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What physical habitat factors determine the distribution of gastropods in neotropical headwater streams?

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What physical habitat factors determine the distribution of gastropods in neotropical headwater streams?

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ABSTRACT

Freshwater gastropods play a pivotal role in the structure and functioning of freshwater ecosystems, but despite their importance, there are still gaps in their ecology. Our goal was to understand what physical habitat factors are the most important for the distribution of freshwater gastropods in headwater stream ecosystems in the Neotropical Savanna and provide a baseline for conservation and management efforts for freshwater gastropods in this biome. We identified five taxa, each with different environmental prefferences. *Littoridina* presence related negatively with stream slope, *Biomphalaria* presence related positively with total dissolved solids and the proportions of cobble, fine sediment and organic matter. *Gundlachia* presence correlated positively with elevation and the proportion of pools in the site. *Physa* presence related negatively with total dissolved solids and positively with alkalinity. *Melanoides tuberculata* presence correlated positively with the proportion of coarse gravel. Our results highlight the challenge for protecting native freshwater gastropod assemblages (and managing non-native invasive species), because environmental preferences vary widely amongst taxa and most are vulnerable to common anthropogenic disturbances.

1. Introduction

Rivers, lakes, ponds and other freshwater ecosystems cover less than 1% of the planet's surface area but hold more than 10% of the known species diversity (Dudgeon et al., 2006; Reid et al., 2019). Freshwater ecosystems also provide irreplaceable ecosystem services to human beings, including drinking water, water supply for multiple human uses, and hydroelectric power generation (van Rees et al., 2021). In spite of these contributions and their importance for global biodiversity and human well-being, freshwater ecosystems are among the most threatened ecosystems worldwide (Collen et al., 2014; Darwall et al., 2018; Reid et al., 2019; Turak et al., 2016). Among these, headwater streams (1st to 3rd order; Strahler, 1957) can be singled out for their high biotic diversity and taxa richness (Meyer et al., 2007) and because they represent ~80% of the channel length in a hydrographic basin (Datry et al., 2014).

Among the taxa that constitute headwater stream biodiversity, freshwater gastropods are one of the most diverse and widespread, with more than 4000 identified species living in all continents (Lopes-Lima et al., 2021; Strong et al., 2008). Freshwater gastropods play a pivotal role in the structure and functioning of lotic ecosystems, contributing to the biodiversity of benthic macroinvertebrate assemblages, water quality, nutrient cycling, and secondary productivity, because of their roles as filter feeders, algal grazers, detritivores and food for predators (Böhm et al., 2021; Johnson et al., 2013). Invasive gastropods are one of the most successful groups of non-native invasive species in freshwater ecosystems (e.g., *Melanoides tuberculata*, an Asian species that has been recorded in most South American river systems (Fernandez et al., 2003; Santos and Eskinazi-Sant'Anna, 2010). Such species are capable of reproducing and generating fertile offspring with a high probability of survival. They also often act as ecosystem engineers, altering the physical habitats and biological processes of the ecosystems where they become established (Jones et al., 1994; Linares et al., 2020; Simberloff et al., 2013).

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Despite their importance, there are still gaps regarding our knowledge of freshwater gastropod ecology (Lopes-Lima et al., 2021). The distribution and structure of gastropod assemblages is influenced by local environmental factors and given their limited movement ability, knowledge about the environmental factors determining their distribution is an important step for conserving native species and managing non-native invasive species (Bae and Park, 2020; Brown et al., 1998; Jörger et al., 2010; Strong et al., 2008).

This lack of knowledge is especially dire in the neotropics, where most studies on these taxa focus only on a few invasive species in reservoirs, large rivers and wetlands (e.g., Linares et al., 2019; Oliveira et al., 2011; Santos and Eskinazi-Sant'Anna, 2010), neglecting the roles of gastropods in headwater streams. For the Cerrado (Brazilian Neotropical Savanna), this study will be the first focusing on freshwater gastropod assemblages in headwater streams.

Here, our goal was to understand what physical habitat factors are the most important for the distribution of freshwater gastropods in headwater stream ecosystems in the Neotropical Savanna. We aimed to provide a baseline for conservation and management efforts for freshwater gastropods in the Neotropical Savanna.

2. Methodology

2.1. Study area

We sampled 40 stream sites (1st to 3rd order, based on Strahler, 1957) within a hydrological unit 35 km upstream of the Três Marias hydroelectric power reservoir, located in the Neotropical Savanna of southeastern Brazil (Fig. 1). The Três Marias Reservoir water comes primarily from the São Francisco River and its tributaries, such as the São Vicente, Paraopeba, Sucuriú, Indaiá, Ribeirão do Boi, Ribeirão da Extrema and Borrachudo Rivers (Esteves et al., 1985). It began operating in 1962 to control floods, improve navigation, encourage development and irrigation, and generate hydroelectric power (CEMIG - Companhia Energética de Minas Gerais, 2014). The stream sites were selected using a probability-based procedure, resulting in a spatially balanced design (Macedo et al., 2014a; Olsen and Peck, 2008). The sites were sampled during the dry season of 2010 and were 40 mean channel widths long or a minimum of 150 m.

2.2. Water quality & physical habitat assessment

To assess water quality, the following physical and chemical characteristics of the water column were measured in the field for each site: pH, conductivity, and total dissolved solids (TDS). Water samples were collected for further analysis in the laboratory for dissolved oxygen, turbidity, alkalinity, total nitrogen, and total phosphorus. These analyses were conducted following APHA (1998) methodology.

To assess physical habitat condition, we followed USEPA protocols (Peck et al., 2006) adapted for the Neotropical Savanna (Ligeiro et al., 2013). In each sampling site, 11 transects (perpendicular to the channel) were established, defining 10 longitudinal sections where physical habitat measurements were taken. At each transect, we recorded channel morphology, habitat features, riparian structure, and anthropogenic alterations. Subsequently, these data were used to calculate 288 physical habitat metrics (Kaufmann et al., 1999, 2022) (Supplementary Material S1).

From the entire pool of physical habitat metrics calculated, we eliminated those with a high number of zeros (0 on ≥ 0.8 of the sites) and those with low variation among sites (coefficient of variation ≤ 0.3). We then determined the Pearson correlations among the remaining metrics, eliminating those that were highly correlated ($|r| \geq 0.7$; Dormann et al., 2013) and retaining the most ecologically relevant based on previous knowledge (Esselman et al., 2013; Macedo et al., 2016; Silva et al., 2017).

We also estimated anthropogenic disturbances at local and catchment scales, based on the methodology described by Ligeiro et al. (2013). The

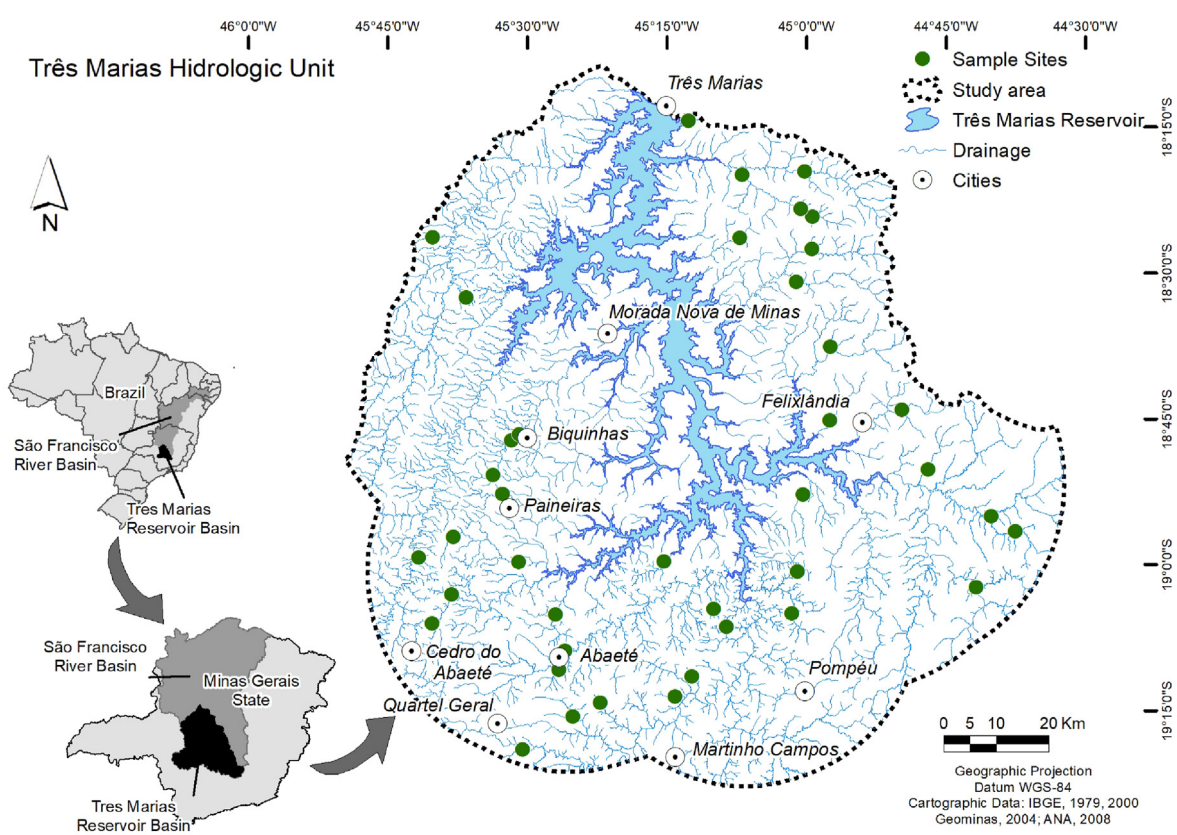

Fig. 1. Sampling site locations in the Três Marias hydrological unit.

Local Disturbance Index (LDI) was calculated based on the amount and proximity of 11 types of anthropogenic disturbances observed in-channel or in the riparian zone of each site (Kaufmann et al., 1999, 2022). Those disturbances included walls, dikes, revetments, rip rap or dams, buildings, pavement or cleared lots, roads or railroads, inlet or outlet pipes, landfills or trash, parks or maintained lawns, row crops, pastures, rangelands, hay fields, or evidence of livestock, logging, or mining.

For calculating the Catchment Disturbance Index (CDI), we estimated the land use in the catchment of each stream site. Land uses were delimited using images obtained through a TM sensor onboard the Landsat 5 satellite, taken in 2010. Polygons for the definition and quantification of land use categories were delimited and classified (pasture, agriculture and buildings), and computed as percentages. Images obtained from Google Earth satellite images were employed as ancillary data in this assessment (Macedo et al., 2014b). CDI was estimated using the land use percentages weighted by the disturbance potential of each (Böhmer et al., 2004; Ligeiro et al., 2013; Rawer-Jost et al., 2004) and calculated as:

$$\mathrm{CDI} = 4 \times (\%\ \text{residential} + \text{urban}) + 2 \times (\%\ \text{agricultural areas} + \%\ \text{bare soil}) + (\%\ \text{pasture} + \%\ \textit{Eucalyptus}\ \text{plantations}).$$

2.3. Freshwater Gastropoda sampling

We collected freshwater gastropods at all stream sites using a D-net (30 cm opening, 0.5 mm mesh sieve), using a kick-net method. The samples were taken following a zig-zag pattern along each stream site, resulting in eleven sub-samples (0.09 m^2 each), totaling a 0.99 m^2 multi-habitat composite sample for each stream site. We fixed the samples in the field with 10% formalin and took them to the laboratory. There, the gastropods were rinsed in tap water, sorted, and identified to the lowest possible level with the aid of specialized literature (Mugnai et al., 2010; Simone, 2006).

Because of the fixation method, the specimens' soft tissue was damaged and could not be used in the identification process, preventing us from identifying all of them to species. Instead, identifications were based on the shells (Geiger et al., 2007 Meier-Brook, 1976; Paraense, 1975). Gastropoda were identified to genus, except for *Melanoides tuberculata*, which were identified to species. Sampling sites were then classified with each identified freshwater gastropod taxon as detected (1) or non-detected (0). All specimens collected were fixed in 70% alcohol and deposited in the Reference Collection of Benthic Macroinvertebrates, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais.

2.4. Data analyses

To understand which physical habitat factors were most important for the distribution of freshwater gastropod species in headwater stream ecosystems in the Três Marias hydrologic unit, we used a model selection approach based on the Akaike information criterion adjusted for small sample size (AICc; Burnham and Anderson, 2002). We used our selected variables as predictor variables in generalized linear models (GLMs) with a binomial distribution, where the response variables were the detection (1)/non-detection (0) of each gastropod taxon. Before the analyses we standardized all variables, which consisted of subtracting each variable value by the variable mean and dividing it by the variable standard deviation. As a result, all variables were centered so that the predictors had their means at 0, which allowed the units of the regression coefficients to be the same. The variables were standardized or scaled using the "scale" function in R. We then constructed models based on all possible additive variable combinations that may have influenced the probabilities of presence for each gastropod taxon (Doherty et al., 2012). This allowed us to calculate the cumulative AICc weights (w_+) for each variable and evaluate which were the most likely ($w_+ \geq 0.50$; Berger and Barbieri, 2004) to have influenced the presence for each gastropod taxon (Burnham and Anderson, 2002). Statistical analyses were implemented using the MuMIn package (Bartón, 2019) in R. To test for overdispersion or extra-binomial variation (i.e., $\hat{c} > 1$ and $p < 0.05$) in the most parametrized model of each model set, we used a simulation-based approach available in the DHARMa package (Hartig, 2022). Because the sampling site locations may have resulted in a lack-of-independence (or spatial autocorrelation) among our sites, we performed a Moran's I test for spatial autocorrelation (Lecocq et al., 2019; Smeraldo et al., 2020). To do so, we used the residuals of our most parameterized model in each model set, using the spdep package (version 1.1.2; Bivand and Wong, 2018) in R (R Development CoreTeam, 2015).

3. Results

A total of five freshwater gastropod taxa were sampled in our stream sites (Supplementary Material S2): *Littoridina* (Hydrobiidae - Caenogastropoda; 40 individuals detected in three sites), *Biomphalaria* (Planorbidae - Panpulmonata; 96 individuals detected in nine sites), *Gundlachia* (Planorbidae - Panpulmonata; 87 individuals detected in eight sites), *Physa* (Physidae – Panpulmonata; 10 individuals detected in five sites), and *Melanoides tuberculata* (Thiariidae - Caenogastropoda; 21 individuals detected in four sites). In total, we detected freshwater Gastropods in 18 (out of 40) sites (Fig. 2).

The variable selection process resulted in a total of 27 selected variables (Table 1). We organized them into six categories: Catchment metrics (two metrics), Physio-Chemical metrics (four metrics), Channel Morphology metrics (five metrics), Substrate metrics (nine metrics), Water Flow metrics (five metrics) and Disturbance metrics (two metrics).

Different variables influenced the presence/absence of freshwater gastropods (Table 2). *Littoridina* presence correlated negatively with Mean Site Slope. *Biomphalaria* presence correlated positively with Total Dissolved Solids and the proportions of Cobble, Fine Sediment and Organic Matter. *Gundlachia* presence correlated positively with Basin Elevation Range and the Proportion of Pools in the site. *Physa* presence correlated negatively with Total Dissolved Solids and positively with Alkalinity. *M. tuberculata* presence correlated positively with the proportion of Coarse Gravel. The simulation-based approach revealed no evidence of overdispersion in the tested models (i.e., $\hat{c} \sim 1$ and $p < 0.05$ in all cases; Supplementary Material S3). The Moran's I test for spatial autocorrelation did not show any spatial autocorrelation in the tested models (Supplementary Material S4).

4. Discussion

Littoridina was negatively related to channel slope, likely indicating a preference for flat lowland streams. This preference stems from these streams being comparatively more stable habitats, that are less affected by seasonal effects such as flash floods (Chattopadhyay et al., 2021; Erba et al., 2020), and the same pattern can be applied to *Gundlachia* preference for pools. *Littoridina* preference for lowland streams can have important implications for its conservation, given that lowland freshwater ecosystems are disproportionally affected by anthropogenic disturbances when compared to highland streams (de Vries et al., 2019; Oliveira et al., 2011; Usseglio-Polatera and Beisel, 2002). Lowland streams are easily accessible to humans and more often located near urban centers or agricultural areas. This results in greater occurrence of anthropogenic stressors, including altered basin land use and riparian vegetation, eutrophication, damming, channelization, and introduced invasive species (Graf et al., 2016; Horsák et al., 2009; Shandas and Alberti, 2009).

The positive correlation of *Melanoides tuberculata* with stable hard substrate corroborates previous studies in South American reservoirs (Karatayev et al., 2007; Linares et al., 2020), where high densities of individuals of this species were found in sites with hard substrates. Substrate composition is closely linked to the quality and quantity of

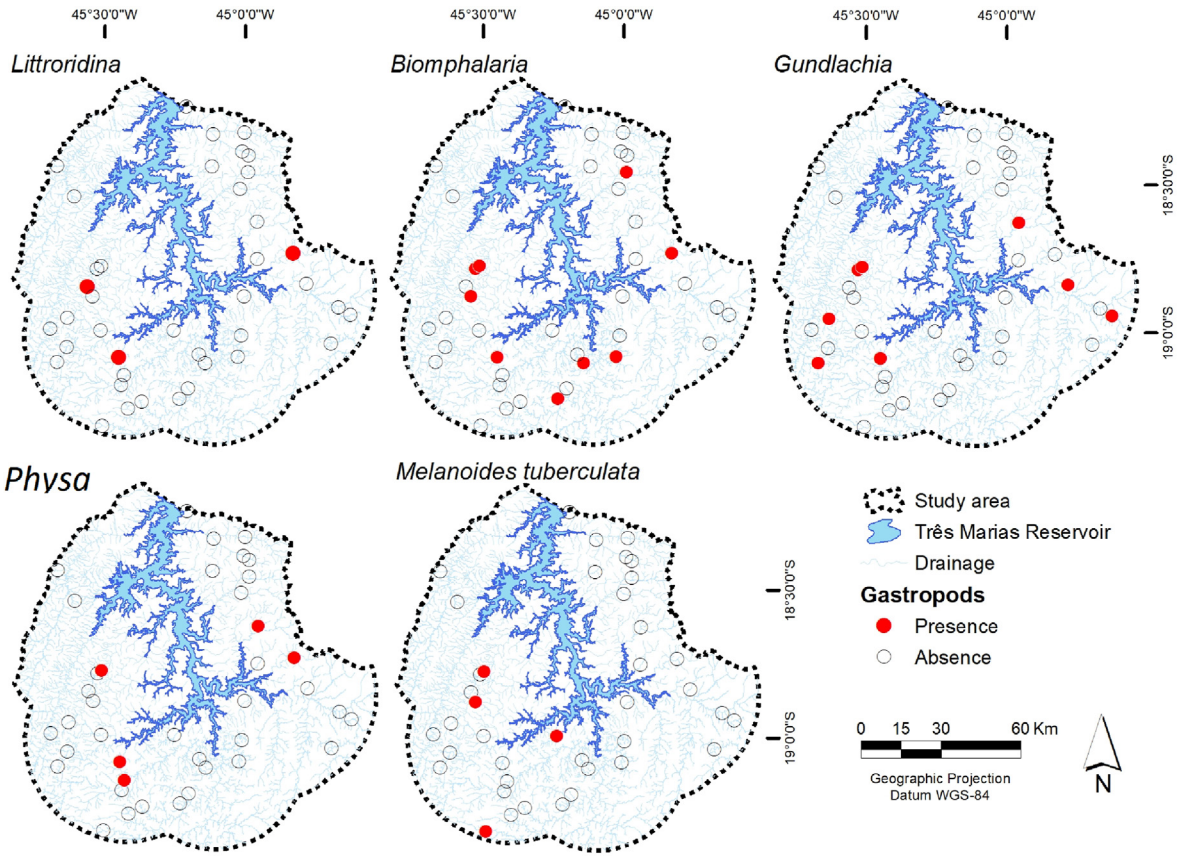

Fig. 2. Spatial distribution of presence/absence of freshwater gastropods in the Três Marias hidrologic unit.

Table 1
Metrics used to determine which physical habitat metrics were most important for the distribution of freshwater Gastropoda in Neotropical Savana streams.

Variable Code	Variable	Metric Category
Basin_elev._range	Basin Elevation Range (m)	Catchment
Basin_slope_range	Basin Slope Range (m)	Catchment
Turbidity	Turbidity (NTU)	Physio-Chemical
Conductivity	Conductivity (μS/cm)	Physio-Chemical
TDS	Total Dissolved Solids (mg/L)	Physio-Chemical
Alkalinity	Alkalinity (μEq/L of CO2)	Physio-Chemical
XBKF_D	Mean Thalweg Depth (m)	Channel Morphology
XBFWD_RAT	Mean Width/Thalweg Depth	Channel Morphology
XWD_RAT_P	Mean Section Width/Section Depth	Channel Morphology
XCDENMID	Mean Channel Canopy Cover (%)	Channel Morphology
XSLOPE	Mean Site Slope (m)	Channel Morphology
XEMBED	Mean Total Embeddedness (%)	Substrate
PCT_BL	Boulder Percentage (%)	Substrate
PCT_CB	Cobble Percentage (%)	Substrate
PCT_GC	Coarse Gravel Percentage (%)	Substrate
PCT_GF	Fine Gravel Percentage (%)	Substrate
PCT_SA	Sand Percentage (%)	Substrate
PCT_FN	Fine Substrate Percentage (%)	Substrate
PCT_ORG	Organic Matter Percentage (%)	Substrate
PCT_WD	Wood Percentage (%)	Substrate
XVEL	Current Velocity (m/s)	Water Flow
PCT_RI	Riffle Percentage (%)	Water Flow
PCT_GL	Glide Percentage (%)	Water Flow
PCT_PL	Pool Percentage (%)	Water Flow
DIV_FLOW	Flow Diversity	Water Flow
CDI	Catchment Disturbance Index	Disturbance
LDI	Local Disturbance Index	Disturbance

resources available for benthic species, such as freshwater gastropods, because hard sediments are substrates for periphytic algae, a major gastropod food source (Aguiar et al., 2015; Linares et al., 2018). As an invasive species, *M. tuberculata* is especially abundant on anthropogenically altered hard substrates (Fernandez et al., 2003; Santos and Eskinazi-Sant'Anna, 2010; Weir and Salice, 2012), such as dams. However, it is less dense in the natural, sandy substrates that characterize most Neotropical Savanna streams (Linares et al., 2019; Miyahira et al., 2020).

Biomphalaria differed from the other Gastropoda taxa, by being the only taxon that was positively correlated with total dissolved solids, a clear link to anthropogenic disturbances. Streams with high levels of total dissolved solids are associated with anthropogenic disturbances, at both local and regional spatial extents (Firmiano et al., 2021). Spatial distributions of many freshwater invertebrates are associated with the level of total dissolved solids in streams, presumably caused by its taxon-specific effects on the maintenance of ion and water balance, which is energetically expensive and thus could affect fitness (Olson and Hawkins, 2017). The positive relation between *Biomphalaria* and total dissolved solids suggests a preference for streams with lower water quality and its resistance to anthropogenic alteration (Firmiano et al., 2021; Mangadze et al., 2019). This genus is often found in wetlands, temporary lakes and other habitats characterized by high amounts of suspended particulate organic matter. Therefore, it is likely that it can successfully colonize streams with similar conditions (Kotzian and Amaral, 2013; Weir and Salice, 2012). The positive relation with both coarse and fine sediments is probably derived from different species in the genus having different habitat preferences, a result supported by previous studies (Estrada et al., 2006; Woke and Aleleye-Wokoma, 2015).

Our results showed that *Physa* preferred clear, alkaline streams. As stated before, high levels of dissolved solids often have adverse physiological effects (Olson & Hawkins, 2017). Because of their thin, fragile shells, *Physa* individuals would benefit from alkaline waters (Brown et al., 1998), indicating a preference for streams in karstic regions (Habdija et al., 1995). It also denotes a preference for streams with good

Table 2
Cumulative AICc weights (w_+) and estimates of variable effects (β parameters) for predictor variables used to model the presence probability of freshwater gastropods taxa in Neotropical Savanna streams. Values of w_+ in bold are those considered to be more likely ($w_+ \geq 0.50$). Estimates of variable effects are based on the most parsimonious model that included that variable and are given only for variables with $w_+ \geq 0.50$.

Variables	*Littoridina*		*Melanoides tuberculata*		*Biomphalaria*		*Gundlachia*		*Physa*	
	w_+	β	w_+	β	w_+	β	w_+	β	w_+	β
Basin_elev_range	0.07	–	0.07	–	0.03	–	**0.76**	**1.974**	0.18	–
Basin_slope_range	0.04	–	0.09	–	0.05	–	0.05	–	0.02	–
Turbidity	0.05	–	0.03	–	0.06	–	0.06	–	0.04	–
Condutivity	0.06	–	0.16	–	0.03	–	0.10	–	0.08	–
TDS	0.08	–	0.17	–	**0.66**	**9.57**	0.22	–	**0.69**	**−436.82**
Alcalinity	0.07	–	0.09	–	0.04	–	0.17	–	**0.67**	**655.04**
XBKF_D	0.12	–	0.19	–	0.03	–	0.13	–	0.03	–
XBFWD_RAT	0.43	–	0.24	–	0.05	–	0.11	–	0.03	–
XWD_RAT_P	0.24	–	0.18	–	0.04	–	0.09	–	0.11	–
XEMBED	0.09	–	0.38	–	0.16	–	0.05	–	0.03	–
XCDENMID	0.07	–	0.04	–	0.04	–	0.05	–	0.03	–
XSLOPE	**0.91**	**−246.16**	0.05	–	0.03	–	0.09	-	0.17	–
PCT_BL	0.06	–	0.02	–	0.05	–	0.05	–	0.22	–
PCT_CB	0.11	–	0.09	–	**0.57**	**14.76**	0.09	–	0.18	–
PCT_GC	0.05	–	**0.62**	**409.91**	0.03	–	0.06	–	0.09	–
PCT_GF	0.26	–	0.03	–	0.04	–	0.09	–	0.12	–
PCT_SA	0.13	–	0.03	–	0.20	–	0.08	–	0.27	–
PCT_FN	0.12	–	0.24	–	**0.70**	**22.36**	0.09	–	0.05	–
PCT_ORG	0.15	–	0.08	–	**0.60**	**10.73**	0.06	–	0.17	–
PCT_WD	0.14	–	0.06	–	0.03	–	0.06	–	0.07	–
XVEL	0.07	–	0.39	–	0.04	–	0.09	–	0.04	–
PCT_RI	0.08	–	0.09	–	0.09	–	0.05	–	0.06	–
PCT_GL	0.09	–	0.07	–	0.03	–	0.42	–	0.06	–
PCT_PD	0.06	–	0.06	–	0.17	–	**0.56**	**2.36**	0.15	–
DIV_FLUXO	0.19	–	0.35	–	0.05	–	0.12	–	0.06	–
CDI	0.07	–	0.05	–	0.04	–	0.06	–	0.16	–
LDI	0.06	–	0.04	–	0.03	–	0.05	–	0.14	–

water quality, suggesting that this genus might be successfully used as a bioindicator (de Kock and Wolmarans, 2007; Wadaan, 2007).

An important caveat to this study is that our taxonomic resolution was mostly limited to genus-level identifications. Although freshwater gastropods of the same genus may be expected to live in the same habitats and have very similar environmental requirements (Narr and Krist, 2019), more diverse genera can have species with markedly different preferences, as highlighted by our *Biomphalaria* results. Our results provide an important baseline, highlighting the environmental preferences of an often-neglected group. However, we recommended that future studies incorporate less damaging field fixation and working closely with taxonomists to obtain proper species inventories.

5. Conclusions

The freshwater gastropods that we collected had differing ecological requirements, but with an underlying tendency for preferring more stable lotic ecosystems. These results highlight the challenge of protecting freshwater gastropod assemblages because their preferred environments are easily disrupted by common anthropogenic stressors.

Authors contributions

Marden S. Linares: Conceptualization, Methodology, Writing – original draft. **Diego R. Macedo**: Methodology, Writing – review & editing. **Rodrigo L. Massara**: Methodology, Writing – review & editing. **Marcos Callisto**: Writing – review & editing.

Conflict of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.watbs.2022.100076.

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