Acta Limnologica Brasiliensia

Publication of the
Brazilian Association of
Limnology

Original Article
Acta Limnologica Brasiliensia, 2023, vol. 35, e23
https://doi.org/10.1590/S2179-975X2923
ISSN 2179-975X on-line version

Beta diversity of Ephemeroptera, Plecoptera and Trichoptera on multiples spatial extents in Xingu River rapids

Diversidade beta de Ephemeroptera, Plecoptera e Trichoptera ao longo de múltiplas escalas espaciais nas corredeiras do rio Xingu

---

Nayara Monteiro Barreiros[1], Tommaso Giarrizzo[1,2] and Bruno Spacek Godoy[1,3]*

[1]Núcleo de Ecologia Aquática e Pesca da Amazônia – NEAP, Universidade Federal do Pará, Rua Augusto Corrêa, 01 – Guamá, Belém, PA, Brasil

[2]Instituto de Ciências do Mar, Universidade Federal do Ceará, Avenida da Universidade, 2853 – Benfica, Fortaleza, CE, Brasil

[3]Instituto Amazônico de Agriculturas Familiares, Universidade Federal do Pará, Rua Augusto Corrêa, 01 – Guamá, Belém, PA, Brasil
*e-mail: bspacek@ufpa.br

Cite as: Barreiros, N.M., Giarrizzo, T. and Godoy, B.S. Beta diversity of Ephemeroptera, Plecoptera and Trichoptera on multiples spatial extents in Xingu River rapids. *Acta Limnologica Brasiliensia*, 2023, vol. 35, e23.

Abstract: Aim: Additive diversity partitioning has been used to explain the accumulation of diversity at different spatial scales with relative success. In lotic ecosystems, the spatial extent is extremely relevant in studies of diversity accumulation, because it encompasses environmental variation that causes changes in the observed communities. Despite of previous knowledge on the effect of extent on biological communities and diversity accumulation, little is known about the topic in aquatic insect communities in large rivers. In this context, we studied the effect of spatial extent and environmental variation on diversity components, alpha and beta, in Ephemeroptera, Plecoptera and Trichoptera (EPT) groups in Xingu River rapids. **Methods:** The sampling was carried out in October 2015 in the dry period of the region, in nine rapids in the Xingu, Bacajá and Iriri rivers. At each collection site, five Surber samples were taken. We also recorded pH, dissolved oxygen, electrical conductivity, water temperature, and geographic coordinates. We used additive diversity partitioning to separate the diversity components α and β. For the spatial component, we generated the spatial filters using PCNM (Principal Coordinates of Neighbour Matrices) and partitioned the variance between space and environment using partial Redundancy Analysis (pRDA). **Results:** We collected 12,249 individuals in 27 genera within 11 families in the EPT orders. The greatest accumulation of diversity was observed among rapids of the river, when the β diversity in this spatial extent was greater than the expected. The spatial structure was an indirect effect at this extent, since it is a relevant drive to environmental variables. **Conclusions:** The results indicate that the effect of spatial extent on rapids is a contributing factor in the diversity components of aquatic insect communities in large river rapids. To the conservation and management of this environment is necessary cover as many rapids as possible, since the preservation of only a few rapids can mean a substantial loss of regional diversity.

Keywords: diversity partitioning; additive beta diversity; large rivers.

Resumo: Objetivo: O particionamento aditivo da diversidade tem sido utilizado para explicar a acumulação de diversidade em diferentes escalas espaciais com relativo sucesso. Em ecossistemas lóticos, a escala espacial é extremamente relevante em estudos de acumulação de diversidade, pois engloba a variação ambiental que causa mudanças nas comunidades observadas. Apesar do conhecimento prévio sobre o efeito da escala nas comunidades biológicas e na acumulação de diversidade, pouco se sabe sobre o tema em comunidades de insetos aquáticos em grandes rios. Neste contexto, estudamos o efeito da escala espacial e da variação ambiental sobre os componentes da diversidade, alfa e beta, em grupos de Ephemeroptera, Plecoptera e Trichoptera (EPT) em corredeiras do rio Xingu. **Métodos:** A amostragem foi realizada em outubro de 2015, no período seco da região, em nove corredeiras nos rios Xingu, Bacajá e Iriri. Em cada local de coleta, foram coletadas cinco amostras de Surber. Também foram registradas as variáveis pH, oxigênio dissolvido, condutividade elétrica, temperatura da água e coordenadas geográficas. Usamos o particionamento aditivo da diversidade para separar os componentes de diversidade α e β. Para o componente espacial, geramos os filtros espaciais usando PCNM (Principal Coordinates of Neighbour Matrices) e particionamos a variância entre espaço e ambiente usando a análise de redundância parcial (pRDA). **Resultados:** Foram coletados 12.249 indivíduos em 27 gêneros dentro de 11 famílias nas ordens EPT. O maior acúmulo de diversidade foi observado entre as corredeiras do rio, quando a diversidade β nessa escala espacial foi maior que a esperada. A estrutura espacial foi um efeito indireto nesta escala, uma vez que é um direcionador relevante para as variáveis ambientais. **Conclusões:** Os resultados indicam que o efeito da escala espacial em corredeiras é um fator contribuinte nos componentes de diversidade das comunidades de insetos aquáticos em corredeiras de grandes rios. Para a conservação e manejo desse ambiente é necessário abranger o maior número possível de corredeiras, uma vez que a preservação de apenas algumas corredeiras pode significar uma perda substancial da diversidade regional.

Palavras-chave: partição de diversidade; diversidade beta aditiva; rios grandes.

1. Introduction

Community ecology aims to explain the patterns of abundance distribution and species interactions and to understand how these patterns change at different spatial extent (Hastings et al., 2011; Hepp & Melo, 2013; Mykrä et al., 2007). An intrinsic component to understanding biological phenomena is the scale of effect, because the various environmental determinants affect biological communities at different spatial extents (Hamer & Hill, 2000; Moraga et al., 2019). However, the theories most often used to explain the patterns observed in communities assume a stability of the environment in the scale of study, observing how communities' structure themselves locally or regionally with little interaction between these levels of organization (Leibold et al., 2004).

When we segment the scale of effects, in the scale regional, the species diversity of a community is influenced by historical and evolutionary processes that determine the number of species present in a region (Ricklefs, 1987; Vellend, 2010). Climatic events, dispersal barriers, and historical-evolutionary events tend to act as natural filters that create the conformation of communities on a regional scale (Jackson & Harvey, 1989; Fukami et al., 2016). In contrast, local factors such as habitat diversity, resource availability, and interspecific interactions determine the composition of the communities found at specific locations in the region (Ricklefs, 1987, 2006; Geho et al., 2007; Godoy et al., 2017).

However, the spatial extend may be observed in the context of ecological hierarchies, and may be an important direct factor in ecological studies in terrestrial and aquatic systems, influencing the observation of patterns in community structure (Moraga et al., 2019). The heterogeneity of environmental and biological characteristics is related to the extent addressed (Hastings et al., 2011), directly influencing the species accumulation function observed at distinctly spatial extent (Patrick & Yuan, 2019). Such species accumulation can be explained by two factors, which are not mutually exclusive: 1) increase in area and 2) increased landscape heterogeneity of larger regions (Whittaker, 1960; Bridgewater et al., 2004).

The accumulation of species generated by difference among communities has become relevant in studies of biological communities, because it indicates that the increase in diversity does not occur simply by increasing the number of species like a nestedness pattern (Barton et al., 2013; Heino et al., 2015). The increase occurs because species would have different capacities to occupy different habitats scattered across the landscape, creating distinct localities with singularities, both environmental and historical (Sepkoski Junior, 1988).

In such a way, the spatial scale would affect in a relevant way the rates of change of species among communities, because different spatial extensions would present rates of change in their environmental variables (Veech & Crist, 2007; Barton et al., 2013; Barros et al., 2022; Godoy et al., 2022a). Thus, it is necessary to observe which factors and to what spatial extent drive these changes in community structure in order to understand possible patterns of community distributions (Balvanera et al., 2002). The species distribution and how the community composition is spatially distributed is essential to understanding how biological diversity is maintained in ecosystems, and it is relevant to biodiversity planning and conservation (Balvanera et al., 2002; Veech et al., 2002; Godoy et al., 2017, 2019).

Aquatic insects are good models for studies with alternating components of biological communities, because they respond strongly to environmental conditions at different scales, from microhabitats to watersheds (Baptista et al., 2014). This group constitutes about 90% of all macroinvertebrate fauna in freshwater environments, playing a relevant role in continental aquatic systems, with participation in various ecological processes, for example, nutrient cycling, leaf decomposition, and food for fish and other invertebrates (Merritt et al., 2008; Hamada et al., 2019). The orders Ephemeroptera, Plecoptera and Trichoptera (EPT) are predominant in terms of abundance which are commonly found in rivers and streams (Rosenberg & Resh, 1993; Bueno et al., 2003; Crisci-Bispo et al., 2007; Godoy et al., 2016).

Variations in river flow and current velocity influence food distribution, nutrient removal, and microhabitat availability, consequently contributing to variation in aquatic insect diversity (Godoy et al., 2016; Leal et al., 2023). Thus, variation in the physical characteristics of the river channel, such as the presence of rapids, can directly influence the structure of aquatic insect communities. If this dependence between the community and the rapids is high, it is expected that the accumulation of diversity will be greater at spatial scales that contain distinct rapids, since each rapids presents distinct environmental conditions. Other effect of space in community composition of aquatic insects in rapids on rivers is the possibility of interchange of individuals through drift movement (Leal et al., 2023).

We evaluated the effect of spatial scale and environmental variables on beta diversity components in the Ephemeroptera, Plecoptera and Trichoptera groups of Xingu River rapids. We used the rapids of the Xingu River, because this habitat was the most accessible to sample, because in the dry period, great portions of stones of the rapids emerge of water column. We tested the hypotheses that: 1) the accumulation of genera of EPT will be greater between than within rapids 2) the accumulation of EPT will be related with the environmental and spatial variables, since these elements influence the structure of EPT communities.

2. Material and Methods

2.1. Study area

The study was carried out on the Xingu, Bacajá and Iriri Rivers (02°51′33.1″S and 52°19′28″W), near the city of Altamira, Pará, during the dry period, October 2015 (Figure 1). The Bacajá and Iriri Rivers are tributaries of the Xingu River, in the Amazon River Basin, located on the right side of the river. With an extension of 1500 km from its source in the Brazilian Central Plateau until its mouth in the Amazon River, the Xingu River drains an area of 531,250 km^2 (CPRM, 2023). The pH ranges from 5.5 to 7.0 with a mean conductivity of 30 µS.cm^{-1}, as well as high concentrations of oxygen (Sioli, 1968; Salomão et al., 2007).

The average flow rate during the flood period varies from 8,000 to 10,000 m^{3}s^{-1} and in the dry period the average is 2,000 m^3.s^{-1} (Norte-Energia, 2016). The flood period occurs between December and April and the dry season occurs between July and November. Because it is located near the equator, the Xingu River basin presents a warm climate and according to Köppen classification the climate is tropical and predominantly humid [Am, Sheffield et al. (2006)]. The mean annual temperature in the Altamira-PA region is 27°C, the rainy season starts in November and the dry season in July (Norte-Energia, 2016). The Xingu River is characterized by a significant number of rapids its course, something not commonly found in other large Amazonian rivers. The rapids of the Xingu are predominantly consolidated substrate formed by rocks of varying sizes [large, medium, small, and even gravel; Salomão et al. (2007)].

The sampling period (October 2015) was chosen because it presents the lowest water discharges facilitating the sample procedure. The dry period has the characteristic of favoring the colonization of high densities of invertebrates, since fast and oxygenated water are favorable conditions for organisms that occur in this environment (Frissell et al., 1986; Bispo et al., 2001).

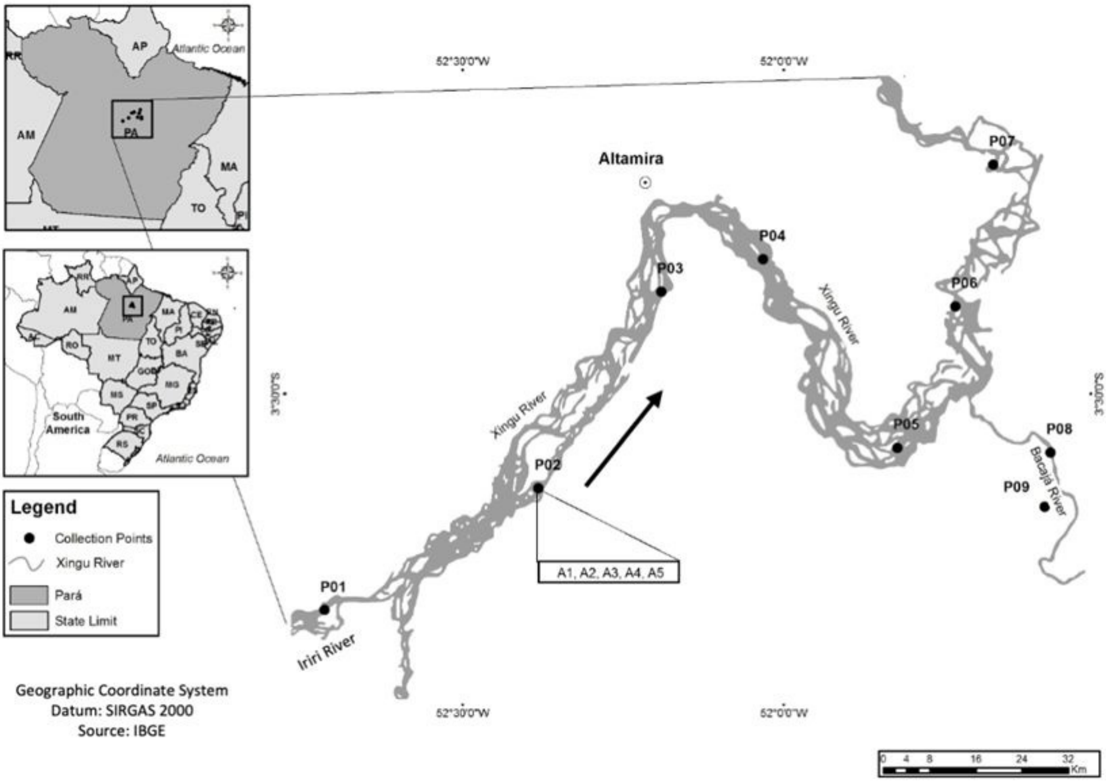

Figure 1. Rapids location in the Xingu, Bacajá and Iriri Rivers. Five Surber sampling units were obtained in each of the nine rapids.

We sampled nine rapids, six in the Xingu River, two in the Bacajá River, and one in the Iriri River. The average distance between samples units in each rapid was five meters, and between rapids was 66.65 km.

2.2. Sampling

We measured *in locus* the environmental variable pH, dissolved oxygen (DO, mg.L^{-1}), electrical conductivity (μS.cm^{-1}) and temperature (°C) in each sampling site using a probe (Hanna HI98194/10). After we measured the environmental variable, we sampled the benthic aquatic insects. We used a *Surber* sample (mesh size of 250 μm, with a 60 cm height and 0.5 m^2 of area) to collect the insects attached in the rocks on the rapids, in five subsample units. The collected insects were identified to the genus level.

2.3. Data analysis

The partition of the total diversity into alpha and beta components was done by the additive approach (Veech et al., 2002). The scales used for this study were: sample unit (α_1), rapid (α_2) and river (γ). The components of diversity accumulation considered in the partition were: average richness of the sample unit (α_1), difference between sample unit (β_1) and difference among rapids (β_2). To test the importance of each of the additive components of diversity, we use a randomization analysis and compared the observed values against the expected values in a null model for the components α, β_1 e β_2 (Veech, 2005). The communities simulated maintained the sums of row and columns to created communities comparable with the observed.

We used a Principal Coordinates of Neighbour Matrices [PCNM; Borcard & Legendre (2002)] to detect spatial relationships among the communities of the sampled points in the rapids. In order to reduce the number of spatial variables we ran a forward selection procedure in the PCNM filters to predict the community matrix (Blanchet et al., 2008). The distances between sampled points used in the PCNM calculations were estimated by the geographic coordinates. We used a partial redundancy analysis (pRDA) to assess the relative importance of environmental (pH, dissolved oxygen, electrical conductivity and temperature) and spatial (PCNM filters selected by the forward selection) variables for the structure of aquatic insect communities (Legendre & Legendre, 2012).

The pRDA allows for the estimation of linear coefficients in the relation of spatial and environmental matrices with the aquatic insect community matrix, as well as the parameters of these relations. In the analyses we used two sources of variability, physical and chemical variables and pre-selected spatial filters.

We repeated the analysis two times, using the number of genera, and to the community composition (abundance per genera), to identify the effects of space and environment in distinctly components of aquatic insect communities (Godoy et al., 2017). In the analysis for genera richness the pRDA had the same characteristics of a partial regression, but we choose to use the pRDA only to standardize the results of partitioned variation in the study. The abundance of the community was standardized using Hellinger transformation, and all environment variables were standardized to normal distribution with mean equal zero and standard deviation equal one [z distribution; Legendre & Legendre (2012)]. All analyses were carried out using the packages *vegan* and *packfor* in the statistical software R (Oksanen et al., 2012; R Development Core Team, 2020).

3. Results

We sampled 12,251 individuals of EPT orders, distributed in 27 genera of 11 families. The Ephemeroptera order was the most abundant (6,888 individuals), followed by Trichoptera (5,329 individuals) and Plecoptera (34 individuals). The average abundance of EPT was 1,361.00 (± 1,481.21) individuals per rapid (minimum of 197 and maximum 4,417). The average number of genera per rapid was 15.44 ± 2.19 (minimum of 13 and maximum 20). The electrical conductivity had the larger variation than other environmental variables (average = 42.17 ± 25.92, and coefficient of variation = 75.87). The dissolved oxygen was intermediary variation (average = 7.32 ± 0.77, and coefficient of variation = 10.53), followed by pH (average = 8.20 ± 0.55, and coefficient of variation = 6.67), and temperature (average = 30.52 ± 1.01, and coefficient of variation = 3.30).

3.1. Addictive diversity partitioning

The observed values of the diversity components α_1, α_2 e β_1 was lower than values estimated by the null model (Table 1). In other hand, the component β_2, difference among rapids, had value greater than the expected by chance. In addition, we observed that all levels of diversity, both local and regional, had important contributions in the accumulation of genera along the Xingu River. Difference of diversity among rapids (β_2) were the highest, contributing the most to regional diversity.

3.2. Diversity partitioning in environmental and spatial components

The percentages of explanation of environmental and spatial variations were different for the number of genera and community composition (Table 2). Two drivers were important to the variation in the number of genera in the rapids, the spatially structured environment and the pure spatial effect. The water temperature variable was relevant in this model, representing the environment spatially structured. For community structure, only space had a relevant effect on the variance partition, although the dissolved oxygen variable was selected for the full model.

Table 1. Observed and expected values of the addictive diversity partitioning of EPT orders in the Xingu River rapids.

Diversity component	Observed	Expected	P
Sample (α_1)	8.67 (0.32)	13.97 (0.52)	< 0.01
Rapid (α_2)	15.44 (0.58)	20.77 (0.77)	< 0.01
Total (γ)	27.00 (1.00)	27.00 (1.00)	1.00
Between sample (β_1)	6.78 (0.25)	6.81 (0.25)	0.93
Between rapid (β_2)	11.56 (0.43)	6.23 (0.23)	< 0.01

The number in the parenthesis are the proportion for the total of diversity.

Table 2. Variation partitioning results (R^2) based on pRDA analyses for different elements of aquatic insect communities.

Community parameters	Environmental variable	Environment	Environment + space	Space	Not explained
Number of genera	Temperature	0.02	0.14	**0.10**	0.73
Community composition	Dissolved oxygen	0.00	0.07	**0.16**	0.77

Bold number represents $P < 0.05$ in pRDA.

The spatial filters selected for variance partitioning for the number of genera and community structure formed distinct sets. For genus numbers the best spatial arrangements were described by PCNM 3 and 9. Using the transformation of the axes into units of space (Guénard et al., 2010) the filters 3 and 9 represent spatial structures at distances of 92 and 36 km. For community composition the spatial filters were PCNM 2 and 3, with distances of 123 and 92 km respectively.

4. Discussion

The main sources for diversity of aquatic insects in Xingu River rapids were the differences among than inside communities in the rapids. At spatial scale comprising distances between rapids showing the greatest accumulation of EPT genera, and presenting the greatest difference between communities. The spatial effect (i.e., distances between sampling points) is an important factor for the structure of aquatic insect communities (Landeiro et al., 2012; Godoy et al., 2017, 2019, 2022a). In our study, the spatial filters were similar in both the number of genera and the community composition both acting at greater distances between rapids. Thus, we can understand that at smaller spatial distances the greater the similarity between communities, as seen in studies in other environments (Heino, 2009; Godoy et al., 2022a).

Increasing diversity at different spatial scales allows us to understand the contributions of alpha and beta diversity over a range of spatial scales. Environmental and spatial factors are also important for aquatic insect community structure. In our study, water temperature and dissolved oxygen were relevant drivers to community of aquatic insects in the rapids. This is very characteristic of tropical regions, where temperature is a conditioning factor for the concentration of dissolved oxygen in water, becoming limiting factors for the stability of aquatic organisms (Thorp et al., 2006). Variations in physicochemical water parameters lead to functional responses of aquatic insect genera, changing the structure of these communities (Monteiro et al., 2008; Godoy et al., 2018, 2019). In addition, spatial distances need to be taken into consideration because it makes it possible to understand how elements such as spatial autocorrelation and dispersal effects can influence the aquatic insect community in rivers and streams (Peltonen et al., 1998; Ligeiro et al., 2010; Ferreira et al., 2017; Godoy et al., 2017).

The main source of variation in aquatic insect diversity in Xingu River rapids was at the meso-regional scale, since the accumulation of genera is greater when observed among different rapids in the river. The distances for selected axis of PCNM (for number of genera and community composition) was related to variation between rapids and also to all abiotic variation inside the river. Such distances would represent variations on a regional scale, suggesting dependence on abrupt physical-chemical variation in the river. The possible explanatory factor for the greater accumulation of EPT genera at the spatial distance covering the rapids may be the different characteristics of each site, creating differential environmental filters. Thus, we can infer that there is an effect of spatial scale on the structure, richness and composition of aquatic insects in the Xingu River. It can be seen that there is a relationship between environment and space, making the environment spatially structured and thus, taking into account how environmental variability is defined in the sample space, becomes important to have a real notion of the relationship between communities and the environment (Godoy et al., 2017, 2019, 2022b). The distribution of aquatic insects is influenced by both overland dispersal (e.g., by flight) and aquatic dispersal (Landeiro et al., 2012). The structural patterns of communities of organisms that disperse by flight are clearer at larger spatial scales. Further studies are needed to observe whether the patterns found in this study are recurrent in communities where the main dispersal mode is passive by drift. In addition, the spatial scale at which the study was conducted has been identified as an important element in structuring aquatic insect communities.

The EPT orders need an environment with specific characteristics for their development, such as good oxygenation of the water and high current, so that the needs of these organisms are satisfied (Wallace & Webster, 1996; Baptista et al., 2001; Godoy et al., 2022b). The environments of rapids are highly utilized by some genera of Trichoptera, (i.e., S*micridea*), and Ephemeroptera (i.e., *Camelobaetidius* and *Baetodes*) that have many representatives of omnivores or fine detritivores feeding organisms, which can only be found in places of rapid flow and which capture suspended or accumulated particles (Cummins & Klug, 1979; Wallace & Webster, 1996; Cummins et al., 2005; Ceneviva-Bastos et al., 2017). This resource is optimally obtained in rapids, highlighting the importance of flow and current velocity, and demonstrating the significance of conserving as many rapids as possible, since they are the point where diversity accumulates. In terms of conservation, the management of this environment should cover as many rapids as possible, since the preservation of only a few rapids can mean a substantial loss of regional diversity.

The Xingu River basin is undergoing major changes in its landscape characteristics due to the construction of the Belo Monte hydroelectric complex (UHEBL), which is drastically changing the water dynamics and affecting the functionality and diversity of the aquatic ecosystem (Freire et al., 2019; Godoy et al., 2023). One of the main environments affected by the damming of the river for the construction of UHEBL are the rapids, since the river level in some reaches has been reduced, causing the rapids to disappear and consequently affecting what was once recognized as an environment rich in species diversity (Araujo et al., 2014; Fearnside, 2014; Freire et al., 2019). Moreover, it can be observed that some environmental characteristics such as turbidity, temperature, riparian forest, among others that directly influence the distribution of genera have presented changes over time (Freire et al., 2019). However, this hypothesis had to be tested in the future, because these additional features lead to the formation of microhabitats that will also influence the structure of the aquatic insect community present there. The river environment is extremely sensitive to environmental changes (either man-made or natural), but the knowledge of its diversity has a deficit of studies in large rivers in the Amazon region, especially related to the EPT fauna. This raises an alert, since there are few public policies aimed at prioritizing these areas for conservation (Suring, 2022).

Acknowledgements

We thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the scholarship of Barreiros NM and Giarrizo (308528/2022-0); to Norte Energia S.A. (PMI-2022) for the field support in the federal environmental assessment in UHE Belo Monte (02001.011114/2020-52); to Universidade Federal do Pará for the support in the production on manuscript (02/2023 – PAPQ/PROPESP); Santos W and Marques L for help in identifying the material.

References

Araujo, M.M.V., Pinto, K.J. & Mendes, F.O., 2014. A usina de Belo Monte e os impactos nas terras indígenas. Planeta Amzôn., 6, 43-51.

Balvanera, P., Lott, E., Segura, G., Siebe, C. & Islas, A., 2002. Patterns of β-diversity in a Mexican tropical dry forest. J. Veg. Sci., 13(2), 145-158. http://dx.doi.org/10.1111/j.1654-1103.2002.tb02034.x.

Baptista, D.F., Buss, D.F., Dorvillé, L.F.M. & Nessimian, J.L., 2001. Diversity and habitat preference of aquatic insects along the longitudinal gradient of the Macaé River basin, Rio de Janeiro, Brazil. Braz. J. Biol., 61(2), 249-258. PMid:11514892. http://dx.doi.org/10.1590/S0034-71082001000200007.

Baptista, V.A., Antunes, M.B., Martello, A.R., Figueiredo, N.S.B., Amaral, A.M.B., Secretti, E. & Braun, B., 2014. Influência de fatores ambientais na distribuição de famílias de insetos aquáticos em rios no sul do Brasil. Ambiente Soc., 17(3), 155-176. http://dx.doi.org/10.1590/S1414-753X2014000300010.

Barros, F.C., Almeida, S.M., Godoy, B.S., Silva, R.R., Silva, L.C., Moraes, K.F. & Santos, M.P.D., 2022. Taxonomic and functional diversity of bird communities in mining areas undergoing passive and active restoration in eastern Amazon. Ecol. Eng., 182, 106721. http://dx.doi.org/10.1016/j.ecoleng.2022.106721.

Barton, P.S., Cunningham, S.A., Manning, A.D., Gibb, H., Lindenmayer, D.B. & Didham, R.K., 2013. The spatial scaling of beta diversity. Glob. Ecol. Biogeogr., 22(6), 639-647. http://dx.doi.org/10.1111/geb.12031.

Bispo, P.C., Oliveira, L.G., Crisci, V.L. & Silva, M.M., 2001. A pluviosidade como fator de alteração da entomofauna bentônica (Ephemeroptera, Plecoptera e Trichoptera) em córregos do Planalto Central do Brasil. Acta Limnol. Bras., 2, 1-9.

Blanchet, F.G., Legendre, P. & Borcard, D., 2008. Forward selection of explanatory variables. Ecology, 89(9), 2623-2632. PMid:18831183. http://dx.doi.org/10.1890/07-0986.1.

Borcard, D. & Legendre, P., 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecol. Modell., 153(1-2), 51-68. http://dx.doi.org/10.1016/S0304-3800(01)00501-4.

Bridgewater, S., Ratter, J.A. & Ribeiro, J.F., 2004. Biogeographic patterns, diversity and dominance in the cerrado biome of Brazil. Biodivers. Conserv., 13(12), 2295-2317. http://dx.doi.org/10.1023/B:BIOC.0000047903.37608.4c.

Bueno, A.A.P., Bond-Buckup, G. & Ferreira, B.D.P., 2003. Estrutura da comunidade de invertebrados bentônicos em dois cursos d’água do Rio Grande do Sul, Brasil. Rev. Bras. Zool., 20(1), 115-125. http://dx.doi.org/10.1590/S0101-81752003000100014.

Ceneviva-Bastos, M., Prates, D.B., Romero, R.M., Bispo, P.C. & Casatti, L., 2017. Trophic guilds of EPT (Ephemeroptera, Plecoptera, and Trichoptera) in three basins of the Brazilian Savanna. Limnologica, 63, 11-17. http://dx.doi.org/10.1016/j.limno.2016.12.004.

Crisci-Bispo, V.L., Bispo, P.C. & Froehlich, C.G., 2007. Ephemeroptera, Plecoptera and Trichoptera assemblages in two Atlantic Rainforest streams, Southeastern Brazil. Rev. Bras. Zoo., 24(2), 312-318. http://dx.doi.org/10.1590/S0101-81752007000200007.

Cummins, K.W. & Klug, M.J., 1979. Feeding ecology of stream invertebrates. Annu. Rev. Ecol. Syst., 10(1), 147-172. http://dx.doi.org/10.1146/annurev.es.10.110179.001051.

Cummins, K.W., Merritt, R.W. & Andrade, P.C., 2005. The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in south Brazil. Stud. Neotrop. Fauna Environ., 40(1), 69-89. http://dx.doi.org/10.1080/01650520400025720.

Fearnside, P.M., 2014. Impacts of Brazil's Madeira River Dams: unlearned lessons for hydroelectric development in Amazonia. Environ. Sci. Policy, 38, 164-172. http://dx.doi.org/10.1016/j.envsci.2013.11.004.

Ferreira, W.R., Hepp, L.U., Ligeiro, R., Macedo, D.R., Hughes, R.M., Kaufmann, P.R. & Callisto, M., 2017. Partitioning taxonomic diversity of aquatic insect assemblages and functional feeding groups in neotropical savanna headwater streams. Ecol. Indic., 72, 365-373. http://dx.doi.org/10.1016/j.ecolind.2016.08.042.

Freire, L., Lima, J. & Silva, E., 2019. Belo Monte: fatos e impactos envolvidos na implantação da usina hidrelétrica na região Amazônica Paraense. Soc. Nat., 30(3), 18-41. http://dx.doi.org/10.14393/SN-v30n3-2018-2.

Frissell, C.A., Liss, W.J., Warren, C.E. & Hurley, M.D., 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environ. Manage., 10(2), 199-214. http://dx.doi.org/10.1007/BF01867358.

Fukami, T., Mordecai, E.A. & Ostling, A., 2016. A framework for priority effects. J. Veg. Sci., 27(4), 655-657. http://dx.doi.org/10.1111/jvs.12434.

Geho, E.M., Campbell, D. & Keddy, P.A., 2007. Quantifying ecological filters: the relative impact of herbivory, neighbours, and sediment on an oligohaline marsh. Oikos, 116(6), 1006-1016. http://dx.doi.org/10.1111/j.0030-1299.2007.15217.x.

Godoy, B.S., Camargos, L.M. & Lodi, S., 2018. When phylogeny and ecology meet: modeling the occurrence of Trichoptera with environmental and phylogenetic data. Ecol. Evol., 8(11), 5313-5322. PMid:29938055. http://dx.doi.org/10.1002/ece3.4031.

Godoy, B.S., Faria, A.P.J., Juen, L., Sara, L. & Oliveira, L.G., 2019. Taxonomic sufficiency and effects of environmental and spatial drivers on aquatic insect community. Ecol. Indic., 107, 105624. http://dx.doi.org/10.1016/j.ecolind.2019.105624.

Godoy, B.S., Ishihara, J.H., Aguiar, R.L. & Teixeira, O.N., 2023. 50 years of the water-flow variance in Tucuruí reservoir related with Brazilian energy consumption. Heliyon, 9(2), e12640. PMid:36761823. http://dx.doi.org/10.1016/j.heliyon.2022.e12640.

Godoy, B.S., Queiroz, L.L., Lodi, S. & Oliveira, L.G., 2017. Environment and spatial influences on aquatic insect communities in Cerrado streams: the relative importance of conductivity, altitude, and conservation areas. Neotrop. Entomol., 46(2), 151-158. PMid:27909952. http://dx.doi.org/10.1007/s13744-016-0452-4.

Godoy, B.S., Queiroz, L.L., Simião-Ferreira, J., Lodi, S., Camargos, L.M. & Oliveira, L.G., 2022a. The effect of spatial scale on the detection of environmental drivers on aquatic insect communities in pristine and altered streams of the Brazilian Cerrado. Int. J. Trop. Insect Sci., 42(3), 2173-2182. http://dx.doi.org/10.1007/s42690-022-00738-1.

Godoy, B.S., Simião-Ferreira, J., Lodi, S. & Oliveira, L.G., 2016. Functional process zones characterizing aquatic insect communities in streams of the Brazilian Cerrado. Neotrop. Entomol., 45(2), 159-169. PMid:26830433. http://dx.doi.org/10.1007/s13744-015-0352-z.

Godoy, B.S., Valente-Neto, F., Queiroz, L.L., Holanda, L.F.R., Roque, F.O., Lodi, S. & Oliveira, L.G., 2022b. Structuring functional groups of aquatic insects along the resistance/resilience axis when facing water flow changes. Ecol. Evol., 12(3), e8749. PMid:35356588. http://dx.doi.org/10.1002/ece3.8749.

Guénard, G., Legendre, P., Boisclair, D. & Bilodeau, M., 2010. Multiscale codependence analysis: an integrated approach to analyze relationships across scales. Ecology, 91(10), 2952-2964. PMid:21058555. http://dx.doi.org/10.1890/09-0460.1.

Hamada, N., Nessimian, J. & Querino, R., 2019. Insetos aquáticos na Amazônia brasileira: taxonomia, biologia e ecologia. Manaus: Editora INPA.

Hamer, K.C. & Hill, J.K., 2000. Scale-dependent effects of habitat disturbance on species richness in tropical forests. Conserv. Biol., 14(5), 1435-1440. http://dx.doi.org/10.1046/j.1523-1739.2000.99417.x.

Hastings, A., Petrovskii, S. & Morozov, A., 2011. Spatial ecology across scales. Biol. Lett., 7(2), 163-165. PMid:21068027. http://dx.doi.org/10.1098/rsbl.2010.0948.

Heino, J., 2009. Biodiversity of aquatic insects: spatial gradients and environmental correlates of assemblage-level measures at large scales. Freshw. Rev., 2(1), 1-29. http://dx.doi.org/10.1608/FRJ-2.1.1.

Heino, J., Melo, A.S. & Bini, L.M., 2015. Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. Freshw. Biol., 60(2), 223-235. http://dx.doi.org/10.1111/fwb.12502.

Hepp, L.U. & Melo, A.S., 2013. Dissimilarity of stream insect assemblages: effects of multiple scales and spatial distances. Hydrobiologia, 703(1), 239-246. http://dx.doi.org/10.1007/s10750-012-1367-7.

Jackson, D.A. & Harvey, H.H., 1989. Biogeographic associations in fish assemblages: local vs. regional processes. Ecology, 70(5), 1472-1484. http://dx.doi.org/10.2307/1938206.

Landeiro, V.L., Bini, L.M., Melo, A.S., Pes, A.M.O. & Magnusson, W.E., 2012. The roles of dispersal limitation and environmental conditions in controlling caddisfly (Trichoptera) assemblages. Freshw. Biol., 57(8), 1554-1564. http://dx.doi.org/10.1111/j.1365-2427.2012.02816.x.

Leal, T.B., Oliveira, R.S., Giarrizzo, T. & Godoy, B.S., 2023. The drift effect on nestedness of Ephemeroptera, Trichoptera and Plecoptera orders in the Xingu River. Biota Neotrop., 23(1), e20221354. http://dx.doi.org/10.1590/1676-0611-bn-2022-1354.

Legendre, P. & Legendre, L.F.J., 2012. Numerical ecology (3rd ed.). Amsterdam: Elsevier.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett., 7(7), 601-613. http://dx.doi.org/10.1111/j.1461-0248.2004.00608.x.

Ligeiro, R., Melo, A.S. & Callisto, M., 2010. Spatial scale and the diversity of macroinvertebrates in a Neotropical catchment. Freshw. Biol., 55(2), 424-435. http://dx.doi.org/10.1111/j.1365-2427.2009.02291.x.

Merritt, R.W., Cummins, K.W. & Berg, M.B., 2008. An introduction to the aquatic insects of North America (4th ed.). Dubuque: Kendall/Hunt Publishing Company.

Monteiro, T.R., Oliveira, L.G. & Godoy, B.S., 2008. Biomonitoramento da qualidade de água utilizando macroinvertebrados bentônicos: adaptação do índice biótico BMWP' à bacia do rio Meia Ponte - GO. Oecol. Aust., 12(3), 553-563. http://dx.doi.org/10.4257/oeco.2008.1203.13.

Moraga, A.D., Martin, A.E. & Fahrig, L., 2019. The scale of effect of landscape context varies with the species' response variable measured. Landsc. Ecol., 34(4), 703-715. http://dx.doi.org/10.1007/s10980-019-00808-9.

Mykrä, H., Heino, J. & Muotka, T., 2007. Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. Glob. Ecol. Biogeogr., 16(2), 149-159. http://dx.doi.org/10.1111/j.1466-8238.2006.00272.x.

Norte-Energia, 2016. UHE Belo Monte [online]. Retrieved in 2023, August 11, from https://www.norteenergiasa.com.br/pt-br/uhe-belo-monte/vazoes-e-niveis-do-rio-xingu-100755

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H. H., & Wagner, H., 2012. Community ecology package. R Package Version [online]. Retrieved in 2023, September 06, from http://vegan.r-forge.r-project.org.

Patrick, C.J. & Yuan, L.L., 2019. The challenges that spatial context present for synthesizing community ecology across scales. Oikos, 128(3), 297-308. PMid:32467652. http://dx.doi.org/10.1111/oik.05802.

Peltonen, M., Heliövaara, K., Väisänen, R. & Keronen, J., 1998. Bark beetle diversity at different spatial scales. Ecography (Online), 21(5), 510-517. Retrieved in 2023, August 11, from http://www.jstor.org/stable/3682887

R Development Core Team, 2020. R: a language and environment for statistical computing [online]. Retrieved in 2023, August 11, from https://www.r-project.org/

Ricklefs, R.E., 1987. Community diverstiy: relative roles of local and regional processes. Science, 235(4785), 167-171. PMid:17778629. http://dx.doi.org/10.1126/science.235.4785.167.

Ricklefs, R.E., 2006. Evolutionary diversification and the origin of the diversity-environment relationship. Ecology, 87(Suppl. 7), S3-S13. PMid:16922298. http://dx.doi.org/10.1890/0012-9658(2006)87[3:EDATOO]2.0.CO;2.

Rosenberg, D. & Resh, V.H., 1993. Freshwater biomonitoring and benthic macroinvertebrates. New York: Chapman & Hall.

Salomão, R.P., Vieira, I.C.G., Suemitsu, C., Rosa, N.A., Almeida, S.S., Amaral, D.D. & Menezes, M.P.M., 2007. As florestas de Belo Monte na grande curva do rio Xingu, Amazônia Oriental. Bol. Mus. Para. Emílio Goeldi. Ciênc. Nat., 2(3), 57-153.

Sepkoski Junior, J.J., 1988. Alpha, beta, or gamma: where does all the diversity go? Paleobiology, 14(3), 221-234. PMid:11542147. http://dx.doi.org/10.1017/S0094837300011969.

Serviço Geológico do Brasil – CPRM, 2023. Bacia do Rio Xingu – características [online]. Retrieved in 2023, August 11, from https://www.cprm.gov.br/sace/xingu_caracteristicas.php.

Sheffield, J., Goteti, G. & Wood, E.F., 2006. Development of a 50-year high-resolution global dataset of meteorological forcings for land surface modeling. J. Clim., 19(13), 3088-3111. http://dx.doi.org/10.1175/JCLI3790.1.

Sioli, H. 1968. Hydrochemistry and Geology in the Brazilian Amazon Region. Amazoniana, 1(3), 267-277.

Suring, L.H., 2022. Imperiled freshwater ecosystems: an overview. In DellaSala, D.A. & Goldstein, M.I., eds. Imperiled: the encyclopedia of conservation. Amsterdam: Elsevier, 345-350. http://dx.doi.org/10.1016/B978-0-12-821139-7.00221-X.

Thorp, J.H., Thoms, M.C. & Delong, M.D., 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. River Res. Appl., 22(2), 123-147. http://dx.doi.org/10.1002/rra.901.

Veech, J.A. & Crist, T.O., 2007. Habitat and climate heterogeneity maintain beta-diversity of birds among landscapes within ecoregions. Glob. Ecol. Biogeogr., 16(5), 650-656. http://dx.doi.org/10.1111/j.1466-8238.2007.00315.x.

Veech, J.A., 2005. Analyzing patterns of species diversity as departures from random expectations. Oikos, 108(1), 149-155. http://dx.doi.org/10.1111/j.0030-1299.2005.13506.x.

Veech, J.A., Summerville, K.S., Crist, T.O. & Gering, J.C., 2002. The additive partitioning of species diversity: recent revival of an old idea. Oikos, 99(1), 3-9. http://dx.doi.org/10.1034/j.1600-0706.2002.990101.x.

Vellend, M., 2010. Conceptual synthesis in community ecology. Q. Rev. Biol., 85(2), 183-206. PMid:20565040. http://dx.doi.org/10.1086/652373.

Wallace, J.B. & Webster, J.R., 1996. The role of macroinvertebrates in stream ecosystem function. Annu. Rev. Entomol., 41(1), 115-139. PMid:15012327. http://dx.doi.org/10.1146/annurev.en.41.010196.000555.

Whittaker, R., 1960. Vegetation of the Siskiyou mountains, Oregon and California. Ecol. Monogr., 30(3), 279-338. http://dx.doi.org/10.2307/1943563.

Received: 06 April 2023
Accepted: 11 August 2023

Associate Editor: Victor Satoru Saito.