



Macroinvertebrate taxa display increased fidelity to preferred biotopes among disturbed sites in a hydrologically variable tropical river

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Abstract Understanding the biotope requirements of the various aquatic biota is crucial for effective biomonitoring. Yet, the biotope preferences of macroinvertebrates in Afrotropical rivers have been poorly studied. In this study, we investigated the influence of human disturbance and flow-driven biotope changes on the β -diversity and biotope preferences of macroinvertebrates in the Mara River, Kenya. Macroinvertebrates were sampled from various biotopes at seven reference and nine impaired sites

in wet and dry seasons. β -Diversity was determined (i) for each biotope and (ii) at the site scale, combining all biotopes sampled, and macroinvertebrate biotope preferences were assessed among biotopes between reference and impaired sites. Minor β -diversity differences were observed between reference and impaired sites based on relative abundance data, but differences were greater when the presence–absence data were used. There were no statistically significant changes in macroinvertebrate biotope preference due to human disturbance, but fidelity to preferred biotopes increased at impaired sites. In fast-flowing waters, Simuliidae, Baetidae, Tricorythidae, and Hydropsychidae dominated stable rocky substrates and were the most sensitive to flow alteration. This study adds valuable information on the effects of

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biotope reduction/loss and flow alteration on the diversity and biotope preferences of macroinvertebrates in Afrotropical rivers, and contributes to improvement of relevant bioassessment protocols and biodiversity conservation efforts.

Keywords Biotope preferences · Bioindicators · Flow alteration · Macroinvertebrates · Rheophilic taxa

Introduction

Worldwide, there has been considerable hydro-morphological alteration as a result of land use change from forested to agricultural and urban areas, uncontrolled infrastructural development, and increased water withdrawal (Arthington, 2012; Grill et al., 2019). These human-induced modifications resulted in an upsurge of studies on the equitable allocation of freshwater resources between humans and the environment (Arthington et al., 2010; Johansson et al., 2016). There has been particular interest in understanding the effects of human development on biodiversity and ecological integrity of streams and rivers. But in order to maintain natural flow regimes in rivers, research has also focused on studying flow–ecology relationships and on applying bioindicators as decision support tools for allocating freshwater among uses, including the ecosystems (Poff & Zimmerman, 2010; Webb et al., 2013).

Impacts arising from land use changes are manifested through alterations of natural flow regimes that further influence aquatic communities. In rivers, flow is a master variable (Poff et al., 1997), which exerts a direct physical force on aquatic communities, but also affects them indirectly by influencing biotope availability and suitability (Hart & Finelli, 1999; Dallas, 2007; Demars et al., 2012). Studying river biotopes has emerged as a practical and meaningful way of linking the ecology of macroinvertebrates and river hydromorphology and can be used to assess hydromorphological degradation in rivers. Biotopes are often defined based on hydraulic (flow velocity, water depth) and substrate characteristics (stones, vegetation, or sand) (Bonada et al., 2006; Dallas, 2007). Differences in biotope availability and suitability at a river reach or site influence macroinvertebrate communities, which include various taxa with different

preferences and requirements (Demars et al., 2012). For instance, stone and vegetation biotopes generally support a diverse array of macroinvertebrates (Chutter, 1970; Dallas, 2007), while sandy biotopes support few macroinvertebrates (Quinn & Hickey, 1990; Brewin et al., 1995).

In spite of the growing popularity of using macroinvertebrate communities in bioassessments of ecological integrity of streams and rivers across the Afrotropics (e.g., Chakona et al., 2008; Kasangaki et al., 2008; Masese et al., 2013), studies investigating relationships between aquatic communities and hydrologic and/or hydraulic parameters, which is a prerequisite for understanding flow–ecology relationships, are very limited (Dallas, 2007; Muñoz-Mas et al., 2019). This limits their use in environmental flow assessments (EFAs). Studies have shown that macroinvertebrate communities are sensitive to small-scale changes in biotope availability (Brooks et al., 2005; Minaya et al., 2013; Muñoz-Mas et al., 2019). Thus, identifying macroinvertebrate taxa that are most responsive to changes in environmental conditions and biotope availability as a result of land use change and flow alteration would contribute significantly to improve their use as bioindicators in EFAs.

While most East African rivers are currently free flowing, plans are underway to dam many of them to provide water for irrigation and industrial and domestic use (UN-Water Africa, 2003). In addition, many rivers are experiencing significant flow-regime alteration due to the replacement of previously forested areas by agricultural and urban land, increased water abstractions, and prolonged, often human-induced, droughts (Kashaigili et al., 2007; McClain et al., 2014). There have been efforts to define and deliver environmental flows in some of these rivers, but data on the response of aquatic communities to flow alteration and flow-related habitat modifications and loss are limited (Muñoz-Mas et al., 2019). More specifically, there are limited data on indicator taxa among aquatic communities that can be used for assessing the ecological effects of flow-related changes in water quality, biotope availability, and ecological integrity in rivers of the region. River flow or hydrology has been considered as a key variable affecting the dynamics and distributional patterns of aquatic communities (Schiemer, 2016).

In this study, we investigated the influence of human disturbance and flow-driven hydraulic and biotope availability changes in on the diversity and biotope preferences of benthic macroinvertebrates in the transboundary Mara River (Kenya and Tanzania). Our specific objectives were to (1) determine the influence of human disturbance on β -diversity of macroinvertebrate communities; (2) determine the frequency of occurrence of taxa among biotopes (within and among sites), and assess whether differences are greater among biotopes than among sites at various levels of human disturbance; and (3) identify macroinvertebrate taxa that are most affected by biotope loss/ reduction and flow alteration, to be potentially used as indicator taxa in EFAs.

Materials and methods

Study area

This study was conducted on the Mara River that originates from the Mau Escarpment in Kenya and drains into Lake Victoria through Tanzania (Fig. 1). The Mara River has its source in the Mau Forest Complex, which is an extensive tropical moist broad-leaf forest.

Until the 1950s, the upper reaches of the Mara River Basin were mainly covered by montane forest. The middle and lower reaches were characterized by a mixture of scrublands and grasslands, with often occurring signs of forest clearance. Two perennial tributaries, the Nyangores and Amala Rivers, drain the forested headwaters and join to form the Mara River mainstem. In the middle and lower reaches, all tributaries draining the grasslands and scrublands are ephemeral, including the Talek and Sand Rivers despite their extensive drainage basins. The Talek River and the Upper Sand River drain the Kenyan part before the Mara River crosses into Tanzania.

On the Mau Escarpment, climate is cooler and seasonal due to the high altitude characterized by distinct rainfall seasons and reduced ambient temperatures during January and February. Rainfall varies across the basin based on altitude, with the highlands receiving around 2,000 mm of rainfall per annum and the lowlands around 1,000 mm (Camberlin et al., 2009). On the Mau Escarpment, dry conditions are experienced from January to March and wet

conditions during April–May and October–November. The rest of the basin is drier, with a dry–wet sequence that does not match that of the upper basin (Jackson & McCarter, 1994).

Among the rivers that drain into Lake Victoria, the Mara is unique because of its transboundary nature and role in the economy of both Kenya and Tanzania as it supports two of the region's most renowned conservation areas and tourist attractions; the Maasai Mara National Reserve in Kenya and the Serengeti National Park in Tanzania. The basin is also ecologically diverse with the wetter upper reaches supporting mixed agriculture of both livestock and subsistence crops, while the drier middle reaches upstream of the conservation areas support large-scale cultivation of mainly wheat and maize and grazing. Pressures on the conservation areas both in the headwater and middle reaches are high, and there is evidence that the shifting land use in the basin has had significant effects on flow regimes in the river and its tributaries (Melesse et al., 2008). As a result, there have been increased incidences of reduced baseflow in the river during the dry season.

Data collection

Seven unimpacted—reference—sites were sampled in the upper Mara River reaches (six sites) and in the Maasai Mara National Reserve (one site), and nine impaired sites were sampled in the upper- and mid-reaches of the basin (Fig. 1). Sites were considered as reference if they were either in a forested basin, or in agricultural areas but with no towns or communities within 1 km upstream, riparian vegetation intact, and no detectable effects of grazing or human activity within 100 m of the riparian zone, including no signs of unnatural turbidity or hydrologic modification in the watershed. Impaired sites were identified as those with damaged and eroded riverbanks associated with livestock and hippos and obvious point and non-point sources of pollution such as municipal discharges within 10 river km upstream. Some sites in the Maasai Mara National Reserve and conservancies were categorized as impaired because of the presence of large populations of hippos which have been associated with organic pollution caused by their dung, loss of species richness of fish and invertebrates, and fish kills (Dutton et al., 2018; Masese et al., 2018).

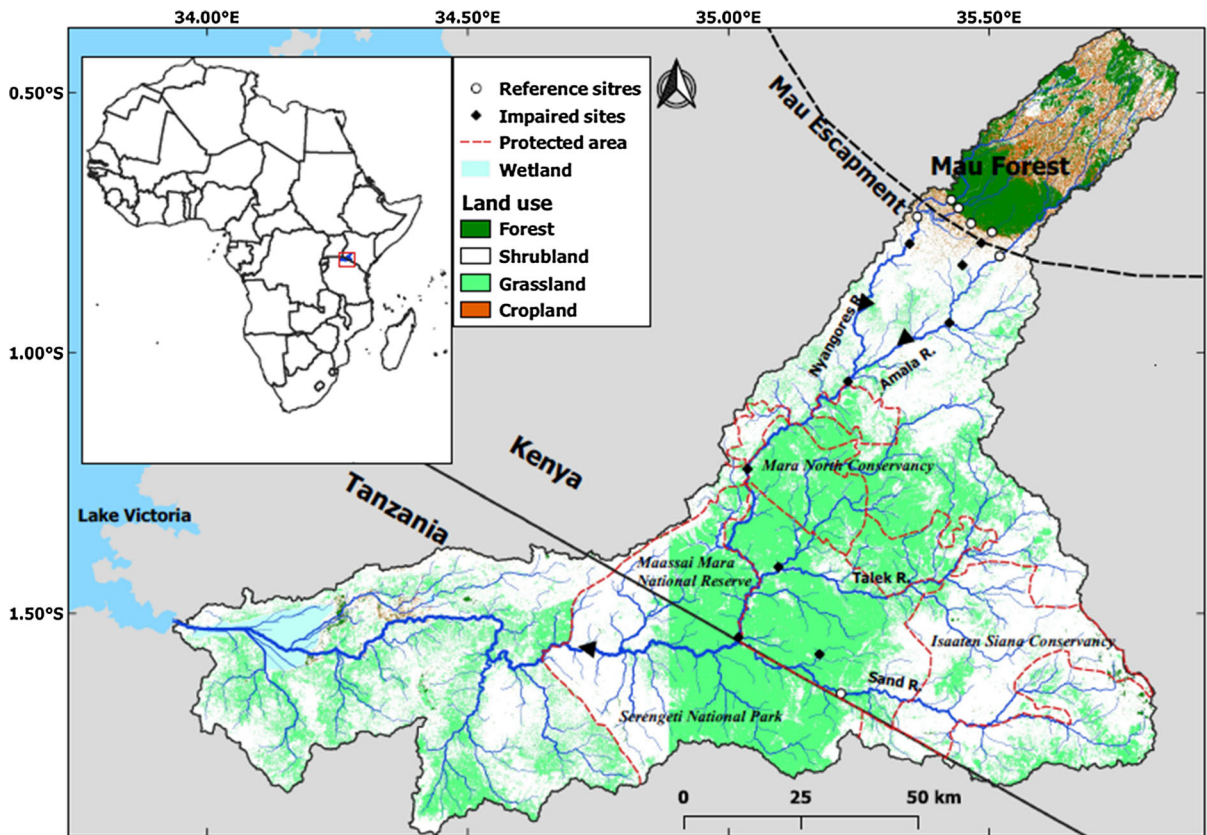


Fig. 1 Study sites in the Mara River Basin, Kenya/Tanzania

To capture the effects of flow variation on water quality and macroinvertebrate communities, sampling was carried out in January–March (dry period), May–July (wet periods), from 2013 to 2016. At the reference and impaired sites, pH, dissolved oxygen (DO), temperature, and electrical conductivity were measured in situ using a YSI multiprobe water quality meter (556 MPS, Yellow Springs Instruments, Ohio, USA). Water samples were collected for analysis of soluble reactive phosphorus (SRP), nitrate (NO_3^-), total suspended solids (TSS), and major ions (Cl^- , SO_4^{2-} , Na^+ , K^+ , Ca^{2+} and Mg^{2+}). Water samples for SRP, NO_3^- , and major ions were filtered on site through pre-combusted (450°C for 4 h) and pre-washed Whatman GF/F filters into acid-washed HDPE bottles, and stored at 4°C until analysis. For TSS, water was filtered on site through pre-combusted and pre-weighed GF/F filters. We measured SRP and NO_3^- using standard colorimetric methods, while TSS was determined gravimetrically (American Public Health Association, APHA, 1998). Major anions

NO_3^- , Cl^- , and SO_4^{2-} were determined using a Dionex ICS-1000 ion chromatograph equipped with an AS-DV auto sampler, and the major cations Na^+ , K^+ , Ca^{2+} , and Mg^{2+} using an ICP-MS.

Macroinvertebrate sampling was done according to Dickens & Graham (2002) using a semi-quantitative kick-net sampling method. Within each site, the following biotopes were delineated and sampled: (i) GSM: gravel, sand and mud; (ii) STONES: bedrock, boulders, cobbles, and pebbles, either in flowing or no-flow conditions; (iii) VEG: aquatic and marginal/riparian vegetation. The sampling method involved disrupting/kicking the bottom upstream of the net (500- μm mesh size), so that when dislodged, invertebrates are washed into and collected in the net. Kicking was conducted for a standard 1 minute per biotope in an area that was approximately 1 m^2 . Larger substrates (including cobbles and boulders) were disturbed and washed into the net by hand. Three random kick samples were collected per biotope, pooled and preserved in ethanol (75%) for further

processing in the laboratory. For each biotope sampled, data on water depth and velocity were collected. At the impaired sites, additional data on substrate types and coverage were collected for each biotope. Visual estimates of substrate sizes and coverage were made using a sampling quadrat adapted from Simonsen (1993). A biotope was divided into nine equal-size sub-sampling units and the number of units occupied by different substrate types was counted. The substrate type (based on a modified Wentworth scale: boulders, cobbles, pebbles, gravel, sand, and mud) with > 50% coverage within the quadrat was considered dominant. The first three substrate categories (boulders, cobbles, and pebbles) constituted the STONES biotope, while the last three (gravel, sand, and mud) constituted the GSM biotope. In addition to substrate types, the instream area covered by coarse particulate organic matter (CPOM) and vegetation or grasses was also estimated.

Macroinvertebrate samples were sorted in the laboratory, enumerated, and identified mostly to family level using a number of taxonomic keys, such as Gerber & Gabriel (2002), Day & de Moor (2002a, b), Day et al. (2002), de Moor et al. (2003a, b), and Merritt et al. (2008). For species-rich families (Baetidae, Caenidae, and Hydropsychidae) whose taxa display varied responses to environmental degradation (Dickens & Graham, 2002; Masese & Raburu, 2017), identifications were done to genus level.

Data analysis

We used two-sample *t* tests to compare water quality variables between reference and impaired sites separately for the dry and wet seasons. Non-metric multidimensional scaling (NMDS) ordination was used to explore variation in the composition of macroinvertebrate taxa among biotopes (VEG, STONES, GSM) and between disturbance classes (reference and impaired). Bray–Curtis dissimilarity matrices (1957) were derived based on absolute abundance (count) data of all macroinvertebrate taxa across all biotopes and sites using the R function “vegdist” (Gardener, 2014). Permutational multivariate analysis of variance (PERMANOVA) was used as implemented in the “adonis” function of the vegan R package (Oksanen et al., 2018) to test for significant differences among communities with biotope nested

within sites in each disturbance class as explanatory variables. For pairwise differences between biotope community compositions, PERMANOVA tests were run for all biotope pairs using “adonis.pair” function of the EcolUtils R package (Salazar, 2018), and used Bonferroni correction to set significance levels for *P* values. Analysis of multivariate homogeneity of group dispersions (variances) to test whether one biotope was more variable than the others was performed using the “betadisper” function of the vegan R package. In all the aforementioned tests, statistical significance was determined by 999 permutations.

To illustrate relationships between environmental data (temperature, TSS, and hydraulic variables) and taxa abundances (response variables), redundancy analysis (RDA) was used. Before RDA was performed, the gradient length in standard deviation (SD) units was estimated using detrended correspondence analysis to test the suitability of a canonical correspondence analysis and a posterior numerical analysis involving techniques based on a unimodal species response model (ter Braak & Smilauer, 2004). Gradient length was < 3 SD, justifying the use of RDA to determine which factors were responsible for the structure or groupings of taxa among biotopes (ter Braak & Smilauer, 2004). To determine which key macroinvertebrate taxa were responsible for the differences observed between biotopes, and hence the preferred biotopes for the taxa, similarity percentages analysis (SIMPER) was used. The percentage contribution of each taxon to the overall dissimilarity between biotopes was quantified. SIMPER is a strictly pairwise analysis between two factor levels (Clarke & Warwick, 2001), and in this case comparisons were made between GSM and STONES, GSM and VEG, and lastly STONES and VEG.

We estimated β -diversity with the method of multivariate dispersion, which estimate β -diversity as the average dissimilarity (i.e., distance) of sites or biotopes from a group centroid in multivariate space (Anderson et al., 2006). We defined groups at two levels, first by site (grouped as either reference or impaired disturbance classes) and then by the sampled biotopes within each site (STONES, GSM, VEG). We calculated β -diversity in two ways: (1) by taking the group average distance from the centroid of all biotopes (STONES, GSM, VEG) at each site (between biotope dispersion) and (2) within each biotope,

calculating the mean distance to the centroid of that biotope within the site (within biotope dispersion). We then calculated a measure of overall dispersion for each site as the ratio of between biotope dispersion and within biotope dispersion. We used the Bray–Curtis distance based on the presence–absence data and Morisita–Horn distance based on abundance data as metrics of dissimilarity (or average distance) using the R function “vegdist” (Gardener, 2014), to determine how much of the dissimilarity is driven by differences in community composition and relative abundances of taxa (Anderson et al., 2006). Morisita–Horn distance takes into account the relative abundances of species and is reported to be robust to under-sampling and unequal sampling sizes, while putting most weight on shifts in the dominant community composition (Barwell et al., 2015). Differences in β -diversity were measured with the “betadisper” function of the vegan package in R.

For all statistical analyses, family-level identifications of macroinvertebrates were used. ANOSIM and SIMPER analyses were performed using Paleontological Statistics (PAST) software package (Version 2.17; Hammer et al., 2001). NMDS, PERMANOVA, RDA, and multivariate dispersion were performed using the “vegan” package (Oksanen et al., 2018) and some of the default functions in R environment (R Development Core Team, 2017).

Results

Water quality

Statistically significant physical and chemical differences were detected between reference and impaired sites (Table 1). The concentration of most physical and chemical variables was significantly higher at impaired sites than at reference sites during both dry and wet seasons. Electrical conductivity, water temperature, total suspended solids, nutrients, and major ions were significantly higher at impaired sites. Dissolved oxygen was significantly lower at impaired sites (Table 1).

Macroinvertebrate community composition

A total of 117 biotopes were sampled across the seven reference sites—59 during dry seasons and 58 during

wet seasons—and 77 biotopes were sampled across the 9 impaired samples—43 during dry seasons and 34 during wet seasons. The orders Coleoptera, Diptera, Ephemeroptera, Hemiptera, Odonata, and Trichoptera were the most diverse, each with four or more families at both reference and impaired sites. A total of 13 families occurred only at the reference sites, some sensitive to disturbance, such as Calamoceratidae, Polycentropodidae, Scirtidae, Pisuliidae, Dixidae, and Psychomyiidae, while 6 families occurred only at impaired sites, some very tolerant to poor water quality, such as Ephyridae, Lymnaeidae, and Syrphidae. The families Hydropsychidae and Philopotamidae (Trichoptera); Baetidae, Caenidae, Heptageniidae, and Tricorythidae (Ephemeroptera); Simuliidae and Chironomidae (Diptera); and Elmidae (Coleoptera) were the most widespread, occurring at most sites, both reference and impaired ones. At reference sites, other abundantly encountered families included Perlidae (Plecoptera), Crambidae (Lepidoptera), Tipulidae (Diptera), Potamonautidae (Decapoda), and Lepidostomatidae (Trichoptera). At the impaired sites, other abundantly encountered families included Gomphidae, Libellulidae, and Lestidae (Odonata); Naucoridae, Corixidae, and Belostomatidae (Hemiptera); and Tubificidae (Oligochaeta).

Both reference and impaired sites were dominated by 10 macroinvertebrate families (comprising more than 80% of all individuals during both seasons), which, however, differed between reference and impaired sites. At reference sites, the most abundant families for all seasons combined were Baetidae (18.14%), Simuliidae (16.6%), Tricorythidae (12.5%), Hydropsychidae (12.4%), Heptageniidae (10.7%), and other Diptera (7.8%). At the impaired sites, the most abundant families were Tricorythidae (18.4%), Hydropsychidae (16.6%), Baetidae (15.9%), Simuliidae (9.1%), Chironomidae (6.1%), and Gomphidae (4.8%).

Patterns of community structure

NMDS based on abundance data showed a clear differentiation between STONES and VEG biotopes in the impaired sites (Fig. 2c, d) at both the wet ($F = 8.02$, $P = 0.001$) and the dry ($F = 6.59$, $P = 0.003$) seasons. STONES and VEG were not differentiated for the reference sites (Fig. 2a, b) at both seasons (wet: $F = 1.88$, $P = 0.11$, /dry: $F = 2.93$, $P = 0.05$). This

Table 1 Means (\pm SD) of water quality and site characteristics at reference and impaired sites in the Mara River

Variables	Season	Impaired sites	Reference sites	<i>t</i> Value	<i>P</i> value
Calcium (mg/l)	Dry	16.8 \pm 6.2	2.3 \pm 27	3.80	0.004
	Wet	9.7 \pm 3.9	0.8 \pm 0.9	5.76	< 0.001
Chloride (mg/l)	Dry	4.6 \pm 2.4	3.9 \pm 1.5	0.72	0.487
	Wet	3.8 \pm 2.6	3.5 \pm 1.5	0.34	0.775
Electrical conductivity (μ S/cm)	Dry	211.8 \pm 127.6	74.6 \pm 15.6	3.20	0.013
	Wet	183.9 \pm 80.1	60.7 \pm 9.1	3.64	0.007
Dissolved oxygen (mg/l)	Dry	5.1 \pm 1.3	7.2 \pm 0.5	6.74	< 0.001
	Wet	5.9 \pm 1.3	8.1 \pm 0.5	6.96	< 0.001
Potassium (mg/l)	Dry	6.4 \pm 3.3	3.0 \pm 1.2	5.90	< 0.001
	Wet	5.1 \pm 2.1	2.3 \pm 2.1	4.11	0.001
Magnesium (mg/l)	Dry	2.1 \pm 0.7	0.6 \pm 0.5	5.40	< 0.001
	Wet	1.7 \pm 1.3	0.7 \pm 0.8	3.62	0.003
Sodium (mg/l)	Dry	17.2 \pm 5.5	5.6 \pm 1.9	5.90	< 0.001
	Wet	14.5 \pm 7.8	6.1 \pm 3.4	4.11	0.001
Nitrates (mg/l)	Dry	2.3 \pm 0.8	0.9 \pm 0.6	4.12	0.001
	Wet	3.7 \pm 0.6	1.0 \pm 0.7	5.21	< 0.001
pH (units)	Dry	7.8 \pm 0.9	7.2 \pm 0.6	0.87	0.398
	Wet	7.4 \pm 0.6	6.9 \pm 0.4	1.41	0.231
Soluble reactive phosphorus (mg/l)	Dry	107.7 \pm 29.3	45.9 \pm 21.4	4.82	< 0.001
	Wet	137.1 \pm 36.1	94.3 \pm 29.4	2.61	0.021
Sulfate (mg/l)	Dry	4.3 \pm 3.0	3.4 \pm 1.9	0.89	0.398
	Wet	8.5 \pm 6.1	3.1 \pm 2.1	1.08	0.310
Temperature ($^{\circ}$ C)	Dry	20.7 \pm 2.4	17.0 \pm 3.6	1.54	0.005
	Wet	19.6 \pm 2.7	16.1 \pm 1.8	3.77	0.002
Depth (m)	Dry	0.9 \pm 0.6	0.4 \pm 0.1	5.47	< 0.001
	Wet	1.4 \pm 0.9	0.9 \pm 0.6	1.41	0.840
Total suspended solids (mg/l)	Dry	95.3 \pm 33.0	44.6 \pm 13.6	2.87	0.034
	Wet	356.3 \pm 171.9	82.6 \pm 23.5	4.73	0.001
Velocity (m/s)	Dry	0.64 \pm 0.3	1.04 \pm 0.5	2.110	0.066
	Wet	1.04 \pm 0.5	1.2 \pm 0.5	1.11	0.290

Two-sample *t* test was used for significant differences between impaired and reference sites. *P* values in bold face indicate significant differences ($P < 0.05$) between reference and impaired sites

suggests that macroinvertebrate taxa display increased fidelity to the specific biotopes under human disturbance. There were no clear patterns of separation among biotopes that would be attributed to seasonality, suggesting that the biotope preferences of taxa remained similar across seasons. Taxa among Simuliidae, Tricorythidae, Hydropsychidae, and Baetidae displayed preference for and high abundances on the STONES biotope. The GSM biotope was preferred by species among Naucoridae, Corixidae, Gomphidae, Lumbriculidae and Tubificidae families, while the

VEG biotope was preferred by species among Notonectidae, Lestidae, Leptoceridae, Lepidostomatidae families, among others.

Macroinvertebrate community composition based on relative abundance data did not differ between reference and impaired samples in the dry season (PERMANOVA $F = 0.75$, $df = 1$, $P = 0.590$) but differed significantly in the wet season (PERMANOVA $F = 3.38$, $df = 1$, $P = 0.003$). However, differences were observed among the three biotopes (STONES, GSM, and VEG) during both the dry

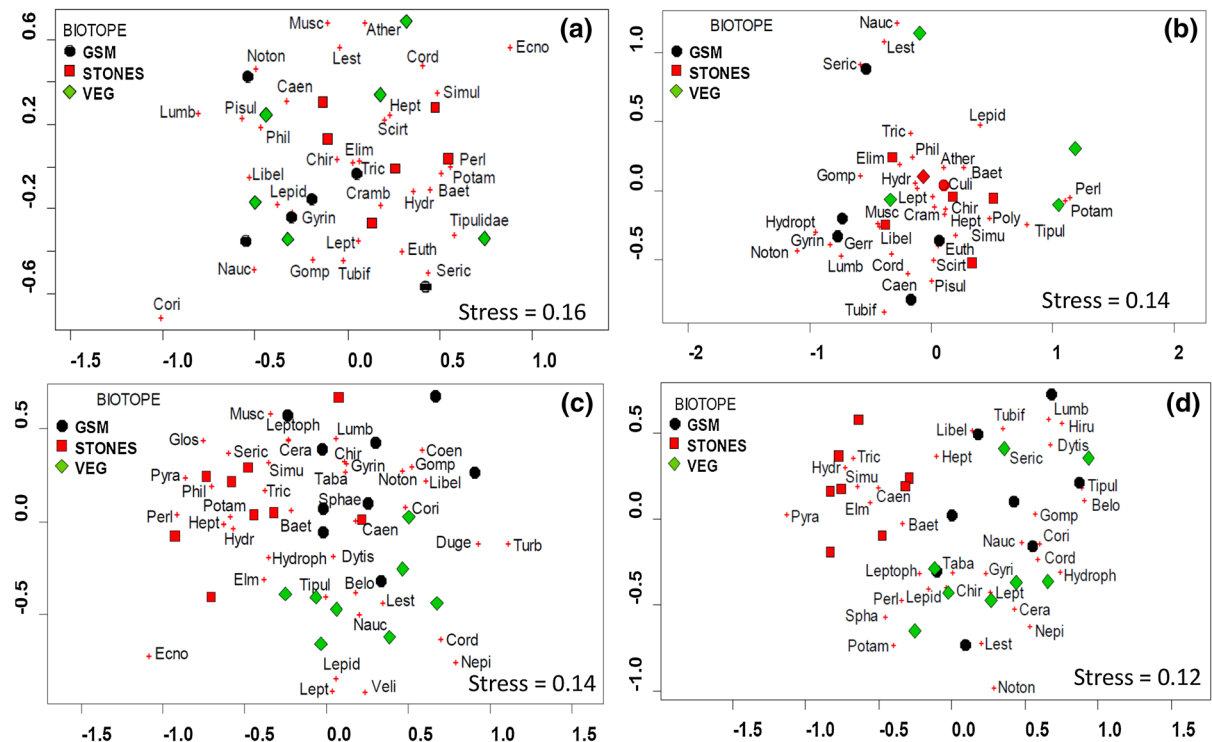


Fig. 2 Non-metric multidimensional scaling (NMDS) ordination of macroinvertebrate abundance data with respect to occurrence on biotopes in the reference sites data set [upper panel (a, b) and impaired sites data set (c, d) during the dry (a, c) and wet (b, d) seasons]. The first two axes of the NMDS accounted for > 65% of the total variance. *Nau* Naucoridae, *Lest* Lestidae, *Seric* Sericostomatidae, *Lepid* Lepidostomatidae, *Tric* Tricorythidae, *Phil* Philopotamidae, *Elim* Elmidae, *Ather* Athericidae, *Hydr* Hydropsychidae, *Baet* Baetidae, *Culi* Culicidae, *Lept* Leptoceridae, *Chir* Chironomidae, *Perl* Perlidae, *Potam* Potamonautidae, *Musc* Muscidae, *Cram* Crambidae,

Hept Heptageniidae, *Simu* Simuliidae, *Poly* Polycentropodidae, *Tipu* Tipulidae, *Noton* Notonectidae, *Hydropt* Hydroptilidae, *Gyrin* Gyrinidae, *Gerr* Gerridae, *Libel* Libellulidae, *Lumb* Lumbriculidae, *Cord* Corduliidae, *Scirt* Scirtidae, *Caen* Caenidae, *Pisul* Pisuliidae, *Tubif* Tubificidae, *Gomp* Gomphiidae, *Ecno* Ecnomidae, *Glos* Glossosomatidae, *Pyra* Pyralidae, *Veli* Veliidae, *Belo* Belostomatidae, *Dytis* Dytiscidae, *Sphae* Sphaeriidae, *Taba* Tabanidae, *Cera* Ceratopogonidae, *Leptoph* Leptophlebiidae, *Coen* Coenagrionidae, *Turb* Turbellaria, *Nepi* Nepidae, *Cori* Corixidae, *Hir* Hirudinea

(PERMANOVA $F = 7.51$, $df = 2$, $P = 0.001$) and wet (PERMANOVA $F = 5.14$, $df = 2$, $P = 0.001$) seasons. Using the presence–absence data, macroinvertebrate community composition differed between reference and impaired samples during both the dry (PERMANOVA $F = 4.85$, $df = 1$, $P = 0.001$) and wet (PERMANOVA $F = 2.15$, $df = 1$, $P = 0.038$) seasons. Similarly, differences were observed among the three biotopes during the dry (PERMANOVA $F = 4.66$, $df = 2$, $P = 0.001$) and wet (PERMANOVA $F = 4.18$, $df = 2$, $P = 0.001$) seasons.

Pairwise comparisons of β -diversity in the same biotope between reference and impaired sites (e.g., GSM-Reference vs. GSM-Impaired) differed in dispersion when using the presence–absence data during the dry season (permutest $F = 2.91$, $df = 5$, $P = 0.021$),

but only marginal differences were observed during the wet season (permutest $F = 2.03$, $df = 5$, $P = 0.065$). Greatest differences between impaired and reference sites were observed between GSM and STONES biotopes, with greater differences during the dry season. However, when using abundance data, no differences were observed during both the dry and wet seasons.

Multivariate dispersion was not significantly different between disturbance classes during both the dry and wet seasons based on the Bray–Curtis distance metric (Fig. 3). However, there was a significant difference in β -diversity between reference and impaired disturbance classes during the dry season based on the Morisita–Horn distance metric. Between biotopes dispersion was higher at the impaired sites

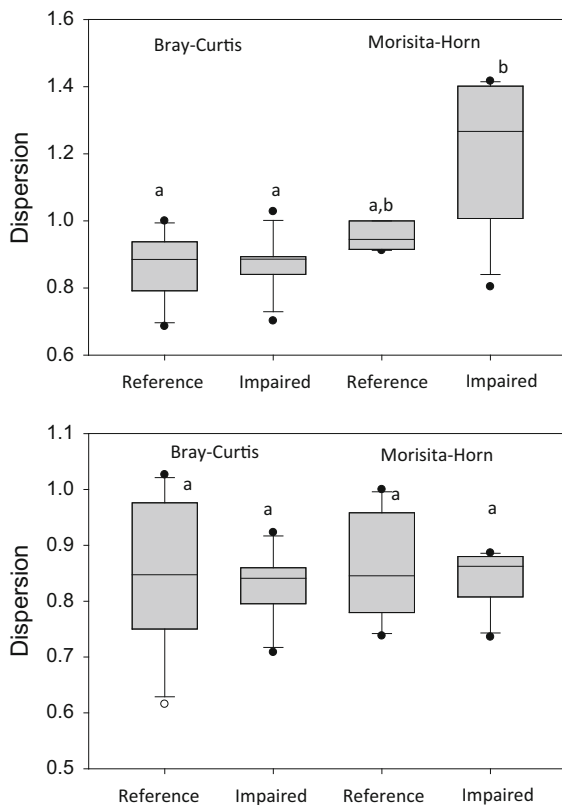


Fig. 3 Mean sample distances from beta diversity centroid for reference and impaired disturbance classes using Bray–Curtis and Morisita–Horn distance (dissimilarity) index during the dry season (upper panel) and wet season (lower panel). Median values (middle line), 1st and 3rd quartiles (boxes), 1.5 times inter-quartile range (whiskers), and outliers (dots) are shown. Boxes topped by the same letter (a or b) do not differ significantly at $P \leq 0.05$ by ANOVA

(1.19 ± 0.24) than at reference sites (0.95 ± 0.04) (Fig. 3).

The RDA ordination of macroinvertebrate taxa with hydraulic parameters (depth, velocity, and substrate) and other physical variables (temperature, width, and TSS) showed similar associations of taxa with specific biotopes (Fig. 4) as observed with the NMDS ordination. RDA Axis 1 accounted for the greatest variance (% explained variance, range 26.3%–49.1%) in the data for all ordinations at the reference and impaired sites for both the dry and wet seasons (Fig. 4a–d), while the second RDA Axis accounted for 15.0–27.4%. Species and hydraulic variables displayed significant correlation for the first 2 axes for all ordination, with RDA Axis 1 positively correlated with velocity and stable substrate (boulders

and cobbles), while RDA Axis 2 was positively associated with water depth and TSS (Fig. 4a–d). For the reference sites, there was no clear differentiation of biotopes unlike the case for impaired sites where the STONES biotope was clearly differentiated from the VEG and GSM biotopes along RDA Axis 1. This suggests that with minimal or no human disturbance, taxa displayed limited preference for specific biotopes, while at the impaired sites preference for specific biotopes was high. This further confirmed that fidelity to biotopes increased among taxa with human disturbance in the study area.

There were clear associations of specific taxa with hydraulic parameters and other physical variables, and, again, associations of specific taxa with particular biotopes were clearer for the impaired sites (Fig. 4). Taxa associated with the STONES biotope, which was characterized by bedrock, boulders, and cobbles, included Simuliidae, Baetidae, Philopotamidae, Tricorythidae and Hydropsychidae, Pyralidae and Elmidae. On the other hand, Lumbriculidae, Leptophlebiidae, Tubificidae, Gyrinidae, Corixidae, and Gomphidae displayed associations with GSM (silt, mud, and sand). The VEG biotope (mainly grass) was associated with Lestidae, Nepidae, Hydrometridae, Notonectidae, Naucoridae, among others.

Biotope preferences among taxa

The relative frequency of occurrence of each taxon on GSM, STONES, and VEG biotopes were investigated separately for the reference (Table 2) and impaired sites (Table 3). Some taxa displayed particular preference for one biotope (relative % > 50), while most did not. For both the reference and impaired sites, the wet season supported a similar number of taxa across biotopes, with the VEG biotope supporting a slightly higher number than the other two biotopes. During the dry season, differences among biotopes were greater than during the wet season. The VEG biotope supported the largest number of biotope-specific taxa followed closely by the STONES biotope. For taxa collected during the dry and wet seasons, fidelity remained unchanged with respect to biotope preferences.

SIMPER analysis identified ten families that contributed greatest to the dissimilarity between biotopes: GSM vs. STONES, GSM vs. VEG, and STONES vs. VEG biotopes, for each season (Tables 4, 5). Families

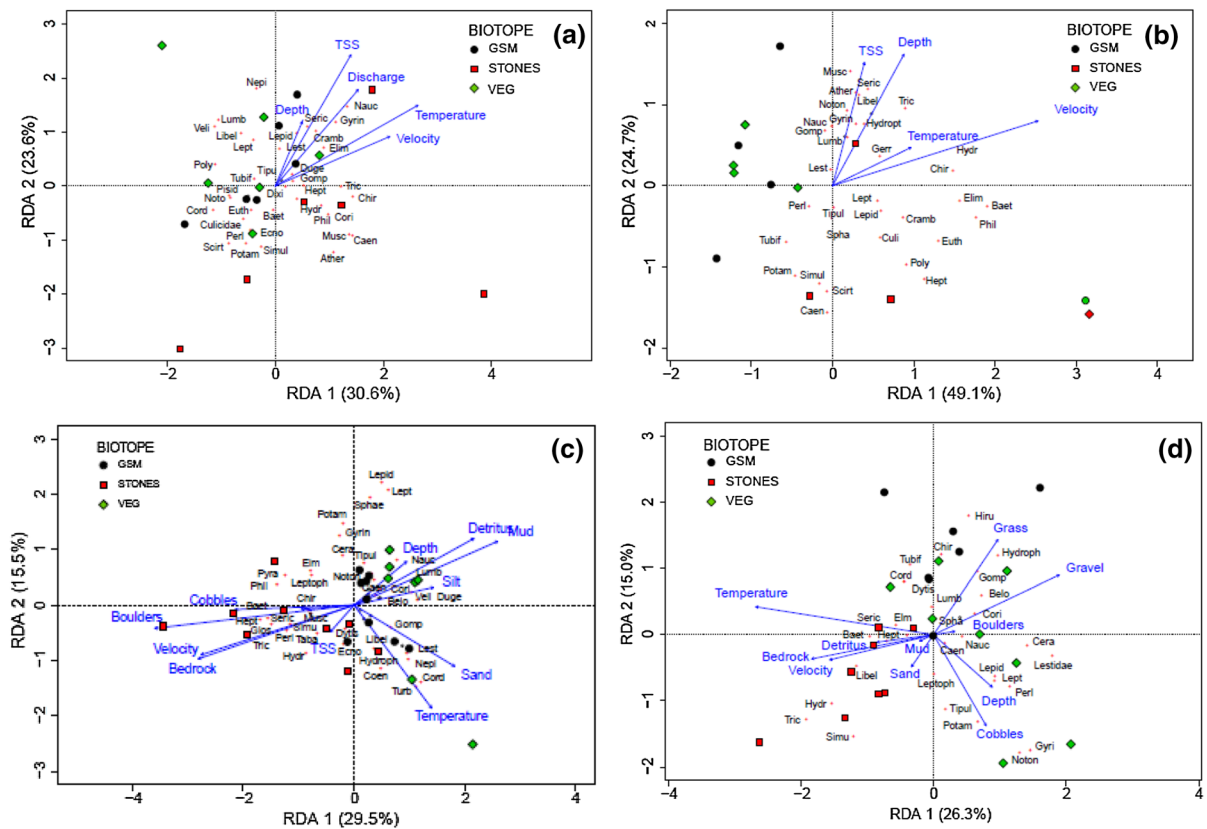


Fig. 4 Redundancy analysis (RDA) used to elucidate relationship between hydraulic parameters and biotope preferences for various macroinvertebrate taxa in the Mara River based on the

Hydropsychidae, Tricorythidae, Simuliidae, and Baetidae were more abundant on the STONES biotope, whereas Gomphidae and Tubificidae were more abundant on the GSM biotope during both the dry and wet seasons. Genera among the key families with biotope-specific requirements for stable substrate (STONES) included Simuliidae, *Centroptiloides* sp. (Baetidae, Ephemeroptera), *Baetis* sp. (Baetidae), *Tricorythus* sp. (Tricorythidae), *Hydropsyche* sp., and *Cheumatopsyche* sp. (Hydropsychidae) which displayed similar hydraulic requirements as the families they belong to by being more abundant in fast flows in the stable STONES biotope (Table 3; Fig. S1). Families that were identified to contribute greatest to the dissimilarity between GSM and VEG biotopes were Baetidae, Chironomidae, Corixidae, Gomphidae, Lestidae, Naucoridae, and Tubificidae (Tables 4, 5). Rheophilic families such as Hydropsychidae, Tricorythidae, and Simuliidae also featured in

reference sites data set (a, b) and impaired sites data set (c, d) during the dry season (a, c) and wet season (b, d). Acronyms for taxa names remain as in Fig. 1

the VEG biotope, as they attached themselves to vegetation in current. Families Hydropsychidae, Tricorythidae, Simuliidae, and Baetidae were also identified as contributing greatest to the dissimilarity between STONES and VEG biotopes. Families Belostomatidae, Naucoridae, and Lestidae showed preference for the VEG and STONES biotopes.

Twenty key macroinvertebrate families that were identified by SIMPER analyses can be used to monitor biotope availability and suitability for a diverse macroinvertebrate community in the Mara River (Table 6). Taxa within these families belong to all five major functional feeding groups (Cummins & Klug, 1979), which are adapted to different biotopes, hence able to capture different forms of disturbance in the river, including riparian disturbance, deposition, and organic pollution (Masese et al., 2014; Merritt et al., 2017).

Table 2 Relative frequency of occurrence (%) of each taxon in three major biotopes (GSM, STONES, and VEG) at reference sites in the Mara River Basin during the dry and wet seasons

Taxa	Wet season			Dry season		
	GSM	STONES	VEG	GSM	STONES	VEG
Lumbriculidae	52.7	14	33.3	100	–	–
Tubificidae	67.1	–	32.9	19.3	21.1	59.6
Salifidae	44.6	55.4	–	–	–	–
Glossiphoniidae	33.5	41.7	24.7	73.2	26.8	–
Dugesidae	61.6	38.4	–	–	41.5	58.5
Potamonautidae	28.8	35.8	35.4	14.4	41.1	44.5
Arachnida			100			100
Perlidae	19.1	43.5	37.5	30.4	42.8	26.8
Baetidae	30.6	40	29.3	32	35.1	32.9
Caenidae	27.9	23.6	48.5	43.4	37.4	19.2
Ephemeridae	44.6	55.4	–	–	–	–
Heptageniidae	28.7	40.7	30.6	29.1	41	29.9
Leptophlebiidae	26.4	21.9	51.8	21.1	46.3	32.6
Oligoneuriidae	–	100	–	–	100	–
Polymitarcyidae	100	–	–	–	–	–
Propistomatidae	–	100	–	–	100	–
Tricorythidae	31.6	42.9	25.4	30.6	38	31.5
Coenagrionidae	57.6	–	42.4	19.3	21.1	59.6
Lestidae	29.3	11.4	59.3	51.4	16.9	31.7
Aeshnidae	32.3	20.1	47.6	64.6	35.4	0
Corduliidae	–	45.8	54.2	100	–	–
Gomphidae	52.2	32.5	15.4	58.9	13.4	27.8
Libellulidae	40.6	29.5	29.9	31.8	43.6	24.6
Crambidae	25.7	52.6	21.7	19.7	39.6	40.6
Belostomatidae	60.6	39.4	–	100	–	–
Gelastocoridae	–	–	100	–	–	–
Corixidae	61.6	38.4	–	100	–	–
Gerridae	50.4	0	49.6	35.5	9.7	54.8
Hydrometridae	–	100	–	–	–	100
Naucoridae	55.3	9.8	34.9	21.6	11.8	66.6
Nepidae	40.4	0	59.6	–	–	–
Notonectidae	76.3	23.7	–	39.3	–	60.7
Pleidae	–	–	–	–	–	100
Veliidae	40.4	–	59.6	–	–	100
Sisyidae	–	100	–	–	–	–
Ecnomidae	–	29.7	70.3	–	–	100
Hydropsychidae	31.3	50.9	17.7	27.6	38.3	34.1
Philopotamidae	24.9	31	44.1	30.8	37.5	31.7
Polycentropodidae	40.4	–	59.6	47.7	52.3	–
Psychomyiidae	0	100	–	–	100	–
Calamoceratidae		56.3	43.7			
Hydroptilidae	–	–	–	47.7	52.3	–

Table 2 continued

Taxa	Wet season			Dry season		
	GSM	STONES	VEG	GSM	STONES	VEG
Lepidostomatidae	29.2	23.6	47.3	25.3	17.7	57
Leptoceridae	42.4	26.4	31.2	14.4	26.3	59.3
Pisuliidae	–	–	–	100	–	–
Amphizoidae	–	44.2	55.8	–	–	–
Carabidae	–	–	100	–	–	–
Curculionidae	–	–	100	–	–	–
Dytiscidae	–	100	–	–	–	–
Noteridae	0	0	100	31.3	68.7	0
Elmidae	35.7	34.7	29.6	31.9	36.6	31.4
Gyrinidae	55.5	17.3	27.3	43.9	28.9	27.2
Haliplidae	30.2	38.2	30.6	29	47	22
Scirtidae	39.2	27.9	33	46.4	29.7	23.9
Hydrophilidae	–	100	–	–	–	–
Psephenidae	–	66	34	–	63.1	36.9
Athericidae	33.5	41.7	24.7	–	100	–
Chaoboridae	–	–	–	–	100	–
Ceratopogonidae	11.1	6.9	82	39.3	–	60.7
Chironomidae	31.9	36.1	32	31.6	30.2	38.2
Culicidae	57.6	–	42.4	19.3	21.1	59.6
Dixidae	100	–	–	100	–	–
Muscidae	22	45.6	32.4	54.9	45.1	–
Psychodidae	100	–	–	–	–	–
Simuliidae	10.5	53.3	36.2	27.4	34.1	38.5
Stratiomyidae	–	–	100	64.6	35.4	–
Sciomyzidae	100	–	–	100	–	–
Tabanidae	–	100	–	–	100	–
Tipulidae	27.7	39.6	32.7	21.3	35	43.8
Hydrobiidae	–	44.6	55.4	–	–	–
Planorbidae	–	–	–	100	–	–
Sphaeriidae	31	9.6	59.4	28.7	15.8	55.5

A dash (–) indicates that the taxon was not collected during that particular season. Taxa with a relative percentage $\geq 50\%$ are given in bold

NB: *GSM* gravel, sand, and mud, *STONES* stones-in-current and stones-out-of-current, *VEG* aquatic and marginal vegetation

Discussion

In this study, we explored macroinvertebrate community composition, β -diversity, and biotope preferences of different taxa in a range of sites at two levels of human disturbance (reference vs. impaired). Most of the water quality variables differed significantly between reference and impaired sites, with high seasonal variability in some of the variables, such as

TSS, concentrations of dissolved oxygen and major ions. Water quality was poorer during the low-flow dry season as a result of accumulation of solids and organic matter from large populations of livestock and wildlife (hippos) in the middle Mara and Talek River. The middle Mara and Talek regions are naturally erosion-prone (Sombroek et al., 1982), but this has also been accentuated by overgrazing and agricultural

Table 3 Relative frequency of occurrence (%) of each taxon in each biotope group at impaired sites in the Mara River during the dry and wet seasons

Taxon	Wet season			Dry season		
	GSM	STONES	VEG	GSM	STONES	VEG
Lumbriculidae	40	30	30	40	20	40
Tubificidae	34	25	41	71	–	29
Glossiphoniidae	–	–	–	–	100	–
Dugesiiidae	61.6	38.4	–	58.5	41.5	–
Potamonautidae	–	43	57	16	52	32
Arachnida	–	–	–	–	–	100
Perlidae	48	52	–	20	80	–
Baetidae	24	57	19	18	52	30
Caenidae	25	23	52	30	25	45
Heptageniidae	18	62	20	19	52	29
Leptophlebiidae	–	35	65	36	36	27
Oligoneuriidae	–	–	100	–	–	–
Polymitarcyidae	73	0	27	60	–	40
Prosopistomatidae	–	100	–	–	–	–
Tricorythidae	16	55	29	9	67	24
Coenagrionidae	–	–	–	55	18	27
Lestidae	38	–	62	32	16	52
Protoneturidae	–	–	–	–	–	100
Aeshnidae	–	63	24	18	55	27
Corduliidae	–	–	–	52	23	25
Gomphidae	51	22	27	58	18	24
Libellulidae	35	21	44	58	30	12
Crambidae	29	31	39	–	100	–
Belostomatidae	32	11	57	48	–	52
Corixidae	56	18	26	51	23	26
Gerridae	–	–	100	–	–	100
Hydrometridae	–	–	–	–	–	100
Naucoridae	32	15	53	39	5	55
Nepidae	–	–	–	–	–	100
Notonectidae	–	–	–	45	10	45
Veliidae	52	28	20	–	–	100
Mesoveliidae	–	–	–	–	100	–
Ecnomidae	100	–	–	–	–	100
Hydropsychidae	28	42	30	18	45	37
Philopotamidae	–	62	38	–	67	33
Hydroptilidae	–	–	–	–	40	60
Lepidostomatidae	14	30	56	–	50	50
Leptoceridae	43	–	57	–	67	33
Curculionidae	46	–	54	–	–	–
Dystiscidae	–	44	56	50	–	50
Elmidae	22	52	26	24	43	32
Gyrinidae	–	21	79	56	21	23

Table 3 continued

Taxon	Wet season			Dry season		
	GSM	STONES	VEG	GSM	STONES	VEG
Haliplidae	–	–	–	50	–	50
Helophoridae	63	–	37	–	–	–
Hydrophilidae	29	31	39	40	–	60
Athericidae	50	–	50	–	100	–
Chaoboridae	–	–	100	–	–	100
Ceratopogonidae	–	–	–	38	25	38
Chironomidae	40	42	18	31	34	36
Culicidae	46	–	54	63	–	37
Empididae	–	–	–	57	6	37
Ephydriidae	–	–	100	–	–	–
Muscidae	29	31	39	30	40	30
Psychodidae	100	–	–	–	–	–
Simuliidae	17	59	24	12	63	25
Syrphidae	–	–	–	100	–	–
Stratiomyidae	–	–	100	–	–	–
Sciomyzidae	–	–	–	100	–	–
Tabanidae	–	100	–	38	25	38
Tipulidae	–	75	25	35	12	54
Lymnaeidae	–	–	100	–	–	100
Planorbidae	–	–	100	–	–	100
Sphaeriidae	43	–	57	–	31	69
Unionidae	–	–	–	67	–	33

A dash (–) indicates that the taxon was not collected during that particular season. Taxa with a relative percentage $\geq 50\%$ are given in bold

NB: *GSM* gravel, sand, and mud, *STONES* stones-in-current and stones-out-of-current, *VEG* aquatic and marginal vegetation

expansion (Serneels & Lambin, 2001; Dutton et al., 2013).

There were significant differences in community composition between reference and impaired sites based on the presence–absence of taxa, but not taxa abundances. This suggests that species turnover assessment at the family level, and not the relative abundance of the various taxa, was more indicative of changes in environmental conditions and biotope availability and suitability. Lack of differences in relative abundance of various taxa between reference and impaired sites can be explained by a number of factors. First, it indicates that relative abundance of taxa was the same across sites despite the different levels of disturbance. Replacement of taxa within one family can also occur whereby intolerant taxa with high abundances at reference sites can be replaced by

tolerant taxa at impaired sites with equally high abundances. Indeed, differences in taxa identity between reference and impaired sites reflected in the number of taxa (taxa richness), whereby 73 families were recorded at reference sites and 64 families at impaired sites. Higher resolution in identification of the families to generic or species levels would have likely led to further differentiation between reference and impaired sites in terms of taxon richness. There is also potential for replacement of taxa between reference and impaired because of environmental (e.g., water quality and geomorphology), hydrological, and ecological differences (de Moor 2002). For instance, 13 families occurred only at the reference sites, some sensitive to disturbance, such as Calamoceratidae and Polycentropodidae, while 6 families occurred only at impaired sites, some very tolerant to poor water

Table 4 SIMPER contributions to differences in macroinvertebrates families between biotopes (GSM, STONES, and VEG) at reference sites in the Mara River during the wet and dry seasons

Wet season		Dry season	
Taxon	Cumulative %	Taxon	Cumulative %
GSM vs. STONES			
Simuliidae ²	16.4	Hydropsychidae ²	16.0
Baetidae ²	29.5	Baetidae ²	32.0
Heptageniidae ²	41.2	Simuliidae ²	47.5
Hydropsychidae ²	51.6	Tricorythidae ²	60.6
Chironomidae ²	60.9	Heptageniidae ²	69.2
Tricorythidae ²	68.8	Chironomidae ²	77.0
Elmidae ²	73.9	Philopotamidae ²	81.8
Philopotamidae	77.8	Caenidae ²	86.4
Lumbriculidae ¹	80.9	Elmidae ²	88.2
Caenidae ¹	84.0	Lumbriculidae ¹	89.5
Potamonautidae ²	86.5	Sphaeriidae ¹	90.6
Perlidae ²	88.6	Perlidae ²	91.6
Sphaeriidae ¹	90.5	Tubificidae ¹	92.3
Tipulidae ²	91.4	Ecnomidae ²	93.1
Lestidae ¹	92.3	Crambidae ²	93.8
GSM vs. VEG			
Baetidae ³	13.0	Baetidae ³	15.0
Chironomidae ³	25.3	Chironomidae ³	27.2
Heptageniidae ³	34.1	Caenidae ³	35.9
Tricorythidae ³	41.3	Tricorythidae ¹	42.8
Simuliidae ³	47.9	Hydropsychidae ³	49.1
Elmidae ³	54.3	Sphaeriidae ³	55.1
Hydropsychidae ³	60.4	Lestidae ³	60.7
Sphaeriidae ³	65.9	Lumbriculidae ¹	66.2
Philopotamidae ¹	69.5	Heptageniidae ¹	71.5
Caenidae ¹	73.1	Lepidostomatidae ³	75.4
Lumbriculidae ¹	76.6	Simuliidae ³	79.2
Leptoceridae ³	79.1	Philopotamidae ¹	82.7
Potamonautidae ³	81.4	Tubificidae ¹	85.0
Perlidae ³	83.6	Elmidae ¹	87.2
Lepidostomatidae ³	85.6	Leptoceridae ³	88.5
STONES vs. VEG			
Baetidae ²	15.3	Baetidae ²	16.0
Simuliidae ²	29.7	Hydropsychidae ²	31.6
Heptageniidae ²	41.8	Simuliidae ²	46.7
Chironomidae ³	51.7	Tricorythidae ²	58.8
Hydropsychidae ²	61.1	Heptageniidae ²	66.5
Tricorythidae ²	69.8	Chironomidae ²	74.2
Elmidae ³	75.7	Caenidae ²	79.5
Sphaeriidae ³	79.0	Philopotamidae ²	83.8

Table 4 continued

Wet season		Dry season	
Taxon	Cumulative %	Taxon	Cumulative %
Perlidae ²	81.5	Lestidae ³	85.8
Potamonautidae ²	83.8	Sphaeriidae ³	87.5
Caenidae ²	85.9	Elmidae ²	89.1
Leptoceridae ³	87.9	Lumbriculidae ³	90.7
Philopotamidae ³	89.7	Lepidostomatidae ³	92.1
Lepidostomatidae ³	91.2	Perlidae ²	93.0
Tubificidae ³	92.5	Tipulidae ³	93.7
Naucoridae ³	93.7	Ecnomidae ²	94.4

Superscript numbers on each macroinvertebrate taxon highlight at which biotope abundance was higher (1: GSM, 2: STONES, 3: VEG)

quality and low dissolved oxygen concentration, such as Lymnaeidae and Syrphidae that are air breathers (Dickens & Graham, 2002). Although identification of taxa to genus or species levels would have been more appropriate at uncovering differences in community composition between reference and impaired sites, a number of factors currently preclude the use of higher resolution identifications in bioassessment studies in the Afrotropics. Firstly, most biotic indices, such as SASS5 (Dickens & Graham, 2002), TARISS (Kaaya et al., 2015), and ETHbios (Aschalew & Moog, 2015), use family-level identifications and this study would like to contribute to the development of similar indices across the Afrotropics, including the Kenya Invertebrates Scoring System (KISS) that is currently being developed. Secondly, identification guides for identification of larval stages of aquatic invertebrates beyond the family level are not available for most taxonomic groups in Africa. Moreover, when we used genus-level identifications for reference sites and re-run the RDA, the outputs (Fig. S1) confirmed that genera display similar biotope preferences as those at the family level.

It has been predicted that increased disturbance in streams and rivers may result in greater homogeneity of communities (Brooks et al., 2005), but the findings of this study do not follow this prediction. It is probable that despite the differences noted in water physical and chemical variables between impaired and reference sites, the level of disturbance was not large enough to result in significant homogenization of the aquatic environment. Reference sites were not

different from disturbed sites, as measured by β -diversity, in any of the measures of dispersion used. Yet, there are important, nuanced differences in the internal spatial structure of β -diversity and community composition between reference and impaired sites that are important for evaluating the effects of disturbance on macroinvertebrate communities in Afrotropical streams. Differences in macroinvertebrate assemblages were greater among biotopes than between disturbance classes, although this varied with season. Differences in β -diversity between biotopes support the importance of biotope availability and suitability as major drivers of macroinvertebrate diversity in rivers. This also means that even if other requirements are met, such as water quality and food resources, lack or shortage of suitable biotopes would lead to a decrease in diversity of macroinvertebrates in the study area.

There were seasonal differences in the composition of macroinvertebrate communities in the study area. During the low-flow dry season, some impaired sites were characterized by disconnected biotopes whereby riffles dried up and stable substrate (mainly cobbles and boulders) remained exposed, to the detriment of rheophilic taxa. In response, macroinvertebrate composition changed and was dominated by Odonata, Coleoptera, and Hemiptera. Taxa among these three orders are fast colonizers and tolerant to flow reduction and poor water quality (Velasco & Millan, 1998; Boulton & Lake, 2008). Odonata were particularly abundant at impaired sites but which had a good coverage of emergent and submerged macrophytes

Table 5 SIMPER contributions to differences in macroinvertebrates families between biotopes (GSM, STONES, and VEG) at impaired sites in the Mara during the dry and wet seasons

Wet season		Dry season	
Taxon	Cumulative %	Taxon	Cumulative %
GSM vs STONES			
Simuliidae ²	13.0	Tricorythidae ²	8.3
Tricorythidae ²	22.2	Hydropsychidae ²	15.8
Baetidae ²	31.3	Baetidae ²	21.2
Gomphidae ¹	40.4	Simuliidae ²	26.4
Tubificidae ¹	48.8	Gomphidae ¹	31.0
Hydropsychidae ²	56.3	Heptageniidae ²	35.1
Lumbriculidae ¹	61.5	Belostomatidae ¹	39.3
Chironomidae ²	66.3	Chironomidae ²	43.2
Naucoridae ¹	71.0	Leptophlebiidae ²	47.0
Caenidae ²	73.9	Corixidae ¹	50.6
Corixidae ¹	76.7	Libellulidae ¹	54.0
Belostomatidae ¹	78.9	Elmidae ²	57.3
Lestidae ¹	81.0	Tubificidae ¹	60.2
Elmidae ²	82.9	Caenidae ²	63.1
Libellulidae ¹	84.7	Naucoridae ¹	65.8
GSM vs VEG			
Baetidae ³	9.3	Corixidae ¹	5.0
Gomphidae ¹	18.3	Gomphidae ¹	9.7
Tubificidae ¹	26.6	Chironomidae ¹	14.2
Lestidae ³	34.7	Baetidae ³	18.7
Simuliidae ³	42.0	Libellulidae ¹	23.0
Naucoridae ³	48.3	Naucoridae ³	27.3
Tricorythidae ³	54.7	Lestidae ³	31.6
Lumbriculidae ¹	60.1	Hydropsychidae ³	35.8
Caenidae ³	64.3	Leptophlebiidae ¹	39.6
Hydropsychidae ³	67.9	Tubificidae ¹	43.4
Chironomidae ¹	71.1	Caenidae ³	47.0
Belostomatidae ³	74.3	Notonectidae ¹	50.3
Libellulidae ³	77.1	Simuliidae ³	53.4
Heptageniidae ³	79.7	Tricorythidae ³	56.4
Lepidostomatidae ¹	81.5	Veliidae ³	59.3
STONES vs VEG			
Tricorythidae ²	21.3	Tricorythidae ²	7.2
Baetidae ²	29.0	Hydropsychidae ²	12.9
Hydropsychidae ²	36.6	Naucoridae ³	17.7
Lestidae ³	44.1	Simuliidae ²	22.4
Tubificidae ³	50.1	Belostomatidae ³	26.9
Naucoridae ³	55.5	Heptageniidae ²	31.0
Gomphidae ³	60.2	Chironomidae ²	34.5
Chironomidae ²	64.5	Leptophlebiidae ²	38.0
Caenidae ³	68.5	Caenidae ³	41.4
Lumbriculidae ³	72.5	Elmidae ²	44.5

Table 5 continued

Wet season		Dry season	
Taxon	Cumulative %	Taxon	Cumulative %
Gyrinidae ³	75.4	Baetidae ²	47.7
Heptageniidae ³	78.2	Lestidae ³	50.8
Corixidae ²	80.5	Corixidae ³	53.9
Elmidae ²	82.6	Gomphidae ³	56.9

Superscript numbers on each macroinvertebrate taxon highlight at which biotope abundance was higher (1: GSM, 2: STONES, 3: VEG)

(VEG biotope) and soft sediments (GSM biotope). In similar savanna river systems with high flow variation, marginal vegetation has been found to support Odonata larvae and adults (Samways & Steytler, 1996). Although Odonata have been identified as one of the groups sensitive to disturbance, especially riparian deforestation (Monteiro-Júnior et al., 2013), some species among Odonata are tolerant to flow variation and high water temperature (Stewart & Samways, 1998; Hardersen, 2008), which can partly explain their high abundance and diversity at impaired sites where flows were very low during the dry season.

Biotope availability and preferences of various taxa

This study showed differences in frequency of occurrence of families among biotopes, with species within several families demonstrating biotope specificity, most likely reflecting substratum and hydraulic requirements of species within families. Seasonality was a major factor determining biotope availability for colonization. During the low-flow season, biotopes which were more distinct as riffles (STONES biotope) were shallower and exposed. Similar findings have been reported with boundaries among biotopes most distinct under low-flow, as opposed to high-flow, conditions (Dallas, 2007). Changes in discharge also modify the hydraulic parameters of biotopes, such as marginal vegetation, which may change from a lentic to a lotic environment as discharge and flow velocities increase (Dallas, 2007). Notable within the Mara River mainstem was the apparent lack of the marginal vegetation biotope. The Mara River is quite incised and experiences flash flooding (Melesse et al., 2008),

which can clear instream and marginal vegetation (Beeson & Doyle, 1995), making the biotope unavailable for dependent taxa during low flows.

The effect of seasonality and biotope availability on taxa occurrence are major considerations during bioassessments. While developing an empirical biotic index of water quality as well as the development of the SASS5 Protocol, it has been noted that wet season samples are unreliable because of homogenization of biotopes, and hence sampling for bioassessment should be restricted to the dry season only (Chutter, 1972; Dickens & Graham, 2002). In this study, the STONES and VEG biotopes were the most diverse and sensitive to flow variation/seasonality. The STONES biotope supported taxa among the EPT that are most sensitive to habitat disturbance and deterioration in water quality (Masese & Raburu, 2017). The STONES biotope is also considered to be more consistent, in terms of the taxa that are most sensitive to flow variation, than either the VEG or GSM biotopes (Dallas, 2007). On the other hand, the VEG biotope supported a high number of taxa because of its propensity to take on different forms during different flow conditions. Under low-flow conditions, vegetation traps sediments and provides depositional habitats for burrowing collector-gatherers (Pardo & Armitage, 1997). Aquatic vegetation in flowing water also resembles the STONES biotope as the usually lentic habitat turns lotic and supports taxa normally associated with stable substrate in flowing water (Dallas, 2007). Compared with the other biotopes, the GSM biotope recorded the lowest diversity and number of biotope-specific taxa. The GSM biotope has been identified as the most variable and inconsistent in

Table 6 Functional feeding groups and tolerances to disturbance of key macroinvertebrate families that account for differences observed among the three common biotopes (GSM, STONES, and VEG) in the Mara River, Kenya/Tanzania

	Collector-gatherers	Collector-filterers	Shredders	Scrapers	Predators	Tolerance to disturbance
Baetidae	✓			✓	✓	Mixed
Belostomatidae					✓	Tolerant
Caenidae ^a	✓			✓		Mixed
Chironomidae	✓	✓	✓	✓	✓	Mixed
Corixidae	✓			✓		Moderately tolerant
Elmidae			✓	✓		Intolerant
Gomphidae					✓	Moderately tolerant
Heptageniidae	✓					Intolerant
Hydropsychidae		✓			✓	Mixed
Lepidostomatidae			✓			Intolerant
Leptoceridae	✓	✓	✓	✓	✓	Moderately tolerant
Leptophlebiidae	✓					Intolerant
Lestidae					✓	Moderately tolerant
Libellulidae					✓	Moderately tolerant
Naucoridae					✓	Moderately tolerant
Perlidae					✓	Moderately tolerant
Simuliidae		✓				Moderately tolerant
Tricorythidae	✓			✓		Intolerant
Tubificidae	✓					Tolerant
Lumbriculidae	✓					Tolerant

Mixed tolerance means that some taxa within the family are intolerant and some are tolerant or moderately tolerant to disturbances

^aCorixidae are also piercers that feed on plant matter piercing cells and imbibing their contents

terms of number of taxa and their tolerance or sensitivity to degradation (Dickens & Graham, 2002).

Implications for bioassessment

This study shows the importance of taxon identity as opposed to richness and relative abundance of different macroinvertebrate taxa as measures of disturbance in streams and rivers. Taxa identified to be sensitive to flow variation, and which will be very important for monitoring flow alteration and setting environmental flow requirements in this river and others in the Afrotropics include Hydropsychidae (*Dipletronella* sp., *Hydropsyche* sp., *Cheumatopsyche* spp., *Leptonema* sp., and *Macrostemum* sp.); Simuliidae, Tricorythidae (*Tricorythus* sp.); and some Baetidae (*Afroptilum* sp., *Centroptiloides* sp., *Pseudocloeon* sp.). Species within families Simuliidae, Hydropsychidae, Tricorythidae, and Baetidae have been

previously identified to be sensitive to flow alteration (O'Keeffe & de Moor, 1988; Dallas, 2007; Rivers-Moore et al., 2007; Thirion, 2016). Their preference for fast flows and stable substrate implies that as water levels drop, filter-feeders are not able to obtain food or enough dissolved oxygen, and as a consequence they will be eliminated. In addition, 20 other taxa were identified to display strong associations with flow-related environmental variables such as flow velocities, substrate type, water depth, temperature, and suspended solids (Figs. 2, 4). For bioassessment, it means that if these biotopes are reduced or lost to any form of degradation, these taxa will be reduced in number or lost altogether, and this will be indicative of loss of ecological integrity of the river. These 20 taxa also represent all the major functional feeding groups (FFGs), namely collector-gatherer, collector-filterers, scrapers, shredders, and predators (Merritt et al., 2008; Masese et al., 2014) (Table 6). They also have high to

moderate sensitivity to different forms of disturbances in streams and rivers, including flow cessation (Shivoga, 2001; Mathooko et al., 2005; Kasangaki et al., 2008; Masese et al., 2009). The presence of all these taxa at a site suggests that diverse biotopes and food sources are available on a temporal scale, as opposed to a single biotope or food source dominating the site, which would be an indication of disturbance and change in ecosystem functioning.

The findings of this study reflect the diversity and composition of benthic macroinvertebrate assemblages in riverine ecosystems in the Lake Victoria Basin and larger Eastern Africa (Masese et al., 2009; Raburu et al., 2009; Aura et al., 2010; Minaya et al., 2013; Kilonzo et al., 2014), and the Afrotropics (Dallas, 2007; Kasangaki et al., 2008; Mbaka et al., 2014; Arimoro et al., 2015; Aschalew & Moog, 2015; Kaaya et al., 2015; Kaboré et al., 2016). Therefore, taxa in this study have wider application in river systems in eastern Africa and, by extension, the Afrotropics and beyond. Most of these families, such as Baetidae, Heptageniidae, Tricorythidae (Ephemeroptera); Hydropsychidae (Trichoptera); Elmidae (Coleoptera); and Simuliidae, Chironomidae (Diptera) are often used as indicators during environmental flow assessments and bioassessment studies in many parts of the world (Harby et al., 2007; Biggs et al., 2008; Holt et al., 2015). However, because of the high diversity among some of these families, such as Baetidae, Hydropsychidae and Chironomidae, they contain genera and species with different environmental requirements (Rivers-Moore et al., 2007; Odume & Muller, 2011; Thirion, 2016). It will therefore be necessary in future studies to try and use genus or species-level identifications, and also consider different life stages that might have different environmental requirements.

Conclusions

This study highlights the importance of biotope availability and seasonality as major drivers of macroinvertebrate community structure in Afrotropical rivers and recognizes the importance of taxon identity, as opposed to richness or diversity alone, as measures of disturbance in streams and rivers. Indeed, at the family level, measures of β -diversity did not differ between reference and impaired sites: neither

did the abundances of various taxa. This calls for careful analysis of community composition to reveal region-specific tolerances of taxa to different influences and flow characteristics. This has significant implications in bioassessment whereby it is not only important to compare and contrast sites in terms of levels of disturbance and community composition of taxa, but also in terms of their biotope availability, its extent, and suitability. In general, the STONES biotope was the most consistent in terms of the number of taxa and their tolerance or sensitivity to degradation. The GSM biotope was the most variable, and because of this it can be ignored so that sites are assessed using only the STONES and VEG biotopes. Importantly, the STONES biotopes (riffles, stones in- and out-of-current) have a remarkable similarity in faunal composition throughout the world, which makes this biotope universally comparable and preferred for biomonitoring purposes (Chutter, 1972; Hynes, 1975; Dallas, 2007). The STONES biotopes occurred in fast flows in riffles and was associated with rheophilic taxa such as *Diplectronella* sp., *Hydropsyche* sp., and *Cheumatopsyche* spp. (Hydropsychidae); Simuliidae, *Tricorythus* sp. (Tricorythidae); and *Afroptilum* sp., *Centroptiloides* sp., *Pseudocloeon* sp. (Baetidae). These taxa were identified to be very important for monitoring habitat and flow alteration and can be used in other river systems in the Afrotropics.

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