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Research paper

Aquatic macroinvertebrate community colonisation and succession in macadamia orchard and communal area reservoirs: a case study of Luvuvhu River valley, South Africa

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The demand for macadamia nut production worldwide has led to increased use of pesticides and chemicals for pest and disease control. Reservoirs in these macadamia farming sectors are at risk, since these chemicals can enter and contaminate the water through direct application, runoff, and atmospheric deposition, subsequently negatively affecting aquatic organisms. The current study investigated macroinvertebrate colonisation and succession associated with two macadamia orchards and two communal area reservoirs. The potential effects of stressors from these land uses was tested for and compared using stone substrates over a 6-week period. Stone substrates from both reservoir types were abundantly colonised over time and the total macroinvertebrate taxa and abundance showed an increasing trend across the sampled weeks, with macadamia orchards having the highest number of macroinvertebrate taxa. Strong ecological succession was observed across reservoirs, with the initial succession of early colonisers – i.e., Chironominae (collector-gatherers), Ostracoda (collector-filterers) and *Anax* sp. (predator) within communal area reservoirs, and Chironominae, Ostracoda and *Radix natalensis* (scrapers) in macadamia orchard reservoirs – followed by predatory colonisers such as Gyrinidae larvae, *Trithemis* sp. (macadamia orchard reservoirs), and *Ranatra* sp. (communal area reservoirs). Macroinvertebrate community structure differed significantly across sites and weeks, with no similarity being observed for communities across the different reservoirs. Redundancy analyses further highlighted 11 sediment chemistry variables (i.e., pH, resistivity, P, K, Na, Ca, Mg, Cu, B, Fe and S) which were significantly related to macroinvertebrate community structure. Thus, sediment variables were found to be better predictors of macroinvertebrate community structure in macadamia orchard reservoirs than communal area reservoirs. Consequently, we concluded that differences in colonisation ability among taxa and environmental stressors were important factors driving succession. These results add to the understanding of the macroinvertebrate colonisation processes and environmental stressors within agricultural landscapes, which can aid in the development of conservation management of freshwater ecosystems.

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INTRODUCTION

Tropical reservoirs are dynamic habitats that support significant biological diversity and provide important ecosystem services (Moberg et al., 2003; Barbier et al., 2011). The degree to which ecological and biological features determine aquatic species distribution and abundance has intrigued ecologists for a long time (Heino et al., 2018). Among aquatic species, macroinvertebrates are the most diverse and abundant organisms in freshwater ecosystems. They are also a key component of ecosystem functioning (Kratzer, 2002; Dalu et al., 2021; Wasserman and Dalu, 2022). Macroinvertebrate species differ in their response to local environmental variables, and this has implications for composition dynamics at the community level (e.g., Dalu et al., 2012; Mutshekwa, 2020; Mutshekwa et al., 2020; Mofu et al., 2021).

In many developing regions, landscapes are comprised of a mosaic of communal human settlements dominated by agricultural activities such as livestock grazing and cultivation. In subtropical regions, these landscapes are often closely associated with natural water bodies (Desmarais et al., 2002) and associated reservoirs. Within large-scale agricultural areas, reservoirs are usually located within a delineated farm area and vulnerable to pesticide contamination, while communal reservoirs are located outside of farms and thus exposed to reduced levels of pesticide pollution. These mosaics of reservoirs exposed to different stressors provide an opportunity to assess the discrete effects of each stressor type on ecosystem dynamics. Assessing the link between these different anthropogenic activities (e.g., pastoral farming vs. commercial agriculture) and aquatic organisms within aquatic ecosystems is important for understanding the broader impacts of agriculture. This also has implications for broader patterns of species distribution and colonisation in a changing world (Verberk, 2011).

With rising global demand for agricultural commodities for food, feed, and bioenergy, the pressure on land is increasing (Ramankutty et al., 2006). In recent decades, many aquatic ecosystems have

been threatened or disappeared because of increasing agricultural land-use activities (Marchetti et al., 2010). Furthermore, the advances in technology have increased land-use intensification in subtropical landscapes (Ramankutty et al., 2006). Unsustainable, unmanaged agricultural activities continue to put pressure on aquatic ecosystems (Sivakumar et al., 2000). As the demand for agricultural production is expected to continue increasing over the next few decades, especially in developing countries in subtropical areas, the effects of agricultural activities on aquatic ecosystems are becoming more intensive. This constitutes an immense potential threat for populations of aquatic organisms.

In shallow aquatic ecosystems, benthic habitats are particularly important for macroinvertebrate communities. These habitats are sites for the accumulation of autochthonous and allochthonous organic matter, and serve as sources of nutrients, organic compounds, and solutes which interact with the water column (Sivakumar et al., 2000). They are also characterised by diverse substrate types such as rocks, sand, silt, and clay, with implications for macroinvertebrate community structures (Sivakumar et al., 2000). The preferences of macroinvertebrates for various artificial substrates in aquatic ecosystems has been the focus of much research in the past decade (Geist and Hawkins, 2016). Colonisation of artificial stones by macroinvertebrates has been extensively studied (e.g., Khalaf et al., 1980; Rosa et al., 2013), and artificial stones have been highlighted as a useful experimental substrate for assessing colonisation and succession (Rosa et al., 2013). Artificial stones provide stable and suitable substrates for colonisation (Pfeiffer et al., 2022) as they are less susceptible to being carried by flowing water (Friedmann and Galun, 1974; Death and Winterbourn, 1995). Furthermore, their uneven surfaces facilitate the movement and attachment of macroinvertebrates in reservoirs or slow-flowing river system, offering greater stability and availability of microsites for colonisation (Ayres-Peres et al., 2006). Due to their roughness, stones provide a three-dimensional habitat that protects macroinvertebrates from various disturbances (Ayres-Peres et al., 2006). As such, focusing on stones in freshwater ecosystems is a useful means toward understanding macroinvertebrate communities and associated environmental stressors.

Aquatic macroinvertebrates play a crucial role in transferring nutrients to higher tropic levels (Berger et al., 2017). Pesticides that affect macroinvertebrates can thus alter the structure and function of biota in these ecosystems (Berger et al., 2017). As large amounts of pesticides are used in macadamia cultivation, macadamia orchard and communal area reservoirs were considered to be suitable for this study, since they are exposed to different environmental stressors. The macadamia orchards were located in a nut-growing area to the east of Makhado town (Levubu), which is dominated by extensive monocultures of macadamia plantations (*Macadamia integrifolia* Maiden & Betche, *Macadamia tetraphylla* L.A.S. Johnson) and high levels of pesticide use (e.g., Karate Zeon 10 CS, Mulan 20 SP, Pyrinex 250 CS). These macadamia orchards require a lot of management for profit and good nut quality since they are susceptible to many pests and disease, resulting in regular monitoring and extensive pesticide applications. The pesticides in the macadamia sectors are applied during the flowering season, which typically occurs from late spring to early summer; however, the exact time can vary from year to year due to weather conditions. The communal area reservoirs were located in residential areas and had high levels of human activities along their shorelines, such as irrigated crop and orchard farming, fishing, and other domestic activities (i.e., laundry, swimming, picnics, bathing) and lower pesticide pollution (Mutshekwa et al., 2023). The current study sought to determine the effects of agricultural land use on the occurrence and distribution of macroinvertebrates in macadamia orchard and communal area reservoirs. We assessed: macroinvertebrate colonisation and succession in reservoirs located in landscapes with different agricultural practices to explore the impacts of environmental stressors on the macroinvertebrate community, the relationship of physico-chemical variables (water and sediment) to macroinvertebrate community structure within the macadamia orchard and communal area reservoirs, and functional feeding group structure of macroinvertebrates related to different agricultural practices. We hypothesised that (1) primary colonisation and abundance would differ between the reservoirs, given the varying agricultural practices (2), water and sediment characteristics would differ between the two reservoir types and that sediments are more likely to influence macroinvertebrate communities due to a strong adsorption capacity for pollutants, and (3) the changes in the functional feeding groups would be site-specific and vary with time. Artificial stone substrates were chosen instead of the conventional sweep-sampling method since they provide a valid alternative method for sampling macroinvertebrates over a period of time (Anderson et al., 2013).

MATERIALS AND METHODS

Study area

The study was conducted between 2 March and 13 April 2022 in similar-sized macadamia orchard and communal reservoirs in Limpopo Province, South Africa. This time of year was found to be suitable for the study due to high rainfall from November through to March which resulted in deposition of pesticide chemicals through runoff from the macadamia orchards. All four reservoirs in this study are mainly used for domestic water supply and irrigation. Macadamia orchard reservoirs (Site 1, –23°06'31.6"S, 30°15'54.2"E; Site 2, –23°06'54.5" S, 30°15'46.5" E) are located in the southern foothills of the Soutpansberg Mountains, 20 km east of Makhado town (previously Louis Trichardt). The communal area reservoirs (Site 3 – 22°96'58.12.19"S, 30°39'56.45"E; Site 4 – 22°59'57.24"S, 30°39'57.53" E) are located in Duthuni village, Thulamela Local Municipality, within the same region (Fig. 1). The macadamia orchard reservoirs had an estimated surface area of 224 m^2 and 350 m^2 and a depth of 6 m and 8 m, respectively, whereas the communal area reservoirs had an estimated surface area of 140.02 m^2 and 211.3 m^2 and a depth of 5 m and 6 m, respectively.

Macadamia orchard reservoirs were selected due to their high concentrations of pesticides, whereas communal area reservoirs were selected due to low or absence of pesticide concentrations (Mutshekwa et al., 2023). The macadamia orchard reservoirs were located where they was no housing and were surrounded by macadamia nut plantations (*Macadamia integrifolia* Maiden & Betche, *Macadamia tetraphylla* L.A.S. Johnson). The reservoirs were characterised by water lilies *Nymphaea sp.* and sedge *Cyperus latifidius*. The communal area reservoirs were located where there was housing and were mainly used for fish farming (e.g., Mozambique tilapia), storage of water for regular irrigation (i.e., litchis, maize and vegetables), and collection of water during the off-season for later use. The communal area reservoirs were characterised by tape grass, *Vallisneria* spp.

Pesticide (i.e., acetamiprid and chlorpyrifos) concentrations in the macadamia orchard reservoirs were found to range from 5.67 to 14.48 μg L^{-1} in sediments and were <6.51 μg L^{-1} in surface water. Pesticide concentrations in the communal area reservoirs were <0.13 ug L^{-1} in water and not detected in sediments. Pesticides in the macadamia orchards (e.g., Karate Zeon 10 CS, Mulan 20 SP, Pyrinex 250 CS) are usually applied in early October and towards the end of March.

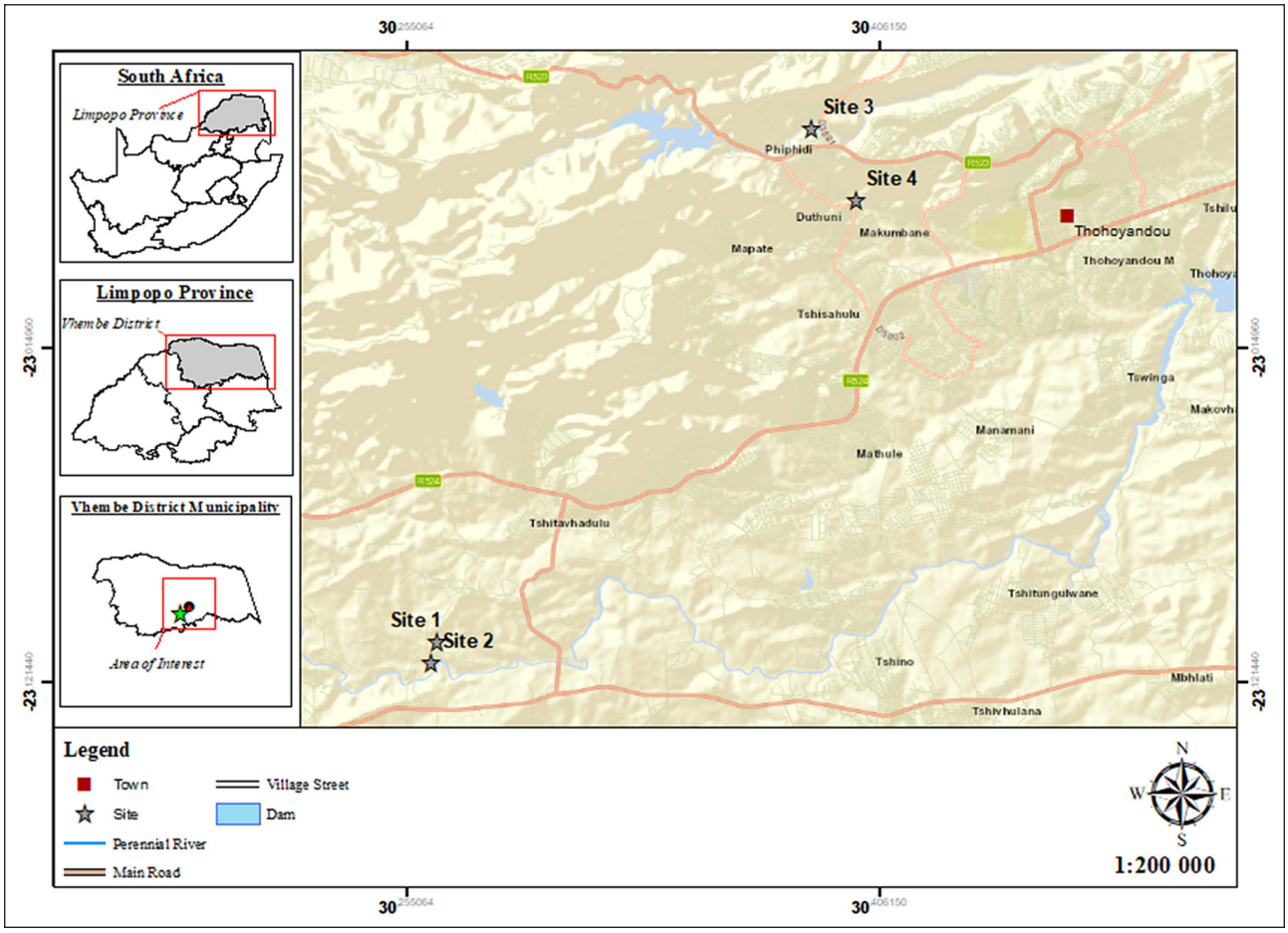

Figure 1. Location of the sample collection sites (Site 1 and 2 – macadamia orchards; Site 3 and 4 – communal area) in Limpopo Province, South Africa

Experimental design

Mesh bags with stones were deployed in macadamia orchard and communal area reservoirs to assess macroinvertebrate colonisation and succession over time, following Suárez et al. (2022). Similar-sized stones (length 15–20 mm; width and depth, range 10–15 mm) were collected from the Mutshundudi River and scrubbed with a brush to ensure the stones were macroinvertebrate-free. The stones were added to 15 cm × 15 cm coarse mesh bags (5 mm mesh size) to allow easy macroinvertebrate movement, with 48 mesh bags (i.e., 4 sites × 2 replicates × 6 weekly sampling events) deployed. Each bag was filled with stones and closed with zip ties. All bags were randomly introduced into both study reservoirs on Day 0 (2 March 2022) at a depth of ~0.5 – 1 m and approximately 1 m away from the shoreline. The bags were attached to ropes which were then attached to wooden sticks near the reservoir shoreline for easy retrieval. The bags were placed at least 1 m apart, with bag retrieval taking place at Days 7, 14, 21, 28, 35, and 42 (hereafter referred to as Weeks 1 – 6).

Macroinvertebrate colonisation

At each site, two mesh bags were retrieved from each of the four reservoirs per sampling week. The two mesh bags from each reservoir type per treatment were treated as replicates (2 bags × 4 sites × 6 weeks). Once removed from the water, the bags were immediately placed in a tray and the contents emptied, to avoid the loss of macroinvertebrates. The macroinvertebrates were carefully separated from stones, and then preserved in 70% ethanol in labelled in 500 mL polyethylene containers for further processing in the laboratory. In the laboratory, macroinvertebrates were sorted under an Olympus dissecting microscope using forceps, identified to lowest taxonomic level following a guide by Fry (2021), and abundances enumerated. All taxa were further assigned to a functional feeding group (FFG) (i.e., collector–gatherers, collector–filterers, scrapers, and predator) following guides by Merritt and Cummins (1996), Cummins et al. (2005) and Merritt et al. (2008).

Physico-chemical variables (water and sediment)

Water chemistry measurements and sediment collection were completed on each day of mesh bag retrieval. Conductivity (μS cm^{-1}), total dissolved solids (TDS: $mg{\cdot}L^{-1}$), pH and temperature (°C) were measured ~2 m apart using a handheld multi-parameter waterproof Cyber Scan 300 (i.e., 3 replicates × 4 sites × 6 weeks) (Eutech Instruments, Singapore). Sediment samples were collected (n = 2, 1.5 kg, depth ~5–10 cm) at each site during each sampling day using a plastic hand shovel after removing the overlaying debris. Upon collection, the samples were placed into new polyethylene Ziplock bags and immediately packed in a cooler bag with ice and transported to the University of Venda laboratory for further analysis. Upon arrival in the laboratory, sediment samples were oven-dried at 60°C for 48 h to a constant weight before being disaggregated in a porcelain mortar and homogenised using a riffle splitter. Thereafter, a sediment subsample of 0.5 kg was separated. The subsamples were sent for nutrient and metal analysis at the South African National Accreditation System (SANAS) accredited laboratory Bemlab (Cape Town). Cation elements (B, Ca, K, Mg, and Na, metals (Mn, Cu, Fe and Zn), nutrients (P) and abiotic factors (pH and resistivity) were quantified for each site across the 6 sampling weeks (see Dalu et al., 2020a, 2020b, for detailed methods).

Statistical analyses

Macroinvertebrate diversity metrices (evenness, Margalef's diversity, taxa richness, Shannon–Wiener diversity, and Simpson's diversity) were calculated using the macroinvertebrate community dataset in PAST version 4.03. The effects of reservoir type (2 levels; macadamia and communal), site (4 levels; 1, 2, 3, 4) and week (6 weeks), and their interaction with environmental variables (i.e., water and sediments) and macroinvertebrate diversity metrics (i.e., evenness, Margalef's diversity index, taxa richness, Shannon–Wiener diversity, Simpson's diversity index) and total abundance were examined using a linear mixed effects model (LMM). To account for repeated measures of each replicate over time, reservoir types and sites were included as a random effect, with time (weeks) included as a within-subject variable. Tukey's post-hoc tests were employed for multiple pairwise comparisons using the 'emmeans' package in R, where effects were significant across the different study sites and weeks (Lenth, 2018). In all analyses, significance was inferred at $p < 0.05$. All statistical analyses were performed using the R environment (v3.5.1; R Development Core Team, 2018).

Distance-based permutational analysis of variance (Permanova; Anderson, 2001) based on Bray–Curtis dissimilarities was employed for biological data and 9 999 permutations with Monte Carlo tests were utilised to analyse differences in macroinvertebrate communities among sites (macadamia, communal) and weeks (i.e., 1–6) using Permanova + for Primer version 6 (Anderson et al., 2008). Furthermore, a two-way analysis of similarities (ANOSIM; Clarke, 1993), with Tukey-HSD post-hoc multiple comparison was conducted, based on a Bray–Curtis resemblance matrix measure calculated from normalised abundance data, to assess potential differences in macroinvertebrate assemblages across sites over time. A two-dimensional ordination of the Bray–Curtis distance rank orders of similarities among taxa was produced using non-metric multidimensional scaling (NMDS) to visually assess similarities and differences within and between different macroinvertebrate communities across weeks.

To investigate the influence of environmental variables (i.e., water and sediment) on macroinvertebrate community structure, a multivariate ordination was utilised after the removal of collinear environmental variables; i.e., we used the variance inflation factor (VIF) to test for multi-collinearity among all variables and deleted those factors that returned VIF values >3. A detrended canonical correspondence analysis (DCA) was utilised to determine whether unimodal or linear methods were most appropriate for ordination analysis (Ter Braak, 1986). The gradient lengths from the DCA analysis were examined, and since the longest gradient was shorter than 3.0, a linear constrained redundancy analysis (RDA) method was found to be the most appropriate for the data. The macroinvertebrate species abundance data were square root transformed before RDA analysis, whereas the environmental variables, except for pH, were log $(x + 1)$ transformed to stabilise variances. The RDA, based on significant ($p < 0.05$) forward-selected water and sediment environmental variables, was used for analysis using 9 999 Monte Carlo Permutations in Canoco version 5.

RESULTS

Physico-chemical variables

Across sampling sites, temperature (mean range 24.5–30.2°C), pH (mean range 5.9–7.3), conductivity (mean range 274.4–550.4 $\mu S \cdot cm^{-1}$) and total dissolved solids (mean range 136.3–354.2) differed significantly ($p < 0.05$; Table 1). Generally, across sites, high mean temperature (30.2 ± 0.3°C) and pH (7.3 ± 0.2) were observed in the macadamia orchard reservoirs, whereas in the communal area reservoirs high mean conductivity (550.4 ± 12.2 $\mu S \cdot cm^{-1}$) and total dissolved solids (354.2 ± 10.3 $mg \cdot L^{-1}$) were observed. A pattern of increasing conductivity was seen for the macadamia orchard reservoirs over time, whereas this was a decreasing trend for communal area reservoirs. There was no clear pattern for temperature and pH. Additionally, an increasing pattern was seen for TDS across both reservoir types. Non-significant differences were observed for water variables (i.e., temperature, conductivity, total dissolved solids and pH) across sites (all; $p > 0.05$), whilst significant differences were observed for temperature, conductivity, and TDS across monitoring weeks ($p < 0.001$) and site × week interactions for pH, conductivity and TDS ($p < 0.05$) (Table 2).

Generally, across sampling weeks, high mean sediment values were observed in macadamia reservoirs, i.e., pH (6.7 ± 0.1), P (24 ± 1.0 $mg \cdot kg^{-1}$), K (153.5 ± 19.5 $mg \cdot kg^{-1}$), Ca (21.5 ± 1.9 $mg \cdot kg^{-1}$), Mg (14.7 ± 0.3 $mg \cdot kg^{-1}$), K (0.4 ± 0.1 $mg \cdot kg^{-1}$), Na (0.5 ± 0.0 $mg \cdot kg^{-1}$), Cu (27.6 ± 1.0 $mg \cdot kg^{-1}$), Zn (7 ± 0.8 $mg \cdot kg^{-1}$), Mn (309 ± 43.0 $mg \cdot kg^{-1}$), B (0.6 ± 0.02 $mg \cdot kg^{-1}$), Fe (1885 ± 55.0 $mg \cdot kg^{-1}$), and S (346.5 ± 2.5 $mg \cdot kg^{-1}$), whereas, in communal reservoirs, high mean sediment values were observed for resistivity (180 95 ± 1 775 Ω). No significant differences were observed for most sediment variables ($p > 0.05$), with the exception of P ($p < 0.05$), across sites. Across monitoring weeks, no significant differences were observed for all sediment variables (all; $p > 0.05$), whilst site x week interactions indicated significant differences for B ($p < 0.05$).

Macroinvertebrate colonisation

A total of 644 macroinvertebrate individuals, belonging to 8 orders and 4 functional feeding groups, were collected over 6 weeks across the 4 reservoirs (2 macadamia, 2 communal) (Table 3). The orders with high occurrence frequency were Odonata and Diptera, accounting for 35.7% and 14.3%, respectively. Overall, Libellulidae (i.e., *Pantala flavensces*, *Trithemis* sp. And *Zyonyx natalensis*) were the most dominant family group. Non-biting midges, Chironominae, was the most abundant taxon, accounting for 55.1% of the total abundance across sampling sites, with the seed shrimps Ostracoda being the second-most abundant (14.4%). The dropwings *Trithemis* sp. and dragonfly *Anax* sp. were the third and fourth most abundant taxa recorded, accounting for 5.2% combined (Fig. 2). The results of the linear mixed model showed that total abundance varied across weeks ($p < 0.001$) (Table 2). Overall, succession in the macadamia orchard reservoirs was marked by an initial colonisation of Chironominae (collector-gatherers), Ostracoda (collector-filterers) and *Radix natalensis* (scrapers), which remained throughout the sampling

Table 1. Range of mean water chemistry variables measured across reservoirs (macadamia orchard, communal area) over time (6 weeks). Abbreviations: TDS – total dissolved solids. Superscript letters (i.e., a, b, c) indicate the significance differences from pairwise comparisons across weeks. Weeks with the same letter for a given variable do not differ significantly for that variable at $p > 0.05$.

Variables	Unit	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6
Temperature	°C	24.5–25.6^{a}	27.5–28.4^{b,c}	25.4–27.1^{a,b}	25.6–26.6^{a}	28.1–30.2^{c}	24.6–26.7^{a}
pH		6.4–7.0	6.0–7.3	6.0–7.2	6.0–7.2	6.4–7.3	6.8–7.0
Conductivity	$\mu S \cdot cm^{-1}$	274.4–360.0^{a}	404.7–458.0^{a,b}	286.0–333.2^{a}	297.8–426.2^{a}	539.7–550.4^{b}	274.4–360.0^{a}
TDS	$mg \cdot L^{-1}$	136.8–168.5^{a}	205.7–263.2^{c}	193.7–196.5^{a,b}	165.5–207.7^{a,b}	264.8–354.2^{c}	136.3–179.0^{a}

Table 2. Linear mixed effects model results considering key base water and sediment variables and macroinvertebrate diversity metrics as a function of sampling sites (i.e., macadamia orchard and communal area reservoirs; df = 1) and weeks (df = 5), and their interaction (df = 5). F-values are discerned with Type III sums of squares via Satterthwaite's method. Significant *p*-values are in bold.

Variables	Site		Week		Site × Week	
	F	*p*	F	*p*	F	*P*
Water chemistry variables						
Temperature	0.899	0.443	**4.532**	**< 0.001**	1.4485	0.22
pH	3.424	0.205	1.246	0.294	**10.255**	**< 0.001**
Conductivity	0	0.999	**7.567**	**< 0.001**	**3.154**	**0.008**
TDS	1.023	0.418	**16.614**	**< 0.001**	**2.551**	**0.01**
Sediment chemistry variables						
pH	0.352	0.613	0.599	0.701	1.812	0.136
Resistivity	3.905	0.187	1.062	0.399	1.001	0.427
P	**82.137**	**0.011**	1.723	0.156	1.207	0.327
K	2.305	0.268	0.418	0.809	0.728	0.607
Na	5.138	0.152	1.024	0.419	0.716	0.616
K	3.792	0.061	0.458	0.809	0.728	0.607
Ca	1.228	0.383	1.14	0.359	0.539	0.746
Mg	9.666	0.09	2.975	0.250	0.991	0.438
Cu	1.228	0.383	1.14	0.359	0.539	0.745
Zn	0.046	0.849	1.22	0.321	1.853	0.129
Mn	1.372	0.362	2.332	0.064	1.256	0.305
B	2.691	0.243	1.458	0.229	**2.526**	**0.048**
Fe	2.153	0.28	0.306	0.906	1.911	0.118
S	1.632	0.33	1.075	0.391	**2.966**	**0.03**
Macroinvertebrate diversity metrics						
Evenness	0.037	0.865	1.696	0.162	0.678	0.643
Margalef's diversity	1.262	0.31	**4.021**	**0.009**	0.776	0.69
Taxa richness	0.002	0.964	**8.33**	**<0.001**	1.666	0.17
Shannon–Wiener diversity	0.011	0.926	**4.408**	**0.003**	1.255	0.306
Simpson's diversity	0.095	0.879	2.22	0.075	0.869	0.512
Total abundance	0.016	0.91	**8.715**	**<0.001**	1.625	0.18

Table 3. Mean relative abundances (%) of the dominant macroinvertebrate species and metrics observed over 6 weeks for the study site categories: macadamia orchard (MO) and communal area (CA) reservoirs. FFG – functional feeding group; Abbr. – abbreviation.

Taxa	Order	FFG	Abbr.	Week 1		Week 2		Week 3		Week 4		Week 5		Week 6	
				MO	CA	MO	CA	MO	CA	MO	CA	MO	CA	MO	CA
Anax sp.	Odonata	Predator	Ana		19		14		13		10		10	3	8
Ceratopogonidae	Diptera	Predator	Cer		12						10		5		
Chironominae	Diptera	Collector-gatherers	Chi	45	22	39	50	32	40	37	33	31	37	34	41
Gyrinidae larvae	Coleoptera	Predator	Gyr							4	12	8	10	7	8
Ostracoda	Podocopida	Collector -filterers	Ost	18	19	18	14	13	9	10	8	10	12	12	19
Pantala flavescens	Odonata	Predator	Pan							10		8		6	
Physella acuta	Gastropoda	Scrapers	Phy						12						
Planaria sp.	Platyhelminthes	Predator	Pla							8		12			
Potamonautes sp.	Decapoda	Collector -gatherers	Pot												5
Pseudagrion sp.	Odonata	Predator	Pse	21				13		7		5		8	
Radix natalensis	Mollusca	Scrapers	Rad	16		21		15		6		10		14	
Ranatra sp.	Hemiptera	Predator	Ran								5		5		5
Trithemis sp.	Odonata	Predator	Tri			14		19		9		6		7	
Zyonyx natalensis	Odonata	Predator	Zyo			8				9		4		5	
Other taxa					30		22	8	26		22	6	21	4	14
Macroinvertebrate diversity metrics															
Evenness				0.9	0.9	0.9	0.8	0.9	0.8	0.7	0.8	0.8	0.8	0.7	0.8
Margalef's diversity				0.9	1.4	0.8	0.9	1.4	1.2	1.6	1.5	1.8	1.4	1.7	1.4
Taxa richness				4	5	5	5	6	6	9	8	10	8	10	8
Shannon–Wiener diversity				0.8	1.1	0.8	0.9	1.3	1.1	1.3	1.4	1.5	1.3	1.5	1.2
Simpson's diversity				0.5	0.6	0.5	0.5	0.7	0.6	0.6	0.7	0.7	0.6	0.7	0.6

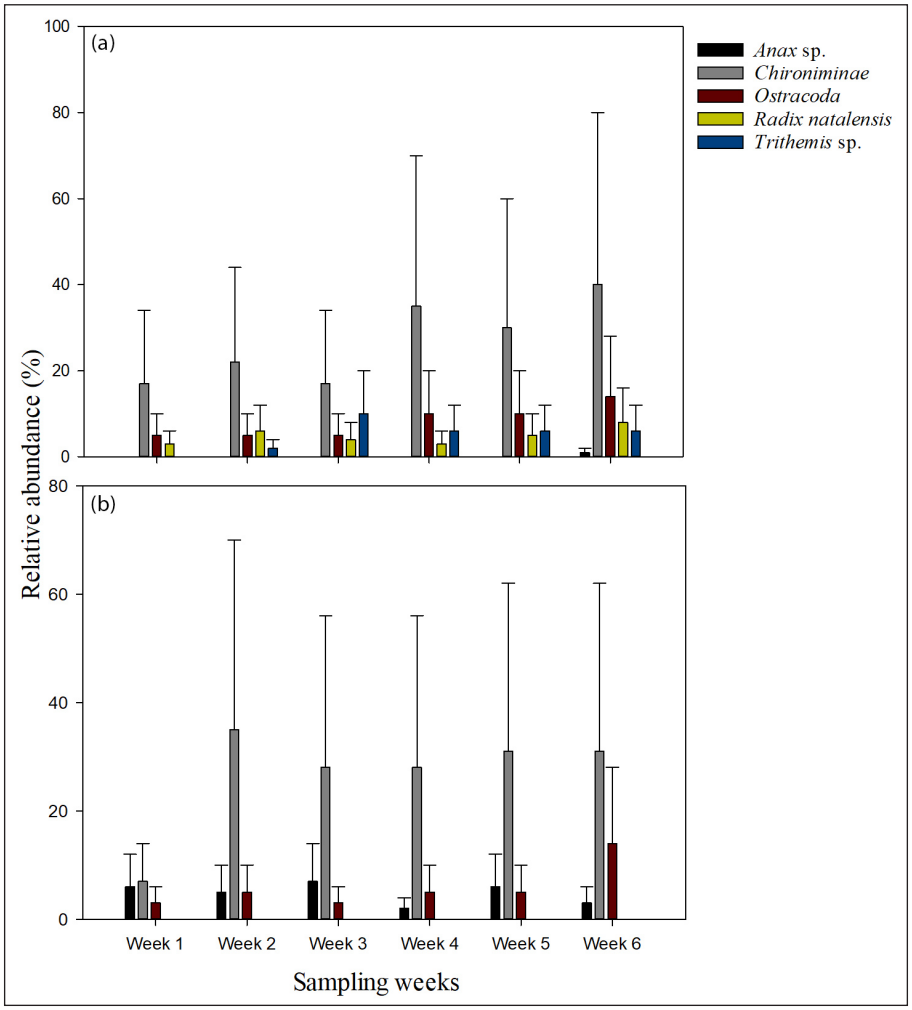

Figure 2. The five most dominant macroinvertebrates (relative abundance (%) ± SD) across, (a) macadamia orchard and (b) communal area reservoirs at the end of the experiment (6 weeks). Different colours denote macroinvertebrate taxa (see legend).

period. Additionally, Chironominae and Ostracoda presented a pattern of increasing abundance over time. Late colonisers were dominated by predators, i.e., Gyrinidae larvae and *Trithemis* sp. The succession in the communal area reservoirs was, however, marked by *Anax* sp. (predator), Chironiminae, and Ostracoda, with Chironiminae, and Ostracoda increasing in abundance over time, similar to macadamia orchard reservoirs. Late colonisers were also dominated by predators, i.e., Gyrinidae larvae and *Ranatra* sp.

Similar macroinvertebrate diversity metric values were observed across macadamia orchard and communal area reservoirs (Table 3, Fig. 3). Significant differences were observed across monitoring weeks for Margalef's diversity, taxa richness and Shannon–Wiener diversity ($p < 0.05$). An increasing pattern in taxa richness was seen for macadamia orchard (Weeks 1–5) and communal area (Weeks 1–3) reservoirs (Fig. 3). Margalef's and Shannon–Wiener diversity exhibited no significant pattern for the communal area reservoirs, whereas in the macadamia orchards Margalef's and Shannon–Wiener diversity increased over time. Simpson diversity exhibited an increasing trend for macadamia orchards, whereas in the communal area reservoirs no clear pattern was observed. Evenness, however, exhibited a decreasing trend over time for both reservoir types.

Using Permanova, significant differences in total macroinvertebrate community structure were observed across sites (pseudo–F = 26.899, p(MC) = 0.001) and weeks (pseudo–F = 2.286, p(MC) = 0.002). Pairwise comparisons highlighted significant differences in macroinvertebrates community structure between weeks; for instance, Weeks 1 vs. 4 (t = 2.341, p(MC) < 0.001), Weeks 1 vs. 6 (t = 2.233, p(MC) = 0.004), Weeks 2 vs. 4 (t = 1.660, p(MC) = 0.011), Weeks 3 vs. 4 (t = 1.545, p(MC) = 0.033), and Weeks 3 vs. 6 (t = 1.590, p(MC) = 0.018).

The n–MDS analysis produced an ordination which separated the two sites (Fig. 4). According to the ANOSIM results, little similarity was observed in macroinvertebrate communities between macadamia orchards and communal area sites (ANOSIM: R = 0.08, p = 0.081), and there were differences across weeks (ANOSIM: R = 0.76, p = 0.001). Pairwise comparison tests indicated significant differences between Week 1 vs. 4 (R = 0.42, p = 0.006), 1 vs. 5 (R = 0.30, p = 0.003), and 1 vs. 6 (R = 0.39, p = 0.002).

The influence of water and sediment chemistry variables on macroinvertebrate community structure

The RDA was conducted to explore the simultaneous effects of all the biotic variables (i.e., water and sediment variables) on macroinvertebrate communities. Based on RDA analysis, first and second axes with eigenvalues of 0.29 and 0.20 were observed, respectively, with selected exploratory variables accounting for 65.9% of the total macroinvertebrate variance. Monte Carlo unrestricted permutation test indicated Axis 1 (permutation) and 2 (999 permutations of Axis 2 with Axis 1 as a covariable) were statistically significant ($p < 0.05$) in all cases. Of the 18 variables (i.e., water and sediment), the abundance of macroinvertebrates

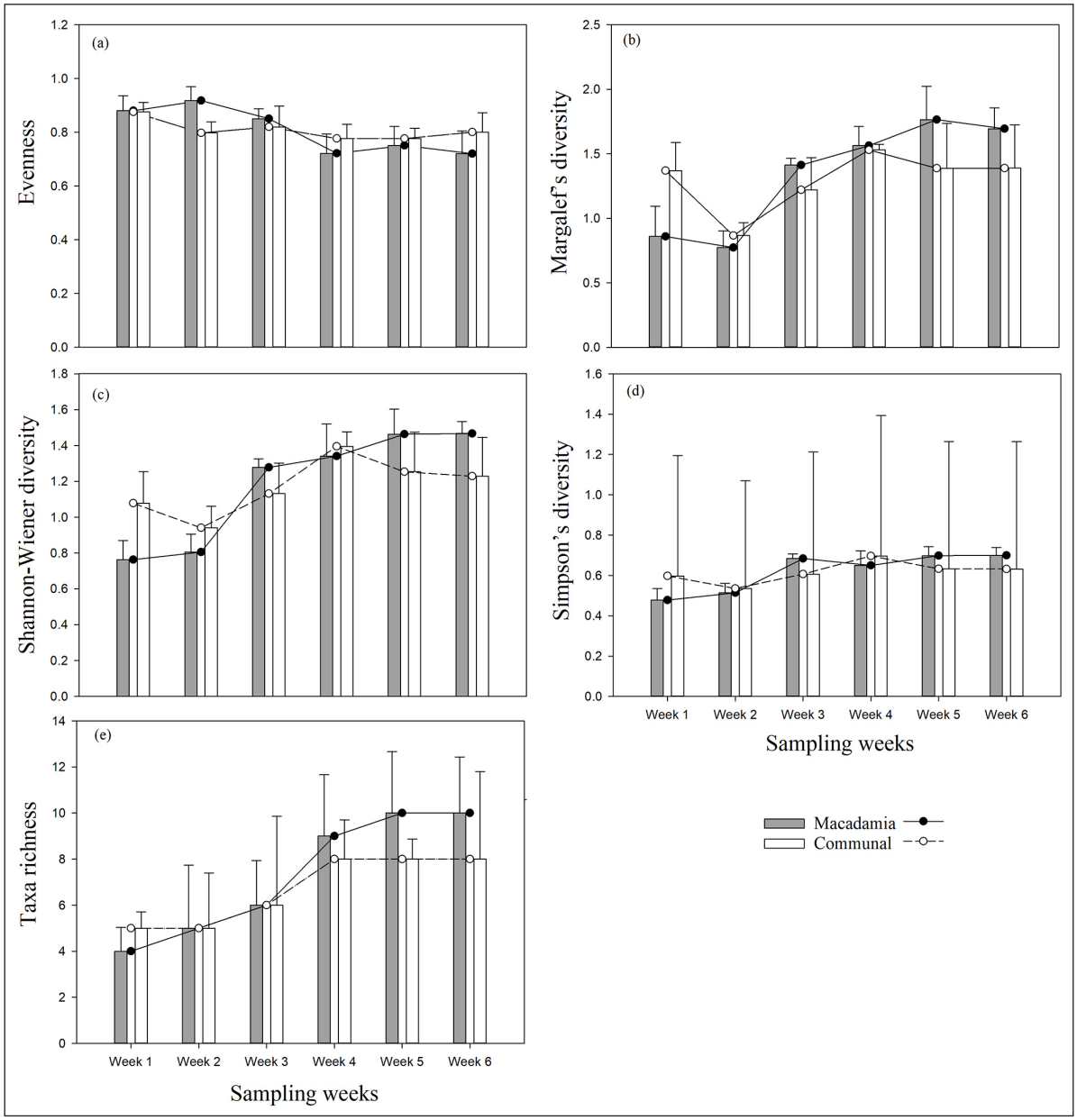

Figure 3. Mean (+ standard deviation) macroinvertebrate diversity metrics, i.e., (a) evenness, (b) Margalef's diversity, (c) Shannon–Wiener diversity (d) Simpson's diversity, and (e) taxa richness across macadamia orchard and communal area reservoirs at the end of the experiment (6 weeks). Different colours denote two reservoir types (see legend).

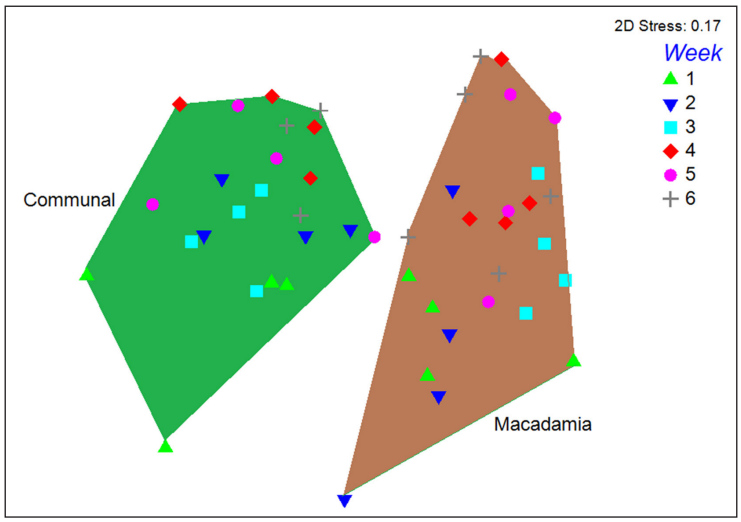

Figure 4. *n*–MDS ordination highlighting variation of macroinvertebrate communities between communal area and macadamia orchard reservoirs over the duration of the experiment (i.e., 6 weeks).

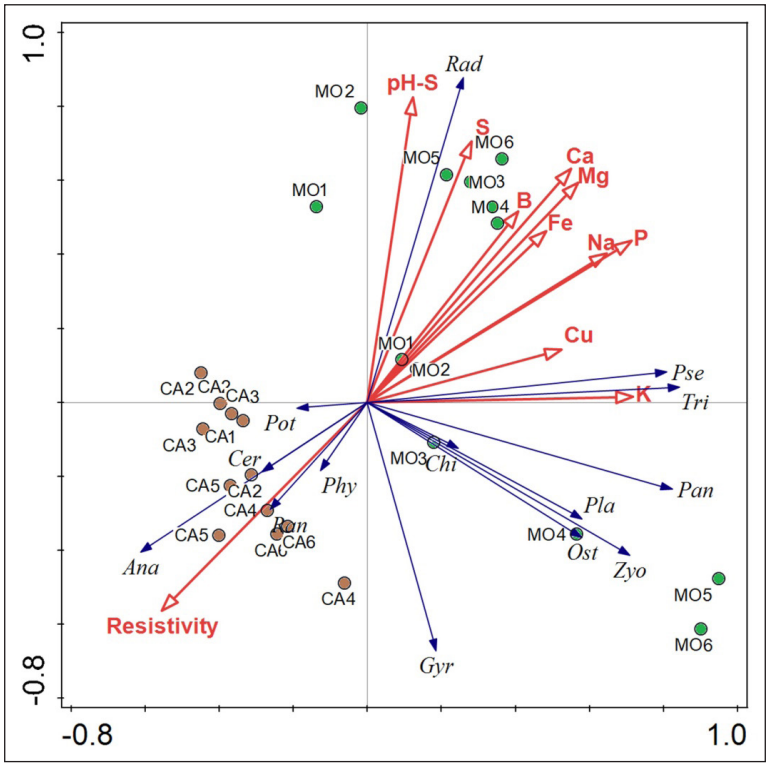

Figure 5. Redundancy analyses ordination showing the relationship between macroinvertebrate colonisation and the significant environmental variables. Letters in sample labels represent sites (MO – macadamia orchard reservoir, CA – communal area reservoir). Numbers in the labels represent sampling weeks (i.e., 1–6). Taxa abbreviations are defined in Table 3.

across two reservoir types and 6 weeks was found to be significantly associated with sediment chemistry (i.e., pH, resistivity, P, K, Na, Ca, Mg, Cu, B, Fe and S) which was significant in structuring macroinvertebrate community (Fig. 5). Sediment pH and S were strongly positively associated with the second axis, while variables such as K, Cu, Na and P were negatively associated with the first axis. Resistivity was highly negatively associated with the first axis. The RDA axis separated the sites based on reservoir types and sampling weeks. Macadamia orchard reservoirs, highly polluted, were generally associated with Axis 1 and Axis 2, being characterised by high values for variables such as pH and S and low resistivity. Moreover, macadamia reservoirs were associated with macroinvertebrates such as Chironominae, Ostracoda, *Plantala flavescens*, *Pseudagrion* sp., *Trithemis* sp., and *Zyonyx natalensis* (Fig. 5). On the other hand, communal area reservoirs, being relatively less polluted, were negatively associated with the first axis, being characterised by high resistivity and macroinvertebrates such as *Anax* sp., Ceratopogonidae, *Physella acuta*, *Ranatra* sp., and *Potamonautes* sp. (Fig. 5).

DISCUSSION

Our results support Hypothesis 1, primary colonisation and abundance would be different between macadamia orchard and communal area reservoirs, given the varying agricultural practices. We found significant differences in macroinvertebrate community structure and few similarities between reservoir types. We also found that at both the pioneer and later successional stages, macroinvertebrate communities were discrete between reservoirs. Our results partially support our second hypothesis, namely, that water and sediment characteristics would differ between the two reservoirs and that sediments were more likely to influence macroinvertebrate communities. The results highlighted that few sediments and water physicochemical variables were significantly different between reservoirs in the different land-use types; however, we observed that sediment variables had a strong significant influence on macroinvertebrate communities. Lastly, our results support Hypothesis 3, namely that the functional feeding groups would vary with time. We found that early colonisers were dominated by collectors and late colonisers were dominated by predators.

According to Layton (1989), the time it takes macroinvertebrates to colonise stone substrates and to reach the state of equilibrium of densities and richness is variable and generally ranges from 4 to 38 days. This corresponded with our findings as macroinvertebrate taxa and abundance showed an increasing trend over time and were significantly different across the weeks. Generally, several macroinvertebrate taxa colonised stone substrates, but Chironominae and Ostracoda were found consistently (representing 55.1% and 14.4%, respectively, of the macroinvertebrates found) and increased in abundance over time across both reservoirs. The colonisation of artificial stone substrates by macroinvertebrates in the present study is not surprising, given that stones are normally stable habitats in periods of high rainfall because they are less susceptible to being carried downstream by the current and because their uneven surfaces facilitate the movement and attachment of macroinvertebrates when the water flow slows, offering greater stability and availability of micro-sites for colonization (Friedmann and Galun, 1974). The high abundance of Chironominae and Ostracoda on the stones might be attributed to the fact that they are small and mobile, live and feed close to the sediment–water interface and reproduce more often. Similar results were observed by Alonso and Camargo (2005), who observed increased diversity of Chironominae for small stone substrates. Early colonisers were dominated by collector-gatherers and collector-filterers, i.e., Chironominae and Ostracoda, respectively, in both reservoirs, whereas late colonisers were dominated by predators, i.e., Gyrinidae larvae, *Trithemis* sp. and *Ranatra* sp. This is not surprising given that predators are known as late arrivals and feed on early colonisers (Hansen et al, 1986). A similar trend was seen by Hansen et al. (1986),

who observed a predator-free pattern during early succession and immigration of predators during the later stage of succession. Although not the key focus of the study, fish (*Tilapia rendalli*) were observed in the macadamia orchard reservoirs, whereas Mozambique tilapia (*Oreochromis mossambicus*) and stream frog (*Strongylopus* sp.) were observed in the communal area reservoir, indicating that artificial stone substrates could also function as habitat for fish and frog communities. As highlighted by Relyea and Diecks (2008), exposure of aquatic fauna such as fish to pesticides, or increased agricultural land-use, results in growth reduction and low reproductive activity, with juveniles more sensitive to pesticides than adults.

Macroinvertebrates are an important part of aquatic ecosystems, and community structure characteristics are related to environmental variables (Munyai et al., 2024). As such, we revealed that changes in water chemistry variables were not reflected in the macroinvertebrate communities, whereas sediment chemistry variables were important as a predictor of macroinvertebrates. Clements (2020) highlighted that sediments contaminated with heavy metals may promote or inhibit macroinvertebrate community structure and colonisation. Macroinvertebrate structural composition has been observed to respond strongly to sediment chemistry variables (Clements, 2020), and this was evident in our study and supported by the RDA analysis, which found sediment chemistry variables (i.e., pH, resistivity, P, K, Na, Ca, Mg, Cu, B, Fe and S) to significantly alter the macroinvertebrate community structure. Furthermore, these variables were crucial factors in structuring macadamia orchard reservoir macroinvertebrate communities, as opposed to communal areas reservoir macroinvertebrate communities, with the exception of resistivity. This was not surprising given that heavy metals are well-known environmental pollutants due to their toxicity, persistence in the environment, and bio-accumulative nature.

Agricultural activities are known for high anthropogenic impacts, resulting in increased pollution compared to communal areas (Sharma and Agrawal, 2005). For instance, Ouyang et al. (2018) highlighted that excessive nutrients can result in water quality deterioration and dissolved oxygen depletion, resulting in a decline in species richness. This further suggests the complexity of the macroinvertebrate–sediment complex relationship, based mainly on B, Fe and Cu. As indicated by Jennings (2021), B is an important sediment chemistry variable involved in structuring macroinvertebrate communities, whereas Dalu et al. (2022) found Cu, Mg and Na among the most important sediment chemistry variables. Bian et al. (2016) highlighted that high levels of Na contributes greatly to water quality in aquatic ecosystems by imparting a salty taste and increase the corrosivity of water, which compromises the osmoregulatory processes in macroinvertebrates and is known to affect macroinvertebrate communities. Lauber et al. (2009) suggested that sediment pH directly imposes a physiological constraint on aquatic fauna by reducing the net growth of individual taxa that cannot survive if the soil pH is outside a certain range.

CONCLUSIONS

The current study contributes to understanding aquatic ecosystem functioning and artificial aquatic substrate colonisation and succession, and interplays between macroinvertebrate community and environmental variables between macadamia orchard and communal area reservoirs. We found that macadamia orchards and communal area reservoirs were important for macroinvertebrate colonisation and succession for artificial stone substrates. Stone substrates supported a distinctive macroinvertebrate community and drove the establishment of macroinvertebrate communities, at least temporarily, for some taxa. Various macroinvertebrates were observed on the stone substrates in both reservoirs, most notably Chironominae and Ostracoda, which contributed a combined 61.5% of the total macroinvertebrate abundance. A consistent succession of macroinvertebrates and functional feeding groups was observed, with early colonisers being marked by collectors and late colonisers being marked by predators. The presence of pesticides in both reservoirs and/or types was most likely to alter primary colonisation and successive community structure in the macadamia orchard reservoirs. Furthermore, macroinvertebrate community structure was found to be more highly affected by sediment chemistry variables than water variables, as shown by RDA analyses. Despite the influence of pesticides on colonisation dynamics, stone substrates are known to represent a complex ecosystem of microflora, including bacteria, algae, fungi, and lichens, which might also have attributed to macroinvertebrate colonisation. This scenario is thus worthy of further investigation, by assessing the abundances associated with stone substrates and their influence on certain macroinvertebrates.

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AUTHOR CONTRIBUTIONS

Thendo Mutshekwa: conceptualisation, methodology, investigation, data curation, formal analysis, writing – original draft, review and editing. Lutendo Mugwedi: methodology, visualization, investigation, supervision, writing – original draft, review & editing. Ryan J Wasserman: visualization, supervision, writing – review and editing. Farai Dondofema: methodology, visualization, investigation, funding, supervision, writing – review and editing. Ross N Cuthbert: visualization, methodology, formal analysis, writing – review and editing. Tatenda Dalu: conceptualisation, methodology, investigation, data curation, formal analysis, funding, supervision, writing – original draft, review and editing.

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DATA AVAILABILITY STATEMENT

The datasets generated and/or analysed during the current study are not publicly available as they are part of larger study that is currently ongoing but are available from the corresponding author on reasonable request.

CONFLICT OF INTEREST

The authors certify that they have no conflict of interest.

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