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RESEARCH PAPER

Stream habitats and human disturbances explain the diversity of Nepomorpha (Heteroptera) assemblages in Neotropical Savanna headwater streams

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Abstract
The organisms of the infraorder Nepomorpha (Heteroptera) present complex habitat requirements in headwater streams, usually being related to local substrate conditions. Therefore, in this study, we evaluated how the diversity of Nepomorpha responded to a wide gradient of habitat and ecological conditions. We tested two hypotheses: (1) local substrate composition is the most important factor determining the diversity of Nepomorpha compared to other physical habitat metrics, (2) Nepomorpha assemblage diversity respond more readily to anthropogenic disturbances at local scale. Our results did not corroborate the first hypothesis, and showed that the assemblage diversity was mostly related to water quality and geomorphology, indicating that substrate requirements are not the only important driver. Our second hypothesis was partially corroborated, as all diversity metrics presented significant correlation with human disturbances at both local and catchment spatial scales. These results show that Nepomorpha assemblages have high potential use as ecological indicators, which should be better explored in future biomonitoring studies of anthropogenic changes.

Keywords Aquatic insects · Biomonitoring · Environmental assessments · Physical habitat

Introduction

Freshwater ecosystems, such as rivers and streams, are among the most impacted by human activities, because human populations tend to develop in their catchments, modifying the surrounding landscape and compromising the ecosystems' structure and functioning (Death and Collier 2009). To protect and improve the ecological condition of freshwater ecosystems, accurate measurements of how their biotic assemblages respond to natural and anthropogenic changes are necessary (Jørgensen and Nielsen 2007). Among the various environmental diagnostic tools available to managers, decision makers and researchers, ecological indicators stand out. A good ecological indicator can be used to assess the ecosystems' structure and functioning and to diagnose the causes of environmental alterations (Jørgensen 2007).

Aquatic insects are useful indicators of ecological condition of streams, because they are highly dependent on the chemical characteristics and physical habitat, thus responding readily to changes in water quality, stream substrate and riparian vegetation (Cunha et al. 2015; Firmiano et al. 2017). Despite not being as diverse as other groups of aquatic insects, the infraorder Nepomorpha (Heteroptera) presents high taxonomic, morphological, and behavioral diversity, and occurs in both lentic and lotic ecosystems worldwide, including temporary habitats and reservoirs (Cunha and Juen 2017).

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Nepomorpha are benthic predators that live submerged or associated with bottom substrates that they use both for shelter (against predators and water current displacement) and for prey searching. They tend to be most abundant in gravel, roots, and aquatic macrophytes, and are more diverse in sites with hard substrates, such as cobbles or stones (Dias-Silva et al. 2013; Suksai et al. 2016). This is consistent with most benthic macroinvertebrate predator taxa, which benefit from hard and complex substrates (Baumgärtner et al. 2008; Maloney et al. 2008; Linares et al. 2022). Therefore, it is expected that local substrate plays a crucial role in the distribution of Nepomorpha (Karaouzas and Gritzalis 2006).

Studies in Neotropical streams show that Nepomorpha assemblages are also influenced by other local physical habitat variables, such as the presence of riparian vegetation, water quality and local anthropogenic stressors (Dias-Silva et al. 2013; Suksai et al. 2016; Giehl et al. 2019). On the other hand, catchment scale variables can also be important for the structure of these assemblages, as land use, topography and channel connectivity often serve as barriers, affecting the distribution of many taxa (Macedo et al. 2014a; Firmiano et al. 2021a, b). However, information is still incipient or non-existent for the relative influence of local and catchment scale variables. Thus, to fulfill this gap we assessed a large geographical area in four river basins in the Neotropical Savanna to investigate how Nepomorpha assemblages respond to a wide gradient of ecological conditions in the catchments of 159 headwater streams.

In this study we evaluated how Nepomorpha diversity, as measured by several commonly used diversity measures (taxa richness, Shannon–Wiener and Simpson (1-D) diversity indices, and Pielou's Evenness), responded to a gradient of stream physical habitat variables and anthropogenic disturbances, measured at both local and catchment scales. For that, we tested two hypotheses. (1) Local substrate composition is the most important factor determining Nepomorpha diversity. We predicted that local substrate variables would comprise the majority of the variables correlated with assemblage diversity measures. (2) Nepomorpha assemblage diversity respond more readily to anthropogenic disturbances at local scale. We predicted that diversity measures would correlate negatively with indices of anthropogenic disturbances measured at both local and catchment scales, but the correlation would be stronger with the index describing local scale disturbances.

Materials and methods

Study area

We sampled 159 stream sites (1st to 3rd order, based on the Strahler classification) located up to 35 km upstream of four hydroelectric reservoirs in southeastern Brazil (Fig. 1): Três Marias (40 sites), Volta Grande (40 sites), São Simão (39 sites) and Nova Ponte (40 sites). All these river basins are located in the states of Minas Gerais, São Paulo and Goiás, central Brazil, sharing similar climatic, edaphic and vegetational characteristics (Ligeiro et al. 2013; Callisto et al. 2019), being located in the Neotropical Savanna (Cerrado biome). The local climate is characterized by temperatures ranging from 22° to 27 °C and an average annual rainfall of 1500 mm (Klink and Machado 2005). It has two well-defined seasons, a dry season from April to September, and a rainy season from October to March. The native vegetation is composed of forest patches, shrubs, and seasonally wet grasslands, all adapted to soils with high acidity, high aluminum and low nutrient concentrations (Fernandes et al. 2018). Because of increased human activities threatening many endemic species, the Cerrado is one of 25 global biodiversity hotspots (Myers et al. 2000).

Within the catchment area of studied river basins, most people live in farming villages (up to 30,000 inhabitants), although a few small cities (up to 100,000 inhabitants) are present. Agriculture (e.g., soy, coffee, corn, and sugar cane) and pasture are the dominant land uses (Ligeiro et al. 2013; Silva et al. 2017). Ecological conditions of the studied streams vary greatly in each river basin, from very disturbed sites within urban areas and large crops to near pristine conditions in protected areas and forest fragments (Martins et al. 2018).

Sampling design

The stream sites were selected using a probability-based procedure and a spatially balanced design, following the generalized random tessellation stratified (GRTS) sampling design developed for the US. EPA's Wadeable Stream Assessment (Olsen and Peck 2008; Macedo et al. 2014b). This methodology is based on the conversion of all reaches of the drainage network to a one-dimensional axis, i.e., a single vector. Then, stream sites are selected randomly, which means that the results obtained with the sampled sites can be extrapolated for the whole spatial extent studied (Hughes and Peck 2008). Since our target were perennial wadeable streams, we excluded all tributaries greater than Strahler order 3 on a digital 1:100,000 scale map.

The field sampling campaigns were all made during the dry season, from 2010 to 2013, with the stream sites of each river basin being sampled each year: Três Marias (2010), Volta Grande (2011), São Simão (2012) and Nova Ponte (2013). We chose to sample at the end of the dry season (September of each year) because usually physical habitats are most exposed, the aquatic insects are bigger and have easier identification, the community are least affected by

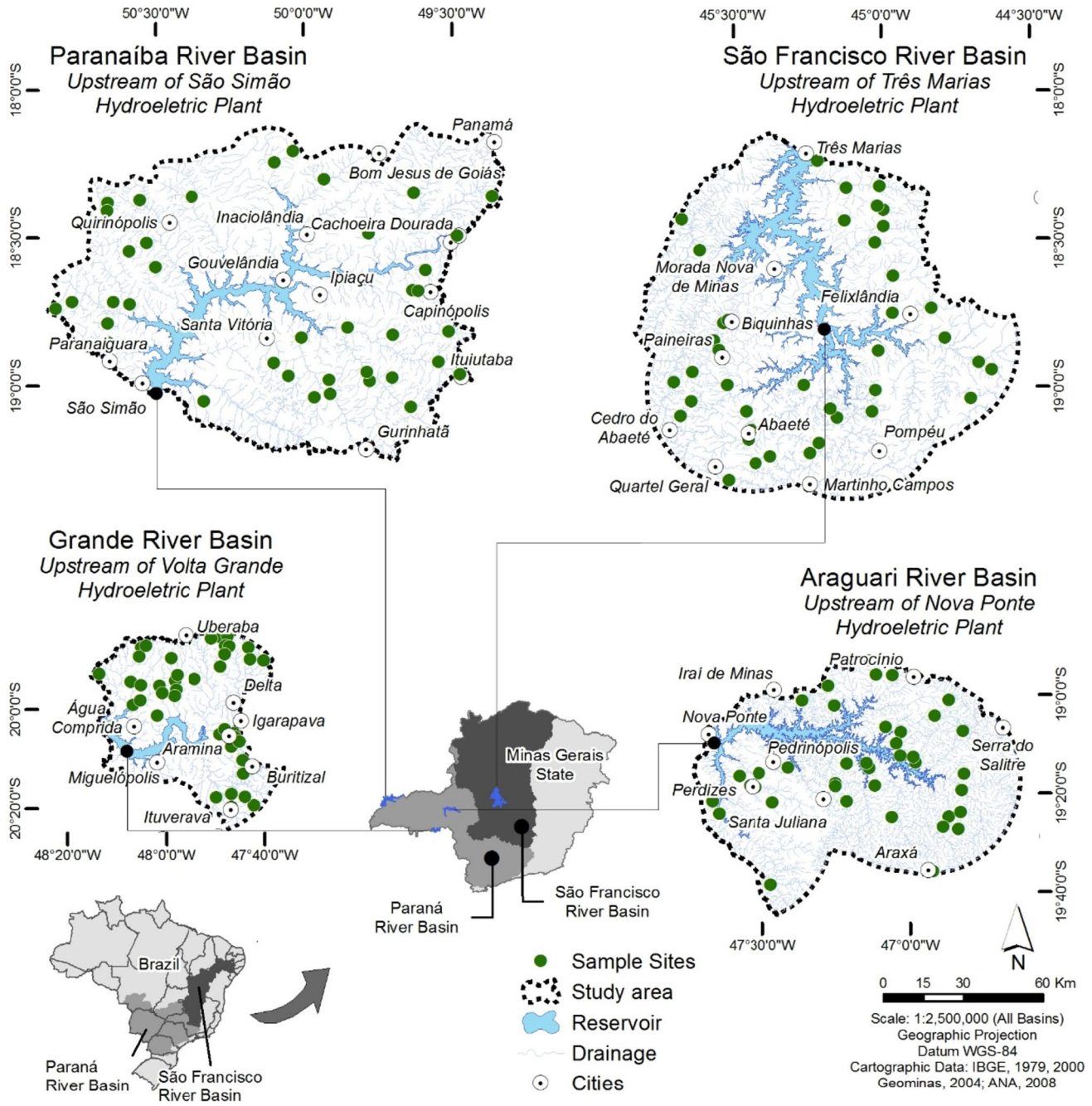

Fig. 1 Sampling locations in the four hydrologic units, southeastern Brazil. Dotted lines represent the limit of the 35 km buffer around the reservoirs that limit our study area

drift processes and researchers are safer from flash floods (Stevens and Olsen 2004; Silva et al. 2017).

Water quality, physical habitat and land use assessment

To assess water quality, the following physical and chemical characteristics of the water column were measured in the field at each stream site: pH, conductivity (µS/cm), and total dissolved solids (TDS; mg/L) were measured using a model YSI 6600 multiprobe meter (YSI, USA). Water samples were collected for further analyses in the laboratory, including concentrations of chlorophyll-a (mg/L), dissolved oxygen (mg/L), turbidity (NTU), total alkalinity (µEq/L of CO_2), total nitrogen (mg/L) and total phosphorus (mg/L). These analyses were conducted following

the APHA methodology (APHA-American Public Health Association 2005). All of these variables were measured once at each stream site.

To assess physical habitat condition, we followed the USEPA protocol (Peck et al. 2006) adapted for the Neotropical Savanna (Ligeiro et al. 2013; Callisto et al. 2019). We first defined a 150 m longitudinal reach at each sampled stream site. Then, 11 transects (perpendicular to the main channel) were established, defining 10 longitudinal sections of the same width per site. At each transect and longitudinal section, many physical habitat measurements were taken. We recorded characteristics of channel morphology (e.g., sinuosity, wetted and bankfull width and depth, incision height), habitat features (e.g., water flow, substrate types, large wood), riparian structure (e.g., riparian cover, stream shading) and anthropogenic alterations (e.g., presence of agriculture, thrash and buildings). Subsequently, these data were used to calculate 288 physical habitat metrics according to Kaufmann et al. (1999) (Table S1).

From the entire pool of physical habitat metrics calculated, we eliminated those with a high number of zeros ($\geq 80\%$ 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 ($|r| \geq 0.7$) and retaining the most ecologically relevant based on previous knowledge (Esselman et al. 2013; Macedo et al. 2016; Silva et al. 2017). Thirty metrics remained after this screening process (Table 1), and were used in the subsequent analyses.

We also estimated anthropogenic disturbance at local and catchment scales, based on the method described by Ligeiro et al. (2013). The Local Disturbance Index (LDI) was equivalent to the metric *w1_hall* (Table S1). This metric is based on the visually observed proportions of 11 types of anthropogenic disturbances (walls, dikes, revetments, riprap

Table 1 Metrics used to determine which physical habitat metrics were most important for Nepomorpha assemblage structure

Metric	Category	Description
Basin_elev_range	Catchment metric	Basin elevation range (m)
Basin_slope_range	Catchment metric	Basin slope range (m)
Turbidity	Physico-chemical metric	Water turbidity (NTU)
Electrical condutivity	Physico-chemical metric	Water conductivity (µS/cm)
Total dissolved solids	Physico-chemical metric	Total dissolved solids (mg/L)
Total_Alkalinity	Physico-chemical metric	Total alkalinity (µEq/L of CO_2)
Total_N	Physico-chemical metric	Total nitrogen (mg/L)
Total_P	Physico-chemical metric	Total phosphorus (mg/L)
Chlorophyll-*a*	Physico-chemical metric	Chlorophyl *a* (mg/L)
FLOW_2	Water flow metric	Water flow (m^3/s)
XVEL	Water flow metric	Current velocity (m/s)
PCT_RI	Water flow metric	Riffle proportion in the stream channel area (%)
PCT_GL	Water flow metric	Glide proportion in the stream channel area (%)
PCT_PD	Water flow metric	Impoundment pool proportion in the stream channel area (%)
SEQ_FLO_2	Water flow metric	Flow sequency
DIV_FLUXO	Water flow metric	Flow diversity (1-D)
XBKF_D	Channel morphology metric	Mean seasonal thalweg depth
XBFWD_RAT	Channel morphology metric	Mean seasonal width/thalweg depth
XWD_RAT_P	Channel morphology metric	Mean site width/depth
XSLOPE	Channel morphology metric	Mean site slope
XEMBED	Substrate metric	Mean total embeddedness (%)
PCT_BL	Substrate metric	Total boulder proportion in the stream channel area (%)
PCT_CB	Substrate metric	Cobble proportion in the stream channel area (%)
PCT_GC	Substrate metric	Coarse gravel proportion in the stream channel area (%)
PCT_GF	Substrate metric	Fine gravel proportion in the stream channel area (%)
PCT_SA	Substrate metric	Sand proportion in the stream channel area (%)
PCT_FN	Substrate metric	Fine sediment proportion in the stream channel area (%)
PCT_ORG	Substrate metric	Total organic matter proportion in the sediment weight (%)
PCT_WD	Substrate metric	Wood proportion in the stream channel area (%)
Dgm_X	Substrate metric	Geometric mean substrate size

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, and mining) in-channel and in the riparian zone of a stream site (Kaufmann et al. 1999).

For calculating the Catchment Disturbance Index (CDI), we first estimated the area of each 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 the same year and same month of the sampling campaigns. Polygons for the definition and quantification of land use categories were delimited and we employed manual interpretation of images with fine resolution (pasture, agriculture and urban area), and computed as the proportional area. Images obtained from Google Earth satellite images were employed as ancillary data in this assessment (Macedo et al. 2014b). The CDI was calculated using the proportional areas of individual land uses, weighted by the disturbance potential of each one (Böhmer et al. 2004; Ligeiro et al. 2013), as follows:

$$\begin{aligned}\mathrm{CDI} = {} & (4 \times \%\ \text{residential and urban areas}) \\ & + (2 \times \%\ \text{agricultural areas and bare soils}) \\ & + (\%\ \text{pasture areas and Eucalyptus plantations})\end{aligned}$$

An Integrated Disturbance Index (IDI) was measured as the Euclidian distance between CDI and LDI, using values standardized for equality of numerical scales, following Ligeiro et al. (2013). This was performed through application of the Pythagorean theorem:

$$\mathrm{IDI} = \left[\left(\frac{\mathrm{LDI}}{5}\right)^2 + \left(\frac{\mathrm{CDI}}{300}\right)^2\right]^{\frac{1}{2}}$$

The higher the IDI value, the farther the site is from the undisturbed condition (zero value in both the LDI and the CDI), that is, more disturbed is the site (Ligeiro et al. 2013).

Nepomorpha sampling

We collected Nepomorpha using the kick-net method with a D-frame net (30 cm opening, 0.25 mm mesh sieve). Samples were taken following a zig-zag pattern along each site (first sampling on the left bank, second sampling in the center of the channel, third sampling on the right bank, fourth sampling in the center again, and so on), resulting in eleven sub-samples (0.09 m^2 each), totaling a 0.99 m^2 multihabitat composite sample taken per site. We fixed the samples in the field with 10% formalin, and took them to the laboratory, where the specimens were identified to genus with the aid of taxonomic keys (Nieser and Chen 2002; Hamada et al. 2014). Genus level identification is more feasible than species level in biomonitoring studies, particularly in megadiverse regions of the Neotropics, where knowledge of species is often incomplete (Bailey et al. 2001; Silva et al. 2016). In addition, many studies have demonstrated the efficacy of genus level identification in biomonitoring and general ecological studies (Lenat and Resh 2001; Marshall et al. 2006; Godoy et al. 2019), including one work made exclusively with Nepomorpha (Giehl et al. 2014). After the fixation of all samples, 10% formalin was replaced with 70% ethanol and deposited in the Reference Collection of Benthic Macroinvertebrates, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais.

Data analyses

To explore our hypothesis that local substrate composition is the most important factor determining Nepomorpha diversity, we used a model selection approach (Burnham and Anderson 2002). We used our 30 habitat metrics indicated in Table 1 as potential predictor variables with genera richness, Shannon–Wiener and Simpson diversity indices and Pielou evenness as response variables. We then constructed models based on all possible additive metric combinations that may have influenced the variation of each response variable (Doherty et al. 2012). In other words, we looked for the combination of habitat metrics that best explained the variation of each response variable. The intercept-only model structure (i.e., null model) was also included in each of the model sets. This strategy resulted in a balanced model set for each analysis, which allowed us to calculate the cumulative AICc weights ($w+$) for each metric and evaluate which were the most likely ($w+ \geq 0.50$) to have influenced the variation of the response variables (Burnham and Anderson 2002). We then tested the fitting of each model made with the selected metrics with a version of the same models made with river basin as a random effect, to test for any effect that the four basins could have on the observed relationships. Statistical analyses were implemented using the MuMIn package (version 1.47.5; Barton 2019) in the R software (R Core Team 2020).

To test our hypothesis that Nepomorpha assemblage diversity respond more readily to anthropogenic disturbances at local scale, we ran generalized linear mixed models (GLMMs), again using genera richness, Shannon–Wiener and Simpson diversity indices and Pielou evenness as response variables, and IDI, CDI and LDI as explanatory variables. The GLMMs used Gaussian (Shannon–Wiener and Simpson diversity indices and Pielou evenness index) and Poisson (genera richness) distributions. These analyses were done using R software version 3.5.1 (R Core Team 2020), using the packages "vegan" (version 2.5; Oksanen et al. 2019) and "lme4" (version 1.1; Bates et al. 2023).

To further understand the effects of anthropogenic disturbances on assemblage diversity, we ran a Pearson

Correlation Matrix between the anthropogenic disturbance indices (LDI, CDI, IDI) and the metrics selected by the GLMMs described above. The significances of the correlations were tested using t tests (significance $p < 0.05$). We ran these analyses using R software version 3.5.1 (R Core Team 2020).

Results

A total of 1457 individuals from 14 genera of the suborder Nepomorpha were identified (Table S2), with an average of 1.43 genera per stream, with a minimum of 0 and a maximum of 6. Different habitat metrics (Table S3) showed significant relationship with the measured aspects of the assemblage structure (Table 2). Genera richness was negatively related to the chlorophyl-a concentration and positively related to the mean seasonal width to thalweg depth ratio (XBFWD_RAT). Shannon–Wiener diversity was positively related to the percentage of boulders (PCT_BL). Simpson diversity was positively related to water conductivity and mean site slope (XSLOPE). Pielou evenness was positively related to the mean seasonal width to thalweg depth ratio (XBFWD_RAT) and to the basin slope range. None of the selected metrics showed significant differences between the regular models and the mixed models, including the random effect, showing that the patterns found were consistent across all river basins.

All the three disturbance indices varied wildly among the sites (IDI: 0.13–1.49; CDI: 3.89–350.00; LDI 0.00–5.96).

Table 2 Cumulative AICc weights (w_+) and estimates of variable effects (β parameters) for predictor variables incorporated to explain variation in Richness, Shannon–Wiener Diversity, Simpson Diversity and Pielou Evenness in Neotropical Savanna stream sites

Metric	Richness		Shannon		Simpson		Pielou	
	w_+	β	w_+	β	w_+	β	w_+	β
Basin_elev_range	0.04	–	0.05	–	0.07	–	0.05	–
Basin_slope_range	0.09	–	0.48	–	0.06	–	**0.62**	**0.0015**
Turbidity	0.20	–	0.26	–	0.09	–	0.17	–
Electrical Conductivity	0.06	–	0.06	–	**0.56**	**0.0009**	0.08	–
TDS	0.05	–	0.04	–	0.18	–	0.08	–
Total_Alkalinity	0.16	–	0.31	–	0.14	–	0.14	–
Total_N	0.04	–	0.07	–	0.05	–	0.11	–
Total_P	0.05	–	0.12	–	0.41	–	0.06	–
Chlorophyll-*a*	**0.51**	**–0.1428**	0.08	–	0.13	–	0.08	–
FLOW_2	0.06	–	0.04	–	0.06	–	0.07	–
XVEL	0.04	–	0.05	–	0.16	–	0.05	–
PCT_RI	0.04	–	0.04	–	0.05	–	0.07	–
PCT_GL	0.04	–	0.05	–	0.05	–	0.05	–
PCT_PD	0.05	–	0.05	–	0.06	–	0.05	–
SEQ_FLO_2	0.05	–	0.04	–	0.06	–	0.05	–
DIV_FLUXO	0.04	–	0.06	–	0.07	–	0.05	–
XBKF_D	0.20	–	0.07	–	0.06	–	0.07	–
XBFWD_RAT	**0.99**	**0.1158**	0.15	–	0.08	–	**0.65**	**0.0380**
XWD_RAT_P	0.11	–	0.04	–	0.22	–	0.05	–
XSLOPE	0.31	–	0.05	–	**0.54**	**0.0093**	0.06	–
XEMBED	0.23	–	0.36	–	0.06	–	0.45	–
PCT_BL	0.08	–	**0.67**	**0.0081**	0.05	–	0.16	–
PCT_CB	0.04	–	0.06	–	0.05	–	0.05	–
PCT_GC	0.09	–	0.14	–	0.05	–	0.07	–
PCT_GF	0.07	–	0.04	–	0.11	–	0.07	–
PCT_SA	0.04	–	0.05	–	0.06	–	0.05	–
PCT_FN	0.04	–	0.06	–	0.06	–	0.09	–
PCT_ORG	0.05	–	0.10	–	0.05	–	0.06	–
PCT_WD	0.06	–	0.23	–	0.1	–	0.15	–
Dgm_X	0.05	–	0.05	–	0.09	–	0.05	–

Values of w_+ in bold are those considered to be more suitable ($w_+ \geq 0.50$). Estimates of variable effects are based on the most parsimonious model that included that variable and are given only for variables with $w_+ \geq 0.50$

Table 3 Nepomorpha richness, Shannon–Wiener and Simpson diversity indices and Pielou evenness response to disturbances: integrated disturbance index (IDI), catchment disturbance index (CDI) and local disturbance index (LDI)

Variable	IDI				LDI				CDI			
	Statistic	*p*	SE	Cor	Statistic	*p*	SE	Cor	Statistic	*p*	SE	Cor
Richness	− 4.658	< 0.0001	0.03621	− 0.162	− 2.981	0.0014	0.00663	− 0.103	− 2.436	0.0074	0.000152	− 0.1
Shannon	− 39.35	< 0.0001	0.01186	− 0.259	− 29.23	< 0.0001	0.002402	− 0.078	− 37.65	< 0.0001	5.52E−05	− 0.216
Simpson	42.077	< 0.0001	0.01185	− 0.09	26.739	< 0.0001	0.002413	− 0.08	40.131	< 0.0001	5.52E−05	− 0.079
Pielou	− 36.31	< 0.0001	0.01165	− 0.177	− 31.31	< 0.0001	0.002341	− 0.102	− 28.72	< 0.0001	5.46E−05	− 0.168

Values for the mixed model Statistic (*z* value for Richness, *t* value for the other variables), *p* equivalent value (*p*), Standard Error (SE) and Correlation of the fixed effects (cor)

Table 4 Pearson correlation matrix between the human disturbance indices (integrated disturbance index (IDI), catchment disturbance index (CDI) and local disturbance index (LDI)) and the selected physical habitat variables: chlorophyll-*a*, mean seasonal width to thalweg depth ratio (XBFWD_RAT), percentage of boulders (PCT_BL), conductivity, mean reach slope (XSLOPE) and basin slope range

Variable	IDI	CDI	LDI
Chlorophyll-*a*	**0.21**	**0.22**	0.13
XBFWD_RAT	**− 0.18**	**− 0.18**	− 0.12
PCT_BL	**− 0.24**	**− 0.27**	− 0.10
Conductivity	**0.20**	0.12	**0.24**
XSLOPE	− 0.02	0.01	− 0.04
Basin slope range	**− 0.18**	**− 0.19**	− 0.08

Numbers in bold indicate significant ($p < 0.05$) correlations

Genera richness, Shannon–Wiener diversity and Pielou evenness showed a weak significant negative correlation to all three disturbance indices (Table 3). Simpson diversity, on the other hand, showed equally weak significant positive correlation with those indices. None of the selected metrics correlated with all three disturbance indices (Table 4). Conductivity was positively correlated with IDI and LDI. Chlorophyll-*a* was positively related to IDI and CDI. Percentage of boulders, on the other hand, was negatively correlated with IDI and CDI, as were mean seasonal width to thalweg depth ratio, and basin slope range. Mean reach slope was the only selected variable that did not relate to any disturbance index.

Discussion

Our results did not corroborate our first hypothesis, that local substrate composition is the most important factor for determining diversity measures of Nepomorpha assemblages, as water quality and geomorphology metrics were the majority of the metrics selected by the models. However, one substrate metric, percentages of boulders in the sediment, was positively related to Shannon–Wiener diversity index. Our second hypothesis, that diversity measures respond mainly to anthropogenic disturbances measured at local scale, was partially corroborated, as the response variables were significantly correlated with the disturbance indices at both spatial scales. Simpson Diversity was the only diversity indicator positively correlated with disturbances.

Despite being more influenced by other metrics, Nepomorpha diversity showed a positive relation to the percentage of boulder, indicating a preference for hard substrates, as reported by previous works (Dias-Silva et al. 2013; Suksai et al. 2016). Higher diversity of predator taxa, such as many Nepomorpha genera, is often associated with hard substrates, which usually offers a complex tridimensional microhabitat with high abundance of prey, and protection against larger predators (e.g., fish, tadpoles, aquatic birds) and hydrological stress (Sylvester et al. 2007; Baumgärtner et al. 2008; Firmiano et al. 2021a).

A higher number of variables of water quality were related to the diversity indices, as shown by a negative correlation between chlorophyll-a, a proxy for water eutrophication, and genera richness, and a positive correlation between conductivity and the Simpson diversity index. Nepomorpha has shown consistent positive relations with sites with higher conductivity globally, usually related to more stagnant environments (Carbonell et al. 2011; Lock et al. 2013). Physiologically, increased conductivity is linked to osmotic stress, increasing the energy costs and decreasing growth performance, and it can cause the loss of more sensitive species and replacement by other more tolerant to osmotic stress (Cañedo-Argüelles et al. 2013). Most species of Heteroptera tolerate moderate conductivity. However, there are records that some species live in environments with low conductivity and others with high conductivity (Lock et al. 2013).

Many geomorphology metrics were adopted by the selected models. Mean seasonal width to thalweg depth ratio was positively correlated with genera richness and Pielou evenness, indicating that relatively wider streams are favorable to the existence of more diverse Nepomorpha

assemblages. Such streams possibly support a higher amount of more stable habitats, that are less affected by seasonal effects, such as flash floods (Erba et al. 2020; Chattopadhyay et al. 2021). The mean slope of the streams was positively related to higher Simpson index values, which suggests that steeper streams may provide Neomorpha assemblages with a variety of microhabitats in terms of flow velocity (Perez Rocha et al. 2018; Sánchez-Bayo and Wyckhuys 2019; Callisto et al. 2021).

We also demonstrated that Nepomorpha assemblages responded to anthropogenic disturbances, as shown by our results that genera richness, Shannon–Wiener diversity and Pielou evenness negatively correlated with the anthropogenic disturbance indices. Thus, these diversity indices may be useful for assessing ecological condition at both local and catchment spatial scales in neotropical biomonitoring studies. On the other hand, Simpson diversity was significantly and positively affected by all the disturbance indices, suggesting that dominant taxa in Nepomorpha assemblages are more sensitive to increased environmental alterations. These results are in agreement with previous studies with Heteroptera in the Neotropical region (Dias-Silva et al. 2013; Suksai et al. 2016; Giehl et al. 2019). As expected, the IDI, being an index integrating both local and catchment scales, significantly explained all diversity measures. This finding supports other studies suggesting that the IDI is an efficient tool for characterizing the disturbance levels in streams (Ligeiro et al. 2013; Silva et al. 2017; Chen et al. 2017; Martins et al. 2021).

The relatively low correlation values between anthropogenic disturbance indices and the assemblage diversity can be attributed to the indirect relation between disturbances and biological responses. Anthropogenic disturbances usually cause alteration in local habitat metrics and in turn can act as stressors that cause alterations in biological diversity (Macedo et al. 2014a; Firmiano et al. 2021a). In our study, all physical habitat metrics related to the Nepomorpha diversity were correlated with anthropogenic disturbances. Conductivity was positively related to disturbances in the riparian zone, likely due to the tendency of disturbances at local scale to increase the entrance of ions and other suspended material into lotic ecosystems (Sponseller et al. 2001; Ferreira et al. 2014). As anthropogenic land uses are closely related to the deposition of fine sediments in streams, it is likely that substrate metrics are related to anthropogenic disturbances, explaining the negative correlation between the percentage of boulders and CDI (Steinhardt et al. 1999; Death and Collier 2009; Oliveira et al. 2016). Mean seasonal width to thalweg depth ratio and basin slope range were also negatively correlated with catchment disturbances, indicating an influence of landscape geomorphology on the human occupation of the catchment, and a preference for pasture and agriculture to be performed in less rugged terrain (Macedo et al. 2018). Concentration of chlorophyll-a in the water was positively related to catchment disturbance, as nutrient inputs coming from the adjacent landscape are likely to increase primary productivity in the water column (Silva et al. 2018). This intrinsic correlation between land uses and the important habitat variables for the Nepomorpha highlights how strongly the niche of this group is threatened by anthropic activities, reinforcing their importance as a bioindicator.

It is important to consider that many of the diversity indices commonly used in ecology and biomonitoring studies are closely related to one another, making them redundant (Strong 2016). Therefore, future research should be focused not only on taxonomic diversity but also on other aspects of the communities, such as functional, phylogenetic or thermodynamic indices (Callisto et al. 2019).

Conclusion

Our results evidenced that water quality and geomorphology variables are the most important factors explaining Nepomorpha diversity in Neotropical Savanna headwater streams. The models indicate that the Nepomorpha diversity increases in wider, mesotrophic streams. This highlight that the interaction of these organisms with the stream habitat is very complex, and cannot be reduced to only their relationships with the substrates. The taxonomic diversity of these assemblages also responded to anthropogenic disturbances at both local and regional scales, which can modify their ecological niches, suggesting that the Nepomorpha may be useful as ecological indicators. In short, our results show that Nepomorpha, dwelling both on the substrates and in the water column, can be a promising tool for biomonitoring programs, capable of providing important insights to policy makers and environmental managers in a changing world.

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Data availability All data generated or analyzed during this study are included in this published article and its supplementary information files.

Declarations

Conflict of interest 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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