary realities, notably recognition of indigenous peoples as a distinct subject of international law with the right to FPIC. Since the Convention promotes the principle of "wise-use," it is not an exclusionary instrument that is emphatic on fortress conservation. It is thus partly compatible to indigenous peoples' rights. What remains is to amend it by inserting in the text, a requirement for States to abide by the principle of FPIC before designation of lands belonging to indigenous peoples (who are stewards of ecosystems including Wetlands of International Importance), as Ramsar sites. This requirement once embedded in the text will shape state actions through binding commitments.

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Appendix I

List of amphibians from seasonally flooded habitats in Amazonia

List of amphibian taxa inhabiting seasonally flooded habitats in Amazonia, compiled from our historically collected data from the margins of Solimões and Negro rivers since 2001, and the results of some inventories at these habitats or that explicitly discriminate the habitats of occurrence of the recorded taxa (Hödl, 1977; Hoogmoed, 1993; Schiesari et al., 2003; Gordo, 2003; Neckel-Oliveira and Gordo, 2004; von May et al., 2010; Pantoja and Fraga, 2012; Bernarde et al., 2013; Waldez et al., 2013; Barros et al., 2014; Upton et al., 2014; Moraes et al., 2016; Ramalho et al., 2016; Böning et al., 2017). The occurrence variation (X = presence) is presented for all taxa according to the river type studied. For taxa recorded at the *várzea* (i.e., at the margins of white-water rivers), their occurrence variations are presented according to the distinct environments of this heterogeneous mosaic: macrophyte banks (MB); sand or mud banks (SB); low *várzea* (LV); high *várzea* (HV); *paleovárzea* (PV); open or anthropic habitats (OA). According with the frequency of the taxa in compiled studies (in percentage), we delimit the most commonly reported taxa (> 30%, 10%, and 5% for anurans, salamanders and caecilians, respectively) as members of a typical assemblage of the *várzea*, with distinct levels of association with this habitat (species groups; see main text); not applicable (NA).

Taxa	River type				*Várzea* environments						Frequency in compiled studies (%)	Species group (*Várzea* association)
	Clear-water	White-water	Black-water	Frequency in river types	MB	SB	LV	HV	PV	OA		
Class Amphibia												
Order Anura												
Family Allophrynidae												
Allophryne ruthveni (Gaige, 1926a)	X	—	—	1/3	NA	NA	NA	NA	NA	NA	NA	NA
Family Aromobatidae												
Allobates femoralis (Boulenger, 1884)	X	X	—	2/3	—	—	X	X	X	X	17	—
Allobates gasconi (Morales, 2002)	—	X	—	1/3	—	—	—	—	X	—	8	—
Allobates paleovarzensis (Lima, Caldwell, Biavati, Montanarin, 2010)	—	X	—	1/3	—	—	—	—	X	—	17	—
Allobates insperatus-juami	—	X	—	1/3	—	—	—	—	X	—	8	—
Allobates trilineatus complex	—	X	—	1/3	—	—	—	X	X	—	8	—

Allobates sp.	—	X	—	1/3	—	—	—	—	X	—	17	—
Family Bufonidae												
Amazophrynella sp.	—	X	—	1/3	—	—	—	X	X	—	8	—
Rhaebo guttatus (Schneider, 1799)	X	X	—	2/3	—	—	X	X	X	—	8	—
Rhinella dapsilis (Myers and Carvalho, 1945)	—	X	—	1/3	—	—	—	—	X	—	8	—
Rhinella castaneotica (Caldwell, 1991)	—	X	—	1/3	—	—	X	X	X	—	8	—
Rhinella magnussoni (Lima, Menin, de Araújo, 2007)	X	—	—	1/3	NA	NA	NA	NA	NA	NA	NA	NA
Rhinella marina (Linnaeus, 1758)	X	X	X	3/3	X	X	X	X	X	X	75	2
Rhinella gr. *margaritifera*	—	X	X	2/3	—	—	X	X	X	—	58	2
Rhinella gr. *granulosa*	X	X	X	3/3	—	X	X	—	—	X	8	—
Family Ceratophryidae												
Ceratophrys cornuta (Linnaeus, 1758)	—	X	—	1/3	—	—	—	X	X	—	25	—
Family Centrolenidae												
Hyalinobatrachium mondolfii (Señaris and Ayarzagüena, 2001)	—	X	—	1/3	—	—	—	X	X	—	8	—

(*Continued*)

(Continued)

Taxa	River type				*Várzea* environments						Frequency in compiled studies (%)	Species group (*Várzea* association)
	Clear-water	White-water	Black-water	Frequency in river types	MB	SB	LV	HV	PV	OA		
Family Craugastoridae												
Oreobates cruralis (Boulenger, 1902)	—	X	—	1/3	—	—	—	X	X	—	8	—
Oreobates quixensis (Jiménez de la Espada, 1872)	—	X	—	1/3	—	—	—	X	X	—	17	—
Noblella myrmecoides (Lynch, 1976)	—	X	—	1/3	—	—	—	X	X	—	8	—
Pristimantis altamazonicus (Barbour and Dunn, 1921)	—	X	—	1/3	—	—	—	X	X	—	8	—
Pristimantis buccinator (Rodríguez, 1994)	—	X	—	1/3	—	—	—	X	X	—	8	—
Pristimantis carvalhoi (Lutz *in* Lutz and Kloss, 1952)	—	X	—	1/3	—	—	—	X	X	—	8	—
Pristimantis conspicillatus (Günther, 1858)	—	X	—	1/3	—	—	X	X	X	—	8	—

Pristimantis divnae (Lehr and von May, 2009)	—	X	—	1/3	—	—	—	X	X	—	8	—
Pristimantis fenestratus complex	—	X	—	1/3	—	—	X	X	X	—	33	2
Pristimantis lacrimosus (Jiménez de la Espada, 1875)	—	X	—	1/3	—	—	X	X	X	—	8	—
Pristimantis ockendeni (Boulenger, 1912)	—	X	—	1/3	—	—	X	X	X	—	17	—
Pristimantis reichlei (Padial and De la Riva, 2009)	—	X	—	1/3	—	—	—	X	X	—	8	—
Pristimantis skydmainos (Flores and Rodríguez, 1997)	—	X	—	1/3	—	—	X	X	X	—	17	—
Pristimantis toftae (Duellman, 1978)	—	X	—	1/3	—	—	—	X	X	—	8	—
Pristimantis zimmermanae (Heyer and Hardy, 1991)	—	X	—	1/3	—	—	X	X	X	—	8	—
Family Dendrobatidae												
Ameerega hahneli (Boulenger, 1884 "1883")	X	X	—	2/3	—	—	X	X	X	—	42	2
Ameerega trivittata (Spix, 1824)	—	X	—	1/3	—	—	—	—	X	—	17	—
Ranitomeya variabilis (Zimmermann and Zimmermann, 1988)	—	X	—	1/3	—	—	—	—	X	—	8	—

(*Continued*)

(Continued)

Taxa	River type				*Várzea* environments						Frequency in compiled studies (%)	Species group (*Várzea* association)
	Clear-water	White-water	Black-water	Frequency in river types	MB	SB	LV	HV	PV	OA		
Family Hylidae												
Boana boans (Linnaeus, 1758)	X	X	X	3/3	X	X	X	—	—	—	58	4
Boana calcarata (Troschel, 1848)	X	X	X	3/3	X	—	X	X	X	—	42	4
Boana cinerascens (Spix, 1824)	X	X	—	2/3	—	—	X	X	X	—	58	2
Boana alfaroi-tetete complex	X	X	X	3/3	—	—	X	X	X	—	58	2
Boana geographica complex	X	X	X	3/3	X	—	X	X	X	—	50	2
Boana aff. *geographica*	—	X	—	1/3	X	—	X	X	X	—	8	—
Boana lanciformis (Cope, 1871)	—	X	—	1/3	X	—	X	—	—	X	83	4

Boana microderma (Pyburn, 1977)	—	X	—	1/3	—	—	—	X	X	—	8	—
Boana multifasciata (Günther, 1859)	—	X	—	1/3	X	—	—	—	—	—	8	—
Boana nympha (Faivovich, Moravec, Cisneros-Heredia, and Köhler 2006)	—	X	—	1/3	—	—	—	X	X	—	8	—
Boana punctata (Schneider, 1799)	—	X	X	2/3	X	—	X	—	—	—	92	3
Boana raniceps (Cope, 1862a)	X	X	—	2/3	X	X	X	—	—	—	67	3
Boana wavrini (Parker, 1936)	X	X	X	3/3	X	X	X	—	—	—	33	4
Dendropsophus acreanus (Bokermann, 1964a)	—	X	—	1/3	X	—	X	X	—	—	8	—
Dendropsophus parviceps complex	—	X	—	1/3	X	—	X	X	—	—	42	2
Dendropsophus bifurcus (Andersson, 1945)	—	X	—	1/3	X	—	—	—	—	—	8	—
Dendropsophus brevifrons (Duellman and Crump, 1974)	—	X	—	1/3	—	—	X	X	—	—	25	—
Dendropsophus frosti (Motta, Castroviejo-Fisher, Venegas, Orrico, and Padial, 2012)	—	X	—	1/3	—	—	X	X	X	—	8	—

(*Continued*)

(Continued)

Taxa	River type				*Várzea* environments						Frequency in compiled studies (%)	Species group (*Várzea* association)
	Clear-water	White-water	Black-water	Frequency in river types	MB	SB	LV	HV	PV	OA		
Dendropsophus haraldschultzi (Bokermann, 1962a)	—	X	—	1/3	X	—	X	X	X	—	50	4
Dendropsophus joannae (Köhler and Lötters, 2001)	—	X	—	1/3	—	—	X	X	X	—	8	—
Dendropsophus koechlini (Duellman and Trueb, 1989)	—	X	—	1/3	—	—	X	X	X	—	33	2
Dendropsophus leali (Bokermann, 1964b)	—	X	—	1/3	X	—	X	—	—	—	33	3
Dendropsophus minusculus (Rivero, 1971)	X	X	X	3/3	X	X	X	X	X	X	8	—
Dendropsophus leucophyllatus (Beireis, 1783)	X	X	X	3/3	X	—	X	—	—	—	75	4
Dendropsophus marmoratus (Laurenti, 1768)	X	—	—	1/3	NA	NA	NA	NA	NA	NA	NA	NA

Dendropsophus minutus (Peters, 1872)	—	X	—	1/3	—	—	X	X	X	X	25	—
Dendropsophus miyatai (Vigle and Goberdhan-Vigle, 1990)	—	X	—	1/3	—	—	—	X	X	—	8	—
Dendropsophus reticulatus (Jiménez de la Espada, 1870)	—	X	—	1/3	X	—	X	X	—	—	8	—
Dendropsophus rhodopeplus (Günther, 1858)	—	X	—	1/3	—	—	—	X	X	—	17	—
Dendropsophus riveroi (Cochran and Goin, 1970)	—	X	—	1/3	X	—	X	—	—	—	17	—
Dendropsophus rossaleni (Goin, 1959)	—	X	—	1/3	X	—	X	X	X	—	67	4
Dendropsophus sarayacuensis (Shreve, 1935)	—	X	—	1/3	—	—	X	X	X	—	8	—
Dendropsophus schubarti (Bokermann, 1963)	X	X	—	2/3	—	—	X	X	X	—	17	—
Dendropsophus timbeba (Martins and Cardoso, 1987)	—	X	—	1/3	—	—	X	X	X	—	17	—
Dendropsophus triangulum (Günther, 1869)	X	X	—	2/3	X	—	X	X	—	—	50	4

(*Continued*)

(Continued)

Taxa	River type				*Várzea* environments						Frequency in compiled studies (%)	Species group (*Várzea* association)
	Clear-water	White-water	Black-water	Frequency in river types	MB	SB	LV	HV	PV	OA		
Dendropsophus walfordi (Bokermann, 1962b)	X	X	X	3/3	X	—	X	—	—	—	50	3
Dryaderces pearsoni (Gaige, 1929)	—	X	—	1/3	X	—	—	—	—	—	17	—
Lysapsus bolivianus (Gallardo, 1961)	X	X	—	2/3	X	—	X	—	—	—	58	3
Osteocephalus castaneicola (Moravec, Aparicio, Guerrero-Reinhard, Calderón, Jungfer, and Gvoždík, 2009)	—	X	—	1/3	—	—	—	X	X	—	17	—
Osteocephalus helenae (Ruthven, 1919)	—	X	—	1/3	—	—	X	X	X	—	25	—
Osteocephalus heyeri (Lynch, 2002)	—	X	—	1/3	—	—	—	—	X	—	8	—
Osteocephalus leprieurii (Duméril and Bibron, 1841)	X	X	—	2/3	—	—	X	X	X	—	25	—

Osteocephalus taurinus (Steindachner, 1862)	X	X	—	2/3	—	—	X	X	X	—	67	2
Osteocephalus vilarsi (Melin, 1941)	—	X	X	2/3	—	—	—	—	—	—	8	—
Scarthyla goinorum (Bokermann, 1962a)	—	X	—	1/3	X	—	X	X	—	—	67	4
Scinax boesemani (Goin, 1966)	X	X	—	2/3	X	—	X	—	—	X	50	4
Scinax cruentommus complex	X	X	—	2/3	X	—	X	X	—	—	33	2
Scinax funereus (Cope, 1874)	—	X	—	1/3	—	—	X	X	—	—	17	—
Scinax garbei (Miranda-Ribeiro, 1926)	X	X	X	3/3	X	—	X	X	X	—	75	2
Scinax ictericus (Duellman and Wiens, 1993)	—	X	—	1/3	—	—	—	X	X	—	8	—
Scinax iquitorum (Moravec, Tuanama, Pérez-Peña, and Lehr, 2009)	—	X	—	1/3	X	—	X	—	—	—	8	—
Scinax nebulosus (Spix, 1824)	X	X	X	3/3	X	—	X	—	—	—	42	4
Scinax pedromedinae (Henle, 1991)	—	X	—	1/3	X	—	X	X	—	—	42	4
Scinax ruber complex	X	X	X	3/3	X	X	X	X	X	X	75	1
Sphaenorhynchus carneus (Cope, 1868)	—	X	—	1/3	X	—	X	X	—	—	67	4

(*Continued*)

(Continued)

Taxa	River type				*Várzea* environments						Frequency in compiled studies (%)	Species group (*Várzea* association)
	Clear-water	White-water	Black-water	Frequency in river types	MB	SB	LV	HV	PV	OA		
Sphaenorhynchus dorisae (Goin, 1957)	—	X	—	1/3	X	—	X	X	—	—	58	4
Sphaenorhynchus lacteus (Daudin, 1800)	—	X	—	1/3	X	—	X	X	—	—	75	4
Trachycephalus coriaceus (Peters, 1867)	—	X	—	1/3	—	—	—	X	X	—	8	—
Trachycephalus cunauaru (Gordo, Toledo, Suárez, Kawashita-Ribeiro, Ávila, Morais, and Nunes, 2013)	X	X	—	2/3	—	—	X	X	X	—	25	—
Trachycephalus typhonius (Linnaeus, 1758)	X	X	—	2/3	X	—	X	X	X	X	50	1
Family Leptodactylidae												
Adenomera andreae (Müller, 1923)	X	X	X	3/3	—	—	X	X	X	—	42	2

Adenomera hylaedactyla (Cope, 1868)	—	X	—	1/3	X	—	X	—	—	—	50	1
Edalorhina perezi (Jiménez de la Espada, 1871 "1870")	—	X	—	1/3	—	—	—	X	X	—	8	—
Engystomops freibergi (Donoso-Barros, 1969)	—	X	—	1/3	—	—	—	X	X	—	8	—
Hydrolaetare schmidti (Cochran and Goin, 1959)	—	X	—	1/3	—	—	X	X	—	—	17	—
Leptodactylus bolivianus (Boulenger, 1898)	—	X	—	1/3	X	—	X	X	—	—	25	—
Leptodactylus discodactylus (Boulenger, 1884 "1883")	—	X	—	1/3	X	—	—	X	X	—	8	—
Leptodactylus didymus (Heyer, García-Lopez, Cardoso, 1996)	—	X	—	1/3	—	—	—	X	X	—	8	—
Leptodactylus leptodactyloides (Andersson, 1945)	—	X	X	2/3	X	X	X	—	—	—	42	4
Leptodactylus fuscus (Schneider, 1799)	X	X	—	2/3	—	X	—	—	—	X	8	—
Leptodacylus knudseni (Heyer, 1972)	X	X	—	2/3	—	—	X	X	X	—	33	2

(*Continued*)

(Continued)

Taxa	River type				*Várzea* environments						Frequency in compiled studies (%)	Species group (*Várzea* association)
	Clear-water	White-water	Black-water	Frequency in river types	MB	SB	LV	HV	PV	OA		
Leptodactylus macrosternum (Miranda-Ribeiro, 1926)	X	X	—	2/3	X	X	X	—	—	X	33	3
Leptodactylus mystaceus (Spix, 1824)	X	X	—	2/3	—	—	X	X	X	—	8	—
Leptodactylus pentadactylus (Laurenti, 1768)	X	X	X	3/3	—	—	X	X	X	—	50	2
Leptodactylus petersii (Steindachner, 1864)	X	X	X	3/3	X	—	X	X	X	—	75	2
Leptodactylus podicipinus (Cope, 1862b)	—	X	—	1/3	X	X	—	—	—	X	17	—
Leptodactylus riveroi (Heyer and Pyburn, 1983)	—	—	X	1/3	NA	NA	NA	NA	NA	NA	NA	NA
Leptodactylus rhodomystax (Boulenger, 1884 "1883")	—	X	—	1/3	—	—	—	X	X	—	25	—

Leptodactylus rhodonotus (Günther, 1869 “1868”)	—	X	—	1/3	—	—	—	X	X	—	8	—
Leptodactylus stenodema (Jiménez de la Espada, 1875)	—	X	—	1/3	—	—	X	X	—	—	8	—
Leptodactylus wagneri (Peters, 1862)	—	X	—	2/3	X	—	—	—	—	—	25	—
Lithodytes lineatus (Schneider, 1799)	—	X	—	1/3	—	—	X	X	X	—	8	—
Family Microhylidae												
Chiasmocleis antenori (Walker, 1973)	—	X	—	1/3	—	—	—	X	X	—	8	—
Chiasmocleis bassleri (Dunn, 1949)	—	X	—	1/3	—	—	X	X	X	—	25	—
Chiasmocleis hudsoni (Parker, 1940)	X	—	—	1/3	NA	NA	NA	NA	NA	NA	NA	NA
Chiasmocleis royi (Peloso, Sturaro, Forlani, Gaucher, Motta, and Wheeler, 2014)	—	X	—	1/3	—	—	X	X	X	—	17	—
Ctenophryne geayi (Mocquard, 1904)	—	X	—	1/3	—	—	—	X	X	—	8	—
Elachistocleis muiraquitan (Nunes-de-Almeida and Toledo, 2012)	—	X	—	1/3	—	—	X	X	X	X	25	—

(*Continued*)

(Continued)

Taxa	River type				*Várzea* environments						Frequency in compiled studies (%)	Species group (*Várzea* association)
	Clear-water	White-water	Black-water	Frequency in river types	MB	SB	LV	HV	PV	OA		
Elachistocleis heliannae (Caramaschi, 2010)	—	X	—	1/3	—	—	X	X	X	X	17	—
Hamptophryne boliviana (Parker, 1927)	—	X	—	1/3	—	—	X	X	X	—	42	2
Synapturanus sp.	—	X	—	1/3	—	—	—	X	X	—	17	—
Family Phyllomedusidae												
Phyllomedusa bicolor (Boddaert, 1772)	—	X	—	1/3	—	—	X	X	X	—	25	—
Phyllomedusa vaillanti (Boulenger, 1882)	—	X	—	1/3	—	—	—	X	X	—	8	—
Pithecopus palliatus (Peters, 1873)	—	X	—	1/3	—	—	—	—	X	—	17	—
Callimedusa tomopterna (Cope, 1868)	—	X	—	1/3	—	—	X	X	X	—	25	—

Family Pipidae												
Pipa pipa (Linnaeus, 1758)	X	X	X	3/3	X	—	X	—	—	—	25	5
Pipa snethlageae (Müller, 1914)	—	X	—	1/3	X	—	X	—	—	—	8	5
Family Ranidae												
Lithobates palmipes (Spix, 1824)	X	X	—	2/3	X	X	X	—	—	—	8	5
Order Caudata												
Family Plethodontidae												
Bolitoglossa altamazonica (Cope, 1874)	—	X	—	1/3	—	—	—	X	X	—	8	—
Bolitoglossa caldwellae (Brcko, Hoogmoed, and Neckel-Oliveira, 2013)	—	X	—	1/3	—	—	X	X	—	—	8	—
Bolitoglossa sp.	—	X	—	1/3	—	—	—	—	X	—	8	—
Order Gymnophiona												
Family Typhlonectidae												
Typhlonectes compressicauda (Duméril and Bibron, 1841)	—	X	X	2/3	X	—	—	—	—	—	17	5

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Appendix II

List of squamates from seasonally flooded habitats in Amazonia

List of squamate taxa inhabiting seasonally flooded habitats in Amazonia, compiled from our historically collected data from the margins of Solimões and Negro rivers since 2001, and the results of some inventories at these habitats or that explicitly discriminate the habitats of occurrence of the recorded taxa (Hoogmoed, 1993; Neckel-Oliveira and Gordo, 2004; Pantoja and Fraga, 2012; Bernarde et al., 2013; Waldez et al., 2013; Moraes et al., 2016; Debien et al., 2019). The occurrence variation (X = presence) is presented for all taxa according to the river type studied. For taxa recorded at the *várzea* (i.e., at the margins of white-water rivers), their occurrence variations are presented according to the distinct environments of this heterogeneous mosaic: macrophyte banks (MB); sand or mud banks (SB); low *várzea* (LV); high *várzea* (HV); *paleovárzea* (PV); open or anthropic habitats (OA). According with the frequency of the taxa in compiled studies (in percentage), we delimit the most commonly reported taxa (>20% and 10% lizards and snakes, respectively) as members of a typical assemblage of the *várzea*, with distinct levels of association with this habitat (species groups; see main text); not applicable (NA).

Taxa	River type				*Várzea* environments						Frequency in compiled studies (%)	Species group (*Várzea* association)
	Clear-water	White-water	Black-water	Frequency in river types	MB	SB	LV	HV	PV	OA		
Class Reptilia												
Order Squamata												
Suborder "Lacertilia"												
Family Alopoglossidae												
Alopoglossus angulatus (Linnaeus, 1758)	—	X	—	1/3	—	—	—	X	X	—	17	—
Ptychoglossus brevifrontalis (Boulenger, 1912)	—	X	—	1/3	—	—	—	X	X	—	17	—
Family Dactyloidae												
Anolis auratus (Daudin, 1802)	—	—	X	1/3	NA	NA	NA	NA	NA	NA	NA	NA
Anolis fuscoauratus (d'Orbigny *in* Duméril and Bibron, 1837)	—	X	X	2/3	—	—	X	X	X	—	67	1

Anolis ortonii (Cope, 1868)	X	X	X	3/3	—	—	X	X	X	X	50	1
Anolis punctatus (Daudin, 1802)	X	X	—	2/3	—	—	—	X	X	—	17	—
Anolis tandai (Ávila-Pires, 1995)	—	X	—	1/3	—	—	X	X	X	—	17	—
Anolis trachyderma (Cope, 1875)	—	X	—	1/3	—	—	X	X	X	—	33	2
Anolis transversalis (Duméril *in* Duméril and Duméril, 1851)	—	X	—	1/3	—	—	—	X	X	—	17	—
Family Gymnophthalmidae												
Arthrosaura reticulata (O'shaughnessy, 1881)	—	X	—	1/3	—	—	—	X	X	—	33	2
Bachia flavescens (Bonnaterre, 1789)	—	X	—	1/3	—	—	X	X	X	—	17	—
Bachia peruana (Werner, 1901)	—	X	—	1/3	—	—	X	X	X	—	17	—
Cercosaura argulus (Peters, 1862)	—	X	—	1/3	—	—	X	X	X	—	17	—
Cercosaura bassleri (Ruibal, 1952)	—	X	—	1/3	—	—	X	X	X	—	17	—
Cercosaura ocellata (Wagler, 1830)	X	—	—	1/3	NA	NA	NA	NA	NA	NA	NA	NA

(*Continued*)

(Continued)

Taxa	River type				*Várzea* environments						Frequency in compiled studies (%)	Species group (*Várzea* association)
	Clear-water	White-water	Black-water	Frequency in river types	MB	SB	LV	HV	PV	OA		
Iphisa elegans (Gray, 1851)	—	X	—	1/3	—	—	—	X	X	—	17	—
Loxopholis percarinatum (Müller, 1923)	—	X	—	1/3	—	—	X	X	X	—	17	—
Loxopholis snethlageae (Ávila-Pires, 1995)	—	X	—	1/3	—	—	X	X	X	—	17	—
Family Iguanidae												
Iguana iguana (Linnaeus, 1758)	X	X	X	3/3	—	X	X	X	X	X	50	1
Family Polychrotidae												
Polychrus marmoratus (Linnaeus, 1758)	—	—	X	1/3	NA	NA	NA	NA	NA	NA	NA	NA

Family Phyllodactylidae												
Thecadactylus rapicauda (Houttuyn, 1782)	—	X	X	2/3	—	—	—	X	X	—	17	—
Thecadactylus solimoensis (Bergmann and Russel, 2007)	—	X	—	1/3	—	—	—	X	X	—	17	—
Family Scincidae												
Copeoglossum nigropunctatum (Spix, 1825)	X	X	X	3/3	—	—	—	X	X	—	33	1
Varzea altamazonica-bistriata	X	X	X	3/3	—	—	X	X	—	—	33	4
Family Sphaerodactylidae												
Chatogekko amazonicus (Andersson, 1918)	—	X	X	2/3	—	—	X	X	X	—	17	—
Gonatodes humeralis (Guichenot, 1855)	X	X	X	3/3	—	—	X	X	X	—	83	2
Lepidoblepharis heyerorum (Vanzolini, 1978)	—	X	—	1/3	—	—	X	X	X	—	17	—

(*Continued*)

(Continued)

Taxa	River type				*Várzea* environments						Frequency in compiled studies (%)	Species group (*Várzea* association)
	Clear-water	White-water	Black-water	Frequency in river types	MB	SB	LV	HV	PV	OA		
Family Teiidae												
Ameiva ameiva (Linnaeus, 1758)	X	X	X	3/3	—	X	X	X	X	X	67	1
Cnemidophorus cryptus (Cole and Dessauer, 1993)	X	X	X	3/3	—	X	—	—	—	X	17	—
Crocodilurus amazonicus (Spix, 1825)	—	X	X	2/3	X	X	X	—	—	—	50	4
Dracaena guianensis (Daudin, 1801)	—	X	—	1/3	X	X	X	—	—	—	50	4
Kentropyx altamazonica (Cope, 1875)	—	X	X	2/3	X	X	X	X	X	—	67	4
Kentropyx calcarata (Spix, 1875)	X	—	—	1/3	NA	NA	NA	NA	NA	NA	NA	NA

Kentropyx pelviceps (Cope, 1868)	—	X	—	1/3	—	—	X	X	X	—	67	2
Kentropyx striata (Daudin, 1802)	—	—	X	1/3	NA	NA	NA	NA	NA	NA	NA	NA
Tupinambis teguixin (Linnaeus, 1758)	X	X	X	3/3	—	X	X	X	X	—	67	4
Family Tropiduridae												
Plica umbra (Linnaeus, 1758)	—	X	X	2/3	—	—	X	X	X	—	67	2
Plica plica (Linnaeus, 1758)	X	—	—	1/3	NA	NA	NA	NA	NA	NA	NA	NA
Uracentron azureum (Linnaeus, 1758)	—	—	X	1/3	NA	NA	NA	NA	NA	NA	NA	NA
Uranoscodon superciliosus (Linnaeus, 1758)	X	X	X	3/3	—	—	X	X	X	—	50	2
Suborder Serpentes												
Family Aniliidae												
Anilius scytale (Linnaeus, 1758)	—	X	—	1/3	—	—	X	X	X	—	33	1
Family Boidae												
Boa constrictor (Linnaeus, 1758)	X	X	—	2/3	—	—	X	X	X	—	17	—

(*Continued*)

(Continued)

Taxa	River type				*Várzea* environments						Frequency in compiled studies (%)	Species group (*Várzea* association)
	Clear-water	White-water	Black-water	Frequency in river types	MB	SB	LV	HV	PV	OA		
Corallus batesii (Gray, 1860)	X	—	—	1/3	NA	NA	NA	NA	NA	NA	NA	NA
Corallus caninus (Linnaeus, 1758)	—	—	X	1/3	NA	NA	NA	NA	NA	NA	NA	NA
Corallus hortulana (Linnaeus, 1758)	X	X	X	3/3	—	X	X	X	X	—	50	1
Eunectes murinus (Linnaeus, 1758)	X	X	X	3/3	X	X	—	—	—	—	50	1
Epicrates cenchria (Linnaeus, 1758)	—	X	—	1/3	—	—	—	X	X	—	17	—
Family Colubridae												
Chironius fuscus (Linnaeus, 1758)	X	X	—	2/3	—	X	X	X	X	X	33	1
Chironius laurenti (Dixon et al., 1993)	—	X	—	1/3	—	X	X	X	X	X	17	—

Chironius multiventris (Schmidt and Walker, 1943)	—	X	—	1/3	—	—	X	X	X	—	17	—
Chironius scurrulus (Wagler *in* Spix, 1824)	X	X	—	2/3	—	X	X	X	X	—	17	—
Dendrophidion dendrophis (Schlegel, 1837)	—	X	—	1/3	—	—	X	X	—	—	17	—
Drymoluber dichrous (Peters, 1863)	—	X	—	1/3	—	—	X	X	—	—	17	—
Leptophis ahaetulla (Linnaeus, 1758)	—	X	—	1/3	—	—	X	X	X	X	17	—
Mastigodryas boddaerti (Sentzen, 1796)	—	X	—	1/3	—	X	X	X	X	X	17	—
Oxybelis aeneus (Wagler *in* Spix, 1824)	—	X	—	1/3	—	X	X	—	—	X	17	—
Oxybelis fulgidus (Daudin, 1803a)	X	X	—	2/3	—	X	X	—	—	X	17	—
Spilotes pullatus (Linnaeus, 1758)	—	X	X	2/3	—	—	X	X	X	X	33	1
Tantilla melanocephala (Linnaeus, 1758)	—	X	—	1/3	—	—	X	X	X	—	17	—
Family Dipsadidae												
Dipsas catesbyi (Sentzen, 1796)	X	X	—	2/3	—	—	X	X	X	—	83	2

(*Continued*)

(Continued)

Taxa	River type				*Várzea* environments						Frequency in compiled studies (%)	Species group (*Várzea* association)
	Clear-water	White-water	Black-water	Frequency in river types	MB	SB	LV	HV	PV	OA		
Dipsas indica (Laurenti, 1768)	—	X	—	1/3	—	—	X	X	X	—	33	1
Dipsas pavonina (Schlegel, 1837)	—	X	—	1/3	—	—	X	X	X	—	17	—
Drepanoides anomalus (Jan, 1863)	—	X	—	1/3	—	—	X	X	X	—	33	2
Erythrolamprus breviceps (Cope, 1860)	—	X	—	1/3	—	—	X	X	X	—	17	—
Erythrolamprus dorsocorallinus (Esqueda et al., 2007)	—	X	—	1/3	—	—	X	X	X	—	17	—
Erythrolamprus reginae (Linnaeus, 1758)	X	X	—	2/3	—	—	X	X	X	X	33	1
Erythrolamprus typhlus (Linnaeus, 1758)	X	X	—	2/3	—	—	X	X	X	—	17	—

Helicops angulatus (Linnaeus, 1758)	X	X	X	3/3	X	—	X	X	X	—	67	1
Helicops hagmanni (Roux, 1910)	—	—	X	1/3	NA	NA	NA	NA	NA	NA	NA	NA
Helicops leopardinus (Schlegel, 1837)	—	X	—	1/3	X	—	—	—	—	—	17	—
Helicops polylepis (Günther, 1861)	X	X	X	3/3	X	—	X	X	X	—	33	2
Hydrodynastes bicinctus (Herrmann, 1804)	X	X	—	2/3	X	X	—	—	—	X	17	5
Hydrodynastes gigas (Duméril et al., 1851)	—	X	X	2/3	X	X	—	—	—	X	17	5
Hydrops martii (Wagler *in* Spix, 1824)	X	—	X	2/3	NA	NA	NA	NA	NA	NA	NA	NA
Hydrops triangularis (Wagler *in* Spix, 1824)	X	—	X	2/3	NA	NA	NA	NA	NA	NA	NA	NA
Imantodes cenchoa (Linnaeus, 1758)	—	X	—	1/3	—	—	—	X	X	—	83	1
Leptodeira annulata (Linnaeus, 1758)	X	X	—	2/3	—	—	—	X	X	—	17	—
Oxyrhopus melanogenys (Tschudi, 1845)	—	X	—	1/3	—	—	—	X	X	—	17	—

(*Continued*)

(Continued)

Taxa	River type				*Várzea* environments						Frequency in compiled studies (%)	Species group (*Várzea* association)
	Clear-water	White-water	Black-water	Frequency in river types	MB	SB	LV	HV	PV	OA		
Oxyrhopus petolarius (Linnaeus, 1758)	—	X	—	1/3	—	—	—	X	X	—	33	1
Philodryas argentea (Daudin, 1803b)	—	X	—	1/3	—	—	—	X	X	—	33	2
Philodryas viridissima (Linnaeus, 1758)	—	—	X	1/3	NA	NA	NA	NA	NA	NA	NA	NA
Pseudoboa coronata (Schneider, 1801)	—	X	—	1/3	—	—	X	X	X	—	17	—
Pseudoboa neuwiedii (Duméril et al., 1854)	X	—	—	1/3	NA	NA	NA	NA	NA	NA	NA	NA
Pseudoeryx plicatilis (Linnaeus, 1758)	—	X	—	1/3	X	—	X	X	X	—	17	5
Sibon nebulatus (Linnaeus, 1758)	X	—	—	1/3	NA	NA	NA	NA	NA	NA	NA	NA
Siphlophis cervinus (Laurenti, 1768)	X	X	—	2/3	—	—	X	X	X	—	17	—

Siphlophis compressus (Daudin, 1803b)	—	X	—	1/3	—	—	X	X	X	—	33	1
Thamnodynastes pallidus (Linnaeus, 1758)	—	X	—	1/3	—	—	X	X	X	—	50	1
Xenopholis scalaris (Wucherer, 1862)	—	X	—	1/3	—	—	—	X	X	—	17	—
Family Elapidae												
Micrurus filiformis (Günther, 1859)	—	X	—	1/3	—	—	—	X	X	—	17	—
Micrurus lemniscatus (Linnaeus, 1758)	—	X	—	1/3	—	—	—	X	X	—	33	1
Micrurus spixii (Wagler *in* Spix, 1824)	—	X	—	1/3	—	—	X	X	X	—	17	—
Micrurus surinamensis (Cuvier, 1816)	X	X	—	2/3	—	—	X	X	X	—	17	—
Family Viperidae												
Bothrops atrox (Linnaeus, 1758)	X	X	X	3/3	—	X	X	X	X	X	83	2
Bothrops bilineatus (Wied-Neuwied, 1821)	—	X	—	1/3	—	—	—	X	X	—	17	—

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Appendix III

List of amphibians from the margins of the Solimões River

List of amphibian taxa recorded in 12 sampling units along the margins of the Solimões River (X = presence), and their respective frequencies of occurrence. Primary data collected in rapid surveys at 39 localities from 2001 to 2018. See the text of the book chapter for clarification on geographic location of the sampling units, localities, and summarized diversity indexes.

Taxa	Sampling units												Frequency (number of sampling units)
	1	2	3	4	5	6	7	8	9	10	11	12	
Family Aromobatidae													
Allobates sp.	—	—	—	—	—	X	—	—	—	X	—	—	**2**
Family Bufonidae													
Rhinella marina (Linnaeus, 1758)	—	—	—	—	X	X	X	X	X	X	X	X	**8**
Rhinella gr. *margaritifera*	—	—	—	—	X	X	X	X	X	X	X	—	**7**
Rhinella gr. *granulosa*	—	—	—	—	—	—	X	—	—	—	—	—	**1**
Family Craugastoridae													
Pristimantis fenestratus complex	—	—	—	—	X	—	—	—	—	—	—	—	**1**
Family Dendrobatidae													
Ameerega hahneli (Boulenger, 1884 “1883”)	—	—	—	—	—	—	X	—	X	—	X	X	**4**
Family Hylidae													
Boana alfaroi-tetete complex	—	—	—	—	X	X	X	X	X	X	X	X	**8**
Boana boans (Linnaeus, 1758)	—	—	X	—	X	—	X	—	X	X	X	X	**7**

Boana calcarata (Troschel, 1848)	—	—	—	—	X	X	—	—	—	—	—	—	**2**
Boana cinerascens (Spix, 1824)	—	—	X	—	—	X	—	—	—	—	X	—	**3**
Boana geographica complex	—	—	—	—	X	X	X	—	X	—	—	—	**4**
Boana lanciformis (Cope, 1871)	—	X	—	—	X	X	X	—	X	X	X	X	**8**
Boana punctata (Schneider, 1799)	X	X	X	X	X	X	X	—	X	X	X	X	**11**
Boana raniceps (Cope, 1862)	X	X	X	X	X	X	X	X	X	X	X	X	**12**
Dendropsophus haraldschultzi (Bokermann, 1962a)	—	—	X	—	—	X	—	X	X	X	X	—	**6**
Dendropsophus joannae (Köhler and Lötters, 2001)	—	—	—	—	—	—	—	—	—	X	—	—	**1**
Dendropsophus koechlini (Duellman and Trueb, 1989)	—	—	—	—	—	—	—	—	—	X	—	—	**1**
Dendropsophus miyatai (Vigle and Goberdhan-Vigle, 1990)	—	—	—	—	—	—	—	—	X	—	—	—	**1**
Dendropsophus riveroi (Cochran and Goin, 1970)	X	X	X	X	—	—	—	—	—	—	—	—	**4**
Dendropsophus rossaleni (Goin, 1959)	—	X	X	—	—	X	—	X	X	X	X	X	**8**

(*Continued*)

(Continued)

Taxa	Sampling units												Frequency (number of sampling units)
	1	2	3	4	5	6	7	8	9	10	11	12	
Dendropsophus walfordi (Bokermann, 1962b)	—	—	—	—	—	X	X	X	X	X	X	X	**7**
Dendropsophus gr. *leucophyllatus*	X	X	X	X	X	X	X	—	X	X	X	X	**11**
Dendropsophus cf. *minusculus*	—	—	—	—	—	—	—	X	X	—	X	X	**4**
Dendropsophus sp.	—	—	—	—	—	—	—	—	X	—	X	—	**2**
Lysapsus bolivianus (Gallardo, 1961)	—	X	X	X	—	X	X	—	X	X	X	X	**9**
Osteocephalus helenae (Ruthven, 1919)	—	—	—	—	X	—	—	—	—	—	—	—	**1**
Osteocephalus leprieurii (Duméril and Bibron, 1841)	—	—	—	—	X	X	X	—	X	—	—	—	**4**
Osteocephalus taurinus (Steindachner, 1862)	—	—	—	—	X	X	X	—	X	X	X	X	**7**
Osteocephalus vilarsi (Melin, 1941)	—	—	—	—	—	—	—	—	X	—	X	—	**2**
Scarthyla goinorum (Bokermann, 1962a)	—	—	—	—	X	X	—	X	X	—	X	X	**6**

Scinax boesemani (Goin, 1966)	—	—	—	—	—	—	—	—	—	—	X	—	**1**
Scinax garbei (Miranda-Ribeiro, 1926)	—	X	X	X	X	—	—	—	X	—	—	—	**5**
Scinax cruentommus complex	X	—	—	—	—	—	—	—	—	X	—	—	**2**
Scinax nebulosus (Spix, 1824)	—	—	—	—	—	—	—	—	X	X	X	X	**4**
Scinax pedromedinae (Henle, 1991)	—	—	X	X	—	X	—	—	—	—	X	—	**4**
Scinax ruber complex	—	—	—	—	X	X	X	—	X	X	X	X	**7**
Sphaenorhynchus carneus (Cope, 1868)	—	X	X	—	—	—	X	—	X	—	X	X	**6**
Sphaenorhynchus dorisae (Goin, 1957)	X	X	X	X	X	X	—	X	X	X	X	—	**10**
Sphaenorhynchus lacteus (Daudin, 1800)	X	X	X	X	—	X	X	X	X	X	X	X	**11**
Trachycephalus cunauaru (Gordo et al., 2013)	—	—	—	—	—	—	—	—	X	—	—	—	**1**
Trachycephalus typhonius (Linnaeus, 1758)	—	—	—	—	X	X	X	—	X	X	X	X	**7**
Family Leptodactylidae													
Adenomera andreae (Müller, 1923)	—	—	—	—	—	X	X	—	X	X	X	X	**6**

(*Continued*)

(Continued)

Taxa	Sampling units												Frequency (number of sampling units)
	1	2	3	4	5	6	7	8	9	10	11	12	
Adenomera hylaedactyla (Cope, 1868)	—	—	—	—	X	—	—	—	X	—	—	—	**2**
Hydrolaetare schmidti (Cochran and Goin, 1959)	—	—	—	—	—	X	—	—	X	X	X	—	**4**
Leptodactylus fuscus (Schneider, 1799)	—	—	—	—	—	—	—	—	X	—	—	—	**1**
Leptodactylus macrosternum (Miranda-Ribeiro, 1926)	—	—	—	—	—	X	X	—	X	X	X	X	**6**
Leptodactylus pentadactylus (Laurenti, 1768)	—	—	—	—	X	X	—	—	X	X	—	—	**4**
Leptodactylus gr. *melanonotus*	X	X	—	—	X	X	X	X	X	X	X	X	**10**
Family Microhylidae													
Elachistocleis heliannae (Caramaschi, 2010)	—	—	—	—	—	—	—	—	—	—	—	X	**1**
Hamptophryne boliviana (Parker, 1927)	—	—	—	—	—	—	—	—	X	—	—	—	**1**

Family Phyllomedusidae													
Callimedusa tomopterna (Cope, 1868)	—	—	—	—	—	—	—	—	X	X	—	—	**2**
Family Pipidae													
Pipa snethlageae (Müller, 1914)	—	—	—	—	—	—	—	—	—	—	—	X	**1**
Raw richness	**8**	**12**	**14**	**9**	**22**	**27**	**22**	**12**	**38**	**27**	**31**	**24**	
Sampling localities	**1**	**3**	**2**	**1**	**2**	**4**	**3**	**1**	**8**	**5**	**6**	**3**	
Mean richness 1	**8**	**8.33**	**11**	**9**	**11**	**12.25**	**13**	**12**	**15.75**	**12.40**	**14.33**	**16.67**	
Mean richness 2	**3.25**		**4.67**		**7.33**	**7**	**9**		**4.75**	**5.60**	**5.17**	**8**	

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Appendix IV

Waterbird species that have been recorded on pans in southern Africa, alongside their population status (obtained from the IUCN)

Family	Species name	Global population status	Migration type	Breeding season	HNP WS trend	HNP DS trend
Accipitridae	African Fish Eagle *Haliaeetus vocifer*	Stab	Resident	Apr–Aug	-	-
	African Marsh Harrier *Circus ranivorus*	Dec	Resident	Dec–Aug	-	-
	European Marsh Harrier *Circus aeruginosus*	Inc	Palearctic	-	-	-
Acrocephalidae	Basra Reed Warbler *Acrocephalus griseldis*	Stab	Palearctic	-	-	-
	European Reed Warbler *Acrocephalus scirpaceus*	Stab	Palearctic	-	-	-
	Greater Swamp Warbler *Acrocephalus rufescens*	Stab	Resident	Apr–Oct	-	-
	Lesser Swamp Warbler *Acrocephalus gracilirostris*	Stab	Resident	Oct–Feb	-	-
	Sedge Warbler *Acrocephalus schoenobaenus*	Stab	Palearctic	-	-	-

Alcedinidae	Giant Kingfisher *Ceryle maxima*	Dec	Resident	Aug–Mar	-	-
	Half-collared Kingfisher *Alcedo semitorquata*	Dec	Resident	All year	-	-
	Malachite Kingfisher *Corythornis cristatus*	Stab	Resident	Jul–Mar	-	-
	Mangrove Kingfisher *Halcyon senegaloides*	Dec	Afrotropical	Mar–April	-	-
	Pied Kingfisher *Ceryle rudis*	Unk	Resident	July–April	Inc	Inc
Anatidae	African Black Duck *Anas sparsa*	Dec	Resident	Jan–Jun	-	-
	African Pygmy Goose *Nettapus auritus*	Dec	Nomadic	Sept–Apr	-	-
	Cape Shoveler *Anas smithii*	Inc	Resident	All year	-	-
	Cape Teal *Anas capensis*	Inc	Nomadic	Opp	Dec	Stable
	Egyptian Goose *Alopochen aegyptiaca*	Dec	Nomadic	May–Dec	Inc	Inc
	Fulvous Duck *Dendrocygna bicolor*	Dec	Nomadic	All year	-	-
	Garganey *Spatula querquedula*	Dec	Palearctic	Apr–Jul	-	-
	Hottentot Teal *Spatula hottentota*	Dec	Nomadic	Feb–May	Inc	InsigDec
	Knob-billed Duck *Sarkidiornis melanotos*	Dec	Nomadic	Sept–Apr	Stable	Dec
	Maccoa Duck *Oxyura maccoa*	Dec	Resident	All year	-	-
	Northern Mallard *Anas platyrhynchos*	Inc	Palearctic	Oct–Mar	-	-

(*Continued*)

(Continued)

Family	Species name	Global population status	Migration type	Breeding season	HNP WS trend	HNP DS trend
	Northern Shoveler *Spatula clypeata*	Stab[r]	Palearctic	Dec–May	-	-
	Pintail *Anas acuta*	Dec	Palearctic	Sep–Apr	-	-
	Red-billed Teal *Anas erythrorhyncha*	Dec	Resident	Nov–May	Inc	InsigInc
	South African Shelduck *Tadorna cana*	Inc	Nomadic	Mar–Dec	-	-
	Southern Pochard *Netta erythrophthalma*	Dec	Nomadic	Dec–Jul	InsigInc	InsigInc
	Spur-winged Goose *Plectropterus gambensis*	Inc	Resident	All year	Inc	InsigInc
	White-backed Duck *Thalassornis leuconotus*	Dec	Nomadic	All year	Stable	InsigDec
	White-faced Duck *Dendrocygna viduata*	Inc	Nomadic	Sept–May	Inc	Dec
	Yellow-billed Duck *Anas undulata*	Stab	Resident	All year	-	-
Anhingidae	African Darter *Anhinga rufa*	Dec	Resident	All year	-	-

Ardeidae	Black Egret *Egretta ardesiaca*	Stab	Resident	Aug–April	-	-
	Black-crowned Night Heron *Nycticorax nycticorax*	Dec	Nomadic	All year	-	-
	Common Bittern *Botaurus stellaris*	Dec	Afrotropical	Sept–Jan	-	-
	Dwarf Bittern *Ixobrychus sturmii*	Unk	Afrotropical	Nov–Apr	-	-
	Goliath Heron *Ardea goliath*	Stab	Resident	All year	InsigDec	Inc
	Great Egret *Ardea alba*	Unk	Nomadic	Sept–Mar	InsigInc	Stable
	Green-backed Heron *Butorides striata*	Dec	Resident	All year	Stable	Dec
	Grey Heron *Ardea cinerea*	Unk	Resident	All year	Inc	Inc
	Intermediate Egret *Ardea intermedia*	Dec	Resident	Jul–Mar	Stable	NA
	Little Bittern *Ixobrychus minutus*	Dec	Resident	Sept–Jun	-	-
	Little Egret *Egretta garzetta*	Inc	Resident	Aug–Mar	InsigInc	Stable
	Madagascar Pond Heron *Ardeola idae*	Dec	Afrotropical	Oct–Mar	-	-
	Purple Heron *Ardea purpurea*	Dec	Resident	All year	-	-
	Rufous-bellied Heron *Ardeola rufiventris*	Unk	Resident	All year	-	-

(*Continued*)

(Continued)

Family	Species name	Global population status	Migration type	Breeding season	HNP WS trend	HNP DS trend
	Squacco Heron *Ardeola ralloides*	Dec	Resident	All year	-	-
	Slaty Egret *Egretta vinaceigula*	Dec	Resident	Feb–May	-	-
	White-backed Night Heron *Gorsachius leuconotus*	Stab	Resident	All year	-	-
Burhinidae	Water Thickknee *Burhinus vermiculatus*	Unk	Nomadic	Aug–Jan	Stable	InsigInc
Caprimulgidae	Natal Nightjar *Caprimulgus natalensis*	Dec	Resident	Aug–Dec	-	-
Charadriidae	African Wattled Lapwing *Vanellus senegallus*	Stab	Resident	Jul–Dec	InsigDec	Dec
	Blacksmith Lapwing *Vanellus armatus*	Inc	Resident	All year	Inc	Inc
	Black-winged Lapwing *Vanellus melanopterus*	Dec	Afrotropical	Mar–Jul	-	-
	Caspian Plover *Charadrius asiaticus*	Dec	Palearctic	Apri–Jun	-	-
	Chestnut-banded Plover *Charadrius pallidus*	Stab	Resident	Mar–Oct	-	-
	Common Ringed Plover *Charadrius hiaticula*	Dec	Palearctic	Apr–Jul	-	-
	Greater Sandplover *Charadrius leschenaultii*	Inc	Palearctic	Apr–May	-	-

	Grey Plover *Pluvialis squatarola*	Dec	Palearctic	May–Jun	-	-
	Kittlitz's Plover *Charadrius pecuarius*	Unk	Nomadic	All year	Inc	InsigInc
	Lesser Black-winged Plover *Vanellus lugubris*	Unk	Resident	Jun–Dec	-	-
	Little-ringed Plover *Charadrius dubius*	Unk	Palearctic	Dec–Jun	-	-
	Long-toed Lapwing *Vanellus crassirostris*	Unk	Resident	Apr–Oct	NA	NA
	Pacific Golden Plover *Pluvialis fulva*	Dec	Palearctic	Jun–Jul	-	-
	Three-banded Plover *Charadrius tricollaris*	Unk	Nomadic	All year	Inc	Inc
	White-crowned Lapwing *Vanellus albiceps*	Stab	Resident	Jan–Mar	-	-
	White-fronted Plover *Charadrius marginatus*	Dec	Afrotropical	All year	NA	NA
Ciconiidae	African Openbill *Anastomus lamelligerus*	Dec	Resident	All year	InsigDec	Inc
	Black Stork *Ciconia nigra*	Unk	Resident	-	NA	InsigInc
	Saddle-billed Stork *Ephippiorhynchus senegalensis*	Dec	Resident	All year	InsigInc	InsigDec
	Woolly-necked Stork *Ciconia episcopus*	Dec	Resident	Dec–Mar	-	-
	Yellow-billed Stork *Mycteria ibis*	Dec	Resident	Jul–Mar	InsigInc	Inc

(*Continued*)

(Continued)

Family	Species name	Global population status	Migration type	Breeding season	HNP WS trend	HNP DS trend
Cisticolidae	Black-backed Cisticola *Cisticola galactotes*	Stab	Resident	Nov—May	-	-
	Chirping Cisticola *Cisticola pipiens*	Stab	Resident	Oct—May	-	-
	Levaillant's Cisticola *Cisticola tinniens*	Stab	Resident	Jul—May	-	-
	Pale-crowned Cisticola *Cisticola brunnescens*	Stab	Resident	Oct—May	-	-
	Red-faced Cisticola *Cisticola erythrops*	Stab	Resident	Nov—Apr	-	-
Cuculidae	Black Coucal *Centropus grillii*	Stab	Resident	Dec—April	-	-
	Coppery-tailed Coucal *Centropus cupreicaudus*	Stab	Resident	Jan—Mar	-	-
	White-browed Coucal *Centropus superciliosus*	Stab	Resident	Mar—June	-	-

Estrildidae	Common Waxbill *Estrilda astrild*	Stab	Resident	Jan–Sept	-	-
	Orange-breasted Waxbill *Amandava subflava*	Stab	Resident	Jun–Sept	-	-
Glareolidae	Black-winged Pratincole *Glareola nordmanni*	Dec	Palearctic	May–Jul	InsigInc	NA
	Red-winged Pratincole *Glareola pratincola*	Dec	Afrotropical	Jun–Dec	Stable	NA
	Rock Pratincole *Glareola nuchalis*	Dec	Afrotropical	Jul–Oct	-	-
Gruidae	Grey Crowned Crane *Balearica regulorum*	Dec	Resident	Nov–Jan	Stable	Dec
	Wattled Crane *Bugeranus carunculatus*	Dec	Resident	All year	-	-
Heliornithidae	African Finfoot *Podica senegalensis*	Dec	Resident	Aug–Apr	-	-
Hirundinidae	African Sand Martin *Riparia paludicola*	Dec	Afrotropical	Apr–Jun	-	-
	Banded Martin *Neophedina cincta*	Inc	Afrotropical	Apr–May	-	-
	European Sand Martin *Riparia riparia*	Dec	Palearctic	-	-	-
	Wire-tailed Swallow *Hirundo smithii*	Inc	Afrotropical	Nov–Mar	-	-
Jacanidae	African Jacana *Actophilornis africanus*	Stab	Nomadic	All year	Inc	InsigInc
	Lesser Jacana *Microparra capensis*	Unk	Nomadic	Feb–Nov	-	-

(*Continued*)

(Continued)

Family	Species name	Global population status	Migration type	Breeding season	HNP WS trend	HNP DS trend
Laridae	African Skimmer *Rynchops flavirostris*	Dec	Afrotropical	Aug–Oct	-	-
	Caspian Tern *Sterna caspia*	Dec	Resident	Dec–Apr	-	-
	Grey-headed Gull *Larus cirrocephalus*	Stab	Resident	Jul–Oct	-	-
	Gull-billed Tern *Gelochelidon nilotica*	Dec	Vagrant	-	-	-
	Lesser Black-backed Gull *Larus fuscus*	Inc	Palearctic	May–Jun	-	-
	White-winged Tern *Chlidonias leucopterus*	Stab	Palearctic	Apr–Aug	InsigInc	NA
	Whiskered Tern *Chlidonias hybrida*	Stab	Afrotropical	Oct–Apr	Inc	NA
Locustellidae	Little Rush Warbler *Bradypterus baboecala*	Stab	Resident	Sept–Mar	-	-
Malaconotidae	Marsh Tchagra *Bocagia minuta*	Dec	Resident	May–Jun	-	-
	Swamp Boubou *Laniarius bicolor*	Dec	Resident	All year	-	-

Meropidae	Blue-cheeked Bee-eater *Merops persicus*	Stab	Palearctic	Oct–Nov	-	-
	Olive Bee-eater *Merops superciliosus*	Stab	Afrotropical	Mar–May	-	-
	Southern Carmine Bee-eater *Merops nubicoides*	Dec	Afrotropical	Aug–Nov	-	-
	White-cheeked Bee-eater *Merops variegatus*	Stab	Resident	Oct–Mar	-	-
	White-fronted Bee-eater *Merops bullockoides*	Inc	Resident	Nov–Apr	-	-
Motacillidae	African Pied Wagtail *Motacilla aguimp*	Stab	Resident	Oct–Mar	-	-
	Pink-throated Longclaw *Macronyx ameliae*	Dec	Resident	Sept–Apr	-	-
Pandionidae	Osprey *Pandion haliaetus*	Inc	Palearctic	Dec–Mar	-	-
Pelecanidae	Great White Pelican *Pelecanus onocrotalus*	Unk	Resident	All year	-	-
	Pink-backed Pelican *Pelecanus rufescens*	Stab	Resident	Jun–Jan	-	-
Phalacrocoracidae	Long-tailed Cormorant *Microcarbo africanus*	Dec	Resident	All year	InsigInc	NA
	White-breasted Cormorant *Phalacrocorax carbo*	Inc	Resident	All year	-	-

(*Continued*)

(Continued)

Family	Species name	Global population status	Migration type	Breeding season	HNP WS trend	HNP DS trend
Phasianidae	African Blue Quail *Synoicus adansonii*	Stab	Resident	Oct–Mar	-	-
	Harlequin Quail *Coturnix delegorguei*	Stab	Resident	Oct–Mar	-	-
Phoenicopteridae	Greater Flamingo *Phoenicopterus roseus*	Inc	Afrotropical	Nov–Feb	-	-
	Lesser Flamingo *Phoenicopterus minor*	Dec	Nomadic	Jan–Aug	-	-
Ploceidae	Brown-throated Weaver *Ploceus xanthopterus*	Dec	Resident	Apr–Jul	-	-
	Golden Bishop *Euplectes afer*	Stab	Resident	Nov–May	-	-
	Red Bishop *Euplectes orix*	Stab	Resident	Nov–May	-	-
	Red-headed Quelea *Quelea erythrops*	Stab	Resident	Mar–May	-	-
	Red-shouldered Widow *Euplectes axillaris*	Stab	Resident	Nov–Apr	-	-
	Yellow Weaver *Ploceus subaureus*	Stab	Resident	Mar–Jun	-	-

Podicipedidae	Black-necked Grebe *Podiceps nigricollis*	Unk	Nomadic	All year	-	-
	Great Crested Grebe *Podiceps cristatus*	Unk	Nomadic	Jan–May	-	-
	Little Grebe *Tachybaptus ruficollis*	Dec	Resident	All year	InsigInc	InsigInc
Rallidae	African Crake *Crex egregia*	Stab	Afrotropical	Oct–Mar	Inc	NA
	African Purple Swamphen *Porphyrio madagascariensis*	Unk	Resident	Jul–Jan	-	-
	African Rail *Rallus caerulescens*	Unk	Resident	Jul–May	-	-
	Allen's Gallinule *Porphyrio alleni*	Dec	Resident	Dec–May	-	-
	Baillon's Crake *Porzana pusilla*	Unk	Resident	Dec–May	-	-
	Black Crake *Amaurornis flavirostra*	Unk	Resident	Aug–Jun	InsigInc	Inc
	Buff-spotted Flufftail *Sarothrura elegans*	Stab	Afrotropical	Sept–Apr	-	-
	Common Moorhen *Gallinula chloropus*	Stab	Resident	All year	Stable	InsigInc
	Corn Crake *Crex crex*	Stab	Palearctic	Apr–Aug	-	-
	Lesser Moorhen *Gallinula angulata*	Unk	Afrotropical	Nov–Mar	InsigInc	NA
	Red-knobbed Coot *Fulica cristata*	Dec	Nomadic	All year	InsigInc	NA
	Red-chested Flufftail *Sarothrura rufa*	Dec	Resident	Sept–May	-	-
	Redtailed Flufftail *Sarothrura affinis*	Dec	Resident	Sept–Mar	-	-
	Spotted Crake *Porzana porzana*	Stab	Palearctic	NA	-	-

(*Continued*)

(Continued)

Family	**Species name**	**Global population status**	**Migration type**	**Breeding season**	**HNP WS trend**	**HNP DS trend**
	Streaky-breasted Flufftail *Sarothrura boehmi*	Dec	Afrotropical	Nov–Mar	-	-
	Striped Crake *Aenigmatolimnas marginalis*	Dec	Afrotropical	Dec–Mar	-	-
Recurvirostridae	Black-winged Stilt *Himantopus himantopus*	Inc	Nomadic	Aug–Dec	Inc	Stable
	Pied Avocet *Recurvirostra avosetta*	Unk	Nomadic	Apr–Aug	NA	InsigDec
Rostratulidae	Greater Painted Snipe *Rostratula benghalensis*	Dec	Afrotropical	Jul–Apr	InsigInc	A
Scolopacidae	African Snipe *Gallinago nigripennis*	Unk	Resident	All year	-	-
	Bar-tailed Godwit *Limosa lapponica*	Dec	Palearctic	May–Aug	-	-
	Black-tailed Godwit *Limosa limosa*	Dec	Palearctic	Apr–Jun	-	-
	Common Greenshank *Tringa nebularia*	Stab	Palearctic	Apr–Jun	InsigInc	Dec
	Common Redshank *Tringa totanus*	Unk	Nomadic	Mar–Aug	-	-

	Common Sandpiper *Actitis hypoleucos*	Dec	Palearctic	May–Jun	Inc	InsigInc
	Common Whimbrel *Numenius phaeopus*	Dec	Palearctic	May–Aug	-	-
	Curlew Sandpiper *Calidris ferruginea*	Inc	Palearctic	Jun–Jul	-	-
	Eurasian Curlew *Numenius arquata*	Dec	Palearctic	Apr–Aug	-	-
	Great Snipe *Gallinago media*	Dec	Palearctic	May–Jul	-	-
	Green Sandpiper *Tringa ochropus*	Stab	Palearctic	Apr–Jun	-	-
	Grey Phalarope *Phalaropus fulicarius*	Unk	Afrotropical	May–Jun	-	-
	Little Stint *Calidris minuta*	Dec	Palearctic	Jun–Jul	Inc	NA
	Marsh Sandpiper *Tringa stagnatilis*	Dec	Palearctic	Apr–Jun	InsigInc	NA
	Red-necked Phalarope *Phalaropus lobatus*	Dec	Afrotropical	May–Jun	-	-
	Ruddy Turnstone *Arenaria interpres*	Dec	Palearctic	May–Aug	-	-
	Ruff *Philomachus pugnax*	Dec	Palearctic	May–Aug	Inc	Stable
	Sanderling *Calidris alba*	Unk	Palearctic	-	-	-
	Terek Sandpiper *Xenus cinereus*	Dec	Palearctic	May–Jul	-	-
	Wood Sandpiper *Tringa glareola*	Stab	Palearctic	May–Jul	InsigInc	Stable
Scopidae	Hamerkop *Scopus umbretta*	Stab	Resident	All year	InsigInc	Inc

(*Continued*)

(Continued)

Family	Species name	Global population status	Migration type	Breeding season	HNP WS trend	HNP DS trend
Strigidae	Marsh Owl *Asio capensis*	Stab	Afrotropical	May–Aug	-	-
	Pel's Fishing Owl *Scotopelia peli*	Stab	Resident	Oct–Jun	-	-
Threskiornithidae	African Spoonbill *Platalea alba*	Stab	Nomadic	Jul–Nov	Inc	Inc
	Glossy Ibis *Plegadis falcinellus*	Dec	Resident	Nov–Apr	Stable	NA
	Sacred Ibis *Threskiornis aethiopicus*	Dec	Resident	All year	Inc	Inc
Tytonidae	Grass Owl *Tyto capensis*	Dec	Resident	Dec–Aug	-	-

Note: The superscript (^{r}) in the global population trend denotes "relatively."
WS trend, wet season trend in HNP; *DS trend*, dry season trend in HNP (data from Tarakini et al., 2020b). For the trend codes, *Inc*, significantly increasing trend; *Stab*, stable; *Dec*, significantly decreasing trend; *InsigInc*, insignificant increase; *Unk*, unknown; *InsigDec*, insignificant decrease. For the breeding season, *Opp*, opportunistic breeder.
Source: Information used in this Appendix was primarily obtained from Hockey, P., Dean, W., Ryan, P., 2005. Roberts Birds of Southern Africa, seventh (ed.) Trustees of the John Voelcker Bird Book Fund, Cape Town; Delany, S., Scott, D., Helmink, T., Martakis, G., 2007. Report on the Conservation Status of Migratory Waterbirds in the Agreement Area, UNEP/AEWA Secretariat, Bonn (Delany et al., 2007); Ferguson-Lees, J., Christie, D., 2001. Raptors of the world (Ferguson-Lees and Christie, 2001) and websites including Birdlife International (http://www.birdlifeInternational.org); Birds of the World (http://www.hbw.com/); the South African electronic bird museum (http://www.biodiversityexplorer.org/birds/) and the International Union for the Conservation of Nature (IUCN) (http://www.iucnredlist.org/details/).

Appendix V

Cited waterbird species in the southern KAZA TFCA alongside the categorized uses

Species common name	Species vernacular names(s)	Uses					
		Meat	Eggs	Dom	BBS	Myths	Fabric
Abdim's Stork	Ngauzane (Nd), Shuramurove (Sh)				x		
African Black Duck	iDada (Nd)	x					
African Fish Eagle	Hungwe (Sh), iNkwazi (Nd)	x			x	x	
African Jacana	Otolo (Nd)	x				x	
African Openbill Stork	isiQhophamnenke (Nd)				x		
African Pygmy Goose	iDada (Nd)	x			x		
African Skimmer	-					x	
African Spoonbill	Imbemba (Nd)	x					
African Wattled Lapwing	Hurekure (Sh)					x	
Black Stork	uNowanga (Nd)						x
Black-crowned Night Heron	-					x	
Blacksmith Lapwing	-	x				x	
Black-winged Stilt	Tekwane (Nd)	x					
Cape Shoveler	Sialwili (T)	x					
Cattle Egret	Amalanda (Nd), Fudzamombe (Sh)					x	

(*Continued*)

(Continued)

		Uses					
Species common name	**Species vernacular names(s)**	**Meat**	**Eggs**	**Dom**	**BBS**	**Myths**	**Fabric**
Common Greenshank	-	x					
Common Moorhen	-	x					
Grey Crowned Crane	Mbowani (Nd), Amahuruhwani (T),					x	x
Crowned Lapwing	oGwelo (Nd), Hurekure (Sh)				x		
Egyptian Goose	Amahansi (Nd), Dhadha (Sh)	x	X	X	x		x
Glossy Ibis	-						X
Goliath Heron	uNozalizingwenyana (Nd)					x	x
Great Egret	-						X
Greater Painted Snipe	-	x					
Green Sandpiper	-					x	
Green-backed Heron	-				x	x	
Grey Heron	Ugogokamzokho (Nd)	x			x		
Hamerkop	uTekwane (Nd)				x	x	
Hottentot Teal	-	x					
Knob-billed Duck	Ingidiva (Nd)	x			x	x	

(*Continued*)

(Continued)

		Uses					
Species common name	**Species vernacular names(s)**	**Meat**	**Eggs**	**Dom**	**BBS**	**Myths**	**Fabric**
Lesser Jacana	-				x		
Little Grebe	Tsvitsitsvi (Sh), Tsviripolo (T)	x		X		x	
Marabou Stork	-				x		
Pied Kingfisher	isiXula (Nd), Chinyururahove (Sh)						x
Red-billed Teal	Amanewenewe (Nd)	x		X			
Reed Cormorant	uLondo (Nd)				x		
Sacred Ibis	umXwagele (Nd)					x	
Saddle-billed Stork	-	x					x
Southern Pochard	iDada (Nd)	x					
Spur-winged Goose	Makhlasi (Nd)	X	X	X	x		x
Squacco Heron	-					x	
White-breasted Cormorant	-				x		
White-faced Duck	iDada (Nd)	x			x		x
Whiskered Tern	-					x	
Wood Sandpiper	-	x					
Woolly-necked Stork	isiThandamanzi (Nd)						x

Dom, those species that people try to domesticate; *BBS*, belief-based superstitions; *Fabric*, use in making various clothing materials or decorations. For vernacular names *Nd*, Ndebele; *Sh*, Shona; *T*, Tonga and those cited in English are marked by a dash (-).

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