

UNIVERSIDADE FEDERAL DO PARÁ
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
EMBRAPA AMAZÔNIA ORIENTAL
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

BEATRIZ DA LUZ SILVA

**Métricas para analisar a heterogeneidade de riachos e padrões de
diversidade beta de assembleias de Gerromorpha na Amazônia Oriental**

Belém
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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia do convênio da Universidade Federal do Pará e Embrapa Amazônia Oriental, como requisito parcial para obtenção do título de Mestre ou Doutor em Ecologia. Área de concentração: Ecologia. Linha de Pesquisa: Ecologia de Comunidades e Ecossistemas

Orientadora: Dr. Maria Cristina Esposito Barthem
Co-Orientadores: Dr. Erlane José Cunha e Leandro Juen

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COMISSÃO JULGADORA

Prof. Dr. Leandro Juen

Universidade Federal do Pará (Presidente)

Prof. Dr. Raphael Ligeiro

Universidade Federal do Pará (Membro Titular)

Prof^a Dr^a Karina Dias-Silva

Universidade Federal do Pará – Campus Altamira (Membro Titular)

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Universidade Federal do Pará (Membro Titular)

Prof. Dr. Leandro Brasil

Universidade Federal de Mato Grosso (Membro Titular)

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Métricas para analisar a heterogeneidade de riachos e padrões de diversidade beta de assembleias de Gerromorpha na Amazônia Oriental

RESUMO

Perdas de biodiversidade em ecossistemas de água doce, especialmente em riachos amazônicos, são uma preocupação crítica impulsionada por muitas atividades humanas que alteram a condição dos corpos d'água. Estudos anteriores mostram que o efeito da complexidade do habitat na biodiversidade difere espacialmente, taxonomicamente e com medidas de complexidade. No entanto, quantificar a complexidade do habitat ainda é um desafio para ecologistas. Desenvolvemos dois indicadores para quantificar a heterogeneidade de riachos com base em variáveis ambientais de um protocolo que mede características físicas e estruturais de riachos amazônicos e as relacionamos com a composição de insetos semiaquáticos (Gerromorpha) em 135 riachos amazônicos. Utilizamos índices de dissimilaridade de diversidade beta taxonômica e singularidade ecológica (LCBD) para compreender quais locais são mais importantes para a diversidade e, assim, poder priorizá-la. Foram selecionadas 18 variáveis ambientais para construir métricas de heterogeneidade de riachos. Nossos resultados mostram que espaço e ambiente contribuem para a diversidade beta total, substituição e diferenças de riqueza de Gerromorpha. A singularidade ecológica apresentou uma relação negativa com o índice de integridade do habitat. Nossos resultados mostraram que tanto espaço quanto ambiente são fatores importantes para a diversidade beta devido a variações nas características do habitat que permitem o estabelecimento de diferentes conjuntos entre diferentes locais e as capacidades de dispersão das espécies. O maior percentual de diversidade beta explicado pela substituição de espécies e sua associação com a heterogeneidade ambiental sugerem que estratégias de conservação para riachos na Amazônia Oriental devem se concentrar em áreas que abrangem habitats ambientalmente heterogêneos com composições locais de insetos semiaquáticos divergentes.

Palavras - Chave: Heterogeneidade ambiental, insetos bioindicadores, singularidade ecológica, substituição, diferença de riqueza.

Metrics for analyzing stream heterogeneity and beta diversity patterns of Gerromorpha assemblages in the Eastern Amazon.

ABSTRACT

Biodiversity losses in freshwater ecosystems, particularly in Amazonian streams, are a critical concern driven by many human activities that alter the condition of water bodies. Previous studies show that the effect of habitat complexity on biodiversity differs spatially, taxonomically and with measures of complexity. However, quantifying habitat complexity remains a challenge for ecologists. We developed two metrics to quantify the heterogeneity of streams based on environmental variables from a protocol that measures physical and structural characteristics of Amazonian streams and related them to the composition of semiaquatic insects (Gerromorpha) in 135 amazonian streams. We used a taxonomic beta diversity dissimilarity indexes and ecological uniqueness (LCBD) to understand which sites are most important for diversity and thus be able to prioritize it. Eighteen environmental variables were selected to construct stream heterogeneity metrics. Our results show that space and environment contribute to the total beta diversity, replacement, and richness differences of Gerromorpha. The ecological uniqueness showed a negative relationship with the habitat integrity index. Our results showed that both space and environment are important factors for beta diversity due to variations in habitat characteristics that allow the establishment of different assemblages between different locations and the dispersal capabilities of species. The higher percentage of beta diversity explained by species replacement and its association with environmental heterogeneity suggest that conservation strategies for Eastern Amazon streams should focus on areas encompassing environmentally heterogeneous habitats with divergent local semiaquatic insects compositions.

Keywords: Environmental heterogeneity, bioindicator insects, ecological uniqueness, replacement, richness difference.

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1. INTRODUCTION

Increased biodiversity has long been associated with elevated habitat complexity or heterogeneity (MacArthur, 1965; Gorman & Karr, 1978; O'Connor, 1991), and habitat destruction stands as a significant contributor to biodiversity loss (Millennium Ecosystem Assessment, 2005; Kaufmann et al., 2022). Despite being similar, these concepts need to be well defined (Kovalenko et al., 2012). Complexity can be understood as the physical structures of a habitat with different numbers and morphologies (Taniguchi et al., 2003), while habitat heterogeneity refers to the diversity of structural elements and concerns the variability of different types of structures (Taniguchi et al., 2003; Kovalenko et al., 2012). However, notable distinctions exist between species and ecosystems regarding which elements of habitat complexity diminish specific aspects of taxonomic or functional diversity and at what spatial extent. Anthropogenic activities, such as deforestation, reduce fish species richness and functional richness (Leitão et al., 2018). Likewise, the assembly of macroinvertebrates varies across ecoregions and in accordance with habitat components (Kaufmann et al., 2022), correlating with patch size and number (Béjar et al., 2020). The effects of habitat complexity on biodiversity differ spatially, taxonomically, and in terms of complexity measures.

The likelihood of biodiversity loss due to habitat loss is a consequence of multiple factors operating at various spatial extents, with their intensity dependent on the sensitivity of ecosystems or taxa involved (Leadley et al., 2022). In aquatic ecosystems, human activities disrupt ecological processes, subsequently degrading water body quality and resulting in imbalances within these environments (Allan, 2004; Vieira et al., 2015). Understanding the impact of resource exploitation and processing on aquatic ecosystems is a primary objective for ecologists today (Tokeshi et al., 2012), and one approach to assess ecological condition is through beta diversity studies. Initially conceptualized as the difference in species composition between locations (Whittaker, 1960), beta diversity is crucial for comprehending how assemblages are organized in space and time (Li et al., 2020).

Seeking to understand more intricate patterns in community assembly, researchers have advanced the partitioning of beta diversity. Among them, Baselga (2010) proposed partitioning beta diversity in spatial turnover and nestedness components, while Podani &

Schmera (2011) introduced replacement and richness differences. Replacement involves the substitution of one species in a particular location by another species in another location, whereas richness difference represents the loss (or gain) of species between locations. In a comparative approach, Carvalho et al. (2012) clarified that the most ecologically meaningful and consistent method for beta diversity partitioning is that of Podani & Schmera (2011), as Baselga's (2010) methods do not represent replacement and species loss accurately not being completely complementary to each other (Schmera et al., 2020). Another approach of this strategy of partitioning is to decompose total beta diversity into Local Contribution to Beta Diversity (LCBD) (Legendre and De Cáceres, 2013), also called ecological uniqueness or compositional uniqueness. Elevated LCBD values indicate that a specific location has a distinct species composition, suggesting it may be more pristine (Legendre, 2014) or with more unique biological ecological information, however, the opposite can also occur, indicating that LCBD despite being helpful, is not an indicator of conservation status, and its results should be analyzed with caution. (Legendre and De Cáceres, 2013). This sheds light on how assemblage composition contributes to beta diversity and assists in prioritizing conservation areas (Heino et al., 2017).

Environmental heterogeneity is linked to beta diversity (Heino et al., 2015; López-Delgado et al., 2020) because of the probability of environments heterogeneous areas offer higher resource availability or diversity, making possible the co-occurrence of a greater number of different species (St. Pierre & Kovalenko, 2014; Tokeshi & Arakaki, 2012). A heterogeneous environment is one with a high availability of abiotic characteristics that can filter the number of species that can inhabit it. Some studies also argue that heterogeneity is not necessarily associated with conserved areas (Lopez-Delgado et al., 2020), and thus, more heterogeneous locations may also harbor disturbance-tolerant species (Guterres et al., 2021). Therefore, it is possible that even in degraded environments with greater variability of conditions, there is a higher uniqueness of tolerant species.

Calculating heterogeneity is, therefore, a challenge as the potential impact of heterogeneity varies. Nonetheless, several qualitative indices of stream habitat quality have been developed (Barbour, 1999; Nessimian et al., 2008; Mishra et al., 2009) and are widely used in stream assessments. Hughes et al. (2010) reported that the four indices that they tested

across the USA were highly correlated with each other, but only moderately correlated with fish and macroinvertebrate biotic index scores. In Brazil, synthesis conducted on the explanatory potential of the integrity index by Nessimian et al (2008) indicate that this index explains approximately around 29% of community variation in streams (Brasil et al., 2020). Despite the great usefulness of these indices due to their simplicity in representing environmental conditions, as with heterogeneity, these indices only explained a portion of the variability in biological condition, and markedly less than multiple regression modeling of multiple habitat variables (Herlihy et al., 2020). Because of this and because aquatic systems have a multidimensional nature, thus, we need to have a good representation of the heterogeneity of streams to precisely assess their effects on biodiversity, it is interesting to consider more complex metrics or to consider multiple dimensions.

For instance, the Distance-Based Tests for Homogeneity of Multivariate Dispersions (PERMIDISP) analyze distances between organized samples and the corresponding centroid of the treatment to which they belong. This method enables the analysis of data (environment and species composition) for distance and dissimilarity matrices, including beta diversity relationships (Anderson et al., 2006). Another way to indicate heterogeneity in environments is through Local Contribution to Environmental Heterogeneity (LCEH), calculated from the environmental matrix that demonstrates the uniqueness of each location in terms of selected environmental characteristics (Legendre & Legendre, 1998; Castro et al., 2019). Despite advancements, environmental categorization (e.g., land use classes) often only applies to some data, and having a metric with raw data that truly indicates heterogeneity without categorizing the data is necessary.

Streams in Amazonian regions suffer from various anthropogenic activities that influence their environmental structure (de Paiva et al., 2021), leading to an anthropogenic and diverse gradient of landscapes and consequently levels of heterogeneity (Faria et al., 2023). To understand and monitor how aquatic biodiversity responds to environmental heterogeneity, aquatic fauna bioindicators, such as aquatic and semi-aquatic insects, are widely used (Linares et al., 2023). Among these insects, semiaquatic Hemiptera stand out as bioindicators because they are well-studied, widely distributed, abundant, and easily collected and identified to species (Andersen, 1982; Andersen & Cheng, 2004; Hu et al., 2003; Vieira et al., 2015; Dias-Silva et al., 2020). They are insect predators with adaptations

for moving on the water's surface, a unique characteristic of this group (Andersen & Cheng, 2004; Hu et al., 2003). Their tolerances vary with the type and degree of stream disturbance, and their wing polymorphism allows species to disperse to more favorable conditions (Cunha et al., 2020; Guterres et al., 2021).

We investigated beta diversity patterns in Amazonian stream sites by assessing site heterogeneity, habitat quality, and among-site distance influences on Gerromorpha assemblage structure. We tested two hypotheses. 1) Both spatial distance and environmental heterogeneity contribute to total beta diversity, as well as replacement e richness difference. 2) The local contribution to total biodiversity exhibits a direct and positive relationship with site heterogeneity, forest cover, and habitat quality.

2. MATERIAL AND METHODS

2.1 Study Area

From 2012-2022, we sampled 135 stream sites in the Brazilian state of Pará, in the Acará, Capim and Murucupi basins (Figure 1). Common anthropogenic pressures in the region include mining, row crop agriculture, and livestock ranching (for more information on land uses in the region, as well as environmental changes, read Piketty et al., 2015). There is rainy season from December to May and a dry season from June to November. The average annual precipitation is approximately 1800 mm (Bastos et al., 2005) and the annual temperature ranges from 24 to 26°C (Fisch et al., 1998).

Each stream site was 150-m long, subdivided into 10 segments of 15-m each, delineated by 11 transects (labeled A to K from downstream to upstream). The samples were collected sequentially along these 10 segments (for details of the collection methodology see Cunha et al. 2015). To reduce possible seasonal effects, all streams were always sampled during the dry period, when the region had the lowest precipitation rates.

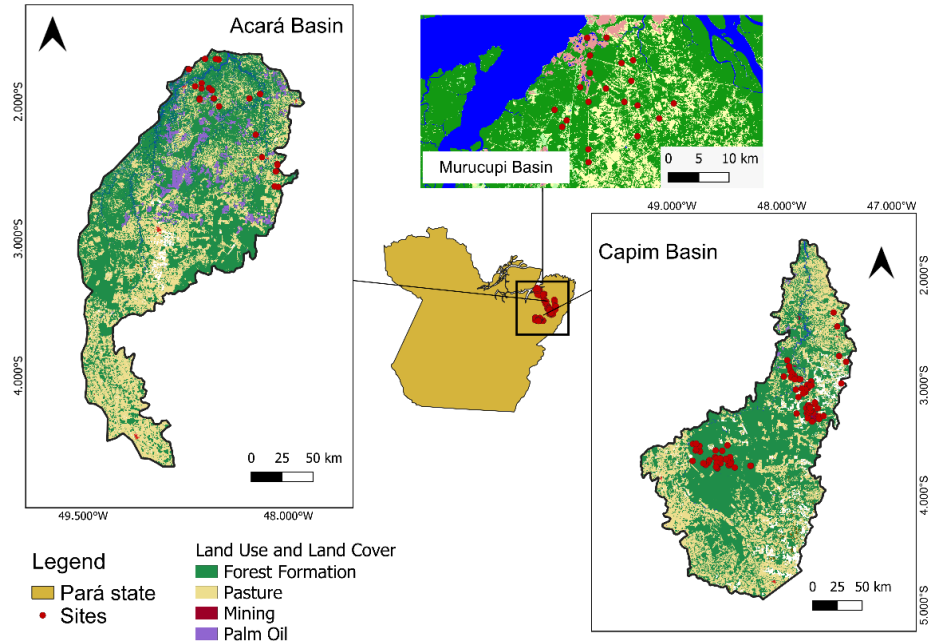


Figure 1 Location of the 135 streams sampled in the state of Pará, Brazil.

2.2 Biological Sampling

We collected Gerromorpha individuals using a sieve (18-cm diameter; 1 mm mesh; Cunha et al., 2015) scanning the surface of the sites for a one hour of sampling effort. The collected individuals were sorted in the field and subsequently identified in the laboratory to the species or morphospecies level using dichotomous keys (Nieser & Mello, 1997; Moreira et al., 2011; Moreira & Barbosa, 2014; Floriano et al., 2017).

2.3 Beta diversity indexes and ecological uniqueness

Dissimilarity among the 135 sites (total beta diversity) was calculated from the species-transformed matrix and the calculations of Podani and Schmera (Podani & Schmera, 2011) with the R package *adespatial* (Dray et al., 2017). As a result, we have a triangular matrix indicating the dissimilarities between pairs of sites considering non-shared species. Total beta diversity (β_T) was then partitioned into replacement (β_{Repl} ; changes in species composition between sites pairs community with the lowest number of species) and richness difference (β_{RichDiff} ; surplus species from one site to another, indicating the loss/gain of species between the pair of communities) (Legendre, 2014). From the triangular matrix, $\text{LCBD}_{\text{Total}}$ (Local contribution to total beta diversity) was also calculated, and for each component $\text{LCBD}_{\text{Repl}}$ (Local contribution to replacement beta diversity) and $\text{LCBD}_{\text{RichDiff}}$ (Local contribution to richness difference beta diversity).

2.4 Habitat Heterogeneity metrics

We measured physical habitat variables following the protocol outlined by Peck et al. (2006), adapted for the tropical region by Callisto et al. (2014). Initially, for calculating environmental heterogeneity, a more comprehensive selection was made to identify metrics from the protocol that represent values across the transects, labeled from A to J. In total, 65 variables were selected, encompassing channel dimensions, bank angle, bed substrate, microhabitat type, and canopy cover (Kaufmann et al., 1999; See Supplementary Material 1). After this selection, environmental variables with >80% zero values and zero covariance were initially removed. Subsequently, Pearson correlation was employed to eliminate variables with correlations >0.7, to reduce dimensionality. Finally, a forward selection method was utilized to choose the most relevant variables, and the selected variables were related to the literature of the group (Vieira et al., 2015; Cunha et al., 2015; Cunha et al., 2017; Cunha et al., 2020).

Habitat heterogeneity was calculated in two ways. The first calculation assessed heterogeneity within each site using principal coordinate analysis (PCoA) on the environmental variables measured at the ten transects. We calculated a local centroid for each site, and within-site heterogeneity consisted of the average distances between the 10 transects and the site centroid. Next, a regional mean centroid was determined from all the stream sites within a basin to calculate among-site heterogeneity. Among-site heterogeneity was then calculated as the distances between the site centroids and the regional centroid.

2.5 Habitat Integrity

A Habitat Integrity Index (HII) was calculated following Nessimian et al. (2008). This index is derived from a 12-question survey based on site visual characteristics. The questions relate to riparian land use patterns, riparian forest width, channel sediments, water flow, and other factors (Nessimian et al., 2008). The index scores range from 0 to 1, where 1 indicates a high-quality site, and 0 denotes a low-quality site.

2.6 Forest Cover

Buffer land use was determined using three geoprocessing software tools. The drainage network was delineated with QGIS by using digital elevation models (SRTM) with a spatial resolution of 30 m. The drainage network was verified using satellite images from 2012 to 2023 and Google Earth images from 2008 (<http://earth.google.com>). We also used

ArcGIS 10.1 to delineate lateral buffers for each site. Landsat 2021 images were employed for Digital Image Processing. All image manipulation steps were conducted through ArcGIS 10.1 (ESRI, 2014), PCI Geomatica V10.1 (PCI, 2007), and Ecognition (Definiens, 2009). These steps included atmospheric correction, mosaic creation, supervised object-oriented classification, and validation using MapBiomass images from the same period (Souza Jr. et al., 2020). The percentage of forest cover was determined within a 30-m linear buffer along each stream bank (60-m total width) for 300-m upstream and 300-m downstream from transect F.

2.7 Data Analyses

In our study, each site represents a sampling unit, therefore totaling 135 sampling units. To test the first hypothesis, which examines the relationship between local heterogeneity and forest cover with beta diversity, we conducted a Distance-Based Redundancy Analysis (dbRDA) (Legendre & Anderson 1999). The total beta diversity dissimilarity matrix was used as the response matrix. The environmental factors (heterogeneity within and among sites, along with individual physicochemical variables) and spatial variables were the predictor variables. The spatial co-variables used to identify correlation among sites were obtained using the MEM (Legendre et al., 2012), which calculates vectors with doubly centered spatial weights on the data and relates them to Moran's indices. Values that were either not calculated or had very low r^2 indicated a lack of significant spatial correlation. This analysis aimed to assess the direct relationship between environmental/space variables and beta diversity among sites (Anderson et al., 2011).

For the second hypothesis, assessing the relationship between environmental variables and assemblage contributions to regional beta diversity, we employed a Beta regression model (Ferrari & Cribari-Neto, 2004). The response variable, ecological uniqueness (LCBD, ranging from 0 to 1), was calculated from the total beta diversity dissimilarity matrix (Legendre & De Cáceres, 2013), with heterogeneity metrics and forest cover as predictor variables. Beta regression is commonly used for modeling response variables that are continuous and range from 0 to 1. This model is based on an alternative parameterization of the beta density in terms of the mean variable and a precision parameter (Cribari-Neto & Zeileis, 2010). Like other Generalized Linear Models (GLM) (McCullagh, 2019), beta regression involves two equations for mean and precision, consequently leading

to two regression matrices, two linear predictors, two sets of coefficients, etc. (Cribari-Neto & Zeileis, 2010). The predictor variables for the model included heterogeneity metrics (within and among sites), forest cover percentage, spatial variables, and Habitat Integrity Index (HII). All analyses were conducted using R software (R Core Team 2023, <http://www.R-project.org>).

3. RESULTS

3.1 *Semiaquatic bugs species*

We collected 12,892 individuals distributed across five families, 18 genera, and 68 species. The family Gerridae comprised 5,107 individuals, with *Brachymetra lata*, Shaw 1933 being the most abundant species, accounting for 1,885 individuals. Vellidae, with 7,664 individuals, represented the most diverse family, and the species *Rhagovelia evidis*, Bacon, 1948 was the most abundant within this family, totaling 2,420 individuals. Hebridae, Hydrometridae, and Mesoveliidae were the other families with fewer individuals, totaling 121 individuals across the three families.

3.2 *Environmental Variables and Heterogeneity*

We selected 18 variables to calculate both within-site and among-site heterogeneity. Five variables represented measures of stream morphology: wet width (m), bank-full width (m), bank-full depth (m), incision height (m), and average depth (m). Additionally, ten variables measured habitat, including substrate embeddedness (%), bank angle (%), bank undercut (m), width/depth ratio, % substrate type (Leaf Bank, Silt/Clay/Mud, Fine Riparian Roots, Sand), amount of wood in the channel, and canopy density (%). Three variables measured the flow dynamics (% slow, % fast, and % rapids). The variables were standardized using z-scores for Principal Component Analyses (PCAs) construction (Legendre and Legendre, 2012). Despite no correlation between within-site heterogeneity and among-site heterogeneity, both were considered in the calculations (Fig. 2). The site exhibiting greater among-site heterogeneity is associated with a mining site in Capim Basin (HYG04 site), while the site with greater within-site heterogeneity is linked to a forest area in Murucupi Basin (M3 site).

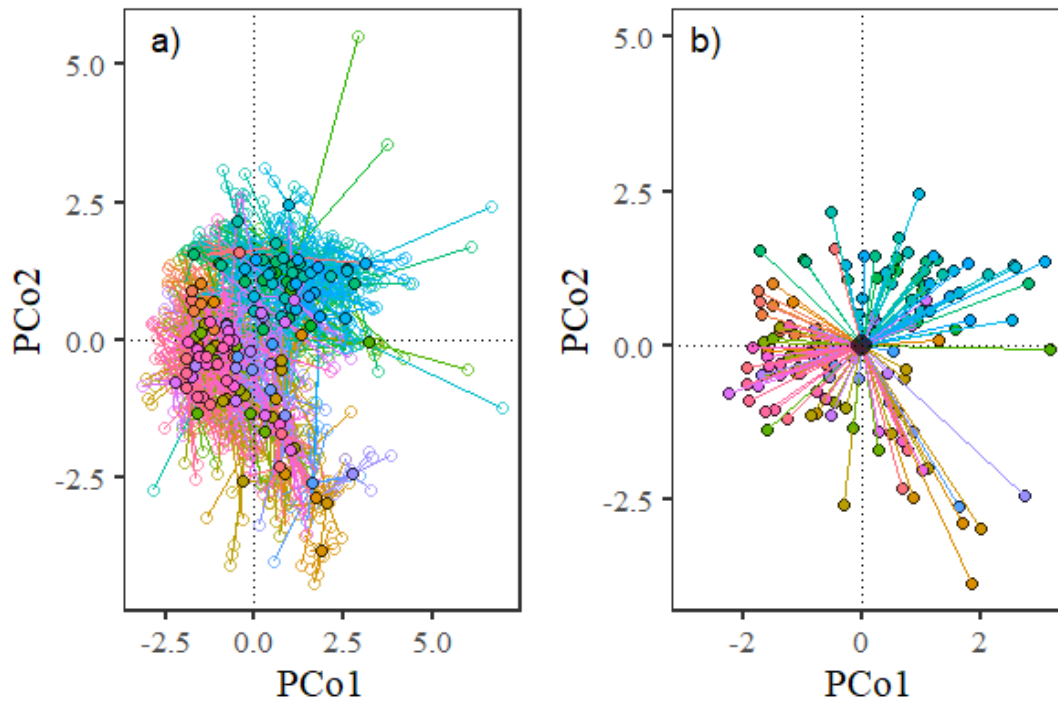


Figure 2: Ordering of heterogeneity within (a) and between (b) sites by Principal Coordinates Analysis (PCoA). Each color corresponds to a site; in (a), empty circles represent variables from the ten cross-sections, while colored circles represent centroids interconnected by lines representing the average distances of the sections, characterizing within-stream heterogeneity. In (b), colored circles represent the centroids of each site, the larger circle at the center represents the regional centroid, and these are interconnected by lines representing the average distance from the sites to the regional centroid, between-stream heterogeneity.

Table 1: Partial distance-based Redundancy Analyses (p-dbrDA) for the partitioning of total beta diversity (β_T) and its components (β_{Repl} and β_{RichDiff}) as a function of environmental and spatial variables. The values presented are the adjusted R-squared values.

Partition	β_T			β_{Rep}			β_{RichDiff}		
	R^2	F	p	R^2	F	p	R^2	F	p
[a] Pure environment	0.052	3.35	0.001	0.047	3.027	0.003	0.057	4.115	0.003
[b] Environment and space shared	0.147			0.147			0.146		
[c] Pure space	0.133	2.85	0.001	0.109	2.464	0.001	0.097	2.313	0.004
[d] Residuals	0.668			0.7			0.7		

3.3 Beta Diversity dissimilarities

The total beta diversity dissimilarity (β_T) was presented a little higher contribution of replacement (59%) than richness difference (41%). The partial dbRDA results showed that β_T was significantly influenced by space (13.3%) and the environment (5.2%), with HII being important in this relationship. β_{Rep} was significantly associated with both space (10.9%) and environment (4.7%), with HII and forest cover being important. Space and environment explained 5.7% and 9.7% of the variation in β_{Ric} , respectively. Heterogeneity within and among sites and forest cover were the most important environmental variables for richness difference.

Spatial variables were selected through forward selection, based on the presence-absence matrix of Gerromorpha. The selected spatial vectors were MEM1, MEM2, MEM3, MEM6, MEM9, MEM10, MEM12, MEM17, MEM23, MEM30, MEM33, MEM37, MEM43, MEM46. The selected vectors represented several spatial scales acting on semiaquatic bugs communities, including the broadest scales (MEM1, 2 and 3) and intermediate scales.

Table 2. Permutation test values from dbRDA of the environment without spatial interference for Total Beta, Replacement, and Richness Difference, showing the significance of the variables for each model (p). Bold values represent variables that were significant.

Beta Total - Pure environment					
	dbRDA1	dbRDA2	F	p	
HII	-0.455	0.278	8.093	0.001	***
Forest cover	-0.001	0.000	1.911	0.058	
Ht.dentro	0.089	0.049	1.025	0.432	
Ht.entre	0.026	0.126	2.370	0.033	*
Beta Replacement - Pure environment					
	dbRDA1	dbRDA2	F	p	
HII	-0.549	-0.017	8.653	0.001	***
Forest cover	-0.001	-0.001	0.999	0.497	
Ht.dentro	0.089	-0.193	1.600	0.294	
Ht.entre	-0.019	0.071	0.855	0.553	
Beta Richness Diference - Pure environment					
	dbRDA1	dbRDA2	F	p	
HII	-0.128	-0.704	7.123	0.006	**
Forest cover	-0.001	0.000	1.398	0.249	
Ht.dentro	0.154	-0.165	2.520	0.090	
Ht.entre	0.079	-0.024	5.418	0.011	*

3.4 Ecological uniqueness

The local contribution to total biodiversity ($LCBD_{Total}$) was negatively related to HII scores ($R^2 = 0,154$; $p < 0,001$) (Figure 3). $LCBD_{Repl}$ ($R^2 = 0,031$) and $LCBD_{RichDiff}$ ($R^2 = 0,017$) had no relationship with any of the model variables.

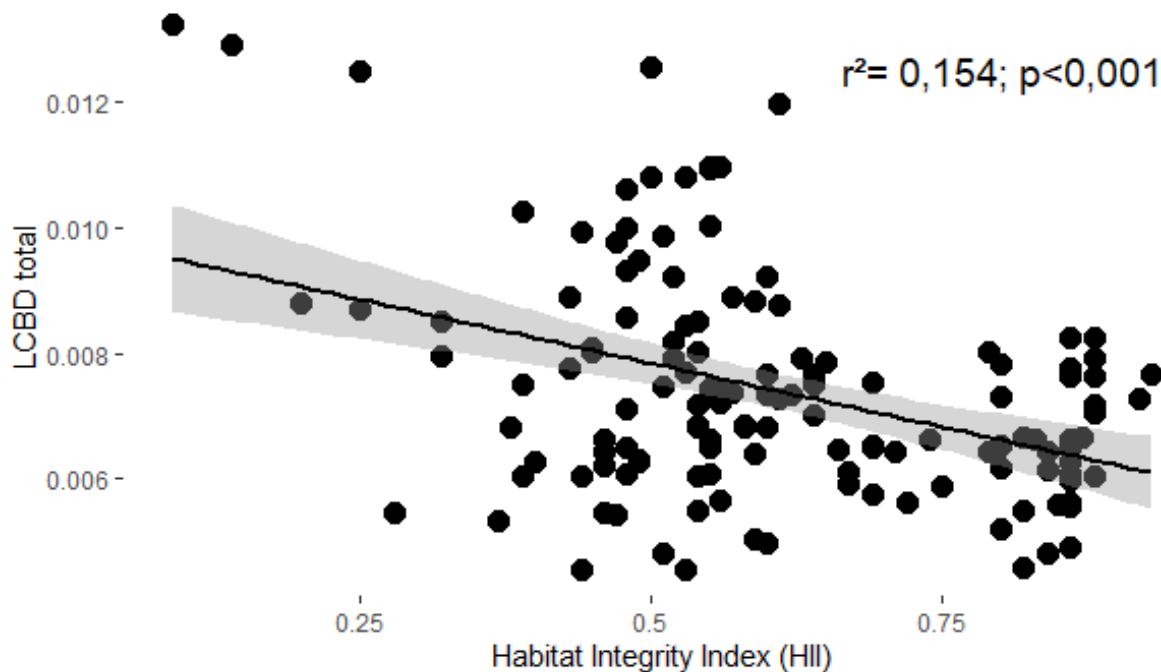


Figure 3. Relationship between the local contribution to total biodiversity ($LCBD_{total}$) and Habitat Integrity Index (HII) scores.

4. DISCUSSION

We confirmed the hypothesis that both space and the environment would contribute significantly to total beta diversity (β_{Total}), as well as to replacement (β_{Repl}) and richness differences ($\beta_{RichDiff}$). The composition was related to both heterogeneity variables as well as spatial variables demonstrated in the variation partitioning and dbRDA. However, the second hypothesis that ecological uniqueness (Local Contribution to Beta Diversity - LCBD) would have a direct and positive relationship, mainly with within-stream heterogeneity, forest cover, and HII (Habitat Integrity Index), was not corroborated. $LCBD_{Total}$ showed a negative relationship with HII.

Beta diversity patterns in aquatic ecosystems strongly depend on spatial extent (Heino et al., 2015). In our study, spatial variables influenced all components and contributed more

than the environment, indicating that proximity among sites affects beta diversity patterns. Therefore, site proximity and the high dispersal capacity of Gerromorpha species may explain the significance of space in assemblage organization (Heino et al., 2015b). Moreover, the higher percentage of β_{Total} explained by β_{Subs} suggests that species dispersal is the most influential factor. Additionally, communities with weak dispersers tend to be more heterogeneous than those with strong dispersers (Li et al., 2020). Given that Gerromorpha can disperse both by skating on water and flying, winged individuals can disperse to other sites when their home streams do not present favorable abiotic conditions (Cunha et al., 2020; Guterres et al., 2021).

Regarding the environmental variables, heterogeneity, HII, and forest cover were important for β_{Total} , but for β_{Repl} , only HII and forest cover were significant. This highlights the well-known relationship between Gerromorpha and their habitats, directly related to their ability to move on the water surface. This enables them to better exploit environmental resources, such as vegetation along the margins, which they use for shelter (Cunha and Juen, 2017). In contrast, β_{RichDiff} was influenced by both within-site and among-site heterogeneity and forest cover. The relationship between Gerromorpha and environmental heterogeneity suggests their ability to tolerate varying levels and types of habitat alteration. In our study, species richness was higher in less heterogeneous sites, suggesting that altered streams are more likely to support different, tolerant species, ultimately increasing species richness in those locations (Guterres et al., 2021). It further indicates that species richness is an insensitive Gerromorpha indicator for assessing site disturbance, as has been reported for other assemblages (Guterres et al., 2021; Vadas Jr. et al., 2022).

Unexpectedly, the Habitat Integrity Index (HII) was the most important variable explaining the ecological uniqueness ($\text{LCBD}_{\text{Total}}$), but $\text{LCBD}_{\text{Total}}$ was higher in streams with lower HII scores. Previous studies with aquatic insects have shown that heavily altered streams are more likely to support different and tolerant species, ultimately increasing species richness in these locations (Guterres et al., 2021; de Paiva et al., 2021). A study with aquatic insects (Ephemeroptera, Plecoptera and Tricoptera - EPT) in the same region obtained related ecological uniqueness results with taxonomic diversity in an anthropic gradient (de Paiva et al., 2021). Therefore, in these cases, high ecological uniqueness values should not be considered indicative of well-preserved sites (Agra et al., 2021; Legendre et al., 2013) but

rather, divergent assemblage structures, reflecting altered habitats suitable for ecological rehabilitation (López-Delgado et al., 2020).

Although we believed that site heterogeneity would predict aquatic assemblages, it did not do so. Different heterogeneity metrics affect aquatic insect diversity at different disturbance levels, mainly because of the interaction between anthropogenic disturbances and natural ecological conditions (López-Delgado et al., 2020). The 18 metrics that we selected are appropriate for semiaquatic insects, but different stream-types influence heterogeneity effects to different degrees and at different spatial extents (St. Pierre & Kovalenko, 2014; Kaufmann et al., 2022). Thus, increased habitat complexity or heterogeneity does not necessarily result in increased biodiversity, at least for Gerromorpha, as presumed by others (MacArthur, 1965; Gorman & Karr, 1978; O'Connor, 1991).

The heterogeneity metrics did not show a relationship with site uniqueness (LCBD). Nevertheless, the results of dbRDA revealed that both within-site ($p= 0.027$) and among-site ($p= 0.009$) heterogeneity played a significant role in the models of total beta diversity. Additionally, the limited environmental explanation in the outcomes, compared to other works involving Heteropteran (Cunha & Juen 2020; Cunha et al. 2022), is attributed to the peculiarities of the group. Specifically, certain group-specific variables function more effectively as explanatory environmental filters (Godoy et al., 2023). However, this observation does not apply to the interpretation of how heterogeneity impacts beta diversity, indicating that the metrics are suitable for such analyses. Other aquatic macroinvertebrates, such as EPT, may serve as appropriate models for employing these metrics, given their consideration of a diverse array of substrate variables. These groups are highly associated with such variables, primarily due to their benthic lifestyle and the elevated sensitivity of this group to disturbances (De Castro et al., 2017; Brasil et al., 2020).

5. CONCLUSION

Finally, heterogeneity metrics were important variables for beta dissimilarities, although they did not influence the ecological uniqueness of the sites. The role of these metrics was also significant as it used information on environmental variation to explain patterns of differentiation among communities and should be employed in future studies with other aquatic groups and environmental variables. The higher percentage of beta diversity explained by space indicates that Gerromorpha dispersal is the most important factor for the community, mainly due to the characteristics of this group, such as wing polymorphism and species tolerance. In our study, site uniqueness was negatively related to the habitat integrity index, demonstrating that sites with lower index values are suitable for conservation. We emphasize that both heterogeneity and water variables are important for decision making regarding the conservation of aquatic ecosystems.

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