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Beta diversity of aquatic insects (Ephemeroptera, Plecoptera and Trichoptera) across stream microhabitats

Diversidade beta de insetos aquáticos (Ephemeroptera, Plecoptera e Trichoptera) em microhabitats de riachos

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Abstract: Aim: We evaluated how the combination of environmental characteristics affects the beta diversity of the EPT (Ephemeroptera, Plecoptera and Trichoptera) community across stream microhabitats. **Methods:** The samples were collected in 12 streams around the Itaipu Reservoir (Paraná, Brazil). We sampled four types of substrates in triplicate with the aid of a Surber sampler. The samples were classified into CSD (sand and clay) and STO (gravel, pebbles, and boulders). The composite substrate of leaf packs (leaves and twigs) was divided into RLP (rapid leaf packs) and BLP (backwater leaf packs). **Results:** We recorded a significant change in EPT composition among the microhabitats evaluated and different genera associated with each substrate category. However, beta diversity did not significantly differ among microhabitats. Thus, we found the highest beta diversity value in the CSD (sand and clay) category and the greatest contribution of the turnover component. **Conclusions:** The partitioning of beta diversity into its components helped understand ecological patterns at local scales, highlighting the importance of microhabitat diversity in stream systems for maintaining the structure and composition of aquatic fauna.

Keywords: small scales; turnover; nestedness; aquatic insects; streams.

Resumo: Objetivo: Nós avaliamos como a combinação de características ambientais afeta a diversidade beta da comunidade EPT (Ephemeroptera, Plecoptera e Trichoptera) em microhabitats de riachos. **Métodos:** As amostras foram coletadas em 12 riachos ao redor do Reservatório de Itaipu

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(Paraná, Brasil). Amostramos quatro tipos de substratos em tréplica com o auxílio de um amostrador *Surber*. As amostras foram classificadas em CSD (areia e argila) e STO (cascalho, seixos e pedregulhos). O substrato composto de pacote de folhas (folhas e galhos) foi dividido em RLP (pacote de folhas de corredeira) e BLP (pacote de folhas de remanso). **Resultados:** Registramos uma mudança significativa na composição de EPT entre os microhabitats avaliados e diferentes gêneros associados a cada categoria de substrato. No entanto, a diversidade beta não diferiu significativamente entre os microhabitats. Assim, encontramos o maior valor de diversidade beta na categoria CSD (areia e argila) e a maior contribuição do componente de substituição. **Conclusões:** A partição da diversidade beta em seus componentes auxiliou na compreensão de padrões ecológicos em escalas locais, destacando a importância da diversidade de microhabitats em sistemas de riachos, para manutenção da estrutura e composição da fauna aquática.

Palavras-chave: pequenas escalas; substituição; aninhamento; insetos aquáticos; riachos.

1. Introduction

Ecological communities are controlled by many factors acting at multiple scales, both temporal and spatial (Fornaroli et al., 2020). The dependence of environmental variables at multiple spatial scales results in complex dynamics between biota and their environment (Zhou et al., 2020). Physical and biological variables at small scales are typically influenced by variables at larger scales. In streams, more specifically, aquatic communities can be seen as a product of a series of filters, from broad to fine scales (e.g., continental, regional, basin, stream, and habitat), through which individuals that persist have had to pass (Johnson et al., 2004).

In streams, the interaction of physical environmental conditions and substrate characteristics (Allan & Castillo, 2007; Leal et al., 2023) promotes different mesohabitats including "slow flow" as in backwater areas or "fast flow" as in rapid areas (Principe et al., 2007). At a smaller scale, a variety of microhabitats can be identified, ranging from fine sediment (more unstable for organisms) to rocks (more complex and stable, providing more diverse and abundant fauna) and organic material (important resources for benthic organisms) (Costa & Melo, 2008; Tokeshi & Arakaki, 2012).

The beta diversity (β), which represents the variation in species composition between sites in the same region of interest, is associated with the way species respond to environmental heterogeneity (Whittaker, 1960; Heino, 2009), including stream microhabitats (Bae et al., 2023; Su et al., 2025). The beta diversity index can further be partitioned into two components: turnover and nestedness. Turnover means the species exchange along the gradient, which may be related to natural and historical factors or caused by anthropogenic influences (Baselga, 2010). Nestedness refers to the local loss of species and may be related to factors that promote the orderly disaggregation of communities, such as habitat degradation or spatial isolation (Calderón-Patrón et al., 2012).

Ephemeroptera, Plecoptera and Trichoptera (EPT) are three orders of insects highlighted among aquatic macroinvertebrates, and they are considered sufficiently representative models of ecological patterns occurring throughout the community (Beauchard et al., 2003; Sivaruban et al., 2020). This representativeness is especially due to the responses of these three orders to environmental disturbances, highlighting the importance of local conditions (e.g., vegetation cover, slope, environmental heterogeneity, frequency of disturbances) in the structuring of communities (Bispo & Oliveira, 1998; Bonada et al., 2006; Bispo & Oliveira, 2007). For these reasons, EPTs were selected as model organisms in our study.

We investigated how the combination of local environmental conditions affects the beta diversity of the EPT community across stream microhabitats. To elucidate this question, we elaborated three main hypotheses: (i) more heterogeneous habitats, composed of leaves, trunks, branches and rocks of different textures, may favor EPT turnover, due to the greater availability of resources, possibilities of exploration and refuge for aquatic fauna; (ii) on the other hand, nestedness possibly stands out in more homogeneous/simplified habitats, where the fauna is more exposed and subject to dragging; (iii) the specific characteristics of the EPT genera result in a different composition of taxa for each microhabitat evaluated, resulting in a significant variation in beta diversity for each stream microhabitat.

2. Materials and Methods

2.1. Study area

Samplings were carried out in November 2021 in 12 streams of 2^{nd} and 3^{rd} order, inserted in the Hydrographic Basin of Paraná 3, around the Itaipu

Reservoir – transboundary region (Brazil/Paraguay) (Figure 1).

The Hydrographic Basin of Paraná 3 is located in the western mesoregion of Paraná State, covering an area of more than 8,000 km² and reaching 28 municipalities (IAP, 2010). This region is included in the Atlantic Forest complex, which can be further divided into 15 ecoregions. Our study area comprises the Upper Paraná Forests Ecoregion, where semideciduous seasonal forest predominates, a phytogeographic unit characterized by double climatic seasonality (Di Bitetti et al., 2003; Rocha & Bade, 2018). The topography of the region features relatively flat areas near the Paraná River and other main rivers, with altitudes ranging between 150 and 250 m, and higher altitudes between 550 and 800 m above sea level. The soil of the region is generally deep and reddish near the main rivers, becoming shallower and stonier at higher altitudes (Ligier, 2000). The climate is subtropical, with

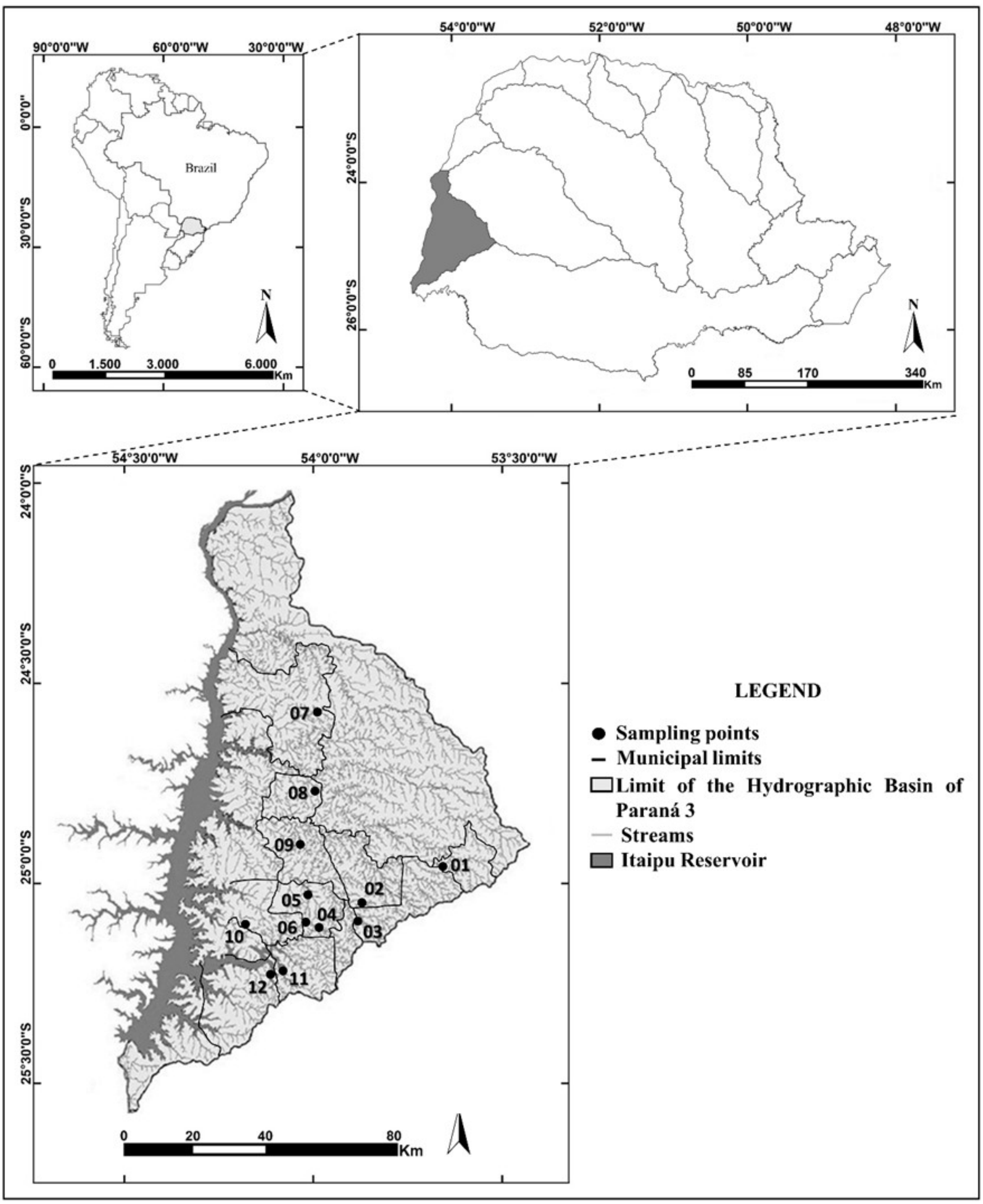

Figure 1. Location of sampling points, inserted in the Hydrographic Basin of Paraná 3 (Datum, SIRGAS - 2000; UTM 22. Cartographic base: IBGE (2019). Prepared by the author).

average temperature ranging from >22 °C in the hottest month to <18 °C in the coldest months. Rainfall is not uniform, with precipitation ranging between 1,600 and 1,800 mm per year, occurring in lesser volumes in the northern part of the ecoregion (Rocha & Bade, 2018).

2.2. Sampling design

All sampled microbasins (belonging to the Hydrographic Basin of Paraná 3) are distributed across 10 municipalities in the western region of Paraná (southern Brazil). The minimum distance between the microbasins was 3.84 km and the maximum distance was 66.61 km, and they are located in landscape areas with different levels of integrity. This is because this region experiences intense agricultural activities, primarily based on no-tillage systems with a predominance of soybean, corn, and wheat crops, along with some pasture areas (Klanovicz & Mores, 2017; Ouchi-Melo et al., 2021). Additionally, the region hosts large livestock farms (poultry, pig, and fish farms), positioning the west of the state of Paraná as the largest producer of animal protein in Brazil (AEN, 2022).

2.3. Data sampling

The samples were classified and grouped according to their granulometry (Santos et al., 2020), in contained sediments (sand and clay, < 5 mm; Figure 2a and 2b), designated as CSD, and stone (gravel, pebbles, and boulders, 25-50 mm and > 50 mm; Figure 2c and 2d), designated as STO. The composite substrate of leaf packs was divided into two types: rapid leaf packs, termed RLP (organic material from fast flow zones; Figure 2e), and backwater leaf packs, termed BLP (organic material from slow flow zones; Figure 2f). The classification of microhabitats composed of different substrates increased our possibilities of capturing a more abundant and diverse fauna (Allan & Castillo, 2007). Thus, four categories of microhabitats were obtained, with three replicates each, providing a total of 12 samples per stream and 144 samples in total.

Macroinvertebrates were collected with a 27x27 cm Surber sampler (therefore, 0.22 m^2 per stream, per microhabitat in each stream) with a 500 µm mesh in a stretch of approximately 50 m. We adopted a minimum distance of five meters between each replicate to be sampled, alternating the type of microhabitat to be sampled each time. Subsequently, the samples were transferred to plastic bags, properly identified, and fixed in 10% formaldehyde.

2.4. Laboratory procedures

Each sample was washed in running water to remove formaldehyde, which was separated for proper disposal. With the aid of sieves with a mesh size of 500 µm, larger substrates, such as stones, leaves and twigs, were separated. The cleaned samples were then transferred to polyethylene jars

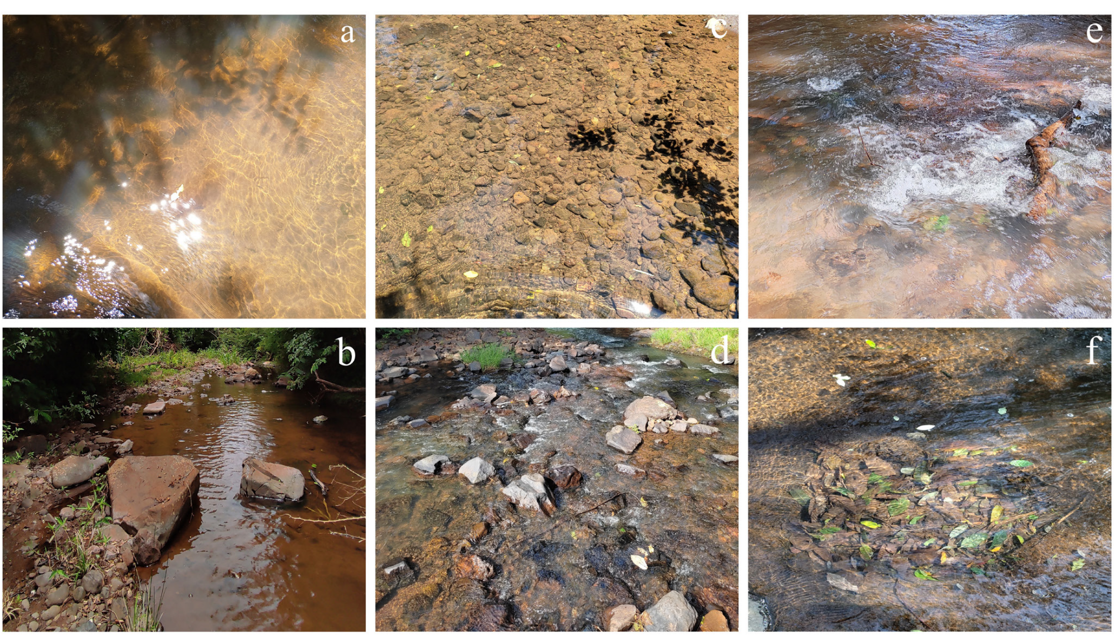

Figure 2. Representation of sampled microhabitat categories **(a-b)** CSD: sand and clay, **(c-d)** STO: gravel, pebbles and boulders, **(e)** RLP: rapids leaf packs and **(f)** BLP: backwater leaf packs.

and stored in 70% alcohol. Subsequently, these samples were sequentially sorted on a tray, and the macroinvertebrates were transferred to properly labeled polyethylene bottles, also stored in 70% alcohol. Organisms were identified at the genus level with the aid of a stereoscopic microscope and identification manuals (Olifiers et al., 2004; Salles et al., 2004; Pes et al., 2005; Gutiérrez & Dias, 2015; Hamada et al., 2018).

2.5. Statistical analyses

We tested the distribution of EPT genera among the four types of microhabitats evaluated (CSD, STO, RLP, and BLP) by permutational variance analysis (PERMANOVA), following Anderson (2001). PERMANOVA was performed based on the transformed data of the observed abundance (Hellinger method) of EPT genera ("*adonis2*" function from *vegan* package; Oksanen et al., 2022). PERMANOVA was followed by a Bonferroni *post-hoc* test to compare the means among the microhabitats evaluated and determine differences between pairs of combinations (Armstrong, 2014). Subsequently, we conducted an analysis of indicator species through the indicator value index (IndVal), following Dufrêne & Legendre (1997). To perform IndVal, we used the package indicspecies ("*multipatt*" function) (Cáceres & Legendre, 2009).

We performed a permutational dispersion analysis (PERMDISP) in combination with a Principal Coordinate Analysis (PCoA) to assess whether the beta diversity of each microhabitat varied significantly. This analysis provided mean distances of the sample points in relation to the centroid of each microhabitat in a multivariate space of principal coordinates (Anderson et al., 2006), as evidenced by PCoA and tested by analysis of variance (ANOVA). For this, the *vegan* package was employed ("*vegdist*" and "*betadisper*" functions).

Beta diversity values were calculated for the set of all sampled microhabitats and subsequently for each category so that we would have a broader comparison reference. Beta diversity was estimated from the observed abundance matrix of recorded EPT genera, and this taxon matrix was transformed using the Hellinger method ("*deconstand*" function) (Legendre & Cáceres, 2013). Then, to calculate the total beta diversity (BDtotal) and partition the turnover and nestedness components, the *adespatial* package ("*beta.div.comp*" function) (Dray et al., 2024) was employed and the Bray-Curtis dissimilarity index was used to perform such analyses. Beta diversity was calculated and partitioned into its components to assess which microhabitats contributed most to beta diversity, and where the replacement and nestedness components stood out most.

3. Results

We collected a total of 9427 individuals of EPT, representing 15 families and 38 genera. Ephemeroptera presented the highest number of genera with 20 records, followed by the order Trichoptera with 16 genera and the order Plecoptera with 2 genera (Online Resource 1).

Permutational variance analysis (PERMANOVA) revealed a significant effect on the change in genera composition among the four categories of microhabitats evaluated ($F_{(3,44)}$=5.861; P=0.001), with a difference between all pairs of categories evaluated according to the Bonferroni *post-hoc* test. Therefore, through the indicator value index (IndVal), we performed the analysis of indicator species (Figure 3). In the CSD category, the associated genus was *Apobaetis* (IndVal=0.645; P=0.015), in STO the genus *Camelobaetidius* (IndVal=0.697; P=0.005), in RLP the genus *Anacroneuria* (IndVal=0.782; P=0.005) and *Chimarra* (IndVal=0.769; P=0.005), and in BLP the associated genus was *Phylloicus* (IndVal=0.910; P=0.005), *Ulmeritoides* (IndVal=0.844; P=0.005) and *Triplectides* (IndVal=0.770; P=0.005).

On the other hand, permutational dispersion analysis (PERMDISP) revealed no significant difference in dispersion among the four categories of microhabitats ($F_{(3,44)}$=2.726; P=0.055; Figure 4). In summary, beta diversity did not significantly vary among microhabitats in the macroinvertebrate community.

For the set of all microhabitats (ALL), the beta diversity (BD) value was 0.23. When evaluated individually for each microhabitat, the BD values ranged from 0.23 to 0.35. The turnover component contributed the most to BD, both for the set of microhabitats and for the CSD, STO, RLP, and BLP categories. The CSD category presented the highest BD value at 0.35 and contributed the most to the turnover component, at 0.33. In contrast, RLP presented the lowest BD value (0.22), and was where nestedness stood out the most (0.05) (Figure 5).

4. Discussion

The quality and integrity of microhabitats in streams are crucial elements for the structuring of aquatic insects that compose them (Macedo et al.,

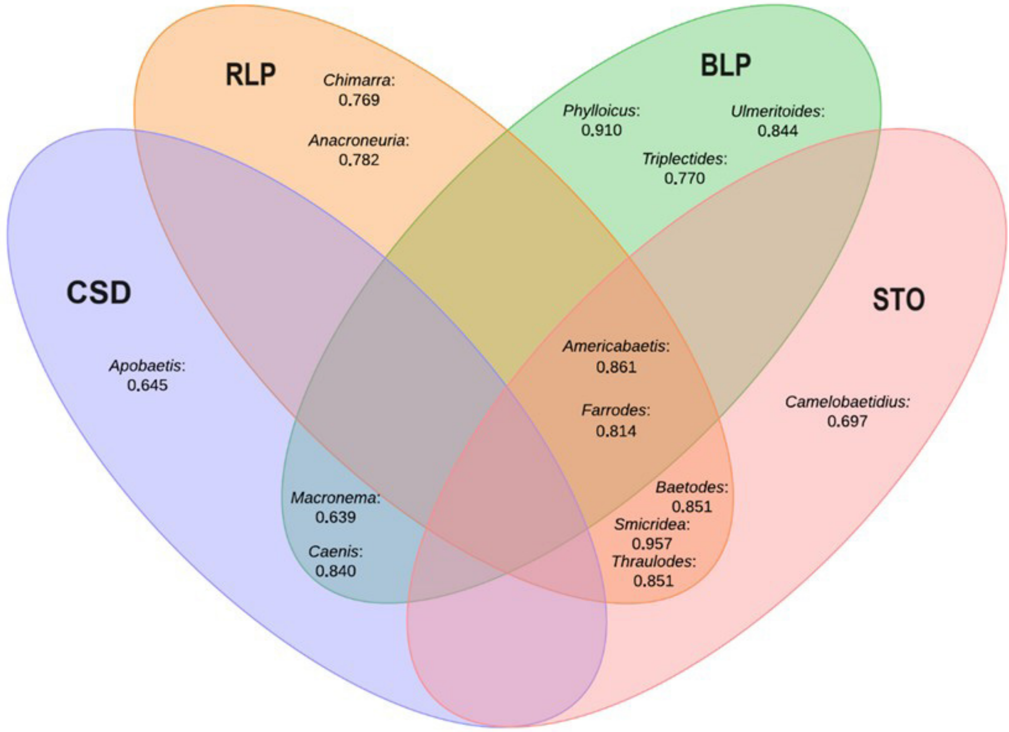

Figure 3. Venn diagram on the association of genera of EPT (Ephemeroptera, Plecoptera, and Trichoptera) with the four categories of microhabitats (CSD: sand and clay; STO: gravel, pebbles and boulders; RLP: rapids leaf packs and BLP: backwater leaf packs), and other combinations.

2019). The different substrates that integrate the physical structure of the streams create a structurally diverse habitat, with greater niche possibilities for the EPT (Yaagoubi et al., 2024). The significant difference in genera composition between the four categories of microhabitats evaluated here reflected this difference. The wide variety of functional groups, morphological characteristics and adaptations found in EPT are relevant to the occurrence of these organisms in different microhabitats (Schmitt et al., 2020).

In addition, the analysis of indicator species revealed some genera associated with specific microhabitats, reinforcing the informative aspect of these taxa regarding the structure, function, and composition of the habitat and its community, making them good indicators (Paripatyadar et al., 2020). In the CSD, the analysis pointed to the genus *Apobaetis* (Ephemeroptera), which is characteristic of sandy substrates and is tolerant to poor water quality (Domínguez et al., 2006). For STO, in our study, the genus *Camelobaetidius* was indicated as an indicator taxon, as also reported by Domínguez et al. (2006) - although the authors highlight that *Camelobaetidius* species can be found in many different habitats.

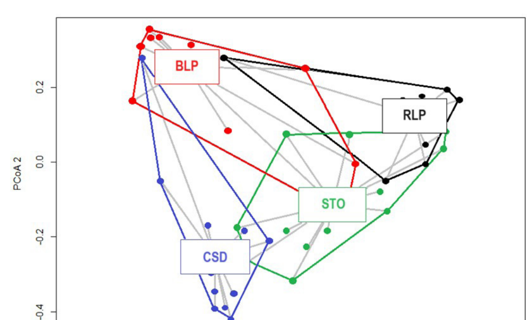

Figure 4. Principal Coordinates Analysis (PCoA) for abundance data of EPT genera (Ephemeroptera, Plecoptera, and Trichoptera) in the four categories of microhabitats (CSD: sand and clay; STO: gravel, pebbles and boulders; RLP: rapids leaf packs and BLP: backwater leaf packs).

In the RLP microhabitat, the analysis of indicator species indicated two genera, *Anacroneuria* (Plecoptera) and *Chimarra* (Trichoptera). *Anacroneuria* is a genus associated with fast-flowing sites as a result of specific adaptations to this microhabitat, such as a strong and flattened body structure (Vázquez et al., 2020), and its occurrence

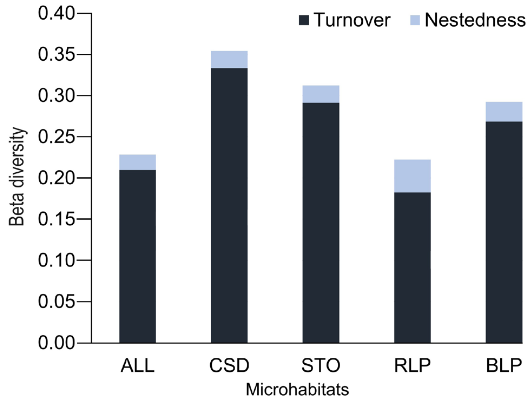

Figure 5. Beta diversity of EPT genera (Ephemeroptera, Plecoptera, and Trichoptera), estimated for the set of microhabitats sampled (ALL) and for the four categories of microhabitats (CSD: sand and clay; STO: gravel, pebbles and boulders; RLP: rapids leaf packs and BLP: backwater leaf packs), with contributions from turnover and nestedness components.

in the RLP was also recorded by Baptista et al. (2001). On the other hand, the genus *Chimarra* is common in small streams and flowing rivers (Almeida et al., 2021).

The BLP microhabitat has been associated with three genera: *Phylloicus* (Trichoptera), *Ulmeritoides* (Ephemeroptera), and *Triplectides* (Trichoptera). The genus *Phylloicus*, which uses leaf fragments found in backwater areas to build shelters, also plays an important role in the fragmentation of organic matter (Wallace & Webster, 1996). In relation to the genus *Ulmeritoides*, it seems to have a preference for calmer waters, for adaptations in its gills that allow more efficient absorption of oxygen, in addition to the occurrence recorded in leaf packs (Domínguez et al., 2006; Shimano & Juen, 2016). Finally, *Triplectides* are characteristic of leaf packs, making use of this sediment mainly for shelter construction (Fidelis et al., 2008).

Despite the distinct composition of genera among microhabitat categories and the associations of some of these genera with each category, aquatic insects beta diversity measured in terms of variability was similar among microhabitats. As noted by Liu et al. (2022), this result demonstrates spatial dynamics that may be strongly influenced by deterministic (environmental filtering by local factors) and stochastic (events related to dispersal) processes in the community. Faced with more abundant genera, for example, stochastic processes may acquire greater relevance in the formation of beta diversity. This is because greater abundance also increases the probability of dispersion and consequent distribution of these organisms in varied habitats (Liu et al., 2015). This can be illustrated in our study by the high abundance of the genera *Caenis*, *Traverhyphes* (Ephemeroptera) and *Smicridea* (Trichoptera), present in all habitat categories evaluated. Especially in insects, which are organisms with a complex life history (they undergo metamorphosis), dispersal can have a strong influence on the processes that regulate the community (Ge et al., 2023).

The dispersion of EPT larvae occurs through the transport of suspended organisms in the water column in a phenomenon known as drift (Brittain & Eikeland, 1988). Drift strongly influences the structure and composition of invertebrate communities and can occur voluntarily or involuntarily. This movement is voluntary when it is associated with the natural behavior of individuals and involuntary when it is the result of factors such as rains, floods and other physicochemical disorders (Gimenez et al., 2015). Drift can favor the arrival and occupation of individuals in different microhabitats (Callisto et al., 2005), which aligns with our findings. Furthermore, it is known that this occupation also depends on favorable conditions such as the availability of food and refuge for individuals, which is associated with their way of life (Szałkiewicz et al., 2022). In our study, this can be translated by the record of EPT genera that presented exclusive occurrence for specific microhabitat categories (e.g., *Austrotinodes* in CSD, *Needhamela* in STO, *Hylister* in RLP and *Cryptonympha* in BLP) or even for those that presented occurrence for some category in a more expressive way than another (e.g., *Ulmeritoides*), which may represent that some taxa can reach certain habitats, but have a greater occupation success in others.

The evaluation of total beta diversity (BD) for the four categories of microhabitats (CSD, STO, RLP, and BLP) revealed the highest value of beta diversity in the CSD category. Species filtering caused by predominant environmental characteristics may be related to substitution under different environmental conditions (Nunes et al., 2016). CSD (contained sediment: sand and clay) represents a microhabitat with limited resources and refuge availability, where the fauna is more susceptible to drag (Castro et al., 2013), which likely favors the turnover component.

On the other hand, the RLP category exhibited the lowest beta diversity value and the greatest contribution of the nestedness component. In contrast to CSD, organisms inhabiting the RLP have access to a wider range of food resources and shelter from potential predators (Osório et al., 2019). Conversely, the faunal characteristics of rapid leaf packs are more susceptible to rigid conditions and need to be adapted to this kind of microhabitat to thrive. Nestedness in RLP may be favored by organisms that can tolerate these conditions (Chase & Myers, 2011).

In addition, although the characterization of the integrity of the sampled points was not the focus of our study, all the points were inserted in a modified gradient, mainly due to land use activities. Different land uses and occupation activities affect riparian vegetation structure, flow regimes, nutrient loading, sediment transport in riverbeds, and habitat quality (Macedo et al., 2014). All these characteristics associated with the identity of the basin where the sampling points are inserted can affect the distribution and structuring of EPT communities (Heino et al., 2017).

In conclusion, the evaluation of EPT genera in each microhabitat supported our hypothesis that these organisms have unique characteristics that result in a different taxon composition for each microhabitat. However, contrary to what we expected, this did not represent a significant variation in beta diversity for each microhabitat evaluated. This demonstrates that microhabitats did not significantly influence the beta diversity of the EPT community, according to the categories evaluated by us. In addition, the EPT fauna also behaved differently than we expected in relation to the use and occupation of microhabitats, contradicting our first and second hypotheses. This highlights the importance of analyses at the microhabitat scale in elucidating diversity patterns, but also highlights the need to consider other variables in the study of beta diversity. Our study offers valuable insights for the management of aquatic ecosystems and their associated biota, highlighting the importance of preserving local conditions at small scales, within streams.

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Data availability

All research data analyzed in the research is available in ALB's Dataverse on SciELO Data. Access is free. It can be accessed in https://data.scielo.org/dataset.xhtml?persistentId=doi:10.48331/scielodata.O8EC4O.

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