Assessing drivers of benthic macroinvertebrate community structure in African highland streams: An exploration using multivariate analysis

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HIGHLIGHTS

- Nutrient concentrations were higher in the impacted Save River system
- Ammonium, channel width and phosphate are important in structuring macroinvertebrates.
- Predator functional feeding group was the most dominant in all river systems.
- Macroinvertebrates are well represented across a broad range of habitats.
- Macroinvertebrate family level data are insufficient to answer key ecological questions.

GRAPHICAL ABSTRACT
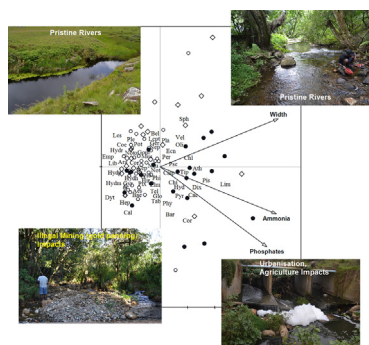
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ABSTRACT

Understanding the drivers of community structure is fundamental for adequately managing ecosystems under global change. Here we used a large dataset of eighty-four headwater stream sites in three catchments in the Eastern Highlands of Zimbabwe, which represent a variety of abiotic conditions and levels of impairment, to examine the drivers of benthic macroinvertebrate community structure. We focused our assessment on macroinvertebrate family level community composition and functional feeding group classifications. Taxonomic richness was weakly positively correlated with ammonium, phosphates and pH, and weakly negatively correlated with detrital cover and dissolved oxygen. Measured abiotic variables, however, had limited influence on both macroinvertebrate diversity and functional feeding group structure, with the exception of ammonium, channel width and phosphates. This reflected the fact that many macroinvertebrate families and functional feeding guilds were well represented across a broad range of habitats. Predatory macroinvertebrates were relatively abundant, with collector-filterers having the lowest relative abundances. The findings of the study suggest that for certain ecological questions, a more detailed taxonomic resolution may be required to adequately understand the ecology of aquatic macroinvertebrates within river systems. We further recommend management and conservation

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initiives on the Save River system, which showed significant impact from catchment developmental pressures, such as urbanisation, agriculture and illegal mining.

1. Introduction

Benthic macroinvertebrates are among the most diverse and abundant organisms in freshwater systems and are key for aquatic ecosystem functioning (Richards et al., 1993; Tolonen et al., 2001; Johnson et al. 2007; Dalu et al. 2013; Nhiwatiwa et al., 2017). They are recognised as an essential food source for amphibians, fish and other invertebrates and are therefore integral components of aquatic food webs (Jiang et al., 2010; Dalu et al., 2013). As such, macroinvertebrates are regarded as useful proxies for determining the ecological status of aquatic ecosystems (Tolonen et al., 2001; Markert et al., 2003; Hodkinson and Jackson, 2005; Bredenhand and Samways, 2009; Li et al., 2012; Tchakonté et al., 2014). According to the river continuum concept, headwaters are small shaded streams where allochthonous inputs of coarse particulate organic matter (CPOM) are a necessary resource for consumers (Vannote et al., 1980). In the headwaters, shredders and collectors occur in large abundances and form a high proportion of total macroinvertebrates due to the presence of CPOM. The predator proportion generally remains largely constant, with changes in species composition being observed, as the reason for the even distribution is not dependent on the CPOM size but on prey availability in the area (Vannote et al., 1980).

Understanding macroinvertebrate community-environment relationships is, therefore, important- particularly within the context of habitat degradation. Performing such investigations at broad spatial scales can however be costly. It is well established that the relationship between macroinvertebrate community and the environment is best performed using species-level identification. However, this is not always possible for biomonitoring research due to budgetary and expertise-related constraints (Ehrlich, 1992; Sparrow et al., 1994; Oliver and Beattie, 1996). As such, practitioners worldwide wishing to characterise the ecological state of rivers and streams regularly use of coarse-level taxonomy for macroinvertebrate assessments (Wright et al., 1984; Rosenberg and Resh, 1993; Chessman, 1995; Dickens and Graham, 2002; Aschalew and Moog, 2015; Kaaya et al., 2015). Such coarse taxonomic approaches are based on the premise of hierarchical taxonomic stress responses, whereby closely related organisms will have more similar stress responses than those that are distantly related (Boesch and Rosenberg, 1981; Ferraro and Cole, 1990). These approaches have been shown to be sufficient to detect environmental conditions at certain scales, particularly in environmental pollution and perturbation studies (Ferraro and Cole, 1990; Dickens and Graham, 2002; Kaaya et al., 2015), and are increasingly incorporated into basic ecological investigations (Jähnig et al., 2015). Here, we aim to understand whether the identification of major environmental drivers of benthic invertebrate communities is possible using coarse taxonomic resolution, particularly at broad spatial scales. We address this question using available data from headwater streams in the Eastern Highlands of Zimbabwe where multiple study sites, representing a variety of abiotic factors and different impairment levels, are analysed based on the relative abundances of macroinvertebrate family level and functional feeding group data. As it is recognised that both regional and local processes can shape communities (Bonada et al., 2006; Li et al., 2012; Jähnig et al., 2015; Stoll et al., 2016), we focus our assessment on both local and regional scale variables.

Few studies (i.e. Chakona (2005) on two upland streams in the central Eastern Highlands), have attempted to quantify the influence of landscape structure on macroinvertebrate communities in headwater streams in parts of the Eastern Highlands of Zimbabwe. The present study aimed to provide a first comprehensive baseline for the entire Eastern Highlands, a region under threat from considerable anthropogenic changes, including illegal mining, invasive species, climate change and agriculture. More specifically, we aimed to assess the structure of aquatic benthic macroinvertebrate communities at the family level in relation to various abiotic factors that characterise the headwater streams of the Eastern Highlands of Zimbabwe. We incorporated a wide range of geomorphological, hydrological and environmental variables in our multi-faceted analysis and further examined whether these communities were environmentally or spatially structured using a distance-decay of community similarity approach. The following predictions were tested: 1) physical and chemical variables would influence macroinvertebrate family and functional feeding group structure within the three catchment zones, due to known differences in land use patterns; 2) given the level of stressors due to land use patterns in the catchments, chemical variables associated with these stressors would be the strongest influence (i.e. nutrients, pH); 3) stronger environmental structuring is expected compared to spatial structuring as these stressors are acting as a strong environmental filter, limiting the pool of available colonists on a site by site basis; and 4) based on the river continuum concept (RCC), we expected more shredders compared to predators, collectors and scrapers in all the study catchments as most of the sampled streams were first to third order streams.

2. Materials and methods

2.1. Study area

The study was conducted across a range of different sized headwater streams (stream orders 1–3) in the Eastern Highlands, a narrow mountain belt (~450 km long north–south) along the eastern Zimbabwe to western Mozambique border (Fig. 1). The area forms part of a mountain chain that runs from the Eastern Africa Ethiopian highlands to Southern Africa Drakensberg Mountains (McGinley, 2008). Most of the Eastern Highlands headwater streams are in mountainous regions, characterised by steep gradients and flow through shallow and narrow channels with a dense riparian canopy. Forestry (e.g. conifer plantations) is the principal form of land use in the central and northern regions, while tea plantations are mainly found in the southern region.

In total, 84 sites along the escarpment were assessed from streams/rivers that flowed into three major river systems: the Búzi River (35 sites), the Save River (26 sites) and the Zambezi River (23 sites) during the summer season (11–23 January 2015). The Búzi River sites were found mostly within communal areas, forestry areas, national parks and tea plantations, with some of the rivers/streams showing impacts of illegal gold and diamond mining (Dalu et al., 2016). The Save River catchment is the longest river in the Eastern Highlands with its entire length dominated by urban and communal areas, crop irrigation, commercial forestry (i.e. pine and gumtree) and mining. The Zambezi River sites were relatively pristine and mostly within national parks and two in communal areas. Site selection was based on representation of a broad range of habitats, altitudes and environmental disturbance gradients. The mean annual temperature ranges from a minimum of 9 °C to 12 °C and a maximum of 25 °C to 28 °C (McGinley, 2008), with a highly variable mean annual rainfall ranging from 1250 mm to 2997 mm per year (Zimbabwe Meteorological Services). The Southern region of the country experiences a drier-warmer climate and as you move towards the North (highlands) cooler-wetter climate prevails (McGinley, 2008).
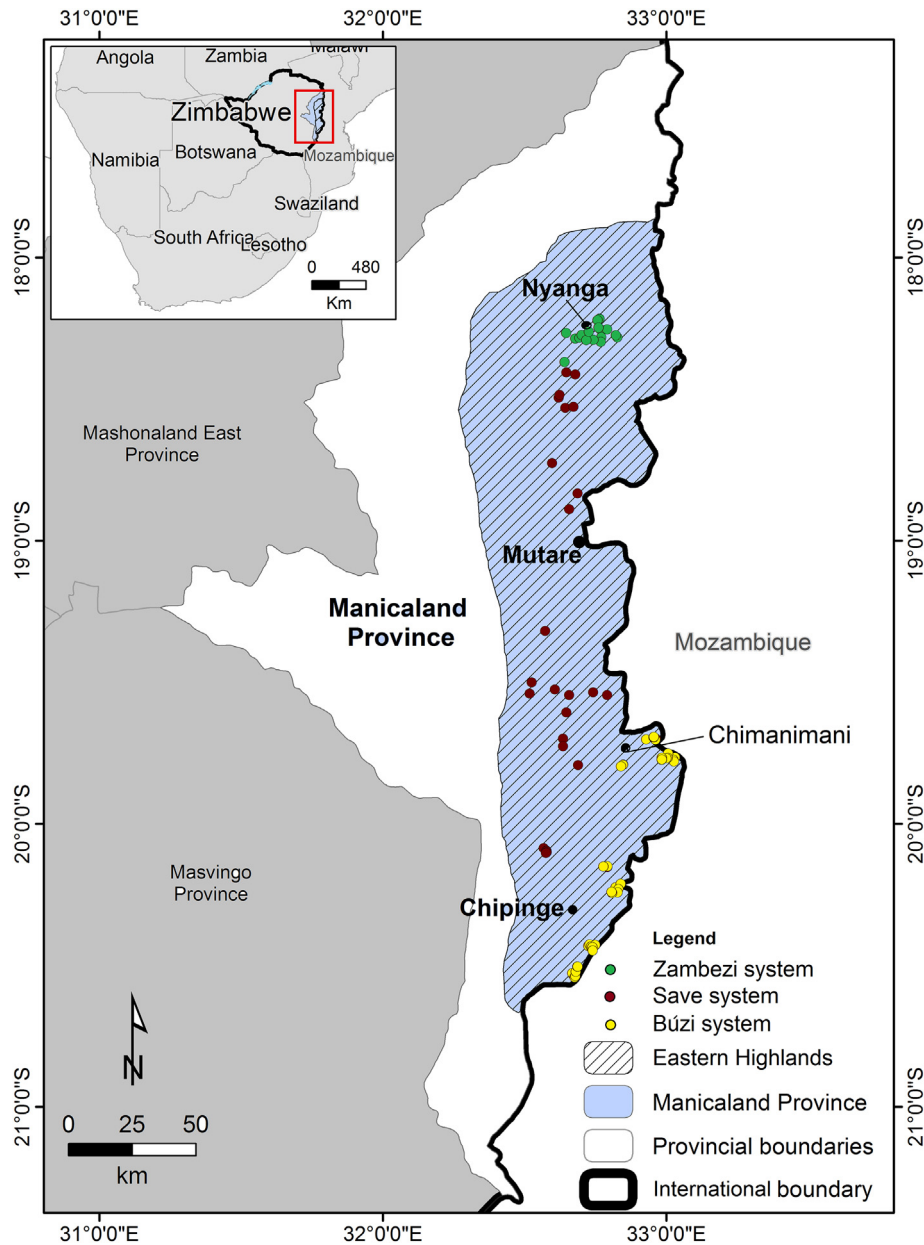
Fig. 1. Location of the macroinvertebrate study sites across the Eastern Highlands, Zimbabwe.

2.2. Environmental variables

In situ measurements of electrical conductivity (EC), pH, total dissolved solids (TDS), salinity (Sal), water temperature and dissolved oxygen (DO) were measured using portable multi-parameter probe PCTestr 35 (Eutech/Oakton Instruments, Singapore) and DO 850045 m (Per Scientific, Taiwan). Water depth was measured using a graduated measuring rod. Integrated water samples (500 mL, $n = 2$) from the two littoral zone edges and main channel centre were collected at each site and stored on ice until they reached the laboratory for nutrient analysis (i.e. ammonium and phosphates). The water samples were analysed within 14 h of collection using the Hanna phosphate high range checker (HI717) and ammonium test kit for freshwater (HI3824) (Hanna Instruments, Romania). The mean phosphate meter detection limit range was 0 to 30 mg L^{-1}, with a resolution of 0.1 mg L^{-1}, whereas ammonium had a range of 0 to 2.5 mg L^{-1}, with a 0.5 mg L^{-1} resolution. The detrital and macrophyte cover of each site was surveyed by wading and expressed as a percentage. Substratum composition was visually assessed at each site and expressed as a percentage, based on the following categories: boulder (>256 mm), cobbles (64–256 mm), pebbles/gravel (2–64 mm), sand (0.06–2 mm) and (silt and clay < 0.06 mm).

2.3. Macroinvertebrate sampling

Macroinvertebrates were sampled semi-quantitatively using a hand-held nylon net (mesh size 500 μm, dimension 30 × 30 cm) in all the available habitat types, such as riffles, macrophytes, pools and bedrock collectively for 6 min per site. At each sampling site, macroinvertebrates were collected by submerging the hand net against the current, sweeping and kicking within a demarcated 10 m transect. This involved walking through the water with the net, dragging and kicking the macrophyte vegetation and benthic substratum to dislodge any attached macroinvertebrates. The hand net was swiftly lifted out of the water to prevent the escape of agile animals and the macroinvertebrates were sorted in a tray from mineral, plant and detrital material before being transferred to 70% alcohol solution in 500 mL polyethylene containers for later identification and counting in the laboratory. The

samples were identified to family level using keys by Gerber and Gabriel (2002a, 2002b). Additionally, macroinvertebrates samples were further sorted according to their functional feeding groups (FFG): collector-gatherer, collector-filterer, scraper, shredder and predator using classifications outlined by Merritt and Cummins (1996), Barbour et al. (1999), Gooderham and Tsyrlin (2002), Allan and Castillo (2007), de Moor et al. (2003a, 2003b), Aschalew and Moog (2015), Kaaya et al. (2015), and Moretti et al. (2007) (see Table S1). However, benthic macroinvertebrate groups with more than one FFG were excluded from further FFG classification and analysis; i.e. Chironomidae, Corbulidae, Ecnomidae, Hydraenidae, Hydropsychidae, Leptoceridae, Leptophlebiidae and Muscidae. Several widely used macroinvertebrate community composition measures were computed to assess community composition and diversity among the three catchments: %Diptera abundance, %Ephemeroptera, Plecoptera and Trichoptera (EPT) abundances, %Ephemeroptera abundance and %Trichoptera abundance (Kaller and Hartman, 2004; Larsen et al., 2011; Bere et al., 2016). Margalef and Shannon-Wiener diversity indices were used as measures of family level diversity.

2.4. Data analysis

The Shapiro-Wilk test indicated non-normality and a Kruskal-Wallis test was consequently run to compare the variation in environmental variables (i.e. ammonium, EC, channel width, detrital cover, DO, macrophyte cover, pH, phosphate, salinity, TDS, water temperature and water depth), substratum (sand, clay/slit, pebbles/cobbles, bedrock), macrophyte cover, detrital composition and biological variables (i.e. taxa richness, dominance, evenness, Margalef, Shannon-Weiner indices, FFGs) among catchment zones (i.e. Búzi, Save and Zambezi). Pairwise comparisons using the Kruskal-Wallis Multiple Comparisons *P* values for biological variables between the three catchment zones was carried out to assess the significant differences indicated by the Kruskal-Wallis test in STATISTICA version 12.0 (StataCorp, 2011). Correlations between the environmental variables and taxa richness, dominance, evenness and diversity indices (Margalef, Simpsons, Shannon-Weiner) were calculated using Spearman-rank correlations in STATISTICA version 12.0 (StataCorp, 2011).

To explore patterns and drivers of multivariate community structure, a detrended correspondence analysis (DCA) was first performed (permutation: $n = 9999$) to determine the appropriate response model (linear or unimodal). The performed DCA illustrated a total gradient length (axes 1 and 2) of 4.34, which was >3 standard deviations and therefore, a unimodal canonical correspondence analysis (CCA) ordination technique was employed (ter Braak and Šmilauer, 2002). Prior to CCA analysis, macroinvertebrate data were square root transformed and the environmental variables were normalized to put them all at the same scale so as to avoid influence on the analysis. The down weighting option was used to reduce the influence of rare taxa and it generally "shortens" the computed ordination axes (Jiang et al., 2010, see Šmilauer and Lepš (2014) for detailed methodology). Canonical correspondence analysis using the automatic step-wise forward selection procedure, with Monte Carlo significance test (permutation: $n = 9999$, $p < 0.05$), was used to examine the effects of environmental variables on the variation in macroinvertebrate biota composition among catchment zones. Prior to running the CCA, a subset of environmental variables that had variance inflation factors of >20, were removed from the analysis (ter Braak and Šmilauer, 2002). All ordination techniques were carried out using CANOCO version 5.1 software (ter Braak and Šmilauer, 2002).

To examine whether the communities were primarily environmentally and/or spatially structured, we correlated community distance matrices at both the regional and catchment scales with both geographic and environmental distance matrices for both the individual catchments and all sites combined. We did this using Mantel tests based on Pearson's product-moment correlation with the 'mantel' function and 1000 permutations in the R ecodist package (Goslee and Urban, 2013). Geographic distance was the pairwise Euclidean distance between sites. Environmental distance was the Euclidean distance between sites based on the normalized environmental variables (highly correlated variables [>0.75] were first removed). Community distance was calculated as the Bray-Curtis distance of log-transformed abundance data, which was performed using the 'vegdist' function in R's vegan package (Oksanen et al., 2016). Both the full and partial mantel tests were performed to disentangle the role of environmental and spatial structuring. First, the three distance matrices were compared individually and second, partial mantel tests were used to examine the role of environmental variables while partialling out the influence of space. Distance decay models were modelled in R statistical package (R Core Team, 2015).

3. Results

3.1. Environmental variables

Significant differences (Kruskal-Wallis, $p < 0.05$) were observed for all water parameters between catchments (EC, [DO], pH, sal, water temperature, [TDS], Table 1). High mean salt concentrations i.e., EC (mean 60 ppm), TDS (mean 45.0 mg L^{-1}) and sal (mean 51 ppm) were observed in the more impacted Save catchment rivers, with the lowest recorded in the Zambezi catchment (EC: mean 37 ppm, TDS: mean 27.8 mg L^{-1}, sal: mean 27 ppm). Nutrients were found to vary significantly (Kruskal-Wallis, $p < 0.05$) within the three catchment zones, with the Save catchment rivers illustrating high ammonium (mean 1.9 mg L^{-1}) and phosphate (mean 2.9 mg L^{-1}) concentrations. Low macrophyte and detrital cover were also recorded in the Save catchment river systems (Table 1). The mean water depth and substratum (i.e. pebbles/cobbles and bedrock) were similar (Kruskal-Wallis, $p > 0.05$) across the three catchment zones (Table 1).

3.2. Macroinvertebrate communities and functional feeding guilds (FFG)

A total of 57 aquatic macroinvertebrate taxa consisting of 23 predators, 12 collector-gatherers, 5 scrapers, 5 shredders, and 4 collector-filterers were identified, with 8 taxa (i.e. Chironomidae, Corbulidae, Ecnomidae, Hydraenidae, Hydropsychidae, Leptoceridae, Leptophlebiidae and Muscidae) having more than two FFGs. Aeshnidae, Baetidae, Potamonautidae and Libellulidae were the most abundant and dominant families in the Búzi and Zambezi catchment river systems, while Gyrinidae were the most abundant in the Save catchment river systems (Table 2). Mean taxon richness per site was relative high in the Save catchment river system (mean 16 families), with Búzi River sites having the lowest richness (mean 11 families). The diversity indices were high in sites in the Save catchment (Simpson: mean 0.9, Margalef: mean 3.8, Shannon-Weiner: mean 3.1), with dominance (mean 0.2) being high in the Búzi River sites (Table 1). Taxon richness, Margalef, dominance, Simpson and Shannon-Wiener were significantly different between the three catchment river systems (Kruskal-Wallis, $p < 0.01$), whereas evenness was similar (Kruskal-Wallis, $p > 0.05$, Table 1). Pair-wise comparisons found differences between the Búzi and Save catchments in mean site taxon richness ($H = 10.330$, $p = 0.001$), dominance ($H = 8.508$, $p = 0.004$), Shannon-Wiener ($H = 10.202$, $p = 0.001$), Simpsons ($H = 8.508$, $p = 0.004$) and Margalef ($H = 11.697$, $p = 0.001$) indices.

Predatory macroinvertebrates were relatively abundant, with collector-filterers having the lowest relative abundance (Table 1). FFG differences (Kruskal-Wallis, $p < 0.01$) were observed between catchments zones for collector-gatherers, collector-filterers and scrapers, with no significant differences (Kruskal-Wallis, $p > 0.05$) for predators and shredders (Table 1). Collector-gatherers, collector-filterers and scrapers were high in the Save catchment (mean 24.2%, 4.2%, 11.7%) and low in the Búzi catchment (mean 16.0%, 1.4%, 4.9%; Table 1). Whereas, predators (mean 62.7%) and shredders (mean 14.9%) were found to be high in the Búzi catchment. Using pairwise comparisons,

Table 1
Summary of all measured environmental variables from different catchment zones in the Eastern Highlands and Kruskal-Wallis and Chi-Square test results for the differences among the catchments. Values in bold represent significance difference at $P < 0.05$, SD – standard deviation.

Parameter	Búzi		Save		Zambezi		Kruskal-Wallis	
	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	H	p
n		35		26		23		
Elevation (m)	673–1646	1063.6 ± 320.9	613–1831	1088.4 ± 330.2	1347–2137	1752.3 ± 180.5	**42.925**	**<0.001**
Chemical								
pH	4.4–8.15	6.82 ± 0.85	5.9–6.95	7.21 ± 0.62	6.5–8.34	7.39 ± 0.45	**14.472**	**0.001**
Temperature (°C)	17.5–26.0	21.58 ± 2.14	17.9–24.6	20.39 ± 1.72	16.2–28.6	20.57 ± 2.37	**7.162**	**0.028**
DO (mg L^{-1})	5.7–8.8	6.82 ± 2.14	4.8–9.4	7.21 ± 2.76	4.3–18.8	12.90 ± 4.06	**23.933**	**<0.001**
TDS (mg L^{-1})	6.6–143.4	43.36 ± 35.99	14.7–93.2	45.10 ± 24.59	11.4–73.4	27.84 ± 14.58	**6**	**0.045**
Conductivity (ppm)	8.5–169.9	59.83 ± 44.88	19.9–113.0	60.01 ± 29.9	14.9–102.9	37.11 ± 20.77	**7.315**	**0.026**
Salinity (ppm)	12.5–122.3	47.52 ± 30.48	12.5–122.3	51.29 ± 27.42	14.2–94.7	27.49 ± 16.64	**8.771**	**0.012**
Nutrients								
Phosphate (mg L^{-1})	0.1–1.4	0.88 ± 0.36	0.1–2.4	1.93 ± 0.91	0.2–3.7	1.04 ± 0.80	**27.164**	**<0.001**
Ammonium (mg L^{-1})	2.0–3.3	2.25 ± 0.31	2.0–4.2	2.90 ± 0.72	2.0–4.2	2.34 ± 0.51	**15.046**	**0.001**
Hydrology								
Water depth (m)	0.1–1.3	0.44 ± 0.36	0.15–0.9	0.43 ± 0.19	0.15–1.2	0.57 ± 0.33	4.988	0.083
Channel width (m)	1.0–15.0	2.95 ± 2.68	1.0–15.0	6.21 ± 4.01	1.0–20.0	6.02 ± 4.77	**17.995**	**<0.001**
Substratum								
Clay/silt (%)	4.0–85.0	20.0 ± 16.0	0.0–45.0	14.0 ± 11.0	0.0–85.0	18.0 ± 23.0	24.549	0.121
Sand (%)	2.0–75.0	26.0 ± 24.0	2–75.0	43.0 ± 22.0	2.0–80.0	35.0 ± 31.0	**16.471**	**0.015**
Pebbles/cobbles (%)	5.0–82.0	45.0 ± 27.0	0.0–0.9	41.0 ± 27.0	5.0–85.0	35.0 ± 27.0	13.442	0.285
Bedrock (%)	0.0–60.0	10.0 ± 17.0	0.0–0.3	38.0 ± 22.0	0.0–83.0	43.0 ± 21.0	21.112	0.061
Vegetation								
Macrophyte cover (%)	0.0–80.0	34.0 ± 21.0	0.0–55.0	30.0 ± 70.0	10.0–70.0	42.0 ± 17.0	**14.527**	**0.003**
Detrital composition (%)	15.0–85.0	54.0 ± 19.0	20.0–80.0	38.0 ± 22.0	10.0–80.0	43.0 ± 21.0	**17.311**	**0.004**
Macroinvertebrate metrices								
Taxa richness	7.0–17.0	10.6 ± 2.8	7.0–26.0	16 ± 6.0	7.0–22.0	12.1 ± 4.0	**10.949**	**0.004**
Dominance	0.1–1.0	0.2 ± 0.1	0.1–0.3	0.1 ± 0.1	0.1–0.3	0.1 ± 0.1	**9.025**	**0.011**
Shannon	0.0–2.7	2.1 ± 0.4	1.6–3.0	2.5 ± 0.4	1.4–2.9	2.2 ± 0.3	**10.893**	**0.004**
Simpson	0.0–0.9	0.8 ± 0.1	0.7–0.9	0.9 ± 0.1	0.7–0.9	0.9 ± 0.1	**9.025**	**0.011**
Evenness	0.6–1.0	0.8 ± 0.1	0.6–0.9	0.8 ± 0.1	0.6–0.9	0.8 ± 0.1	0.828	0.661
Margalef	1.8–4.2	2.8 ± 0.7	2.1–4.6	3.8 ± 1.0	1.8–4.8	3.1 ± 0.8	**12.76**	**0.002**
Collector-gatherers	0.0–18.0	16.0 ± 0.1	0.0–26.0	24.2 ± 0.7	0.0–25.0	16.8 ± 0.7	**9.515**	**0.009**
Collector-filterers	0.0–4.0	1.4 ± 0.1	0.0–20.0	4.2 ± 0.3	0.0–13.0	3.3 ± 0.4	**6.933**	**0.031**
Predators	0.0–37.0	62.7 ± 0.7	5.0–54.0	54.2 ± 1.4	0.0–55.0	66.4 ± 1.8	1.811	0.404
Scrapers	0.0–10.0	4.9 ± 0.2	0.0–15.0	11.7 ± 0.5	0.0–15.0	4.9 ± 0.2	**11.52**	**0.003**
Shredders	0.0–17.0	14.9 ± 0.4	0.0–20.0	5.7 ± 0.3	0.0–20.0	8.7 ± 0.25	4.999	0.082
%Ephemeroptera	0.0–39.3	11.0 ± 11.3	0.0–55.0	14.3 ± 12.4	0.0–25.7	6.0 ± 7.8	**7.403**	**0.025**
%Trichoptera	0.0–31.8	7.1 ± 7.7	0.0–34.5	10.4 ± 7.9	0.0–38.1	10.7 ± 11.0	3.266	0.195
%Plecoptera	0.0–16.7	1.4 ± 3.9	0.0–16.7	1.2 ± 3.6	0.0–12.5	1.6 ± 3.4	0.54	0.764
%EPT	0.0–56.7	19.5 ± 15.4	3.4–65.0	25.9 ± 14.6	0.0–52.4	18.3 ± 15.2	4.421	0.11
%Diptera	0.0–33.3	8.5 ± 10.0	0.0–55.6	13.9 ± 14.5	0.0–22.5	5.9 ± 6.8	5.125	0.077

differences were found for collector-gatherers ($H = 7.487$, $p = 0.006$), scrapers ($H = 10.601$, $p = 0.001$) and collector-filterers ($H = 6.862$, $p = 0.009$) between the Búzi and Save catchments. Similarly, differences were found for shredders ($H = 4.216$, $p = 0.040$) between the Búzi and Zambezi catchments and collector-gatherers ($H = 6.887$, $p = 0.009$) between the Save and Zambezi catchments.

3.3. Macroinvertebrate communities and functional feeding groups (FFG) in relation to environmental variables

Ammonium, phosphates and channel width were found to be significant variables in explaining the variation of aquatic macroinvertebrate community structure across all sampled sites (i.e. regional level) using canonical correspondence analysis (CCA, Fig. 2a, b). Axis 1 (9.4%) and 2 (7.0%) of the CCA explained 16.4% of the explained cumulative variation, thus, indicating low predictive power for the selected environmental variables. Ammonium and phosphate were strongly positively associated with the 1st axis while channel width was positively associated with the second axis (Fig. 2a). CCA axes 1 and 2 separated the sites into roughly three groups based on location. Save sites were generally positively associated with axes 1 and 2 being characterised by a wide channel width, high ammonium and phosphate concentrations. The macroinvertebrate families associated with these sites included Veliidae, Chlorolestidae, Corbulidae, Dixidae, Limnichidae, Oligochaetae and Sphaeriidae. Búzi and Zambezi catchment sites, with some of the Save sites were associated with taxa, such as Baetidae, Dytiscidae,

Lestidae, Libellulidae, Hydrometridae, Notonectidae and Plecoptera (Fig. 2a).

Correspondingly, phosphate concentration and channel width were found to be significant in explaining the variation of FFGs structure across all sites (i.e. regional level, Fig. 2b). Using CCA axes 1 (11.0%) and 2 (9.3%) explained 20.3% of the explained cumulative variation. The phosphate concentration was highly positively associated with the 1st and 2nd axes while channel width was positively associated with the first axis (Fig. 2b). The Save catchment sites were strongly associated with the shredders and scrapers, whereas the Buzi and Zambezi catchment sites were associated with collector-gatherers, collector-filterers and predators (Fig. 2b).

At the regional level (across all sites), taxon richness was positively correlated ($p < 0.05$) with ammonium, phosphates and pH, while weakly negatively correlated ($p < 0.05$) with detrital cover and DO (Table 3). For the diversity indices, Margalef showed a significant ($p < 0.05$) and weak positive correlation with ammonium, phosphates and pH and similarly a significant ($p < 0.05$) and weak negative correlation with water depth and DO (Table 3). At catchment level, few significant ($p < 0.05$) relationships were observed for diversity indices and environmental variables. The Save River systems showed no significant relationships between diversity indices and any measured environmental variables. However, there were significant relationships ($p < 0.05$) between most of the diversity indices with pH (weak) and water depth (strong) at Búzi River system, while in the Zambezi River system, substratum was found to be important (Table 3).

Table 2

Summary of most dominant macroinvertebrate taxa. Symbols: mean abundances + (<1%), ++ (1–4.9%), +++ (>5%).

Taxa	Catchment		
	Búzi	Save	Zambezi
Annelida			
Hirudinea	+	++	++
Coleoptera			
Dytiscidae	++	++	++
Gyrinidae	++	+++	++
Noteridae	+	++	++
Decapoda			
Potamonautidae	+++	++	+++
Diptera			
Chironomidae	+	++	++
Dixidae	+	++	+
Empididae	++	++	+
Muscidae	+	++	++
Tipulidae	++	++	++
Ephemeroptera			
Baetidae	+++	++	++
Caenidae	+	++	+
Heptageniidae	+	++	+
Teloganodidae	++	++	+
Hemiptera			
Belostomatidae	++	++	++
Corixidae	++	++	++
Gerridae	++	++	++
Nepidae	++	+	++
Notonectidae	++	++	++
Pleidae	++	+	+
Veliidae	++	+	++
Mollusca			
Sphaeriidae	+	++	++
Thiaridae	++	++	++
Odonata			
Aeshnidae	+++	++	+++
Chlorolestidae	++	++	
Coenagrionidae	++	++	++
Gomphidae	++	++	++
Lestidae	++	++	++
Libellulidae	+++	++	+++
Trichoptera			
Ecnomidae	+	+	++
Glossosomatidae		++	+
Leptoceridae	++	++	++
Pisuliidae	+	++	++

The only significant relationships found between geographic, environmental and community distance matrices were between environmental and geographic for the Búzi catchment and all sites combined. Thus, environmental conditions were spatially structured for the Búzi catchment and all sites combined, whereby significant relationships between geographic, environmental and community distance matrices were found (Table 4). No other relationships were found.

4. Discussion

Our study assessed aquatic macroinvertebrate community structure and associated environmental variables at sites spanning a considerable range of environmental conditions in the Eastern Highlands of Zimbabwe. The findings of the study highlight that the measured physical and chemical variables had little influence on both macroinvertebrate family and functional feeding group structure, with the exception of marginal contributions from ammonium, channel width and phosphates. This further suggests that variability with regard to environmental tolerances and preferences within a family may be large enough to mask any patterns of spatial structuring in response to such variability. As a result of various processes acting at different scales, benthic macroinvertebrate communities integrate ecosystem changes over space and time and therefore vary across and within aquatic ecosystems (Richards et al., 1993; Tolonen et al., 2001; Johnson et al., 2007; Dalu

et al., 2013; Dézerald et al., 2014; Jähnig et al., 2015; Richards et al., 1993; Li et al., 2012; Dézerald et al., 2014).

Family richness varied among the three river systems, being generally high in Save catchment sites, which may have been due to low number of predators observed. The relatively low diversity in the Búzi catchment can possibly be explained by low water temperature, due to very high elevation/altitude and low topographical heterogeneity which can reflect low habitat heterogeneity between sites leading to reduced taxonomic turnover, and ultimately regional biodiversity (Shah et al., 2015; Astorga et al., 2014). The modification of river channels through gold panning and replacement of indigenous forest species by exotic pine and gumtrees in riparian zones as observed in most parts of the Eastern Highlands, can affect the habitat characteristics, detritus quality and invertebrate colonisation (i.e. migration or dispersal) rates (König et al., 2014; Niba and Mafereka, 2015; Dalu et al., 2016). With most of the Eastern Highlands dominated by pine and gumtree plantations (below 1500 m altitude) from the central zone (Chimanimani) to the north (Nyanga), differences in land use might explain the observed differences in macroinvertebrate diversity between the different catchment zones, especially in the south (Búzi catchment) where tea plantation dominates. Indeed, these differences in land use are reflected in nutrient concentrations and community structure was reflected in the CCA analysis. This is supported by several other studies (e.g. Ormerod et al., 1993; Chakona, 2005; Chakona et al., 2009) that have attributed the low macroinvertebrate diversity in aquatic ecosystems draining pine and gumtree plantations to water chemistry differences.

Ammonium, channel width and phosphate concentrations were the most influential variables explaining macroinvertebrate community structure in the different catchment zones (Fig. 2; Table 3). Environmental (or in-stream water chemistry) variables were limited and inadequate to explain the majority of the variance in this study, where >90% of macroinvertebrate family composition variability remained unexplained. This suggests that unmeasured variables, such as resource availability (Pinna et al., 2004; Wellard et al., 2013), biotic interactions (Gasith and Resh, 1999; Heino et al., 2003) and disturbance, could also be important (Chakona et al., 2008, 2009; Lock et al., 2011; Márquez et al., 2015), or a suite of multiple stressors may have been operating (Leps et al., 2015; Jackson et al., 2016).

Using the distance-decay of community similarity approach to assess whether macroinvertebrate communities were environmentally or spatially structured, we found no significant relationships between geographic, environmental and community distances. Depending on the spatial arrangement of sites in stream networks and the rate of dispersal, spatial structuring may override local environmental control on stream macroinvertebrate community structure (Brown and Swan, 2010; Tonkin et al., 2016). However, we found no clear evidence of either strong environmental or spatial structuring in these communities. Johnson et al. (2007) hypothesised that different organism groups would respond differently to different ecological scales, such as macroinvertebrates to local (i.e. habitat) and fish to regional (i.e. large-scale – geographical [elevation]) factors. This is based on life history strategies of the individual organisms. For example, fish being mobile and long-lived would be affected by or related to regional and large-scale variability, while macroinvertebrates would be affected by or related to local factors. Li et al. (2012) found that local scale, macroinvertebrate community structure is controlled mainly by microhabitat characteristics, whereas at regional scales, the macroinvertebrate community assemblages were controlled by macro-habitat characteristics and they concluded that different findings may depend upon the relative size of the studied area. With this information and findings from this study, we have baseline information to help in improving the implementation and planning of management and conservation programmes and make predictions of how human alterations can affect aquatic ecosystems in this region (Johnson et al., 2007). However, we recommend the use of species or genus level identifications, as family level taxonomic resolution may be a primary cause of the weak patterns observed here.

Fig. 2. CCA triplots showing the effect significant environmental variables on sampled (a) macroinvertebrate communities and (b) functional feeding groups (FFG) on catchment zones (i.e. open circles – Búzi, closed black circles – Save, diamonds – Zambezi). Abbreviations: amm – ammonium, phos – phosphates, collect-filter – collector-filterers, collect-gather – collector-gatherers, Ath – Atheridae, Aes – Aeshnidae, Bar – Barbarochthonidae, Bel – Belostomatidae, Cal – Calopterygidae, Cae – Caenidae, Chl – Chlorolestidae, Coe – Coenogranidae, Cor – Corixidae, Corb – Corbulidae, Chir – Chironomidae, Dix – Dixidae, Ecn – Ecnomidae, Elm – Elmidae, Emp – Empididae, Hir – Hirunidae, Lib – Libellulidae, Lim – Limnichidae, Lept – Leptoceridae, Ger – Gerridae, Glo – Glossosomatidae, Gom – Gomphidae, Gyr – Gyrinidae, Hep – Heptageniidae, Hydr – Hydraenidae, Hydc – Hydrochidae, Hydm – Hydrometridae, Hydp – Hydrophilidae, Hydph – Hydropsychidae, Nau – Naucoridae, Nep – Nepidae, Not – Noteridae, Noto – Notonectidae, Oli – Oligochaetae, Pla – Platycnemididae, Ple – Pleidae, Phy – Physidae, Pse – Psephenidae, Pis – Pisuliidae, Pix – Pixidae, Pot – Potamonautidae, Pro – Prosopistomatidae, Pyr – Pyralidae, Sph – Sphaeriidae, Tab – Tabanidae, Tip – Tipulidae, Tel – Teloganididae, Vel – Veliidae.

There was an equal proportion of collector-gatherers and shredders in the low to middle altitude zones as has been found in other studies (Jiang et al., 2010). This may be related to increased organic matter, from allochthonous inputs, due to increased riparian and littoral vegetation.

In conclusion, we found that geographic and environmental variables had little influence on the macroinvertebrate family level communities across the Eastern Highlands. Variable tolerances and environmental preferences of species within families may be the reason

for the weak relationships observed (with the assumption that there were different species among the sites), as could the presence of few species with wide environmental tolerances. The Save River system was severely impacted based on the macroinvertebrate diversity, physical and chemical variables. We therefore suggest that management and conservation initiatives should focus on the Save River system, due to increased illegal mining activities, urbanisation and agriculture, while also not neglecting the other two river systems. While several studies have demonstrated that macroinvertebrate family level classification

Table 3
Spearman rank correlation coefficient (r) highlighting significant variables and p-values highlighted in parentheses between environmental variables and macroinvertebrate diversity indices for the Eastern Highlands. Abbreviations: DO – dissolved oxygen, TDS – total dissolved solids.

Catchment/index	Variable							
	Ammonium	Channel width	Detrital cover	DO	pH	Phosphates	Substratum	Water depth
All								
Taxa richness	0.42 (<0.001)		−0.24 (0.027)	−0.28 (0.008)	0.32 (0.003)	0.42 (<0.001)		
Shannon	0.29 (0.009)				0.21 (0.050)	0.32 (0.003)		0.44 (<0.001)
Simpsons								−0.32 (0.003)
Evenness		−0.43 (<0.001)		0.23 (0.034)				−0.44 (<0.001)
Margalef	0.36 (0.001)			−0.23 (0.032)	0.29 (0.007)	0.39 (<0.001)		−0.22 (0.042)
Búzi								
Taxa richness					0.36 (0.026)			
Dominance					−0.41 (0.009)			0.56 (<0.001)
Shannon					0.38 (0.018)			−0.51 (0.001)
Simpsons					0.41 (0.009)			−0.56 (<0.001)
Evenness	0.37 (0.020)				−0.39 (0.014)			
Margalef								−0.44 (0.005)
Zambezi								
Taxa richness							0.61 (0.001)	
Shannon							0.54 (0.007)	
Evenness		−0.44 (0.031)						
Margalef							0.58 (0.003)	

Table 4

Results of both full and partial mantel tests between geographic (Euclidean), environmental (Euclidean) and invertebrate community (Bray-Curtis) distance matrices. Environmental distances were calculated based on normalized environmental variables. The partial mantel test examined the pure effect of environmental variables on community structure by controlling for spatial structuring of environmental conditions. We examined these relationships both at the full regional scale (All) and catchment scales. Bold values indicate significance at p < 0.05

Relationship	Test	Data	R	p
Macroinvertebrates vs geographic	Full	Búzi	0.003	0.968
Macroinvertebrates vs geographic	Full	Save	0.045	0.558
Macroinvertebrates vs geographic	Full	Zambezi	0.000	0.994
Macroinvertebrates vs geographic	Full	All	0.019	0.408
Macroinvertebrates vs environmental	Full	Búzi	0.004	0.953
Macroinvertebrates vs environmental	Full	Save	−0.084	0.387
Macroinvertebrates vs environmental	Full	Zambezi	0.11	0.309
Macroinvertebrates vs environmental	Full	All	0.046	0.318
Environmental vs geographic	Full	Búzi	**0.199**	**0.014**
Environmental vs geographic	Full	Save	0.081	0.346
Environmental vs geographic	Full	Zambezi	−0.172	0.255
Environmental vs geographic	Full	All	**0.162**	**0.001**
Macroinvertebrates vs pure environmental	Partial	Búzi	0.004	0.954
Macroinvertebrates vs pure environmental	Partial	Save	−0.088	0.345
Macroinvertebrates vs pure environmental	Partial	Zambezi	0.112	0.262
Macroinvertebrates vs pure environmental	Partial	All	0.044	0.353

can produce meaningful results (e.g. Bailey et al., 2001; Peeters et al., 2004; Kouamé et al., 2011; Bere and Nyamupingidza, 2014), our findings suggest that for a regional-scale study, other physical and chemical variables (e.g. sediment chemistry variables) may be required to better explain the role and importance of abiotic factors as drivers for stream invertebrate ecology within the Eastern Highlands. Finally, this study has highlighted that finer taxonomic resolution (genus/species level) is likely needed both for basic and applied studies on stream invertebrate ecology in order to be able understand the micro- and macro-scale processes structuring biodiversity. It is very likely that family level taxonomic resolution was not sufficient to detect environmental correlations despite strong impacts within the catchments, and despite the fact that several other studies have demonstrated significant relationships between macroinvertebrate families and environmental variables (i.e. Santos et al. (2015), Valle Junior et al. (2015), Bere et al. (2016) and Ferreira et al. (2017)).

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