Unveiling patterns of taxonomic and functional diversities of stream insects across four spatial scales in the neotropical savanna

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ARTICLE INFO

ABSTRACT

The drivers of dissimilarity in biological communities among habitats and the mechanisms that modulate the distribution of functional diversity in streams are still important gaps in ecological knowledge. This study was designed to assess how the taxonomic and functional composition of Cerrado stream insect assemblages are distributed among multiple spatial scales (i.e., habitat, stream sites and hydrological units). To do so we used a hierarchical series of four diversity components: stream transect (α), among transects (β_1), among stream sites (β_2), and among hydrological units (β_3). Our aim was to identify the spatial scales at which variation in aquatic insect assemblage structure was greatest and whether turnover or nestedness mainly explain the patterns of β-diversity. We found that β-diversity among streams (β_2) is highest and contributes most to total richness (γ-diversity) of aquatic insects in Cerrado streams as opposed to dissimilarities among habitats or among hydrological units. Moreover, β-diversity among transects had the lowest contribution to total insect richness (γ-diversity). The turnover component of taxonomic β-diversity was high for all spatial scales, but highest at stream scale. Conversely, for functional β-diversity, nestedness was the main component at stream scale. Understanding how biodiversity changes from local to regional scales is a first step towards understanding the variation in species and trait composition across space. Our results emphasize the importance of conserving Cerrado headwater streams because each stream harbors different taxa and human disturbance of any stream will result in loss of diversity and ecosystem functions.

1. Introduction

A key research topic in ecology is to understand what drives changes in species and trait composition over different time spans and spatial scales (Devictor et al., 2010; Heino et al., 2015a; Villéger et al., 2013). It is widely known that biodiversity variation comes from several kinds of filters (e.g., historical, stochastic, and environmental) (HilleRisLambers et al., 2012). Moreover, ecosystems exhibit heterogeneity in environmental conditions that influence biological communities at multiple spatial scales, ranging from microhabitats to local landscapes and ecoregions (Herlihy et al., 2020; Mykrä et al., 2007). Patterns of biodiversity and compositional variation among communities can be generated by different factors and processes operating at multiple spatial scales (Peláez and Pavanelli, 2019). Environmental variables that shape communities may differ in their range of variation among spatial scales (Borcard et al., 2004). Some variables show large variation at small spatial scales (e.g., substrate types, flow), generating high community dissimilarity in relatively small areas. On the other hand, variables that show variation only at large spatial scales (e.g., land cover, basin slope) will generate community dissimilarity only across large study areas (Declerck et al., 2011). Therefore, to understand the patterns structuring biodiversity, we need to unveil environmental drivers across different spatial scales (Barton et al., 2013; Heino et al., 2007).

Aquatic ecosystems are no exception, in which environmental factors operate at multiple spatial scales, starting from microhabitats (e.g., types of organic and inorganic bottom substrates), to habitat types (e.g., riffles and pools), to stream segments, to hydrological units and catchments, affecting the structure and composition of biological communities (Heino et al., 2004; Leps et al., 2015; Townsend et al.,

2003). Understanding the role of different scales in determining stream invertebrate biodiversity is especially relevant in tropical headwater streams (Ligeiro et al., 2010; Tonkin et al., 2016). These systems are among the most diverse on Earth, present high variation in species composition and are threatened by multiple anthropogenic activities (Callisto et al., 2019; Strayer and Dudgeon, 2010; Sundar et al., 2020).

For spatially nested datasets, species diversity can be decomposed into three components: local species richness (α-diversity), total regional richness (γ-diversity) and the variation in species composition among sites or sampling units within a given area (β-diversity) (Whittaker, 1960). Partitioning of biological diversity along spatial scales and disturbance gradients has been the focus of several studies on aquatic ecosystems (e.g., Ferreira et al., 2017; Hepp and Melo, 2013; Jost et al., 2010; Petsch et al., 2017). Likewise, functional diversity can be analyzed at multiple spatial scales and can help identify changes in the structure of aquatic communities along ecological gradients of human disturbance (Ligeiro et al., 2013), and how species attributes influence the structuring of these communities (Bello et al., 2009; Heino and Tolonen, 2017). It is increasingly recognized that functional diversity is essential to understand community structure and function (Perez Rocha et al., 2019; Villéger et al., 2013). However, most studies addressing diversity partitioning ignore key components of what makes communities different across spatial scales: relative abundance and biological characteristics of the species. Based on the relationships among species, their traits, and evolutionary history, integrating measures of different facets of biodiversity (e.g., taxonomic and functional) at different scales provide valuable information on the determinants of community composition (Cavender-Bares et al., 2009; Perez Rocha et al., 2018). The approach based only on species composition is an incomplete view of the community structure (Villéger et al., 2012). Determining the spatial scale where greater biological variability occurs can help managers and decision makers focus their efforts and resources where biodiversity is most vulnerable and requires more attention.

Regional and local drivers of β-diversity may interact in complex ways to determine community structure (Krynak et al., 2019; Perez Rocha et al., 2018). Theoretical and analytical developments have shown that β-diversity can be decomposed into its turnover (i.e., species replacement between different sites) and nestedness (i.e., addition or loss of species between sites for nested sites) components (Baselga, 2010), allowing insights about the communities. For example, the turnover component of β-diversity might inform us about deterministic niche-related processes (e.g., filtering of different species by prevailing environmental features) related to species replacements between different environmental conditions (Nunes et al., 2016). On the other hand, the nestedness component might be more closely related to stochastic dispersal or extinction processes resulting in gain or loss of species (Heino and Tolonen, 2017).

The drivers of dissimilarity in species among habitats and the mechanisms that modulate the distribution of functional diversity in streams remain gaps in ecological knowledge. Analyzing the partitioning of taxonomic and functional diversity offers a unique tool to understand the ecological processes that structure the biological communities in environmental gradients or spatial scales (Villéger et al., 2013). Thus, the present study aims to contribute to filling these gaps, broadening our understanding of the processes driving the distribution patterns of the functional diversity of aquatic insects in the neotropical savanna. This Brazilian biome is a hotspot of biodiversity (Myers et al., 2000) and contains important hydrographic basins, but their aquatic ecosystems are threatened by habitat fragmentation, sedimentation, flow regulation and water pollution (Callisto et al., 2019; Castro et al., 2018; Strassburg et al., 2017), impairing human well-being and ecosystem services.

This study was designed to assess how the taxonomic and functional composition of stream insect assemblages are distributed among multiple spatial scales (i.e., habitat, stream sites and hydrological units) using a hierarchical series of four diversity components in Cerrado streams: stream transect (α), among transects (β_1), among stream sites (β_2), and among hydrologic units (β_3). Our aim was to identify the scales at which variation in aquatic insect structure was greatest and whether species replacement (turnover) or changes in species richness (nestedness) mainly explain the patterns of β-diversity. Our hypothesis is that β-diversity is not evenly distributed among spatial scales because environmental variables differ greatly at the local scale (e.g., substrate type, current velocity, width and water depth) greatly influence biological communities (Hepp et al., 2012; Ligeiro et al., 2010). Therefore, we expected that taxonomic composition would show greater variability among transects than among streams or hydrologic units. We also expected that the taxonomic β-diversity would be explained mainly by the turnover component because of high habitat variability that allows more species to coexist. We predicted that functional β-diversity would be mainly driven by the nestedness component because of strong environmental filtering and because species can display similar traits over different sites despite substantial variation in species composition among streams.

2. Material and methods

2.1. Study sites and survey design

We conducted our study in streams located in the neotropical savanna (Cerrado biome) of southeastern Brazil. A total of 148 stream sites (1st- to 3rd-order streams sensu Strahler (1957), defined at a 1:100,000 scale) were selected and sampled in four hydrological units (defined as the contributing drainage areas within 35 km upstream of each of four major hydropower reservoirs). The hydrologic units (Três Marias, Volta Grande, São Simão, Nova Ponte) comprised a total geographic area of 45,180 km² and were geographically isolated from each other (Fig. 1). Sampling was conducted in September from 2011 to 2014, one year for each of the aforementioned hydrological units, ensuring that samples were all taken in the low flow season. Site selection followed a generalized random tessellation stratified design (Olsen and Peck, 2008) via a hierarchical, spatially weighted criterion (Stevens and Olsen, 2004). This procedure ensures a balanced selection of sites across the range of stream orders, geographic location, and along different disturbance levels. Lastly, 19 additional sites representing least disturbed conditions (LDC) were also sampled. All sampled sites were treated together. Thus, we analyzed a total of 167 sites at different levels of impact, ranked from least- to most-disturbed, in a well-defined disturbance gradient (see details in Castro et al., 2018).

Each site was a minimum of 150 m long. Randomly selected sites were divided into 11 equally spaced transects and LDC sites were subdivided into six equidistant transects. We employed a standardized multihabitat sampling as described in Hughes and Peck (2008). This method consists in taking one aquatic invertebrate sample unit per transect following a systematic zyg-zag pattern (right-mid-left). For each of these sample units we used a D-frame kick net (30 cm mouth aperture, 500 μm mesh size) in 30 × 30 cm per sample unit (0.09 m²). This method ensures that most of the available habitats, such as substrates and flow profiles, are sampled at each site. Samples were placed in individual plastic buckets and were fixed in 4% formalin. In the laboratory, samples were rinsed on a 500 μm mesh sieve, then sorted. Ephemeroptera, Plecoptera, and Trichoptera (EPT) specimens were identified to genus by using taxonomic keys (Dominguez et al., 2006; Mugnai et al., 2010; Pes et al., 2014). Therefore, we had a set of 1837 samples (1837 transects in 167 streams sites in 4 hydrological units).

2.2. Functional traits

In this study, a trait was defined as a measurable aspect of an organism that affects its performance and interaction with the environment (McGill et al., 2006). We used a trait database recently developed for Cerrado aquatic insects fully described in Castro et al. (2017). This
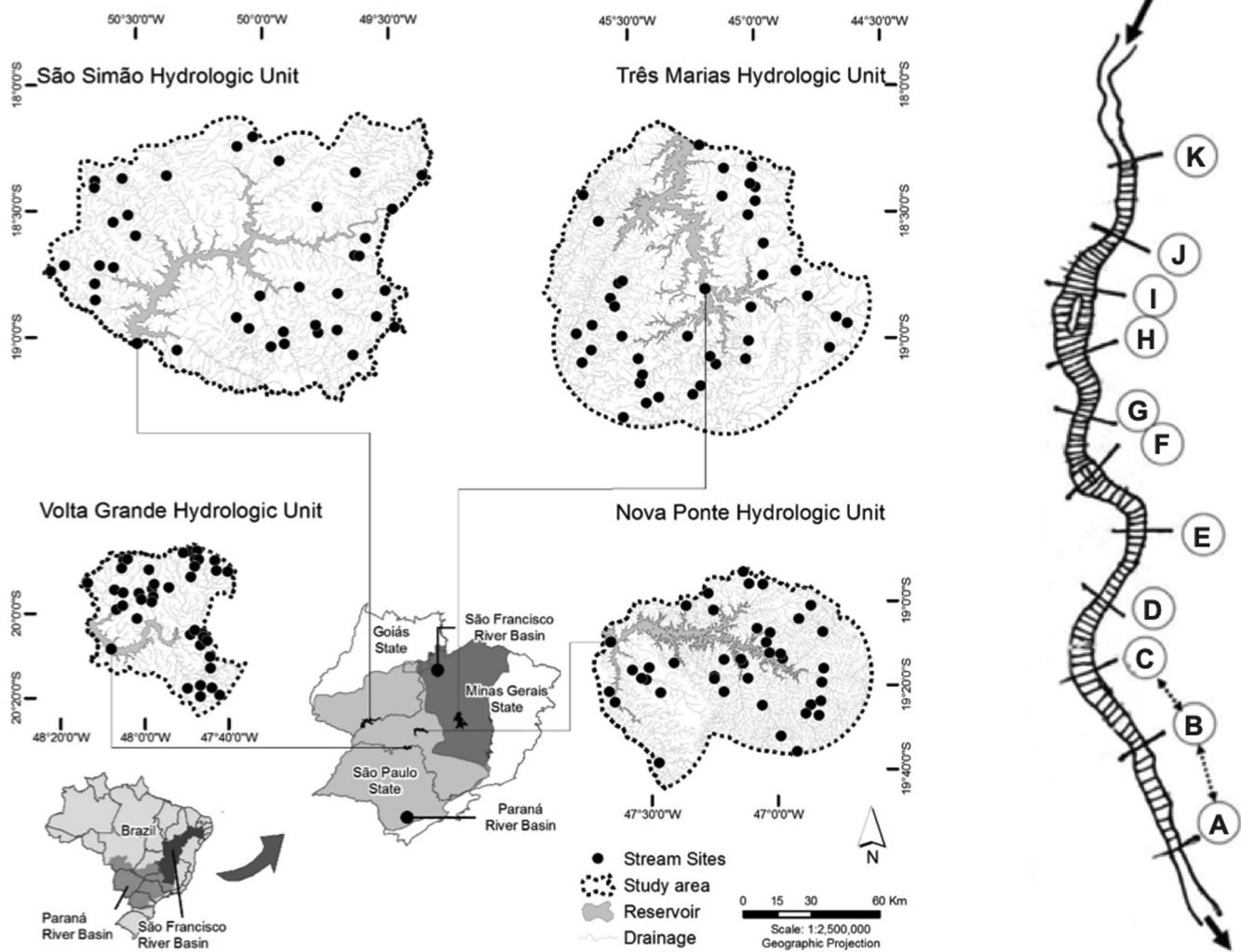
Fig. 1. Location of stream sites in four hydrological units in the Cerrado biome (left) and details of in-stream sample design carried out in each stream site (right).

database contains seven biological traits and their respective 28 trait categories describing EPT genus profiles in terms of morphology, life cycle, resilience or resistance ability to natural disturbance or human disturbance, and feeding behavior. Seven functional traits were considered: maximum body length (mm), voltinism, feeding habits, locomotion, body flexibility, body form, and relation to substrate. The affinity of EPT genera to each trait category was quantified via fuzzy coding (Chevenet et al., 1994) by assigning a score varying from 0 (no affinity) to 3 (strongest affinity). Affinity scores were standardized so that their sum for a given taxon and a given trait equaled 1. We summarized the trait structure of EPT genera in the samples by computing the proportion of each trait category in the invertebrate assemblages at each of the four scales. We performed a Fuzzy Correspondence Analysis (FCA; Chevenet et al., 1994) on the trait table to create synthetic traits based on the FCA axes. The first four FCA axes were then used to calculate the minimum convex hull volume measured in multidimensional space that encompasses all taxa at each scale. The number of dimensions (i.e., FCA axes) was chosen based on the quality of the functional space, i.e., the extent to which it accurately represents the initial functional distances between species pairs, quantified by the mean squared-deviation index (Maire et al., 2015). We kept the minimum number of axes (i.e., four axes) that provides a high-quality functional space to minimize the number of sites we had to exclude to attain computation requirements (i.e., higher number of taxa than FCA axes)

(Villéger et al., 2008). Difference in quality between four and more dimensional spaces was relatively low, allowing us to construct a faithful representation of the initial functional trait values (Fig. 2).

2.3. Data analyses

2.3.1. Diversity partitioning

We used the multiplicative partitioning of diversity (Whittaker, 1972, 1960) to assess the relationships among components of diversity (α, β, γ) at multiple spatial scales only for taxonomic composition. In partitioning analysis, α-diversity is defined as the number of taxa per sample unit, γ-diversity as the total number of taxa found in the entire study, and β-diversity consists of dissimilarities of taxonomic composition among samples.

In this hierarchical study, one value of β-diversity is associated with each spatial level. Accordingly, the first β-diversity is associated with variation in taxonomic composition among transect sample units and is defined as $\beta_{1\text{-among\_transects}}$ hereafter. This first β component can be interpreted as the ratio in mean taxon richness among transect sample units within a stream. Similarly, $\beta_{2\text{-among\_streams}}$ is the ratio in mean taxon richness among stream sites, and $\beta_{3\text{-among\_hydrological\_units}}$ the ratio among hydrological units. We calculated multiplicative β-diversity for each scale because it is a measure of the effective number of distinct assemblages or samples in a unit, also not being mathematically
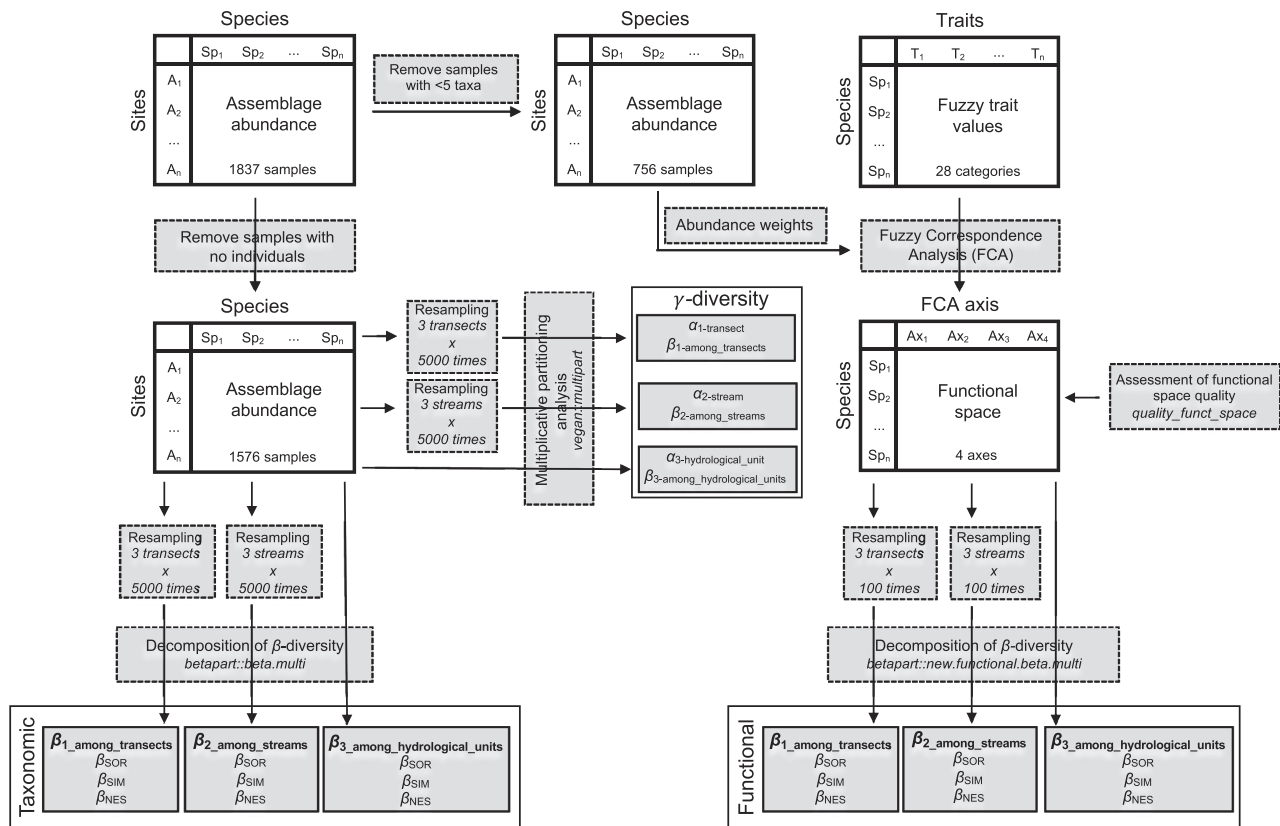
Fig. 2. Schematic diagram presenting the methodological design of statistical analyses used in this study.

affected by the number of taxa in each assemblage (Jost, 2007). We organized our data according to the following hierarchical scheme: $\alpha_{1\text{-transect}}$ as the number of species (genera) per transect, $\alpha_{2\text{-stream}}$ as the total number of species per stream, and $\alpha_{3\text{-hydrological\_unit}}$ as the total number of species per hydrological unit. $\gamma_{(regional\_diversity)}$ was the total number of species in all hydrological units. Thus, the diversity model evaluated was: $\gamma_{(regional\_diversity)} = \alpha_{1\text{-transect}} \times \beta_{1\text{-amog\_transects}} \times \beta_{2\text{-among\_streams}} \times \beta_{3\text{-among\_hydrological\_units}}$. We calculated all values for each spatial scale separately, and used multiplicative partitioning as a measure of the magnitude of differentiation, independent of α-diversity (and therefore of taxon loss), thus indicating the amount by which diversity (e.g., taxonomic richness) increased across scales. We computed diversity values using both genus richness (Hill numbers of order 0) and the exponent of Shannon entropy (Hill numbers of order 1). Whereas simple genus richness includes all genera irrespective of their frequency, the exponential of Shannon entropy weights genera by their frequencies, thereby reducing the influence of rare species (Chao et al., 2014).

Before performing all analyses, we removed transects having no individuals; therefore, sample sizes differed for different spatial scales. This could lead to biased results for analyses of β-diversity that may be sensitive to sample size. Therefore, we resampled the data to obtain comparable values of β-diversity (Baselga, 2010). To calculate $\beta_{1\text{-among\_transects}}$, we randomly sampled without replacement three transects within each stream 5000 times. To calculate $\beta_{2\text{-among\_streams}}$, we randomly sampled without replacement three streams (all transect data per stream were pooled) within each hydrological unit 5000 times (Fig. 2). Diversity partitioning analysis was conducted using the *vegan* R package (Oksanen et al., 2019).

2.3.2. Decomposition of β-diversity

Taxonomic β-diversity measures the number of taxa in common and unique among assemblages where functional β-diversity uses convex

hull volume to measure the volume shared and unique among assemblages (Baselga, 2012; Baselga et al., 2018; Villéger et al., 2013). We decomposed taxonomic and functional $\beta_{1\text{-among\_transects}}$, $\beta_{2\text{-among\_streams}}$, and $\beta_{3\text{-among\_hydrological\_units}}$ diversities into two components: the dissimilarity resulting from genera gain/loss (nestedness) and from genera replacement (turnover) by calculating, respectively, nestedness (β_{NES}) and Simpson (β_{SIM}) indices (Baselga, 2012, 2010). To do this, we used the Sørensen coefficient of dissimilarity (i.e., β-diversity). Differences between Sørensen and Simpson values are representative of the nestedness component of β-diversity: $\beta_{NES} = \beta_{SOR} - \beta_{SIM}$ (Baselga, 2012, 2010). Multi-site β-diversity calculations based on the Sørensen coefficient are sensitive to sample size, so we calculated β-values using a resampling procedure. We took 5000 random samples from the total number of stream sites and from the total number of transects in the same way that we did for each scale of β-diversity partitioning to have comparable measures of β_{SOR} and β_{SIM} diversities. Similarly, the *functional.beta.multi* function in the *betapart* R package modified by Krynak et al. (2019) was used to partition functional β-diversity into its turnover and nestedness components of functional β-diversity. Multi-site functional β-diversity requires computing the intersection of convex hulls, which is a demanding computational task, and the time required increases with increased number of sites and trait axes. Therefore, we used a resampling procedure as described for the taxonomic approach, whereby we took 100 random samples at each spatial scale. β-diversity calculations were performed using the *betapart* R package (Baselga et al., 2018) or modified functions (Krynak et al., 2019) (Fig. 2). All data analyses were completed using R version 3.4.3 (R Core Development Team, 2015).

3. Results

A total of 57,672 organisms were collected, distributed across 83 EPT genera, being 42 genera of Ephemeroptera, 5 genera of Plecoptera,
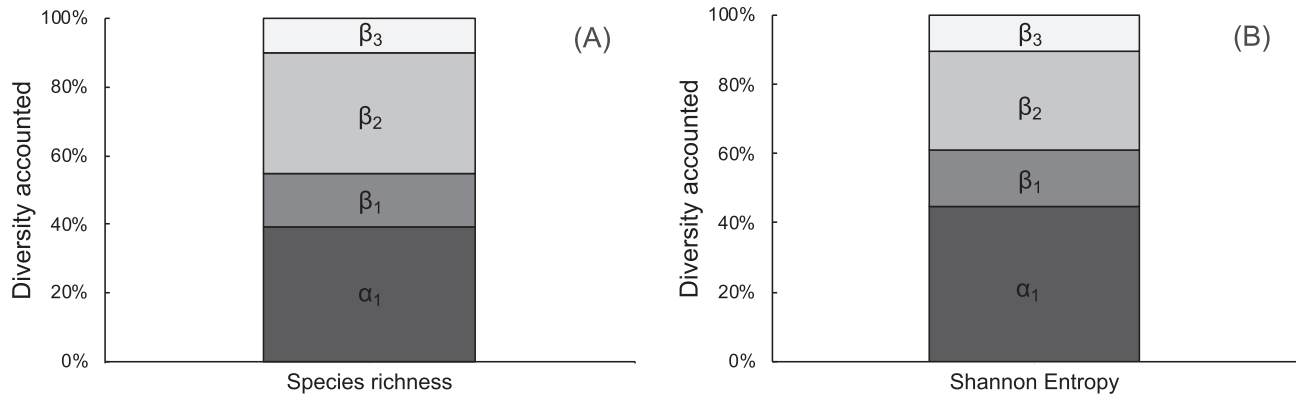
Fig 3. The contribution of α_1, β_1, β_2, and β_3 to taxonomic diversity (A) and Shannon entropy diversity (B) to γ-diversity.

and 36 genera of Trichoptera. Ephemeroptera was the most abundant order with 44,074 individuals (76.4% relative abundance), followed by Trichoptera with 12,038 (20.9%) and Plecoptera with 1560 individuals (2.7%).

3.1. Diversity partitioning

EPT genera richness varied among spatial scales. Mean taxonomic richness by transects ($\alpha_{1\text{-transect}}$) was 5.33 genera, by streams ($\alpha_{2\text{-stream}}$) was 10.9 genera, and by hydrological units ($\alpha_{3\text{-hydrological\_unit}}$) 52.4 genera. The multiplicative partitioning showed that the richness observed at the smallest scale was those who most contributed to the total γ-diversity, where $\alpha_{1\text{-transect}}$ represented 39.1% of total richness. The observed β-diversity component of the first scale, $\beta_{1\text{-among\_transects}}$, accounted for 15.5%, $\beta_{2\text{-among\_streams}}$ accounted for 35.2% and $\beta_{3\text{-among\_hydrological\_units}}$ represented 10.2% of total diversity (Fig. 3A). We observed similar patterns for Shannon entropy diversity (Fig. 3B).

The full hierarchical taxonomic diversity partitioning showed that β-diversity is higher among streams ($\beta_{2\text{-among\_streams}}$ = 4.8 (30%), followed by among transects ($\beta_{1\text{-among\_transects}}$ = 2.1, 28%). The lowest value of β-diversity was observed among hydrologic units ($\beta_{3\text{-among\_hydrological\_units}}$ = 1.4, representing 2%) (Fig. 4A). For Shannon entropy, we observed a slightly different pattern, whereby $\beta_{1\text{-among\_transects}}$ was higher, accounting for 27%, followed by $\beta_{2\text{-among\_streams}}$, accounting 25% and $\beta_{3\text{-among\_hydrological\_units}}$ representing for only 3.5% of the total Shannon entropy β-diversity (Fig. 4B).

3.2. Decomposition of β-diversity

When we partitioned taxonomic and functional β-diversity into their respective turnover and nestedness components, we verified that for taxonomic β-diversity, the turnover contribution was high for all scales, and highest at stream scale (Table 1, Fig. 5A). This means that species turnover mainly occurs across streams. We observed a similar pattern for functional β-diversity among transects, where the turnover

component was higher. On the other hand, nestedness was the higher component of functional β-diversity at stream and hydrological unit scales (Table 1, Fig. 5B). This means that functional nestedness mainly occurs across streams and hydrological units.

4. Discussion

Streams are highly heterogeneous habitats and this condition is reflected in the variation of their taxonomic species composition (Hepp and Melo, 2013). We were able to show that this heterogeneity also affects both within- and among-streams functional diversity. We found that β-diversity among streams is higher and contributes most to the total richness (γ-diversity) of aquatic insects in Cerrado streams in comparison to dissimilarity among habitats and among hydrologic units. Contrary to our expectation, we observed that β-diversity among transects had the lowest contribution to total insect richness (γ-diversity). On the other hand, corroborating our expectations, we found that the turnover component of taxonomic β-diversity was high for all scales, being higher at stream scale. Conversely, nestedness was the main component of functional β-diversity at stream scale, i.e., functionally poorer assemblages are only subsets of the richer ones.

Taxonomic β-diversity was mainly driven by the turnover component across all scales, whereas the contribution of the nestedness component was minor. This pattern is consistent with the results of a recent meta-analysis showing that the taxonomic turnover component is around 6 times larger than the nestedness component for different biological groups and geographical areas (Soininen et al., 2018). On the other hand, the nestedness component contributed more to functional β-diversity among streams than the turnover component. This is similar to results observed in other studies (e.g., Perez Rocha et al., 2019; Villéger et al., 2013). Because of environmental filtering, some traits are presumably more common than others, resulting in low functionally diverse assemblages being subsets of high functionally diverse assemblages (Heino and Tolonen, 2017).

The high turnover component of β-diversity among transects and streams can be explained by the high habitat variability at the within-
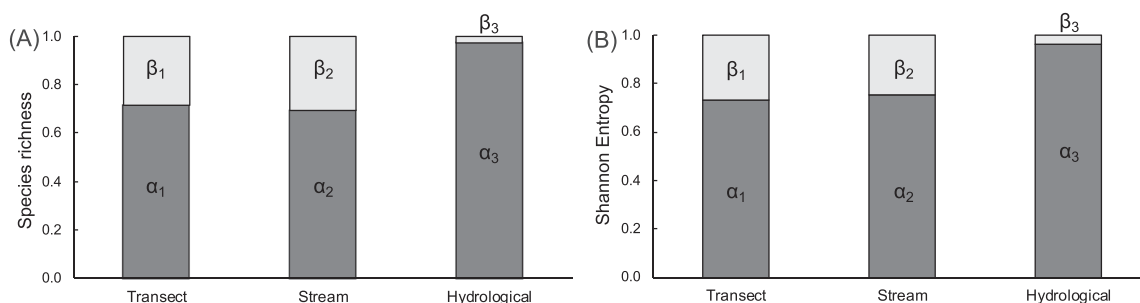

Fig. 4. Proportional contribution of α_1, α_2, α_3, β_1, β_2, and β_3 of taxonomic diversity (A) and Shannon entropy diversity (B) for each scale evaluated.

Table 1
Multi-site taxonomic and functional dissimilarities among spatial scales and their components (i.e., total (β_{SOR}), turnover (β_{SIM}), and nestedness (β_{NES})). For transects and streams, the values are means of 5000 resampled calculations. SD = standard deviation.

	Among transects (β_1)			Among streams (β_2)			Among hydrological units (β_3)		
Taxonomic	β_{SOR}	β_{SIM}	β_{NES}	β_{SOR}	β_{SIM}	β_{NES}	β_{SOR}	β_{SIM}	β_{NES}
Min	0.000	0.000	0.000	0.333	0.095	0.000			
Max	1.000	1.000	0.875	0.939	0.905	0.612			
Mean	0.674	0.508	0.166	0.732	0.612	0.120	0.271	0.179	0.092
SD	0.181	0.250	0.132	0.089	0.113	0.057			
Functional	β_{SOR}	β_{SIM}	β_{NES}	β_{SOR}	β_{SIM}	β_{NES}	β_{SOR}	β_{SIM}	β_{NES}
Min	0.113	0.000	0.000	0.149	0.002	0.028			
Max	1.000	1.000	0.996	0.983	0.832	0.941			
Mean	0.845	0.498	0.348	0.640	0.230	0.410	0.024	0.011	0.014
SD	0.159	0.306	0.254	0.187	0.168	0.198			
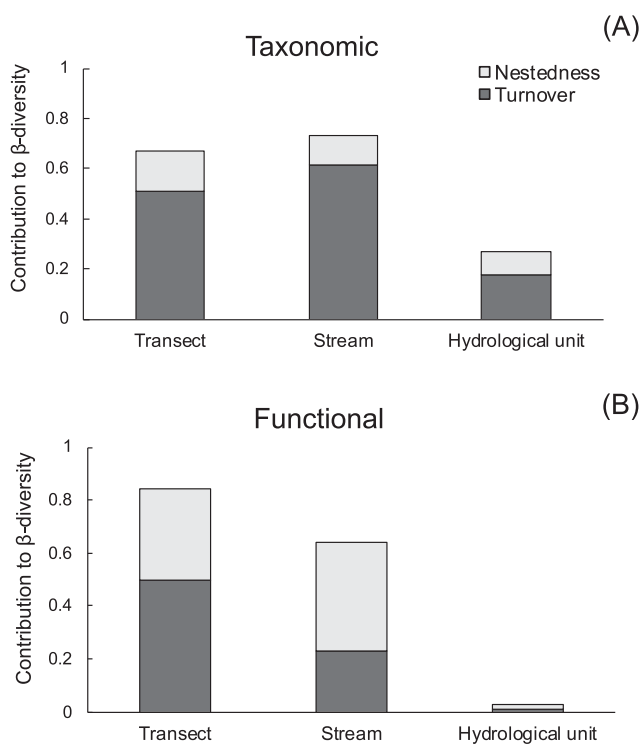
Fig. 5. Contribution of turnover and nestedness to taxonomic (A) and functional (B) β-diversity for each spatial scale.

and between-stream scales (e.g., depth, water flow, substrates, and physical habitats). Species differ in their environmental and micro-habitats requirements and, thus, assemblage compositional differences are likely related to heterogeneity within streams (Libório and Tanaka, 2016; Soininen et al., 2007). High habitat variability within a stream allows more species to coexist locally and it is a key structuring factor of aquatic communities (Boyero, 2003). Previous studies have shown that stream biodiversity patterns are related to local-scale variables, such as current velocity, substratum, physical and chemical water parameters (e.g., Ferreira et al., 2017; Firmiano et al., 2017; Heino et al., 2007; Perez Rocha et al., 2018). The high turnover components of β-diversity among transects and streams shows the strong linkage between local habitat features and changes in aquatic insect assemblages over short spatial distances. At fine spatial scales, dispersal limitation is expected to have minor effects and increases with increasing geographic distances among sites and the spatial extents surveyed (Soininen, 2012; Heino et al., 2015b).

The observed low values of both taxonomic and functional β-diversity among hydrological units show that aquatic insects are

widespread among basins, a pattern that also has been observed by other studies (Maasri et al., 2018; Zbinden and Matthews, 2017). Heino et al. (2015b) showed that species composition in streams changes mostly because of among-site environmental differences, whereas spatial distances are generally less important in accounting for compositional changes. Our study suggests that sorting resulting from heterogeneity of in-stream habitats (environmental filter) is the main reason of the high taxonomic turnover component of aquatic insects in neotropical savanna streams. In addition, there are other mechanisms, such as dispersal ability, that can also be a strong factor influencing assemblage composition, but has not been evaluated in this study (Cañedo-Argüelles et al., 2015; Kärnä et al., 2015).

Despite the high turnover of aquatic insects occurring among streams, the nestedness component of functional β-diversity among streams was higher than the turnover component. Nestedness can be a result of different dispersal limitations (McAbendroth et al., 2005) and environmental tolerances among species (Driscoll, 2008). Factors such as habitat heterogeneity (Hylander et al., 2005) or isolation (Patterson, 1990) also cause nested patterns. One reason for this pattern in Cerrado streams may be the strong anthropogenic environmental filtering, where low trait-diversity assemblages are subsets of high trait-diversity assemblages. Although it was not assessed in our analyses, there is a gradient of human disturbance across stream sites (Ligeiro et al., 2013), ranging from low to high disturbed sites, which directly influences habitat heterogeneity. This heterogeneity in the physical habitats, substrate, and hydromorphology between streams are key factors controlling taxonomic and functional composition of stream insect assemblages (Castro et al., 2017; Ligeiro et al., 2020). Thus, assemblages having a small set of traits would occur in the low heterogeneity sites and assemblages with a large variety of traits would occur in the high heterogeneity sites (Perez Rocha et al., 2019).

The low values of functional β-diversity observed among hydrological units may result from functional convergence (i.e., adaptation of different species to similar habitat conditions; Villéger et al., 2013), which was expected. Even though each hydrological unit is geographically separated, they occur in the same Cerrado biome and suffer similar anthropogenic threats (e.g., agriculture, livestock) to varying degrees (Macedo et al., 2018; Silva et al., 2018). Taxonomic β-diversity observed among hydrological units was low when compared to other spatial scales, but accounted for almost 27% of dissimilarity, mainly due to species replacement (66%). Thus, distinct species found in different streams share similar traits within hydrological units, leading to low functional differentiation between them (Heino and Tolonen, 2017). However, this pattern changes greatly when functional β-diversity is evaluated within and between streams. This topic has not been studied extensively from the functional perspective (Hill et al., 2019) and generalized patterns are not yet possible as for taxonomic β-diversity components (Soininen et al., 2018).

We did not evaluate the effects of disturbance as drivers of dissimilarity in aquatic assemblages, but we aimed to simply understand at which scale variation in aquatic insect assemblages is most important.

Nonetheless, understanding how biodiversity changes from local to regional scales is a first step to disentangle the mechanisms governing the variation or dissimilarity in species and trait composition across space (Socolar et al., 2016). As suggested by Jost et al. (2010), to effectively conserve regional biodiversity, it is essential to know how diversity is distributed geographically within a region, how homogeneous and how much each assemblage contributes to regional diversity. We found that the spatial scales that most contribute to taxonomic and functional β-diversity of aquatic insects in the Cerrado biome differ. This highlights the value of diversity decomposition as a tool to support the adoption of different management and conservation strategies, which are particularly relevant for ecological indicators and biomonitoring programs. For example, we show that most of the regional diversity of aquatic insects in Cerrado results from high dissimilarity among streams, even over relatively short geographic distances. This indicates that sampling at a few stream sites is not enough for an efficient assessment of diversity in a region. Moreover, even though species change greatly among streams, which contributes to regional diversity, low functionally diverse assemblages are subsets of high functionally diverse assemblages. Our results emphasize the importance of considering spatial planning in conserving Cerrado headwater streams, which are key to water supply for multiple human uses by millions of people. Also, these systems are home to several species, including endemics, and marked stream alterations will result in a loss of diversity and ecosystem functions.

Author contributions

D.M.P.C and M.C. elaborated the research design, collected and processed the data. D.M.P.C, P.G.S. and R.S. conducted the statistical analyses. All authors wrote the paper.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

References

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, 639–647. https://doi.org/10.1111/geb.12031.

Baselga, A., 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Glob. Ecol. Biogeogr. 21, 1223–1232. https://doi.org/10.1111/j.1466-8238.2011.00756.x.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x.

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., Logez, M., Henriques-Silva, R., 2018. Partitioning beta diversity into turnover and nestedness components. Cran 1–42.

Bello, F., Thuiller, W., Leps, J., Choler, P., Clement, J.C., Macek, P., Sebastia, M.T., Lavorel, S., 2009. Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence. J. Veg. Sci. 20, 475–486. https://doi.org/10.1111/j.1654-1103.2009.01042.x.

Borcard, D., Legendre, P., Avois-Jacquet, C., Tuomisto, H., 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology 85, 1826–1832. https://doi.org/10.1890/03-3111.

Boyero, L., 2003. The quantification of local substrate heterogeneity in streams and its significance for macroinvertebrate assemblages. Hydrobiologia 499, 161–168.

Callisto, M., Macedo, D.R., Linares, M., Hughes, R.M., 2019. Multistatus and Multispatial Scale Assessment of Landscape Effects on Benthic Macroinvertebrates in the Neotropical Savanna. In: Hughes, R.M., Infante, D.M., Wang, L., Chen, K., Terra, B.F. (Eds.), Advances in Understanding Landscape Influences on Freshwater Habitats and Biological Assemblages. American Fisheries Society Symposium, Bethesda, MD. https://doi.org/10.5281/zenodo.3519460.

Cañedo-Argüelles, M., Boersma, K.S., Bogan, M.T., Olden, J.D., Phillipsen, I., Schriever, T.A., Lytle, D.A., 2015. Dispersal strength determines meta-community structure in a dendritic riverine network. J. Biogeogr. 42, 778–790. https://doi.org/10.1111/jbi.12457.

Castro, D.M.P., Dolédec, S., Callisto, M., 2017. Landscape variables influence taxonomic and trait composition of insect assemblages in Neotropical savanna streams. Freshw. Biol. 62, 1472–1486. https://doi.org/10.1111/fwb.12961.

Castro, D.M.P., Dolédec, S., Callisto, M., 2018. Land cover disturbance homogenizes aquatic insect functional structure in neotropical savanna streams. Ecol. Indic. 84, 573–582. https://doi.org/10.1016/j.ecolind.2017.09.030.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A., Kembel, S.W., 2009. The merging of community ecology and phylogenetic biology. Ecol. Lett. 12, 693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.x.

Chao, A., Chiu, C.-H., Jost, L., 2014. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through hill numbers. Annu. Rev. Ecol. Evol. Syst. 45, 297–324. https://doi.org/10.1146/annurev-ecolsys-120213-091540.

Chevenet, F., Dolédec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long-term ecological data. Freshw. Biol. 31, 295–309.

Declerck, S.A.J., Coronel, J.S., Legendre, P., Brendonck, L., 2011. Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of High-Andes wetlands. Ecography (Cop.) 34, 296–305. https://doi.org/10.1111/j.1600-0587.2010.06462.x.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S., Mouquet, N., 2010. Defining and measuring ecological specialization. J. Appl. Ecol. 47, 15–25. https://doi.org/10.1111/j.1365-2664.2009.01744.x.

Dominguez, E., Molineri, C., Pescador, M.L., Hubbard, M.D., Nieto, C., 2006. Ephemeroptera of South America, in: Aquatic Biodiversity in Latin America Biodiversidad Acuatica En America Latina. p. 646.

Driscoll, D.A., 2008. The frequency of metapopulations, metacommunities and nestedness in a fragmented landscape. Oikos 117, 297–309. https://doi.org/10.1111/j.2007.0030-1299.16202.x.

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. https://doi.org/10.1016/j.ecolind.2016.08.042.

Firmiano, K.R., Ligeiro, R., Macedo, D.R., Juen, I., Hughes, R.M., Callisto, M., 2017. Mayfly bioindicator thresholds for several anthropogenic disturbances in neotropical savanna streams. Ecol. Indic. 74, 276–284. https://doi.org/10.1016/j.ecolind.2016.11.033.

Heino, J., Louhi, P., Muotka, T., 2004. Identifying the scales of variability in stream macroinvertebrate abundance, functional composition and assemblage structure. Freshw. Biol. 49, 1230–1239. https://doi.org/10.1111/j.1365-2427.2004.01259.x.

Heino, J., Melo, A.S., Bini, L.M., 2015a. Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. Freshw. Biol. 60, 223–235. https://doi.org/10.1111/fwb.12502.

Heino, J., Melo, A.S., Siqueira, T., Soininen, J., Valanko, S., Bini, L.M., 2015b. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. Freshw. Biol. 60, 845–869. https://doi.org/10.1111/fwb.12533.

Heino, J., Mykrä, H., Kotanen, J., Muotka, T., 2007. Ecological filters and variability in stream macroinvertebrate communities: Do taxonomic and functional structure follow the same path? Ecography (Cop.) 30, 217–230. https://doi.org/10.1111/j.2007.0906-7590.04894.x.

Heino, J., Tolonen, K.T., 2017. Untangling the assembly of littoral macroinvertebrate communities through measures of functional and phylogenetic alpha diversity. Freshw. Biol. doi: 10.1111/fwb.12934.

Hepp, L.U., Landeiro, V.L., Melo, A.S., 2012. Experimental assessment of the effects of environmental factors and longitudinal position on alpha and beta diversities of aquatic insects in a neotropical stream. Int. Rev. Hydrobiol. 97, 157–167. https://doi.org/10.1002/iroh.201111405.

Hepp, L.U., Melo, A.S., 2013. Dissimilarity of stream insect assemblages: Effects of multiple scales and spatial distances. Hydrobiologia 703, 239–246. https://doi.org/10.1007/s10750-012-1367-7.

Herlihy, A.T., Sifneos, J.C., Hughes, R.M., Peck, D.V., Mitchell, R.M., 2020. The relation of lotic fish and benthic macroinvertebrate condition indices to environmental factors across the conterminous USA. Ecol. Indic. 112, 105958. https://doi.org/10.1016/j.ecolind.2019.105958.

Hill, M.J., Heino, J., White, J.C., Ryves, D.B., Wood, P.J., 2019. Environmental factors are primary determinants of different facets of pond macroinvertebrate alpha and beta diversity in a human-modified landscape. Biol. Conserv. 237, 348–357. https://doi.org/10.1016/j.biocon.2019.07.015.

HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M., Mayfield, M.M., 2012. Rethinking community assembly through the lens of coexistence theory. Annu. Rev. Ecol. Evol. Syst. 43, 227–248. https://doi.org/10.1146/annurev-ecolsys-110411-160411.

Hughes, R.M., Peck, D.V., 2008. Acquiring data for large aquatic resource surveys: the art of compromise among science, logistics, and reality. J. North Am. Benthol. Soc. 27, 837–859. https://doi.org/10.1899/08-028.1.

Hylander, K., Nilsson, C., Gunnar Jonsson, B., Göthner, T., 2005. Differences in habitat quality explain nestedness in a land snail meta-community. Oikos 108, 351–361. https://doi.org/10.1111/j.0030-1299.2005.13400.x.

Jost, L., 2007. Partitioning diversity into independent alpha and beta components. Ecology 88, 2427–2439. https://doi.org/10.1890/06-1736.1.

Jost, L., Devries, P., Walla, T., Greeney, H., Chao, A., Ricotta, C., 2010. Partitioning diversity for conservation analyses. Divers. Distrib. 16, 65–76. https://doi.org/10.1111/j.1472-4642.2009.00626.x.

Kärnä, O.-M., Grönroos, M., Antikainen, H., Hjort, J., Ilmonen, J., Paasivirta, L., Heino, J., 2015. Inferring the effects of potential dispersal routes on the metacommunity structure of stream insects: as the crow flies, as the fish swims or as the fox runs? J. Anim. Ecol. 84, 1342–1353. https://doi.org/10.1111/1365-2656.12397.

Krynak, E.M., Lindo, Z., Yates, A.G., 2019. Patterns and drivers of stream benthic macroinvertebrate beta diversity in an agricultural landscape. Hydrobiologia 837, 61–75. https://doi.org/10.1007/s10750-019-3961-4.

Leps, M., Tonkin, J.D., Dahm, V., Haase, P., Sundermann, A., 2015. Disentangling environmental drivers of benthic invertebrate assemblages: The role of spatial scale and riverscape heterogeneity in a multiple stressor environment. Sci. Total Environ. 536, 546–556. https://doi.org/10.1016/j.scitotenv.2015.07.083.

Libório, R.A., Tanaka, M.O., 2016. Does environmental disturbance also influence within-stream beta diversity of macroinvertebrate assemblages in tropical streams? Stud. Neotrop. Fauna Environ. 51, 206–214. https://doi.org/10.1080/01650521.2016.1237801.

Ligeiro, R., Hughes, R.M., Kaufmann, P.R., Heino, J., Melo, A.S., Callisto, M., 2020. Choice of field and laboratory methods affects the detection of anthropogenic disturbances using stream macroinvertebrate assemblages. Ecol. Indic. 115, 106382. https://doi.org/10.1016/j.ecolind.2020.106382.

Ligeiro, R., Hughes, R.M., Kaufmann, P.R., Macedo, D.R., Firmiano, K.R., Ferreira, W.R., Oliveira, D., Melo, A.S., Callisto, M., 2013. Defining quantitative stream disturbance gradients and the additive role of habitat variation to explain macroinvertebrate taxa richness. Ecol. Indic. 25, 45–57. https://doi.org/10.1016/j.ecolind.2012.09.004.

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

Maasri, A., Hayford, B., Erdenee, B., Gelhaus, J., 2018. Macroscale drivers influencing the structural and functional organization of stream macroinvertebrate metacommunities: Potential role of hydrological connectivity. Freshw. Sci. 37, 159–168. https://doi.org/10.1086/695945.

Macedo, D.R., Hughes, R.M., Kaufmann, P.R., Callisto, M., 2018. Development and validation of an environmental fragility index (EFI) for the neotropical savannah biome. Sci. Total Environ. 635, 1267–1279. https://doi.org/10.1016/j.scitotenv.2018.04.216.

Maire, E., Grenouillet, G., Brosse, S., Villéger, S., 2015. How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. Glob. Ecol. Biogeogr. 24, 728–740. https://doi.org/10.1111/geb.12299.

McAbendroth, L., Foggo, A., Rundle, S.D., Bilton, D.T., 2005. Unravelling nestedness and spatial pattern in pond assemblages. J. Anim. Ecol. 74, 41–49. https://doi.org/10.1111/j.1365-2656.2004.00895.x.

McGill, B., Enquist, B., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185. https://doi.org/10.1016/j.tree.2006.02.002.

Mugnai, R., Nessimian, J.L.J.L., Baptista, D.F., 2010. Manual de Identificação de Macroinvertebrados Aquáticos do Estado do Rio de Janeiro., Technical Books Editora. Rio de Janeiro – RJ. Technical Books, Rio de Janeiro.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., Kent, J., da Fonseca, G.a.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501.

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, 149–159. https://doi.org/10.1111/j.1466-8238.2006.00272.x.

Nunes, C.A., Braga, R.F., Figueira, J.E.C., Neves, F. de S., Fernandes, G.W., 2016. Dung beetles along a tropical altitudinal gradient: environmental filtering on taxonomic and functional diversity. PLoS One 11, e0157442. https://doi.org/10.1371/journal.pone.0157442.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. vegan: Community Ecology Package.

Olsen, A.R., Peck, D.V., 2008. Survey design and extent estimates for the Wadeable Streams Assessment. J. North Am. Benthol. Soc. 27, 822–836. https://doi.org/10.1899/08-050.1.

Patterson, B.D., 1990. On the temporal development of nested subset patterns of species composition. Oikos 59, 330. https://doi.org/10.2307/3545143.

Peláez, O., Pavanelli, C.S., 2019. Environmental heterogeneity and dispersal limitation explain different aspects of β-diversity in Neotropical fish assemblages. Freshw. Biol. 64, 497–505. https://doi.org/10.1111/fwb.13237.

Perez Rocha, M., Bini, L.M., Domisch, S., Tolonen, K.T., Jyrkänkallio-Mikkola, J., Soininen, J., Hjort, J., Heino, J., 2018. Local environment and space drive multiple facets of stream macroinvertebrate beta diversity. J. Biogeogr. 45, 2744–2754. https://doi.org/10.1111/jbi.13457.

Perez Rocha, M., Bini, L.M., Grönroos, M., Hjort, J., Lindholm, M., Karjalainen, S.M., Tolonen, K.E., Heino, J., 2019. Correlates of different facets and components of beta diversity in stream organisms. Oecologia 191, 919–929. https://doi.org/10.1007/s00442-019-04535-5.

Pes, A.M., Santos, A.P.M., Barcelos-Silva, P., Camargos, L.M. De, 2014. Ordem Trichoptera. Insetos aquáticos na Amaz. Bras. Taxon. Biol. e Ecol. 724.

Petsch, D.K., Schneck, F., Melo, A.S., 2017. Substratum simplification reduces beta diversity of stream algal communities. Freshw. Biol. 62, 205–213. https://doi.org/10.1111/fwb.12863.

R Core Development Team, 2015. R: a language and environment for statistical computing, 3.2.1. Doc. Free. Available internet http//www. r-project. org. doi: 10.1017/CBO9781107415324.004.

Silva, D.R.O., Herlihy, A.T., Hughes, R.M., Macedo, D.R., Callisto, M., 2018. Assessing the extent and relative risk of aquatic stressors on stream macroinvertebrate assemblages in the neotropical savanna. Sci. Total Environ. (in press).

Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016. How should beta-diversity inform biodiversity conservation? Trends Ecol. Evol. 31, 67–80. https://doi.org/10.1016/j.tree.2015.11.005.

Soininen, J., Heino, J., Wang, J., 2018. A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. Glob. Ecol. Biogeogr. 27, 96–109. https://doi.org/10.1111/geb.12660.

Soininen, J., McDonald, R., Hillebrand, H., 2007. The distance decay of similarity in ecological communities. Ecography (Cop.) 30, 3–12. https://doi.org/10.1111/j.0906-7590.2007.04817.x.

Stevens, D.L., Olsen, A.R., 2004. Spatially balanced sampling of natural resources. J. Am. Stat. Assoc. 99, 262–278. https://doi.org/10.1198/016214504000000250.

Strahler, A.N., 1957. Quantitative analysis of watershed geomorphology. Trans. Am. Geophys. Union 38, 913–920. https://doi.org/10.1130/0016-7606.

Strassburg, B.B.N., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R., Latawiec, A.E., Oliveira Filho, F.J.B., Scaramuzza, C.A. de M., Scarano, F.R., Soares-Filho, B., Balmford, A., 2017. Moment of truth for the Cerrado hotspot. Nat. Ecol. Evol. 1, 0099. doi: 10.1038/s41559-017-0099.

Strayer, D.D.L., Dudgeon, D., 2010. Freshwater biodiversity conservation: recent progress and future challenges. J. North Am. Benthol. Soc. 29, 344–358. https://doi.org/10.1899/08-171.1.

Sundar, S., Heino, J., Roque, F. de O., Simaika, J.P., Melo, A.S., Tonkin, J.D., Gomes Nogueira, D., Silva, D.P., 2020. Conservation of freshwater macroinvertebrate biodiversity in tropical regions. Aquat. Conserv. Mar. Freshw. Ecosyst. 1–13. doi: 10.1002/aqc.3326.

Tonkin, J.D., Arimoro, F.O., Haase, P., 2016. Exploring stream communities in a tropical biodiversity hotspot: biodiversity, regional occupancy, niche characteristics and environmental correlates. Biodivers. Conserv. 25, 975–993. https://doi.org/10.1007/s10531-016-1101-2.

Townsend, C.R., Doledec, S., Norris, R., Peacock, K., Arbuckle, C., 2003. The influence of scale and geography on relationships between stream community composition and landscape variables: description and prediction. Freshw. Biol. 48, 768–785. https://doi.org/10.1046/j.1365-2427.2003.01043.x.

Villéger, Mason, Mouillot, Villéger, S., Mason, N.W.H.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301. doi: 10.1890/07-1206.1.

Villéger, S., Grenouillet, G., Brosse, S., 2013. Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. Glob. Ecol. Biogeogr. 22, 671–681. https://doi.org/10.1111/geb.12021.

Villéger, S., Miranda, J.R., Hernandez, D.F., Mouillot, D., 2012. Low functional β-diversity despite high taxonomic β-diversity among tropical estuarine fish communities. PLoS One 7. https://doi.org/10.1371/journal.pone.0040679.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 213–251. https://doi.org/10.2307/1218190.

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30, 279–338. https://doi.org/10.2307/1943563.

Zbinden, Z.D., Matthews, W.J., 2017. Beta diversity of stream fish assemblages: partitioning variation between spatial and environmental factors. Freshw. Biol. 62, 1460–1471. https://doi.org/10.1111/fwb.12960.