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Drivers of aquatic macroinvertebrate communities in a Ramsar declared wetland system

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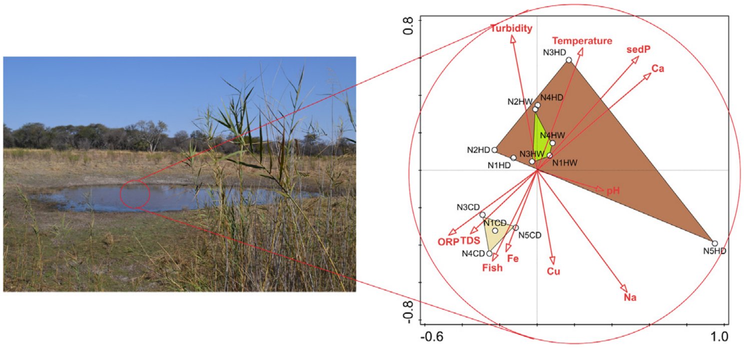
HIGHLIGHTS

- Baetidae, Corixidae, Coenogrionidae, Dytiscidae and Physidae were the most abundant families.
- Functional feeding group ratios indicated that all sites were strongly autotrophic.
- Environmental variables and fish had an influence on macroinvertebrate community.
- Different macroinvertebrate taxa respond differently to seasonal changes.

GRAPHICAL ABSTRACT



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ABSTRACT

Wetlands in the Global South are under increasing pressure due to multiple stressors associated with global change. Water and sediment quality assessments, as well as biomonitoring using macroinvertebrate communities, are fundamental tools for informing wetland condition and management strategies. Here, we examine water and sediment parameters affecting aquatic macroinvertebrates in Nlyslvey Wetland, Limpopo Province, South Africa. Water quality, sediments, fish and macroinvertebrate community data were collected across three seasons (hot-dry, hot-wet, cool-dry) from five sites. Baetidae, Corixidae, Coenogrionidae, Dytiscidae and Physidae were the most abundant and dominant families, with functional feeding group (FFG) ratios indicating that all sites were strongly autotrophic, had high predator-prey ratios, few shredders and had a stable substrate across seasons. Fish abundances increased significantly towards the cool-dry season. Based on redundancy analysis, P, Ca, pH, Cu and Na were strongly positively associated with macroinvertebrates, including Physidae, Corixidae, Planorbidae, Ostracoda, Potamonautidae and Hydropyschidae; turbidity and sulphur were associated with Dytiscidae, Oligochaetae, Libellulidae, Gerridae and Dixidae; and fish abundance, Fe, oxygen reduction potential and total dissolved solids were negatively associated with Baetidae, Belostomatidae, Hydrophilidae and Leptoceridae. Therefore, these variables accounted for high levels of variation in macroinvertebrate families, with the cool-dry season clearly distinguished from the hot-wet and hot-dry

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seasons according to functional feeding groups. Being a protected area, this information could provide a useful baseline for further studies into wetlands in the region subject to greater anthropogenic stresses, as well as future studies in this Ramsar site. Further studies are required to assess the importance of environmental factors influencing the richness and distribution of macroinvertebrate communities in wetlands under growing anthropogenic pressures.

1. Introduction

Floodplain wetlands are essential habitats for a rich diversity of plants, invertebrates and amphibians, and represent important foraging grounds for a variety of birds and watering points for many large mammals (Vanschoenwinkel et al., 2011; O'Neill and Thorp, 2014; Dalu and Wasserman, 2022). These systems are shaped by biotic interactions, particularly top-down processes, which act as strong ecosystem structuring determinants, together with abiotic conditions (Hanson and Riggs, 1995; Maurer et al., 2014; Hanson et al., 2005). Floodplain habitats represent the buffer zones between rivers and adjacent terrestrial systems (Carter, 1996; Polis et al., 1997). Different forms of nutrients and energy move across the conceptual boundaries of ecosystems via organisms' activities or physical processes, such as wind or water currents, and these transfers can represent important food subsidies. Biotic and abiotic influences can impact aquatic communities in a predictable manner along a habitat permanence gradient (Hanson et al., 2005).

Many floodplain wetlands are, however, ecologically degraded due to poor land use practices and freshwater abstraction (Dalu et al., 2017a; Shen et al., 2019). Despite their ecological importance and growing risk, for the great majority of these systems, we have a poor understanding of their functioning or structuring, particularly within the Global South context. In Africa, the quantification of ecosystem service loss is often impossible to determine given the scarcity of extant pre-degradation conditions (Dalu et al., 2017a). Working in protected areas with largely-intact floodplains can provide information on the factors that govern ecosystem functioning and productivity, with the ultimate goal of informing management of these systems elsewhere or in future. Central to issues of habitat quality and water availability is the question of whether organisms (including humans) are under threat due to pollution, food scarcity, or overharvesting in freshwater ecosystems.

Macroinvertebrates play an important role in controlling primary productivity, decomposition, nutrient cycling, and translocation of materials (Wallace and Webster, 1996; Nhiwatiwa et al., 2017a; Dalu et al., 2017b). These organisms are ubiquitous and abundant in ecosystems and have been widely used as biological indicators of aquatic health due to their wide pollution tolerance ranges (Hauer and Resh, 2017; Nhiwatiwa et al., 2017a, 2017b; Mangadze et al., 2019). Groups such as Ephemeroptera (mayflies), Plecoptera (stoneflies), Trichoptera (caddisflies) and Uniondale (mussels, freshwater clams) are accepted and widely-used indicators of aquatic degradation (Herman and Nejadhashemi, 2015), and tend to survive at high dissolved oxygen levels and are not found in polluted ecosystems. Contrastingly, taxa such as Oligochaetae (worms) and Diptera (fly/midge larvae) tolerate low dissolved oxygen levels, and are considered good indicators of impacted ecosystems (Xu et al., 2014). Hence, monitoring of the diversity and composition of taxa present within a particular ecosystem can foster a better understanding of its state.

Macroinveterbrate diversity encompasses the spatial structure of aquatic systems and landscape diversity patterns, playing a central ecological role in many aquatic ecosystems such as wetlands, because they are among the most ubiquitous and diverse organisms in freshwaters (Strayer, 2006). In southern Africa, there is scant information on the macroinvertebrate distribution and hydro-period dynamic effects of floodplain wetlands on these organisms (e.g., Dalu and Chauke, 2020). Both physico-chemical and biotic variation is considerable over a hydroperiod, confounding the identification of drivers of community dynamics. For example, during periods of low water, less aquatic habitat is available, and there is a concentration of dissolved solutes in the water body with certain large bodied predators often largely excluded or reduced in number (e.g., fish). High water periods are characterised by water quality influenced by catchment dynamics and the presence of longer aquatic food chains which include fish in greater abundance. Fish are generally considered as major natural enemies of macroinvertebrates in freshwater ecosystems, and are largely responsible for top-down trophic effects on macroinvertebrate communities (e.g., do Nascimento Filho and do Nascimento Moura, 2021; Gusha et al., 2021). As such, fish were collected across sites and seasons during this study as a factor of macroinvertebrate abundance and diversity. The role that these various potential drivers play in structuring macroinvertebrate communities is complex and highly variable across floodplain wetland systems. The present study aimed to characterize the macroinvertebrate communities and assess their relationship with water and sediment chemistry parameters, as well as fish predation pressure dynamics, within a subtropical Rasmar-declared wetland system. We hypothesised that top down pressure would shape macroinvertebrate communities during the low water hydroperiod due to greater predatory encounters, and that bottom-up drivers would cause a stronger influence on macroinvertebrates during high water periods.

2. Materials and methods

2.1. Study area

The study was conducted in the upper reaches of the Ramsar declared Nylsvley Wetland (24°16′25″S, 28°58′37″E) within the Waterberg District, Limpopo Province of South Africa (Fig. 1). The upper reaches generally fall within the protected Nylsvley Nature Reserve, but are downstream of the towns of Modimolle and Bela Bela. The reserve has a total area of 2425 km^2 and occurs at an elevation of between 1080 m and 1155 m above sea level. The wetland is made up of extensive reed beds of *Typha capensis* and *Phragmites australis* and grass veld, surrounded by open savannah woodlands (Dalu et al., 2020a). The area is subtropical, with mean temperatures ranging from 20.5 °C in winter to 28.9 °C in summer, and the mean annual rainfall is 648 mm, mostly occurring in summer. The wetland consists of central sandy Bushveld and Springbokvlate Thornveld soils (LEDET, 2013).

To investigate the influence of water level/hydro-period dynamics on macroinvertebrate distribution and structure, the study was carried out at five randomly selected sites (i.e., N1, N2, N3, N4, N5), during three contrasting hydro periods; the hot-dry (September 2018), hot-wet (March 2020) and cool-dry (June 2019) seasons (Fig. 1). The five sites were chosen to capture spatial variation in physico-chemical properties/environmental variables across the water body. No sampling was done at sites N2 (cool-dry season) and N1 (hot-wet season) due to low rainfall, causing the wetland to become dry, and a lack of access to the site as it was located on private property and owners were not available on the sampling occasion, respectively.

2.2. Environmental (abiotic and biotic) variables

2.2.1. Water

Measurements of electrical conductivity (EC), pH, total dissolved solids (TDS), salinity, water temperature, and resistivity were taken using a portable multi-parameter probe PCTestr 35 (Eutech/Oakton Instruments, Singapore) at each site ($n = 3$ per site (N1–N5)) and season (i.e., hot-dry, hot-wet, cool-dry) from the edge, middle (between edge and centre) and centre points of the wetland at each site. Water depth was measured using a graduated measuring rod from the deepest point. Furthermore, integrated water samples (500 mL, $n = 3$) from the permanent wetland

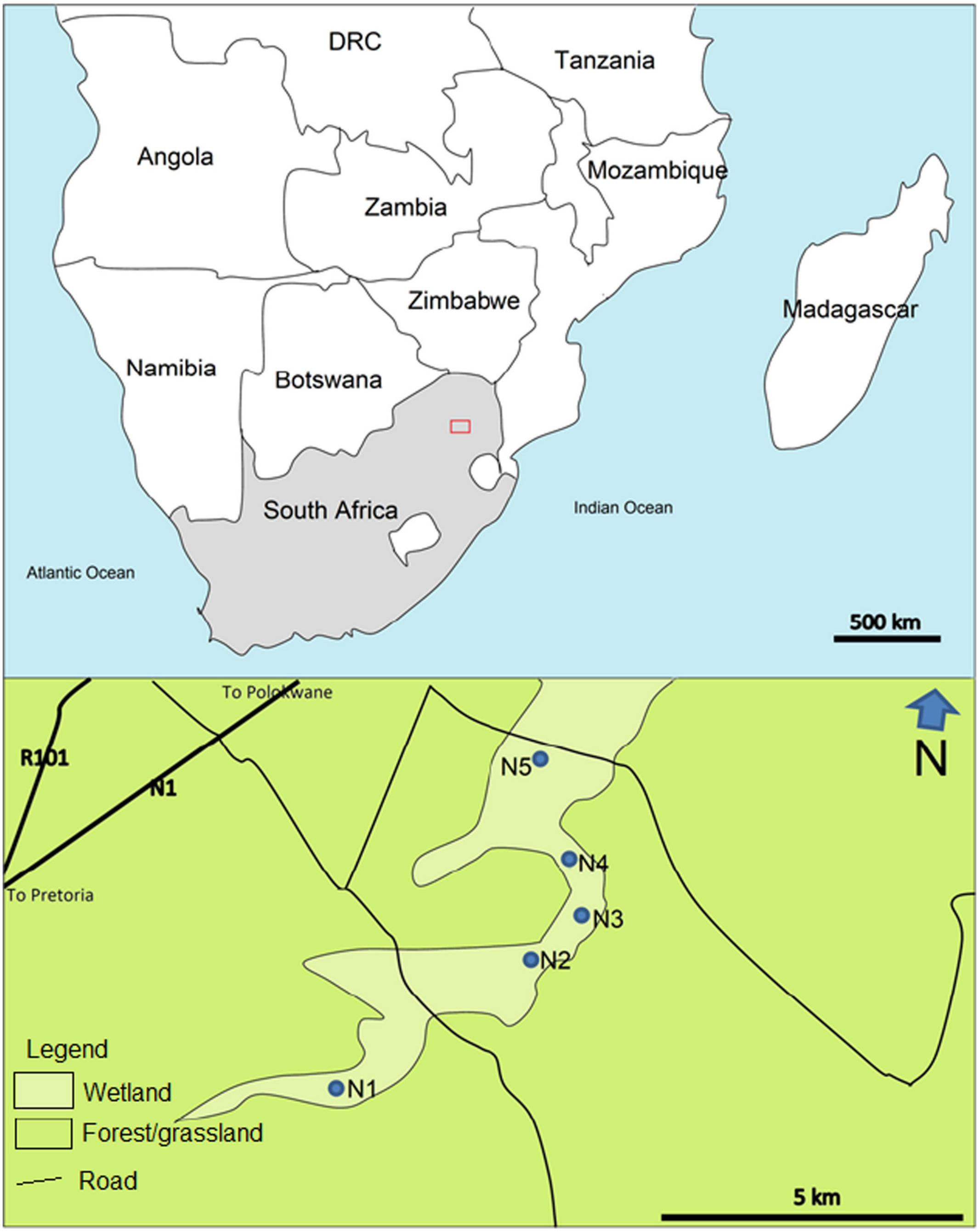

Fig. 1. Location of the study sites within Nylsvley wetland, Limpopo Province of South Africa.

zone were collected and stored on ice until they were processed in the field laboratory for nutrient (i.e., ammonium ($NH^+{}_4$, phosphates ($PO^{3-}{}_4$)) analysis. The water nutrients were analysed within 12 h of collection using a HI717 HANNA phosphate high range checker (range 0.0 to 30.0 mg L^{-1}, resolution 0.1 mg L^{-1}, accuracy 1.0 mg L^{-1}) and HI3824 HANNA ammonium test kit for freshwater (range 0.0 to 100.0 mg L^{-1}, resolution 0.5 mg L^{-1}, accuracy 1.0 mg L^{-1}).

2.2.2. Sediment

Integrated 1.5 kg sediment samples ($n = 2$) from five random depositional zones were collected from each of the five study sites per sampling event. The sampling was done using acid washed wooden splints and placed in new labelled ziplock bags, packed in a cooler box with ice and transported to the laboratory for analysis. In the laboratory, the sediment samples were dried at 60 °C in an oven for 48–72 h before disaggregation in a porcelain mortar and straining through a sieve (mesh size 0.05 mm) to remove plant roots and other debris. All sediment sample were sent for analysis at a South African National Accreditation System (SANAS) certified laboratory i.e. BEMLAB. Cation elements (boron (B), calcium (Ca), potassium (K), magnesium (Mg), sodium (Na)), heavy metal (manganese (Mn), copper (Cu), iron (Fe), zinc (Zn)) and nutrients (N, P) were analysed (see Dalu et al., 2020a, 2020b for detailed methods).

2.2.3. Fish

Electrofishing along a 5 m length was conducted using a SAMUS-725G backpack electrofisher from all the different habitat biotopes (i.e., pools, marginal vegetation). The electrofisher settings were standardised at 0.3 ms duration and 90 Hz frequency. At each sampling site and season, three-passes were conducted with an electrofisher, with fish captured during each pass being placed into separate buckets and reported as catch per unit effort (CPUE). After being identified to species level according to Skelton (2002) and counted, all fishes in the field were safely released into their natural environment without harm.

2.3. Macroinvertebrates sampling

Macroinvertebrates were collected using a handheld kick net (frame 30 cm × 30 cm, mesh size 500 μm) by disturbing and kicking the bottom sediment and macrophytes for 5 min at each site and season. The collected macroinvertebrates were placed into a tray and sorted to remove plant material before being preserved in 70% ethanol in 400 mL polyethylene containers for later identification and counting in the laboratory (Hauer and Resh, 2017). In the laboratory, the samples were hand-sorted under a disserting microscope and the macroinvertebrates were identified to family level (Gerber and Gabriel, 2002a, 2002b; Gooderham and Tsyrlin, 2002), with all individuals per family counted.

2.4. Data analysis

We tested for significant differences in environmental variables among the study sites (i.e., N1–N5) and seasons (i.e., hot-dry, cool-dry, hot-wet) using a two-way ANOVA in SPSS v16.0 (SPSS Inc., 2007). This was after the data were found to meet all assumptions of parametric testing. Diversity matrices (i.e., taxa richness, evenness, Shannon–Weiner) were calculated using the macroinvertebrate community dataset in PAST version 2.0 (Hammer et al., 2001) to assess for differences in species diversity among sites and seasons. A non-parametric Kruskal–Wallis tests was used to test for differences in diversity matrices among study sites and seasons using SPSS v16.0 (SPSS Inc., 2007).

The collinearity of environmental variables was tested using correlation analysis, with all highly significantly ($r > 0.8$) correlated variables removed. To determine the relative importance of variables structuring macroinvertebrate community and sites/seasons, an ordination multivariate approach was utilised which included all measured environmental variables and fish CPUE. First, to determine whether to use linear or unimodal methods for the macroinvertebrate community and environmental data analysis, a Detrended Correspondence Analysis (DCA) was used. The gradient lengths were examined, and since the longest gradient was <3.0, a Redundancy Analysis (RDA) — a constrained linear ordination method based on significant ($p < 0.05$) forward selected environmental variables using 9999 Monte Carlo Permutations — was used for analysis in Canoco version 5.1 (Ter Braak and Šmilauer, 2012). Furthermore, a cluster analysis (CA) was performed using PC-ORD to define macroinvertebrate groups based on their similarities among sites and seasons (McCune and Mefford, 2006).

The functional feeding group (FFG) contributions of the different communities were determined for each season, but not sites as we expected site variation to be similar across sites. Macroinvertebrate families with more than one FFG classification were divided equally among the possible functional groups before the proportions were determined (e.g. four baetids were calculated as two scrapers and two collector–gatherers) (Dudgeon, 1994). Furthermore, we used FFG ratios as surrogates for ecosystem functioning within the wetland. Ecosystem condition changes have been known to impact upon the food base of invertebrates FFGs, and they can be captured by the relative proportion of measurements within these groups (see Cummins et al., 2005 for more details; Table 1).

3. Results

3.1. Environmental variables and fish community structure

The mean environmental variables recorded across the three seasons are presented in Table 2. Most of the environmental variables were significantly different ($p < 0.05$) among sites, with the exception of three water (i.e., ORP, pH, chl-*a*) and eight sediment (chl-*a*, pH, resistivity, H^+, B, Fe, SOC, S) parameters which were found to be non-significant ($p > 0.05$) (Table 3). Seasonal variations were also pervasive according to most water and sediment variables, excepting $PO^{3-}{}_4$ (water) and Chl-*a*, pH, Resistivity, H^+, SOC and S (sediment, Table 2). For example, high values of conductivity, salinity, $PO^{3-}{}_4$, water depth, pelagic chl-*a*, Cu, Zn, B and Fe were observed during the cool-dry season, whereas, water pH, sed $PO^{3-}{}_4$, K, Mg and Na were high during the hot-dry season for the significant variables. Water temperature, ORP, TDS and Ca were high during the hot-wet season (Table 2).

Table 1

Functional feeding group ratios as ecosystem attribute indicators. Based on Cummins et al. (2005). Abbreviations: CPOM – coarse particulate organic matter, FPOM – fine particulate organic matter, TFPOM – fine particulate organic matter in transport (suspended) BFPOM – fine particulate organic matter storage in sediments (deposited in benthos).

FFG ratios	Ecosystem attribute	Ratio levels
Scrapers to shedders + total collectors	Autotrophy to heterotrophy (P/R)	Autotrophic > 0.75
Shredders to total collectors	CPOM to FPOM index (CPOM/FPOM)	Normal shredder association linked to functioning riparian zone > 0.25
Collector-filterers to collector-gatherers	FPOM in transport (suspended) to FPOM storage in sediments (deposited in benthos) (TFPOM/BFPOM)	TFPOM > Normal particulate suspension loading >0.50
Scrapers + collector-filterers to shedders + collector-gatherers	Substrate/channel stability	Stable substrates (e.g., rooted vascular plants, large woody debris, cobbles, boulders) > 0.50
Predators to total of all other functional groups	Predator-prey ratio (P/P)	<0.15 indicates a normal predator/prey ratio

Five fish species were identified within the Nylsvley Wetland i.e., Straightfin barb (*Enteromius paludinosus*), African sharptooth catfish (*Clarias gariepinus*), Nile tilapia (*Oreochromis niloticus*), the Southern mouth-brooder (*Pseudocrenilabrus philander*) and Western mosquitofish (*Gambusia affinis*). Two species (*E. paludinosus* and *C. gariepinus*; CPUE = 14.6 ± 3.2), all five species (CPUE = 30.9 ± 11.0) and two species (*E. paludinosus* and *C. gariepinus*; CPUE = 25.0 ± 5.5) were caught during the hot-dry, cool-dry and hot-wet seasons, respectively.

3.2. Macroinvertebrate communities

Twenty six macroinvertebrate families were identified within Nylsvley Wetlands, with Baetidae (cool-dry), Corixidae (all seasons), Coenogrionidae (cool-dry), Dytiscidae (hot-dry), Physidae (hot-dry, hot-wet) and Planorbidae (hot-wet) being dominant (mean > 10% abundance; Table 4). Taxa richness (TR), Shannon-Wiener (H) and Simpson (D) diversity index were high during the hot-wet season (i.e., mean TR = 12.3, H = 1.81, D = 0.75) and low for select parameters during the hot-dry (i.e., mean TR = 8) and cool-dry (i.e., mean H = 1.57, D = 0.65) seasons. Whereas, evenness (E) was high and low during the hot-dry (mean E = 0.64) and hot-wet (mean E = 0.51) seasons, respectively (Table 4). No significant differences ($p > 0.05$) were observed for all diversity matrices (i.e., TR, H, D, E) among the study sites and seasons.

3.3. Macroinvertebrate communities in relation to environmental variables

Environmental variables (*water* – ORP, TDS, pH, water temperature, turbidity; *sediment* – P, Ca, Na, Cu, Fe; fish) were found to be significant ($p < 0.05$) in explaining the variation of macroinvertebrate community structure across all sampled wetland sites and seasons based on the RDA analysis. The RDA axis 1 (43.6%) and 2 (22.0%) explained 65.6% of the explained macroinvertebrate cumulative variation with selected environmental

Table 2

Range and mean (±standard deviation) environmental variables recorded in Nylsvley Wetland. Abbreviation: Temp – water temperature, ORP – oxygen reduction potential, Cond – electrical conductivity, TDS – total dissolved solids, $PO^{3-}{}_{4}$ – phosphate, $NH^{+}{}_{4}$ – ammonium, Depth – water depth, Chl-*a* – chlorophyll-*a*, SOC – sediment organic carbon.

Variable	Units	Hot-dry		Cool-dry		Hot-wet	
		Range	Mean	Range	Mean	Range	Mean
Water							
Temp	°C	15.1–26.6	20.2 ± 3.1	13.3–16.7	14.5 ± 1.2	19.9–26.7	22.9 ± 2.8
ORP	mV	−128.1 to 1.7	−61.0 ± 41.8	−59.9 to −22.4	−35.1 ± 11.8	−47.4 to −9	−27.3 ± 14.4
pH		7.8–9.8	8.6 ± 0.5	7.3–8.3	7.6 ± 0.3	6.3–8.1	6.8 ± 0.6
Cond	$\mu S\ cm^{-1}$	35.0–250.0	121.9 ± 80.8	304.4–738.9	453.4 ± 140.4	1.1–258.6	129.7 ± 97.0
TDS	$mg\ L^{-1}$	22.0–162.0	77.4 ± 52.7	86.6–144.0	120.1 ± 21.0	48.3–589.9	201.5 ± 227.0
Salinity	ppt	160.1–200.1	180.4 ± 30.0	146.2–344.5	219.3 ± 64.0	59.3–590.2	209.2 ± 232.7
Turbidity	NTU	15.1–789.0	302.2 ± 271.0	15.1–102.5	39.1 ± 39.2	11.7–301.0	155.6 ± 95.8
$PO^{3-}{}_{4}$	$mg\ L^{-1}$	0.5–17.2	2.4 ± 4.1	1.2–10.2	3.9 ± 4.0	0.07–4.0	1.6 ± 1.5
$NH^{+}{}_{4}$	$mg\ L^{-1}$	0.8–7.5	2.6 ± 2.6	1.8–15.3	5.6 ± 6.0	0.07–6.6	2.2 ± 2.2
Depth	m	0.01–0.9	0.3 ± 0.3	0.25–2.1	1.0 ± 0.8	0.2–0.8	0.5 ± 0.2
Chl-*a*	$mg\ m^{3}$	13.4–194.7	73.5 ± 62.7	55.2–836.2	322.5 ± 285.3	5.0–342.8	68.8 ± 124.3
Sediment							
Chl-*a*	$mg\ m^{2}$	7.1–640.6	182.8 ± 162.2	123.4–329.1	228.5 ± 70.5	49.4–512.5	246.8 ± 159.0
pH		3.7–4.1	3.9 ± 0.1	3.8–4.2	4.0 ± 0.1	3.4–4.5	3.7 ± 0.3
Resistivity	Ω	590.0–3170	1473 ± 946	630.0–2010	872.5 ± 461.4	470.0–1160	843.8 ± 314.1
H^{+}	$cmol\ kg^{-1}$	1.0–3.3	2.4 ± 0.8	1.6–3.3	2.8 ± 0.6	0.7–4.0	3.0 ± 1.3
P	$mg\ kg^{-1}$	55.0–450.0	217.6 ± 136.4	0.02–0.05	0.03 ± 0.01	4.8–38.6	19.8 ± 13.2
K	$cmol\ kg^{-1}$	0.5–7.9	3.1 ± 2.3	0.08–0.19	0.1 ± 0.03	0.2–0.91	0.6 ± 0.3
Ca	$cmol\ kg^{-1}$	1.0–18.9	7.5 ± 5.8	0.1–0.29	0.2 ± 0.1	1.3–8.8	6.1 ± 2.6
Mg	$cmol\ kg^{-1}$	0.8–8.3	4.5 ± 2.7	0.03–0.15	0.1 ± 0.03	0.6–4.0	2.9 ± 1.1
Na	$cmol\ kg^{-1}$	0.09–4.2	1.3 ± 1.4	0.9–1.4	1.1 ± 0.2	0.24–0.43	0.3 ± 0.1
Cu	$mg\ kg^{-1}$	5.3–39.2	23.1 ± 13.2	11.4–37.2	25.1 ± 8.6	0.56–12.1	7.9 ± 1.0
Zn	$mg\ kg^{-1}$	8.0–61.9	33.2 ± 18.6	27.2–62.0	47.1 ± 12.4	1.3–19.7	8.7 ± 7.4
Mn	$mg\ kg^{-1}$	54.8–503.0	235.5 ± 165.3	85.5–397.4	260.7 ± 112.6	9.4–424.0	163.7 ± 130.6
B	$mg\ kg^{-1}$	3.5–33.6	9.1 ± 9.0	14.7–46.7	26.4 ± 10.6	0.26–0.65	0.4 ± 0.2
Fe	$mg\ kg^{-1}$	3967–15,215	8933 ± 3734	10,801–25,250	16,755 ± 4979	140.0–1950	1125 ± 719.6
SOC	%	0.6–2.4	1.9 ± 0.6	1.2–4.6	2.5 ± 1.3	0.89–4.02	2.5 ± 1.3
S	$mg\ kg^{-1}$	14.5–97.9	35.6 ± 16.7	15.2–59.8	35.5 ± 16.7	26.4–61.5	46.7 ± 14.8

variables (Fig. 2). High fish abundances, Fe, ORP and TDS were associated with cool-dry season sites and characterised by Baetidae, Belostomatidae, Hydrophilidae, Leptoceridae and Culicidae. Water temperature, sediment P, Ca, pH, Cu and Na were strongly positively associated with RDA axis 1, and characterised by macroinvetebrate families such as Physidae, Corixidae, Planorbidae, Ostracoda, Potamonautidae and Hydropyschidae. Redundancy

Table 3

Two-way ANOVA results for environmental variables measured at Nylsvley Wetlands in three seasons. Abbreviations are listed in the Table 2 caption.

Variable	Site			Season			Site × Season		
	Df	F	*p*	Df	F	*p*	Df	F	*p*
Water									
Temperature	4	74.577	<0.001	2	230.366	<0.001	6	19.006	<0.001
ORP	4	0.797	0.548	2	4.770	0.028	6	1.409	0.283
pH	4	2.097	0.139	2	55.235	<0.001	6	2.385	0.089
Conductivity	4	27.427	<0.001	2	228.952	<0.001	6	14.514	<0.001
TDS	4	369.530	<0.001	2	445.035	<0.001	6	489.643	<0.001
Salinity	4	145.099	<0.001	2	526.214	<0.001	6	177.785	<0.001
Turbidity	4	14.433	<0.001	2	31.042	<0.001	6	14.664	<0.001
$PO^{3-}{}_{4}$	4	3.273	0.046	2	3.686	0.054	6	1.693	0.200
$NH^{+}{}_{4}$	4	31.480	<0.001	2	52.265	<0.001	6	46.350	<0.001
Chl-*a*	4	1.808	0.188	2	5.759	0.016	6	2.181	0.112
Sediment									
Chl-*a*	4	3.135	0.052	2	0.171	0.845	6	0.395	0.870
pH	4	2.982	0.060	2	2.170	0.154	6	0.996	0.468
Resistivity	4	1.526	0.252	2	3.347	0.067	6	0.910	0.517
H+	4	1.406	0.286	2	1.463	0.267	6	0.851	0.554
P	4	16.369	<0.001	2	141.957	<0.001	6	15.571	<0.001
K	4	6.878	0.003	2	42.788	<0.001	6	7.382	0.001
Ca	4	2.821	0.069	2	15.365	<0.001	6	3.553	0.026
Mg	4	6.014	0.006	2	48.840	<0.001	6	8.257	0.001
Na	4	44.579	<0.001	2	66.874	<0.001	6	38.309	<0.001
Cu	4	4.061	0.024	2	14.714	<0.001	6	2.709	0.062
Zn	4	7.138	0.003	2	39.941	<0.001	6	2.269	0.102
Mn	4	8.494	0.001	2	6.902	0.009	6	3.576	0.026
B	4	1.235	0.344	2	15.037	<0.001	6	0.691	0.661
Fe	4	1.153	0.376	2	42.736	<0.001	6	1.871	0.162
SOC	4	0.602	0.668	2	0.830	0.458	6	0.357	0.893
S	4	1.311	0.317	2	1.700	0.221	6	0.882	0.535

Table 4
Range and mean (± standard deviation) relative abundances (%) and diversity metrics of macroinvertebrates recorded in Nylsvley Wetland across three seasons. Abbreviations to functional feeding groups (FFG): CF – Filterers, CG – collector-gatherers, PR – predators, SC – scrappers and SH – shredders.

Family	FFG	Hot-dry		Cool-dry		Hot-wet	
		Range	Mean	Range	Mean	Range	Mean
Aeshnidae	PR	1.2–14.2	5.9 ± 5.2	0.8–6.0	2.6 ± 2.4	1.1–4.1	2.3 ± 2.0
Ancylidae	SC					0.0–6.8	3.1 ± 3.6
Baetidae	CG;SC	0.0–10.7	2.7 ± 4.5	9.3–63.7	42.7 ± 23.8	2.9–9.9	5.4 ± 3.1
Belostomatidae	PR			0.0–0.9	0.7 ± 0.5		
Chironomidae	CG	0.0–1.6	0.5 ± 0.8	0.0–14.2	8.3 ± 6.6	0.0–5.5	2.8 ± 2.6
Corixidae	PR; SC	0.0–45.6	23.4 ± 16.4	0.0–22.2	11.1 ± 11.3	6.3–31.8	15.7 ± 11.3
Coenogranidae	PR	0.0–5.7	1.2 ± 2.6	0.0–45.8	16.8 ± 21.6	0.4–9.2	4.6 ± 4.6
Culicidae	CF	0.0–2.0	0.8 ± 1.1	0.0–5.7	2.3 ± 2.4	0.0–1.5	0.7 ± 0.8
Dixidae	CG					0.0–2.6	0.6 ± 1.3
Dytiscidae	PR	0.0–32.7	11.4 ± 12.5			5.5–13.6	8.0 ± 3.8
Gerridae	PR					0.0–1.7	0.5 ± 0.8
Hirudinea	PR	0.0–6.0	1.7 ± 2.6				
Hydrophilidae	CG			0.0–4.7	1.2 ± 2.3		
Hydropsychidae	CF; SC	0.0–9.4	2.1 ± 4.1			0.0–12.1	3.0 ± 6.1
Leptoceridae	SH	0.0–6.0	1.2 ± 2.4	0.0–3.8	2.7 ± 1.8		
Libellulidae	PR	0.0–18.4	7.4 ± 8.0	0.0–3.2	1.8 ± 1.5	0.0–4.4	1.1 ± 2.2
Notonectidae	PR	0.0–5.7	1.1 ± 2.6	0.0–7.5	1.9 ± 3.8	0.0–4.0	1.7 ± 1.74
Ostracoda	CF	0.0–39.4	7.9 ± 17.6				
Oligochaetae	CG					0.0–0.5	0.2 ± 0.3
Physidae	SC	7.0–39.4	27.2 ± 12.6	0.0–18.7	6.5 ± 8.8	13.1–60.5	36.3 ± 19.5
Philopotamidae	CG					0.0–1.1	0.3 ± 0.6
Planorbidae	SC	0.0–27.7	6.6 ± 11.9	0.0–3.2	1.5 ± 1.7	2.9–28.2	12.5 ± 11.2
Potamonautidae	SH					0.0–0.7	0.3 ± 0.4
Sphaeriidae	CF					0.0–1.1	0.3 ± 0.6
Tabanidae	SH					0.0–0.7	0.2 ± 0.4
Tetragnathidae	PR					0.0–1.3	0.4 ± 0.6
Richness		5–12	8 ± 2.2	7–14	8 ± 1.4	11–14	12.3 ± 21.5
Shannon-Wiener		1.2–2.01	1.57 ± 0.3	1.10–1.55	1.41 ± 0.21	1.38–2.12	1.81 ± 0.31
Simpson		0.63–0.83	0.74 ± 0.08	0.54–0.71	0.65 ± 0.08	0.59–0.84	0.75 ± 0.11
Evenness		0.47–0.80	0.64 ± 0.15	0.43–0.60	0.52 ± 0.09	0.36–0.64	0.51 ± 0.12

DA axis 2 was positively associated with turbidity and S, and was characterised by Dytiscidae, Oligochaetae, Libellulidae, Gerridae and Dixidae (Fig. 2). Based on the cluster analysis, two groups were identified that split macroinvertebrate community according to sampling sites and seasons. Group 1 consisted of the cool-dry season sites and group 2 of the hot-dry and hot-wet season sites (Fig. 3).

3.4. Functional feeding groups (FFGs) as a proxy of ecosystem attributes

The seasonal FFGs relative contributions are presented in Table 5, with scrapers being the dominant FFG across all seasons, whereby the hot-wet season had the highest relative abundances for scrapers at 65.9%. Predators were the second most dominant for the hot-dry (25.5%) and hot-wet

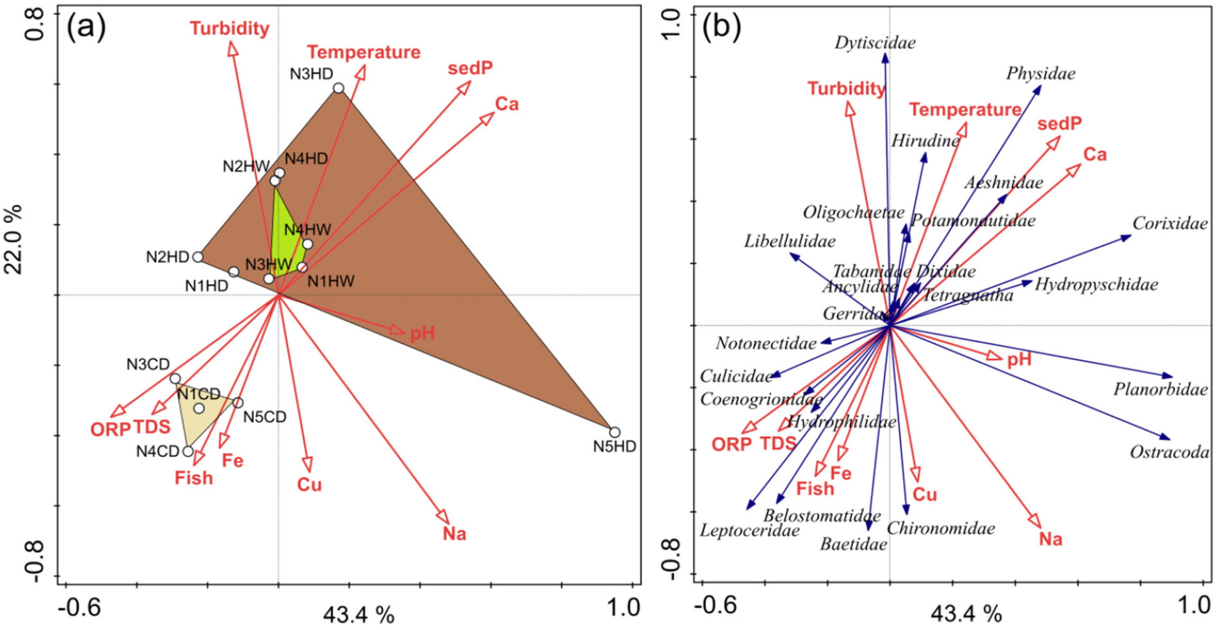

Fig. 2. Redundancy analysis (RDA) of environmental variables in relation to (a) sampling sites/seasons and (b) macroinvertebrate communities. Abbreviations: ORP – oxygen reduction potential, TDS – total dissolved solids, sedP – sediment phosphates, N1–N5 are study sites with lettering HD – hot-dry, HW – hot-wet and CD – cool-dry.

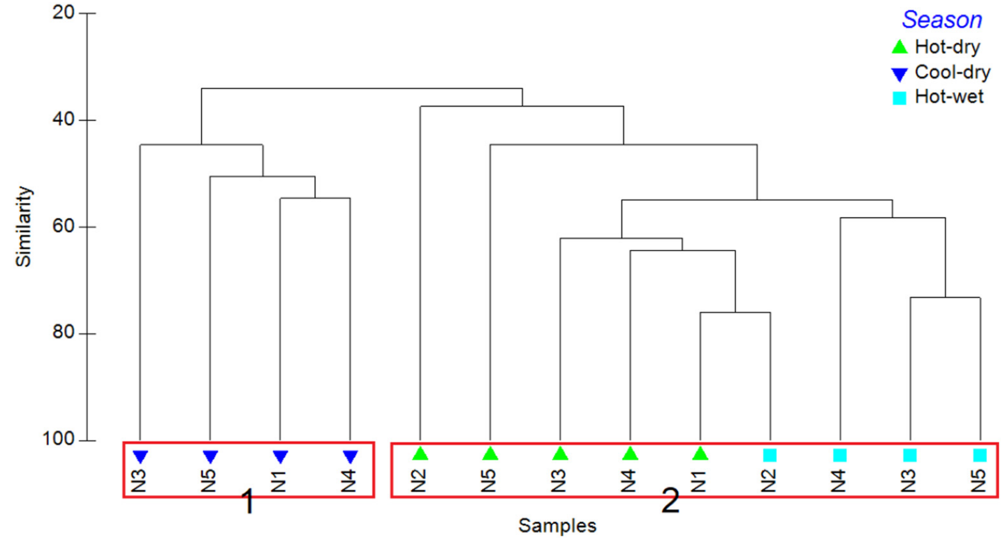

Fig. 3. Cluster analysis highlighting the different groupings for the macroinvertebrate communities across the study sites and seasons in Nylsvely Wetlands, South Africa.

(23.6%) seasons, with the shredders being the least common FFG across all three seasons (abundances <1%; Table 5). The FFG ratios as proxies of ecosystem attributes (Table 1) highlighted that all seasons were very strongly autotrophic (P/R > 0.75) and had a high proportion of predators (P/P > 0.15; Table 6). There was a shredder underrepresentation, suggesting poor linkage with the nearby riparian areas (CPOM/FPOM < 0.25) and abundant and stable substrate across all seasons (channel stability > 0.50). During the hot-dry season, a heavy suspended loading of FPOM was observed (TFPOM/BFPOM > 0.50), with the cool-dry and hot-wet having very light and reduced suspended FPOM loading (TFPOM/BFPOM < 0.50), respectively (Table 6).

4. Discussion

A combination of both abiotic and biotic variables was found to be important in structuring aquatic macroinvertebrate communities within the Nylsvley Wetland system in the present study. We observed reduced fish abundances and diversity during the hot-wet season, which was in turn associated with increased macroinvertebrate abundances, thereby supporting our hypothesis that the macroinvertebrate diversity would be higher during the hot-wet season. High fish abundances and diversity were associated with decreased macroinvertebrate diversity. Previous studies have similarly observed fish to significantly cause declines of macroinvertebrates abundances in shallow ecosystems, even at relatively low fish densities (Marklund et al., 2002). In contrast, Mallory et al. (1994) observed that wetland systems which had fewer fish had fewer macroinvertebrates than fishless wetlands, indicating other potential bottom-up drivers of diversity patterns. Macroinvertebrate community structure also followed the observed water quality changes among the study sites and seasons, with effects of environmental variables being integrated into the overall macroinvertebrate community structuring (Roy et al., 2003). Therefore, the macroinvertebrate variability with regard to environmental tolerances and preferences within the different taxa were not large enough to disguise any patterns of spatiotemporal structuring. Different macroinvertebrate taxa respond differently to seasonal changes (i.e., environmental, fish) which results in community structure shifts (Clement, 2004). The dominance of taxa such as Corixidae, Physidae and Dystisidae during the low water period (i.e., cool-dry season) was potentially also related to high macrophyte cover which increased habitat heterogeneity. Macrophytes provide shelter against predation from taxa such a fish and provide more food resources (Hanson and Butler, 1994; Mereta et al., 2012). Several studies have highlighted the importance of environmental factors which play an important role in the structuring of community patterns, with water temperatures, habitat complexity and alternative resources playing an important role in trophic interaction strengths in wetlands (Cuthbert et al., 2022; Dalu and Wasserman, 2022).

Table 5
Absolute and relative (in parenthesis) abundances of functional feeding groups (FFG) of macroinvertebrates over three seasons in Nylsvely Wetlands. Abbreviations: CF – Filterers, CG – collector-gatherers, PR – predators, SC – scrappers and SH – shredders.

FFG	Hot-dry	Cool-dry	Hot-wet	Total
CF	347 (21.9)	9 (1.7)	25 (2.8)	380 (12.7)
CG	28 (1.7)	176 (34.1)	63 (7.1)	276 (8.9)
PR	404 (25.5)	120 (23.2)	208 (23.6)	731 (24.5)
SC	800 (50.5)	202 (39.1)	580 (65.9)	1589 (53.1)
SH	7 (0.4)	10 (0.6)	5 (0.3)	5 (0.7)
Total	1585 (53.2)	516 (17.3)	879 (29.5)	2980 (100)

Ecosystem health was generally considered to be good among the study seasons, with differences observed being related principally to upper reach activities (i.e., agriculture and urban pollution) and wetland area geology, particularly during the cool-dry season when most variables were high. Similar results were observed for environmental variables, particularly water and sediment chemistry, within the same wetland system (Greenfield et al., 2007, 2012; Musa et al., 2017; Dalu et al., 2020a, 2020b). These differences were highlighted by changes in macroinvertebrate community composition among sites and seasons, and this was further supported by the RDA analysis which found sediment (e.g., Ca, Cu, Na, Fe, ORP, P) and water (e.g., turbidity, temperature, ORP, pH, TDS) to be important, but that responses among taxa were variable. For example, Fe and Cu concentrations were found to significantly alter macroinvertebrate community structure (Cadmus et al., 2018) and these two metals were found to be positively related to the cool-dry season which had low macroinvertebrate abundance and diversity in the present study. Indeed, this system was distinct within both the hot-wet and hot-dry seasons compared to the cool-dry season with regards to functional groupings of taxa.

The low shredder proportion was expected as this group is dependent upon high canopy cover for organic matter provision (Mangadze et al., 2019), which is lacking in this study system. Several studies have additionally attributed shredder distribution and relative abundance to changes in environmental factors and terrestrial organic matter input (Masese et al., 2014; Mangadze et al., 2019). Therefore, limited shredder presence can have substantial implications for ecosystem functioning in riparian zones and can result in significant shifts through trophic cascades. Low

Table 6
Ratios of functional feeding group (FFG) analysis for macroinvertebrates from Nylsvley Wetland categories. For abbreviations see Table 1, seasons: HD – hot-dry, CD – cool-dry, HW – hot-wet.

Ecosystem attribute	HD FFG ratio	Interpretation	CD FFG ratio	Interpretation	HW FFG ratio	Interpretation
P/R	114.52	Very strongly autotrophic	62.41	Very strongly autotrophic	209.09	Very strongly autotrophic
CPOM/FPOM	0.02	Shredders very underrepresented, poor linkage to riparian inputs	0.02	Shredders very underrepresented, poor linkage to riparian inputs	0.03	Shredders very underrepresented, poor linkage to riparian inputs
TFPOM/BFPOM	12.60	Heavy suspended FPOM load (or good FPOM quality)	0.05	Very light suspended FPOM load (or very poor FPOM quality)	0.39	Reduced suspended FPOM load (or poor FPOM quality)
Substrate/channel stability	50.02	Stable substrates abundant	3.50	Stable substrates abundant	9.57	Stable substrates abundant
P/P	0.34	High predators	0.30	High predators	0.31	High predators

abundances of shredders have been attributed to the nutritional quality of leaves (Tomanova et al., 2006; Ferreira et al., 2014) and climate variability, as many shredders are adapted to cold water and may be nearer to their thermal maxima in the tropics (Masese et al., 2014). Thus, it is important to highlight that the low TFPOM to BFPOM ratio in turbid systems, such as the Nylsvley Wetlands, likely reflects the quality rather than quantity of the suspended load.

Within wetland ecosystems, autotrophic production is often dominant and sustains aquatic food webs (Dalu et al., 2016; Hall et al., 2020). Similarly, all seasons were strongly autotrophic, as indicated by high P/R ratio in the present study, with the CPOM/FPOM ratio indicating shredders to be very poorly represented, and with reduced linkage and input to the terrestrial environment. The high P/R ratio was observed due to the dominance of scrapers (i.e., Physidae, Baetidae, Corixidae) across all seasons. Thus, high channel stability can likely also be attributed to the fact that the Nylsvley Wetlands were strongly autotrophic, which increased scrapers and collector-filterer proportions, which are reliant on autotrophy and require stable surfaces for attachment or grazing. It is also important to highlight that environmental variability could lead to macroinvertebrates changing their feeding mode, and taxonomically-linked groups generally exhibit diverse diets across regions (Wallace and Webster, 1996; Cummins et al., 2005). In addition, the FPOM in transport (TFPOM/BFPOM) macroinvertebrate surrogate ratio was low, as indicated by few collector-filterer taxa during the cool-dry season, which may have been compromised due to the rains experienced during our sampling dates and increased wildlife activity (T.D., *personal observation*).

In conclusion, we found that selected environmental variables and fish had an influence on macroinvertebrate community structuring across Nylslvey Wetland, with strong spatiotemporal differences for many parameters. Being a protected area, this information could provide a useful baseline for further studies into wetlands in the region subject to greater anthropogenic stresses, as well as future studies in this Ramsar site under global changes. Further studies are required to assess the importance of biotic factors for macroinvertebrate composition and distribution within tropical wetlands.

CRediT authorship contribution statement

Tatenda Dalu: Conceptualization, Investigation, Data curation, Formal analysis, Supervision, Funding acquisition, Writing – original draft. **Ross N. Cuthbert:** Conceptualization, Methodology, Writing – original draft. **Mathapelo J. Methi:** Investigation, Writing – review & editing. **Farai Dondofema:** Investigation, Visualization, Writing – review & editing. **Lenin D. Chari:** Investigation, Visualization, Writing – review & editing. **Ryan J. Wasserman:** Conceptualization, Investigation, Visualization, Writing – review & editing.

Declaration of competing interest

All co-authors have seen and agree with the contents of the manuscript and there is no financial interest to report. Thus, all authors have declared that no competing interests exist.

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