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Metacommunities of water bugs are driven by environmental, spatial, and landscape factors in Cerrado freshwater habitats along a land-use gradient

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Abstract

Anthropogenic pressures, particularly changes in land use and land cover, have profound effects on aquatic ecosystems and have motivated extensive research on patterns of biodiversity distribution. In this study, we evaluated the relative influence of environmental, landscape, and spatial factors on the structure of Nepomorpha and Gerromorpha communities in lentic and lotic habitats within a Cerrado region of northeastern Brazil. We tested the following hypotheses: (i) in lentic habitats, Gerromorpha would be jointly influenced by local environmental, landscape, and spatial factors (species sorting + mass effects), whereas Nepomorpha would be predominantly structured by spatial processes, with little or no influence of environmental and landscape variables; and (ii) in lotic habitats, both Gerromorpha and Nepomorpha would be primarily structured by environmental and landscape factors, with limited or no influence of spatial processes (species sorting). We sampled 34 sites and collected 1,052 individuals representing 63 species. Our results showed that environmental conditions, landscape attributes, and dispersal processes jointly contributed to community assembly, although their relative importance varied among groups and habitat types. In lentic habitats, we found that Gerromorpha communities were primarily shaped by environmental filtering, whereas no clear structuring mechanism was detected for Nepomorpha. In lotic habitats, we found that Gerromorpha communities were influenced by spatial and landscape factors, consistent with mass effects, whereas Nepomorpha communities responded to environmental variables, habitat connectivity, and landscape configuration. These findings highlight the combined role of local and regional processes in structuring aquatic insect communities and underscore their importance for biodiversity conservation.

Introduction

The distribution and organization of biodiversity have been extensively studied in the context of environmental changes driven by anthropogenic activities. The distribution and organization of biodiversity have been extensively studied in the context of environmental changes driven by human activities. Among these, alterations to freshwater ecosystems resulting from changes in land use and land cover (Kuemmerlen et al., 2014) are particularly relevant, especially in tropical regions. Land-use changes particularly when riparian vegetation is not preserved alter environmental conditions, affect biodiversity, and can compromise ecosystem services and associated communities (Dias-Silva et al., 2020).. Land-use changes, particularly when riparian vegetation is not preserved, alter environmental conditions, affect biodiversity, and may compromise ecosystem services and the associated communities (Dias-Silva et al., 2020).

The Cerrado is recognized as one of the world's most biodiverse biomes and is considered a global biodiversity hotspot due to its high richness of endemic species and extensive habitat loss (Myers et al., 2000). Its diverse freshwater ecosystems include lotic and lentic habitats, as well as flood-associated systems classified as wetlands, all of which are subject to intense anthropogenic pressures, primarily driven by the expansion of agriculture and livestock production (Fonseca, 2005). Lotic ecosystems are characterized by unidirectional water flow and high connectivity along the drainage network, both of

which are essential for ecosystem functioning and the dispersal of aquatic communities (Pringle, 2006; Salles & Ferreira-Júnior, 2019). In contrast, lentic ecosystems exhibit little or no water flow and are considered semi-closed or closed systems that function as ecological islands supporting distinct biological communities (Salles & Ferreira-Júnior, 2019).

Regarding connectivity among aquatic ecosystems, riparian vegetation also plays a fundamental role in maintaining ecological interactions among different communities, contributing to both the maintenance of local environmental conditions and the facilitation of species dispersal (Naiman & Décamps, 1997). Riparian vegetation degradation may compromise stream longitudinal connectivity, altering dispersal patterns and the distribution of organisms across both local and regional spatial scales, as riparian zones and drainage network connectivity are important drivers of aquatic organism distributions, representing local and regional factors, respectively (Brown & Swan, 2010; Tonkin et al., 2018b). In this context, metacommunity theory (Leibold et al., 2004) seeks to explain how ecological communities are structured through the dynamics of local- and regional-scale processes, such as species dispersal and habitat connectivity (Leibold et al., 2004; Holyoak et al., 2005). Furthermore, intrinsic species characteristics can drive metacommunity structure between these two mechanisms by dispersal limitation through space, depending on spatial extent (Winegardner et al., 2012; Tonkin et al., 2018).

According to this framework, four main paradigms can explain community structuring, with environmental filtering (species sorting) and (mass effects) considered the primary mechanisms structuring aquatic ecosystems (Heino et al., 2015). In environmental filtering, community composition directly reflects local environmental conditions, as species tend to colonize habitats that match their ecological requirements, provided that their dispersal ability is sufficient to reach them (Leibold et al., 2004; Cottenie, 2005; Winegardner et al., 2012). Mass effects, in turn, occur when high dispersal rates promotes species to colonize and persist in habitats with suboptimal environmental conditions, often due to continuous immigration from source populations and higher tolerance to less suitable environments (Leibold et al., 2004).

Aquatic insects play a fundamental role in metacommunity studies due to their sensitivity to environmental conditions and habitat changes, as well as their diverse ecological strategies related to dispersal and colonization, making them suitable models for investigating spatial patterns in ecological communities (Cunha & Juen, 2020; Heino et al., 2015; Tonkin et al., 2018). Among these taxa, aquatic Heteroptera stand out for being widely used as bioindicators and providing valuable information on impacts on aquatic ecosystems, as they occupy different ecological niches and respond to environmental and spatial variations (Dias et al., 2010; Giehl et al., 2014; Cunha & Juen, 2017; Guterres et al., 2021).

These organisms can be classified as semiaquatic and aquatic bugs, respectively represented by the infraorders Gerromorpha and Nepomorpha. Gerromorpha generally exhibit high dispersal capacity, occurring both through flight and locomotion on the water surface (Andersen, 1982; Cunha et al., 2020). Their occurrence often depends on the physical structure of watercourses, including factors such as

shading, presence of retained organic matter in the channel, and habitat heterogeneity, such as pools and riffles (Dias-Silva et al., 2010, 2020).

On the other hand, Nepomorpha exhibit more limited dispersal, occurring mainly through occasional flight events (Ye et al., 2019), and tend to be more influenced by limnological variables than by physical habitat alterations (Dias et al., 2020). However, this pattern is not universal, since different responses in this group suggests high environmental plasticity (Dias-Silva et al., 2010; Cunha et al., 2015).

Thus, we aim to evaluate the influence of environmental, landscape, and spatial factors on the structure of Gerromorpha and Nepomorpha communities in tropical lentic and lotic ecosystems within a Cerrado region, northeastern Brazil. The following hypotheses were tested: (i) in lentic environments, Gerromorpha are simultaneously influenced by local environmental, landscape, and spatial factors, reflecting the combined action of species sorting and dispersal limitation; in contrast, Nepomorpha are predominantly influenced by spatial factors, with reduced or no influence of environmental and landscape variables; and (ii) in lotic environments, both Gerromorpha and Nepomorpha infraorders are primarily influenced by environmental and landscape factors, with little or no influence of the spatial component, indicating the predominance of species sorting.

Material and methods

Area of study

The study was conducted at 34 sampling sites, 15 in lentic and 19 in lotic habitats, with each site considered a sampling unit The sampled sites are located within the Cerrado biome in Maranhão State, northeastern Brazil. The sampling points are distributed across two major river basins: the Itapecuru River Basin and the Parnaíba River Basin (Fig. 1).

The Itapecuru River Basin has an area of approximately 53,216.84 km², corresponding to about 16.03% of the territory of Maranhão (Aranha et al., 1997). This river has its source in the municipality of Mirador, Maranhão, on the northern slope of the Serra da Cinta, and flows for approximately 1,050 km until it reaches the Atlantic Ocean at the Baía de São José, east of São Luís island (Alcântara, 2004). The Parnaíba River Basin has a drainage area of approximately 331,000 km², of which about 20% lies within Maranhão. This river has its source in the Chapada das Mangabeiras, on the border between the states of Piauí, Bahia, and Tocantins, flows for approximately 1,344 km, and discharges into the Atlantic Ocean, forming an extensive delta between the states of Piauí and Maranhão (CPRM, 2017).

The climate of the region is classified as equatorial semi-humid, with mean annual temperatures ranging from 23°C to 38°C and annual precipitation between 1,100 and 1,600 mm, the region exhibits a well-defined seasonality, with a rainy season (December to May) and a dry season (June to November) (Alvares et al. 2014). The vegetation is mainly composed of different Cerrado physiognomies, including typical savannas, forest and grassland formations, and veredas (wetlands with Buriti palms). In recent decades, these areas have been heavily impacted by land-use changes, as the region is considered one

of the main agricultural frontiers in Brazil, resulting in the progressive replacement of natural landscapes by large-scale monocultures, particularly soybean, corn, and cotton cultivation, along with livestock production (Bastos et al., 2019). The region also contains a wide availability of water resources, including springs, headwaters, streams, creeks, wetlands, rivers and their tributaries, as well as artificial reservoirs, ponds, and lakes.

Sampling design and biological sampling

In lotic environments, a 50-m reach was delimited in each stream and subdivided into five 10-m sections (Fig. 2a). The sampling was conducted in an upstream direction to minimize disturbances to the environment during the collection of organisms and environmental variables, following the protocol proposed by Azevedo & Hamada (2007). In lentic environments, the accessible shoreline segments (also 50 m long) were considered, as access to some portions of these environments was restricted. In this case, three sampling points were established according to local physical conditions, without prior standardization of the distances between them (Fig. 2b). Specimens were collected using a D-frame net, a sweep net along the margins of water bodies, or by manual collection.

Different substrate types were examined, including leaf packs, marginal sand, macrophytes, and emergent vegetation on the water surface. Sampling effort was standardized across environments by establishing a sampling time of 1h per water body, following the collection methodology employed. This standardization aimed to account for the diversity of microhabitats, as heteropterans may occur submerged and are associated with sediments and detritus, as well as with riparian vegetation, the water surface, and wet areas adjacent to water bodies. After collection, substrates were preliminarily sorted in the field, and both biological material and substrates were placed in plastic bags containing 80% ethanol. Subsequently, the samples were taken to the laboratory for species-level identification using specialized dichotomous keys, including those of Ribeiro et al. (2014), Magalhães et al. (2016) Floriano et al. (2017), Moreira et al. (2018), Franco et al. (2024), Stefanello (2021), Stefanello & Azevêdo (2024), and Viana et al. (2023, 2025). After identification, specimens were preserved in vials containing 80% ethanol, labeled, organized, and deposited in the collection of the Aquatic Entomology Laboratory (LEAq) at the Universidade Estadual do Maranhão, Caxias, Maranhão.

Physicochemical and environmental parameters

In lotic environments, variables were measured at three points along the sampling reach (upstream, middle, and downstream), distributed along a 50-m transect. At these points, water physicochemical parameters, including electrical conductivity (µS/cm), temperature (ºC), hydrogen potential (pH), dissolved oxygen (mg/L), and turbidity (NTU), were measured, together with the hydrological variables such as water velocity (m/s) and flow rate (m³/s) (Table S1, **Online Resource**). In lentic environments, physicochemical parameters were also measured at three points to obtain a representative average of local conditions. However, water velocity and flow rate were not assessed in these environments due to the absence or low intensity of water flow. Water physicochemical variables were measured using multiparameter probes or individual instruments for each parameter. In lotic environments, current

velocity was estimated and discharge was calculated following the procedures described by Craig (1987), using measurements of channel width, depth, and flow velocity.

Landscape variables

Land use and land cover (LULC) were derived from a mosaic of images obtained from the RapidEye satellite constellation (RapidEye, 2015) corresponding to the sampling period (2024 and 2025). Digital image processing (DIP) was performed to classify land-use and land-cover types using PCI Geomatics 2015 and the ATCOR Ground Reflectance module. After atmospheric correction, a mosaic of the RapidEye scenes was generated using the OrthoEngine module of PCI Geomatics. The resulting RapidEye mosaic was subjected to object-based image classification in eCognition 9, resulting in seven land-use and land-cover classes: forest, savanna, pasture, agriculture, urban areas, bare soil, and water. Classification accuracy was evaluated by comparison with raster layers from MapBiomas Collection 10 and by in situ observations. Landscape variables were obtained for each site using circular buffers with radii of 250, 500, and 1,000 m centered on the midpoint of each sampling transect (25 m). Landscape variables were represented by the percentage of area occupied by each land-use and land-cover class within each buffer.

Spatial variables

We generated connectivity matrices based on the geographic coordinates of the sampling sites to calculate spatial variables using the *spdep* package in R (Bivand at al., 2013). These matrices considered two types of distances: linear overland distances (Euclidean) and fluvial distances, the latter computed using the *riverdist* package (Tyers, 2022), which accounts for the position of sites along the drainage network. From these matrices, Principal Coordinates of Neighbour Matrices (PCNM) were extracted using the *adespatial* package (Dray et al., 2025) to represent spatial structure.

Given the lack of hydrologCical connectivity in lentic ecosystems, fluvial PCNMs were used as spatial variables only in analyses of lotic systems, whereas Euclidean distance was used for lentic systems. These spatial variables (linear and fluvial PCNMs) were used as predictors of community variation in relation to space and represent spatial relationships among sampling sites at different scales, with lower-numbered PCNMs reflecting broader spatial structures and higher-numbered PCNMs representing finer-scale spatial patterns (Dray et al., 2006). As a spatial autocorrelation matrix, only significant and positive spatial eigenvectors were retained.

Statistical analyses

Each water body was treated as an independent sampling unit. To assess environmental patterns in lentic and lotic environments, a Principal Component Analysis (PCA) was performed (Legendre & Legendre, 2012) using an environmental matrix of water physicochemical variables and landscape variables. PCA was conducted separately for each system (lentic and lotic) to reduce data dimensionality to observe the environmental patterns across the forest cover gradient.

To test our two hypotheses regarding the relative importance of local, landscape, and spatial variables, we performed variance decomposition using partial Redundancy Analysis (pRDA) (Borcard et al., 1992; Legendre & Legendre, 2012). This approach allows the assessment of the relative contribution of environmental (physicochemical and hydrodynamics parameters), landscape (land use and land cover), and spatial (linear and fluvial PCNMs) variables in structuring water bugs communities, identifying which factors exert the strongest influence on variation in community structure. For this analysis, a Hellinger-transformed species abundance matrix (Legendre & Legendre, 2012) was used as the response variable. Environmental variables included physicochemical parameters of water such as temperature, pH, electrical conductivity, turbidity, dissolved oxygen, flow, and water velocity. Landscape variables included land use and land cover within a 500 m buffer around each sampling point. Spatial variables were derived from PCNMs (Blanchet et al., 2008).

For lentic environments, only linear PCNM vectors derived from Euclidean distances among sampling sites were used. For lotic environments, both linear and fluvial PCNM vectors were combined, the latter calculated based on distances along the river network, to account for the spatial connectivity typical of these systems. Spatial vectors (PCNMs), as well as environmental and landscape variables, were subjected to forward selection (adespatial package, Blanchet et al., 2008) to retain only the most relevant predictors explaining variation in the community composition of Gerromorpha and Nepomorpha.

Variance partitioning was used to decompose total variation in species composition into pure fractions explained exclusively by environmental, landscape, and spatial factors, as well as the shared variation among these three sets of predictors. Variance partitioning was performed separately for lentic and lotic environments and for Gerromorpha and Nepomorpha. Each pure fraction was assessed using pRDA and evaluated through Monte Carlo permutation tests with 9,999 permutations. All analyses were performed in environment R (R Core Team, 2025, version 4.5.1) using *adespatial* (Blanchet et al., 2008) and *vegan* (Oksanen et al., 2025) packages, and figures were generated using the *ggplot2* package (Wickham, 2016).

Results

Species composition

A total of 1,052 specimens were identified, comprising 11 families, 26 genera, and 63 species. In lentic environments, Nepomorpha accounted for 97.11% of the individuals and was primarily represented by *Tenagobia incerta* (n = 50 specimens), *Buenoa konta* (n = 40), *Buenoa tarsalis* (n = 30), *Belostoma nessimiani* (n = 16), and *Buenoa salutis* (n = 14). Gerromorpha represented 2.89% of the individuals, with *Limnogonus recurvus* being the most abundant species (n = 3 specimens) (Table S2, **Online Resource**). In lotic environments, Gerromorpha accounted for 51.98% of the individuals and was represented mainly by *Rhagovelia hambletoni* (n = 170 specimens), *Rhagovelia tenuipes* (n = 98), *Brachymetra albinervus* (n = 77), and *Cylindrostethus palmaris* (n = 53). Nepomorpha comprised 48.02% of the individuals and was

primarily represented by *Martarega bentoi* (n = 143 specimens) and *Maculambrysus transversus* (n = 52) (Table S2, **Online Resource**).

Lentic versus lotic environments

The Principal Component Analysis (PCA) based on local environmental and landscape variables from lentic environments indicated that the first two axes explained 44.02% of the total variation (PC1 = 26.90%; PC2 = 17.12%). Although no clear clustering pattern was observed, a distinct grouping of ponds was evident. An environmental gradient primarily associated with land use was detected, with temperature, turbidity, exposed soil, and agricultural cover being positively associated, indicating ponds characterized by higher values of these variables. In addition, savanna and forest areas showed contrasting configurations, with forested areas exhibiting higher pH values than savanna areas. Pasture-dominated areas were associated with higher electrical conductivity and lower dissolved oxygen concentrations (Fig. 3a).

For lotic environments, the first two PCA axes jointly explained 41.34% of the total variation (PC1 = 25.78%; PC2 = 15.56%). Streams located in more open landscapes dominated by pasture, agriculture, savanna grasslands, and exposed soil exhibited environmental conditions associated with higher discharge and flow velocity, as well as variation in temperature, pH, and dissolved oxygen. In contrast, streams associated with greater forest cover, despite strong urban influence, displayed a distinct environmental configuration characterized mainly by higher electrical conductivity and turbidity, reflecting differences in hydrological dynamics among environments (Fig. 3b).

Overall, variation in lentic environments was primarily associated with land use and land cover surrounding the ponds, which in turn influenced the physicochemical characteristics of the water. In lotic environments, variation was driven by both land-use patterns and stream hydrological characteristics, indicating that flow dynamics play a key role in shaping environmental conditions.

Variation partitioning of communities in lentic and lotic environments

In lentic environments, variation partitioning for Gerromorpha indicated that the pure environmental fraction explained 28% of the variation, primarily associated with turbidity and dissolved oxygen (R^2 = 0.285; F = 5.290; p = 0.008). The pure spatial fraction accounted for 21% of the variation and was associated with PCNM1 and PCNM2 (R^2 = 0.209; F = 4.140; p = 0.015). The pure landscape fraction was not significant (R^2 = 0.097; F = 2.460; p = 0.062), and 33% of the variation remained unexplained (Fig. 4a; Table S3, **Online Resource**). For Nepomorpha, none of the fractions significantly explained variation in community composition. The pure environmental fraction was negligible (R^2 = -0.001; F = 0.900; p = 0.564), as were the pure landscape (R^2 = 0.037; F = 1.207; p = 0.230) and spatial fractions (R^2 = 0.003; F = 1.015; p = 0.491). Most of the variation (98%) remained unexplained (Fig. 4b; Table S3).

In lotic environments, Gerromorpha showed no significant effect of the environmental fraction (R^2 = -0.012; F = 0.808; p = 0.559). The landscape fraction explained 10% of the variation, mainly associated

with forest cover (adjusted R^2 = 0.101; F = 2.554; p = 0.027). The spatial fraction explained 16% of the variation, related to four fluvial distance-based variables and two linear spatial terms (adjusted R^2 = 0.159; F = 1.591; p = 0.026), while 72% remained unexplained (Fig. 4c, Table S3). For Nepomorpha, the environmental fraction was significant, with discharge explaining 9% of the variation (R^2 = 0.089; F = 2.339; p = 0.016). The landscape fraction was not significant (R^2 = 0.022; F = 1.180; p = 0.248), and the spatial fraction explained 8% of the variation, based on one fluvial and one linear spatial variable (R^2 = 0.075; F = 1.433; p = 0.053). Overall, 87% of the variation remained unexplained (Fig. 4d; Table S3).

Discussion

Our study demonstrates that lentic and lotic ecosystems are shaped by distinct scale-dependent drivers and further highlights the importance of connectivity in structuring metacommunities of aquatic and semiaquatic true bugs across the Cerrado. In lentic ecosystems, environmental variation was primarily associated with land use and land cover surrounding ponds, emphasizing the strong influence of landscape composition on water variables. This pattern is expected, given that ponds and wetlands act as sinks for sediments, organic matter, and nutrients (Esteves, 2011), making them particularly susceptible to changes in the surrounding landscape. Accordingly, ponds embedded within highly modified landscapes receive greater inputs of sediments and nutrients associated with agricultural expansion and deforestation, resulting in increased turbidity, altered water chemistry, and higher water temperatures due to reduced riparian inputs and shading (Allan, 2004).

In contrast, environmental variation in lotic ecosystems was primarily associated with stream hydrology, indicating that local environmental conditions are strongly mediated by flow dynamics. Although land use and land cover also influenced stream functioning, their effects were largely mediated by the removal of riparian vegetation, which reduces shading and increases the exposure of streams to direct solar radiation, thereby resulting in elevated water temperatures. (Hostetler, 1991), and alters pH by modifying the input and processing of allochthonous organic matter (Allan & Castillo, 2007). Stream flow and wtaer velocity also emerged as major drivers of environmental variation by regulating oxygen availability, as greater flow rate and turbulence enhance oxygen diffusion, an effect that may be further modified by landscape alteration.

Community responses differed markedly between Gerromorpha and Nepomorpha in lentic ecosystems, partially supporting our hypothesis i. Gerromorpha communities were shaped primarily by environmental filtering, with a significant contribution of spatial processes, whereas Nepomorpha assemblages showed no detectable relationships with environmental, landscape, or spatial variables, contrary to our expectation of a stronger spatial signal for this group. For Gerromorpha, the joint influence of environmental and spatial components suggests that species-specific niche requirements and environmental tolerances interact with dispersal among habitat patches. In ecosystems with little or no hydrological connectivity, terrestrial dispersal appears sufficient to allow species to colonize habitats that better match their ecological requirements (e.g., suitable environmental conditions, resource availability, and mating opportunities), thereby promoting population persistence (Cunha & Juen, 2020;

Guterres et al., 2021). Consequently, community assembly in these moderately isolated habitats reflects the combined effects of environmental filtering and dispersal, facilitated by the strong flight capacity of most Gerromorpha species (Cunha et al., 2020).

Among the environmental variables, dissolved oxygen and turbidity were the strongest predictors, indicating that water quality plays a key role in structuring Gerromorpha assemblages. These variables likely influence prey availability and behaviour while reducing the visibility of submerged organisms, thereby affecting foraging efficiency. Although several studies have reported declines in abundance or species turnover in disturbed habitats (Dias-Silva et al., 2010; Cunha et al., 2015), some Gerromorpha species persist under degraded conditions. This likely explains the occurrence of *Limnogonus recurvus*, a habitat generalist frequently recorded in open, disturbed, and anthropogenically modified environments (Dias-Silva et al., 2010; Guterres et al., 2021). Thus, environmental filtering in lentic ecosystems does not exclude generalist species but instead favors those with greater tolerance to altered environmental conditions.

According to Cunha and Juen (2020), the spatial influence may be associated with the variable dispersal capacity of semiaquatic bugs and with phenotypic plasticity related to flight. Thus, the spatial component reinforces that the structuring of Gerromorpha assemblages in lentic systems results from the interaction between environmental filters and spatial processes associated with dispersal. This pattern is more consistent with the species-sorting paradigm with spatial influence, rather than with classical mass effects (Leibold et al., 2004). Considering that Gerromorpha exhibit moderate dispersal, but the dispersal range of species depend on suitable connectivity among habitats (Heino et al., 2015; Fares et al., 2025), these results are consistent with the ecology of the group and with the more stable, yet disturbance-susceptible, nature of lentic environments.

Regarding Nepomorpha, the absence of effects of environmental, spatial, and landscape variables suggests that the structuring of these assemblages does not respond to well-defined gradients when considering the variables evaluated in this study. This pattern is consistent with the ecology of the group, as many Nepomorpha species exhibit broad environmental tolerance. They are also strongly influenced by demographic characteristics, as previously observed for species of *Belostoma*, whose populations reflect historical processes that have shaped their dynamics over time (Stefanello et al., 2020). In addition, these insects are recognized as efficient colonizers, capable of persisting in environments with low water quality and reduced oxygen availability—features frequently associated with lentic ecosystems, which tend to exhibit lower habitat heterogeneity and a less uniform distribution of dissolved or suspended nutrients (Salles & Ferreira-Júnior, 2014).

On the other hand, considering lotic environments and patterns of variance partitioning, our hypothesis ii was also partially supported, where Gerromorpha communities in these ecosystems were predominantly explained by spatial and landscape components, indicating the importance of dispersal and regional connectivity, but without influence from local environmental variables, contrary to expectations. Furthermore, Nepomorpha communities were structured mainly by environmental factors, as generally

expected for actively dispersing freshwater aquatic organisms. Overall, our results highlight the importance of both niche-related mechanisms and species dispersal in shaping aquatic communities, given the high environmental variability and the degree of spatial connectivity among these systems.

Although the literature frequently indicates that streams are strongly structured by Although the literature frequently indicates that streams are strongly structured by environmental conditions due to hydrological connectivity, which facilitates organism dispersal toward suitable habitats (Heino et al., 2015; Cunha et al., 2020; Dias-Silva et al., 2020; Guterres et al., 2021), our results show a contrasting pattern in which the spatial component was the main driver of Gerromorpha assemblage structure, followed by landscape-scale variables, while environmental predictors had no detectable effect. This absence may reflect either a relative physicochemical homogeneity among the sampled streams or the broad ecological tolerance of some species within the group (Heino et al., 2013), suggesting that, under conditions of high connectivity, community composition may be governed primarily by regional-scale processes, including landscape configuration and geographic distances among sites. In this context, the observed pattern is consistent with high-dispersal scenarios and the operation of mass effects at a regional scale, as predicted by metacommunity theory (Leibold et al., 2004), whereby community structure is shaped by continuous dispersal among habitat patches, a result also reported by Franco et al. (2023) for Gerromorpha assemblages in Cerrado streams, although with some context-dependent influence of local environmental conditions.

In contrast, studies conducted in the Amazon indicate that habitat structure and water variables often explain most of the variation in Gerromorpha composition (Cunha & Juen, 2020; Guterres et al., 2021). Thus, while Gerromorpha metacommunities in the Amazon tend to be strongly shaped by environmental filtering and organized primarily by species sorting, in the Cerrado their structure may be more strongly modulated by the interaction between spatial processes and landscape structure, particularly when spatial factors are explicitly considered. The importance of forest cover further highlights the role of forest fragments in the Cerrado as corridors or stepping stones, facilitating dispersal to suitable habitats even under suboptimal local conditions (Tonetti et al., 2019).

In lotic ecosystems, unlike Gerromorpha, local environmental variables, especially flow velocity, were the main drivers of Nepomorpha community structure. This relationship indicates that hydrological dynamics play a central role in structuring this group, which is expected given their predominantly aquatic habits and strong association with the substrate, backwaters, and submerged vegetation (Dias-Silva, 2013). This pattern is closely associated with the functional adaptations of Nepomorpha, including morphological traits that enable underwater respiration, such as air retention and the presence of a plastron (Wang et al., 2021). These adaptations may facilitate the exploitation of the water column and benthic habitats, including environments characterized by higher flow velocities. Consistently, the exclusive occurrence of the genera *Australambrysus*, *Maculambrysus*, and *Limnocoris* in lotic environments indicates a strong affinity for higher-flow reaches.

Landscape variables had no effect on Nepomorpha communities, suggesting that local conditions are more important than surrounding landscape context. A similar pattern was reported by Dias-Silva (2020), who found that Nepomorpha were not related to landscape-scale physical changes but responded more strongly to limnological variables. Despite limited terrestrial dispersal, in-stream movement may help maintain population structure within suitable microhabitats, enabling connectivity among environmentally favorable sites. This response is consistent with a species-sorting model, in which assemblage composition is primarily determined by species' responses to local environmental conditions, even when dispersal occurs mainly along the channel network.

Despite uneven sampling across basins—with only three streams in the Parnaíba River basin—the inclusion of streams separated by large distances along rivers may have revealed regional biogeographic turnover, as evidenced by the lack of an environmental effect on lotic Gerromorpha communities. These responses contrast sharply with the structuring of such communities in Amazonian streams, which are strongly influenced by local environmental factors even over great distances (Cunha & Juen, 2020). Another aspect to consider, based on our findings, is that despite incorporating multiple sets of predictor variables, the absence of discernible patterns in lotic Nepomorpha communities suggests that other ecological processes not analyzed here—such as species' morphological and functional traits—may have played a role alongside the stochastic processes driving these communities. Consequently, further studies are needed at broader geographic scales, considering responses beyond the purely taxonomic, to determine the mechanisms governing these aquatic ecosystems within this understudied Amazon-Cerrado-Caatinga transition region.

Conclusion

Our results highlight important differences in the organization of freshwater aquatic metacommunities, based on organisms with distinct life-history strategies and habitat-use modes. We also emphasize that the characteristics of aquatic ecosystems with different hydrological regimes (i.e., lentic and lotic systems) play a key role in structuring these communities. Life habits and dispersal modes were fundamental in shaping community organization, with Gerromorpha and Nepomorpha metacommunities showing differing degrees of environmental tolerance and connectivity-dependent dispersal across sites (streams and ponds). These findings address important gaps by providing an integrated assessment of Gerromorpha and Nepomorpha assemblage structure in lentic and lotic Cerrado environments, while simultaneously incorporating factors associated with variation along a land-use gradient. Overall, the results reinforce the need for freshwater biodiversity conservation strategies in the Cerrado that jointly consider local environmental quality, landscape connectivity, and aquatic habitat heterogeneity, as changes in land use and hydrological dynamics may differentially affect aquatic organisms and ecosystem types.

Declarations

Supplementary Information

Additional data for this study is available.

Ethical approval

All authors have read, understood, and have complied as applicable with the statement on “Ethical responsibilities of Authors” as found in the Instructions for Authors and are aware that with minor exceptions, no changes can be made to authorship once the paper is submitted.

Competing interests

The authors declare no competing interests.

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Author Contribution

TGSA conducted the field collections, identified the specimens, and prepared the manuscript. EJC contributed to the data analyses, produced the maps and figures, and revised the manuscript. FS revised and translated the manuscript into English. CASA reviewed the manuscript.

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Figures

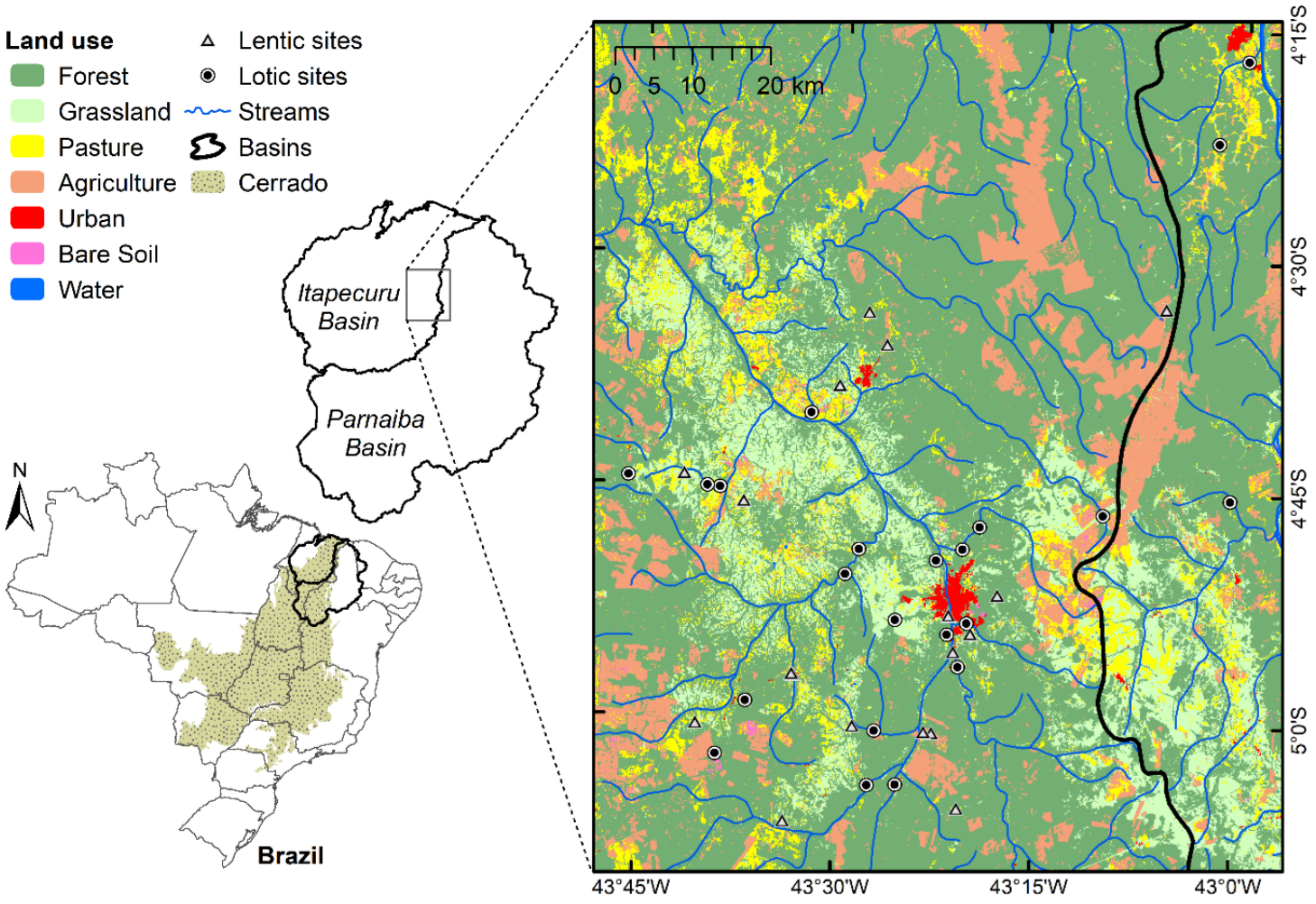


Figure 1

Distribution of sampling sites for aquatic bugs (Heteroptera: Gerromorpha and Nepomorpha) across the Itapecuru and Parnaíba River basins in the Cerrado of eastern Maranhão, Brazil. Land use and land cover classes are shown in the background. Circles indicate lentic sites, and triangles indicate lotic sites

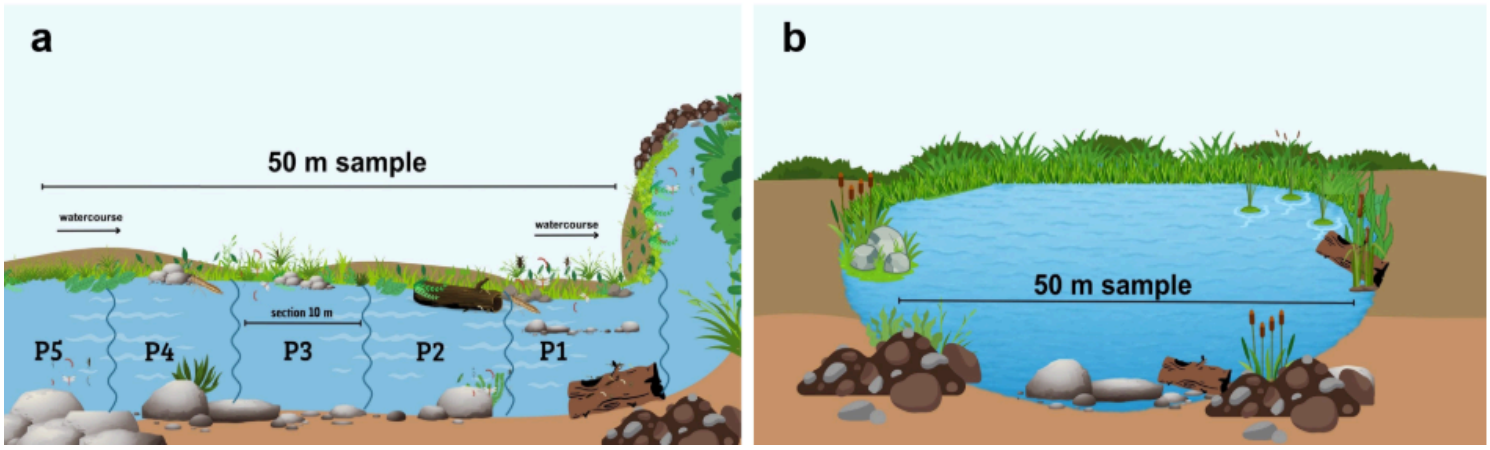


Figure 2

Schematic representation of the sampling protocols used for (a) lotic and (b) lentic environments in the Cerrado of eastern Maranhão, Brazil

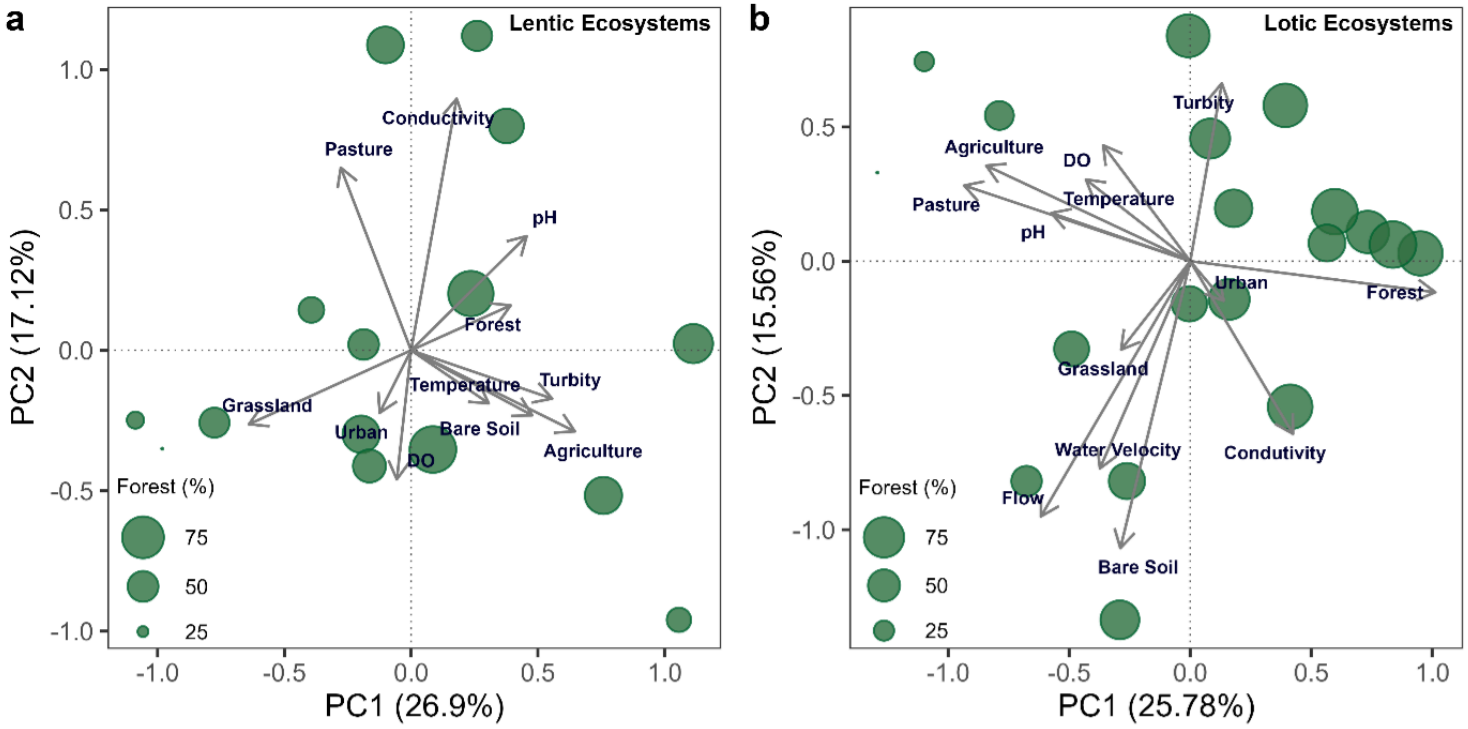


Figure 3

Principal Component Analysis (PCA) of (a) lentic and (b) lotic environments based on physicochemical variables and land-use/land-cover variables. Arrows represent the environmental and landscape variables contributing to the ordination. Each bubble corresponds to a sampling site, and bubble size indicates the percentage of forest cover surrounding the water bodies

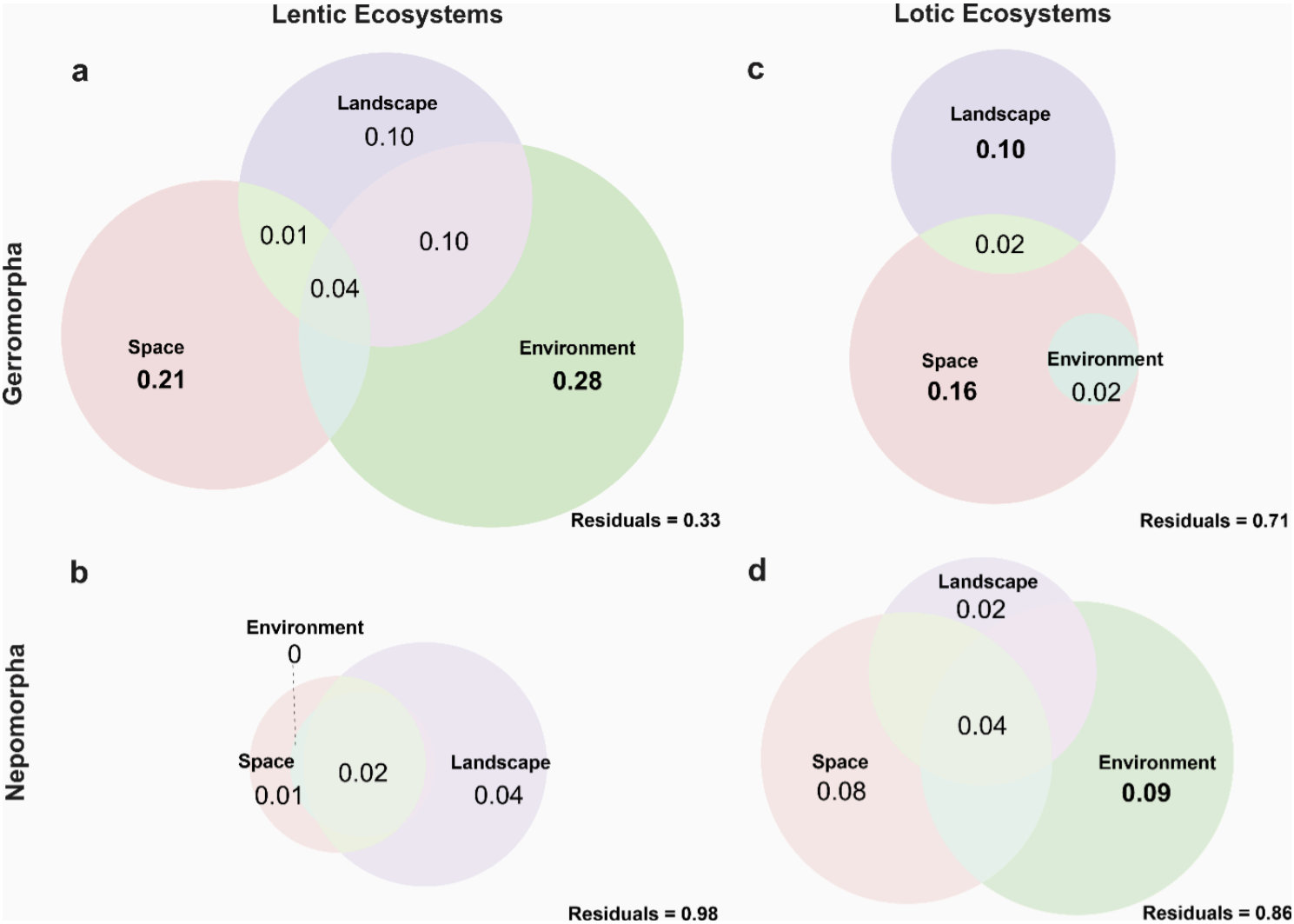


Figure 4

Variation partitioning of water bugs metacommunities across environmental, spatial, and landscape predictors. Circles indicate unique fractions of explained variation and overlaps indicate shared fractions. Values in bold represent significant pure fractions ($p < 0.05$). (a) Lentic–Gerromorpha; (b) lentic–Nepomorpha; (c) lotic–Gerromorpha; (d) lotic–Nepomorpha

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