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Do shrimps and aquatic insects have the same patterns and drivers of beta diversity in eastern Amazon streams? A spatial hierarchical approach

Belém, Pará
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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia (PPGECO) do convênio da Universidade Federal do Pará e Embrapa Amazônia Oriental, como requisito parcial para a obtenção do título de Mestre em Ecologia.
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SUMÁRIO

Camarões e insetos aquáticos têm suas diversidades beta governadas pelos mesmos fatores em riachos da Amazônia oriental? Uma abordagem espacial hierárquica

RESUMO

Os padrões de distribuição espacial dos macroinvertebrados de riachos, em diferentes escalas espaciais, estão geralmente relacionados a processos ambientais e espaciais distintos. Ecólogos analisaram o papel das distâncias espaciais e modos de dispersão nos padrões de diversidade beta. O presente estudo propôs avaliar os padrões de diversidade beta de metacomunidades aquáticas em duas escalas espaciais em riachos na Amazônia Oriental, bem como testar se fatores ambientais e espaciais afetaram esses padrões nas assembleias de camarão (Crustacea: Decapoda) e insetos aquáticos (ordens Ephemeroptera e Trichoptera - ET). Foram amostrados quinze riachos distribuídos em uma bacia amazônica, considerando dois níveis hierárquicos: unidades amostrais (tomadas em segmentos de 5m dentro dos riachos) e riachos (150m de comprimento). Particionamos aditivamente a diversidade gama para testar a importância relativa de cada nível espacial para a diversidade regional. A diversidade beta total (βtotal), em cada nível espacial, foi medida com o índice de Ruzicka e decomposta nos componentes de substituição da abundância (βbal) e diferença de abundância (grad), para testar quais processos (aninhamento ou substituição) foram predominantes. Para testar se houve efeito de distâncias espaciais e variáveis ambientais nas matrizes de diversidade (βtotal, βbal e grad), utilizamos regressão múltipla de matrizes de distância (MRM), usando distâncias espaciais e matrizes ambientais como preditores. No total, foram coletados 2432 macroinvertebrados, 1387 insetos aquáticos (ET) e 1045 decápodes. Nos dois grupos, a diversidade alfa (riqueza média nas unidades amostrais) foi menor que o esperado por acaso (propexp > obs > 0,999). A diferença entre as unidades amostrais foi semelhante entre os grupos, mas não foi diferente do acaso (p = 0,124 nos decápodes, p> 0,9999 no ET). A diferença entre os locais dos riachos apresentou uma maior contribuição para a diversidade gama (45,7% em decápodes, 60,5% em ET), significativamente maior do que o esperado aleatoriamente (p = 0,003 e p < 0,001, respectivamente). A decomposição da diversidade beta foi semelhante nos dois grupos e entre os dois níveis espaciais, com maior contribuição do βgrad, revelando um padrão aninhado. Os modelos de MRM mostraram que para ET apenas a dissimilaridade do ambiente era importante para explicar a variação na diversidade beta, enquanto para camarões as distâncias ambientais e espaciais eram significativas. Concluímos que diferentes processos e variáveis ambientais são importantes para explicar a distribuição de ET e camarão, o que provavelmente está relacionado aos diferentes modos de dispersão e exigências ambientais dos grupos. Portanto, neste estudo avançamos na compreensão dos padrões e fatores da diversidade beta de diferentes grupos de macroinvertebrados e os fatores que afetam sua variação em pequenas escalas, o que tem implicações importantes para fins teóricos e aplicados.

Palavras-chave: Particionamento aditivo, dissimilaridade de assembleias, equilíbrio de abundância, diferença de abundância, dispersão de macroinvertebrados.

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ABSTRACT

Spatial distribution patterns of stream macroinvertebrates at different spatial scales are generally related to distinct environmental and spatial processes. Ecologists have analyzed the role of spatial distances and dispersion modes in beta diversity patterns. The present study proposed to evaluate the beta diversity patterns of aquatic metacommunities at two spatial scales in streams in the Eastern Amazon, as well as to test whether environmental and spatial factors affected these patterns in shrimp (Crustacea: Decapoda) and aquatic insects' assemblages (orders Ephemeroptera and Trichoptera - ET). Fifteen streams distributed in an Amazon basin were sampled, considering two hierarchical levels: sampling units (taken in segments of 5m within streams) and stream sites (150m in length). We additively partition gamma diversity to test the relative importance of each spatial level to regional diversity. The total beta diversity (βtotal), at each spatial level, was measured with the Ruzicka index, and was decomposed into the components of substitution of abundance (βbal) and difference of abundance (βgrad), to test which processes (nesting or substitution) was predominant. To test whether there was an effect of spatial distances and environmental variables on the diversity matrices (βtotal, βbal and βgrad), we used multiple distance matrix regression (MRM), using spatial distances and environmental matrices as predictors. In total, 2432 macroinvertebrates, 1387 aquatic insects (ET) and 1045 decapods were collected. In both groups, the alpha diversity (mean richness in the sample units) was less than expected by chance (propexp > obs > 0.999). The difference between the sampling units was similar between the groups, but it was not different from chance ($p = 0.124$ in decapods, $p > 0.9999$ in ET). The difference between stream sites presented a greater contribution to the gamma diversity (45.7% in decapods, 60.5% in ET), significantly higher than expected at random ($p = 0.003$ and $p < 0.001$, respectively). The decomposition of beta diversity was similar in both groups and between the two spatial levels, with a greater contribution of βgrad, revealing a nested pattern. The MRM models showed that for ET only the dissimilarity of the environment was important to explain the variation in beta diversity, while for shrimp the environmental and spatial distances were significant. We conclude that different processes and environmental variables are important to explain the distribution of ET and shrimps, which is probably related to the different modes of dispersion and environmental requirements of the groups. Therefore, in this study we have advanced in understanding the patterns and drivers of beta diversity of different macroinvertebrate groups, and the factors that affect their variation in small scales, which has important implications for applied and theoretical purposes.

Keywords: Additive partitioning, assemblage dissimilarity, abundance balance, abundance difference, macroinvertebrate dispersion.

1. Introduction

One of the main goals of ecology is to understand the factors that drive the spatial and temporal distribution of biodiversity and how these factors structure natural communities (Poff, 1997; Finn & Poff, 2005). Whittaker (1960, 1972) proposed to characterize different components of species diversity. Alpha diversity (α) is commonly defined as the diversity of species in a single sample unit in a region, usually corresponding to local scale. On the other hand, the broader regional species pool receives the name of gamma diversity (γ). The difference of species composition among sampling units is called beta diversity (β) (Anderson et al., 2011). The dissimilarity between sites can elucidate issues such as whether the same species or number of individuals is found in different sites or how much the average of individuals or species in a region exceeds the average of individuals or species in local units. There is a distinction between beta diversity measures using presence-absence data and using abundance-based data (Anderson et al., 2011). Measures that are based on abundance can detect more subtle relationships making us perceive co-interactions between the same group of species in two locations with different abundances, which may reflect the rarity of some species in certain locations (Cassey et al., 2000; Barwell et. al, 2015). So, incorporating abundance information on beta diversity can provide a richer data and a finer approach. From that, this abundance dissimilarity between sites can be generated by two components: balanced variation in abundances and abundance gradients in assemblages (Baselga, 2017). Balanced variation in abundances consists in individuals of one species at a given site that are replaced by the same number of individuals but of different species in another site (Baselga, 2017). This process happens through substitution patterns, analogously to species replacement, usually as a consequence of environmental sorting or spatial and historical constraints (Legendre, 2014). In the other hand, abundance gradients consist in differences in the number of individuals from one site to another, in which abundance values of species of the sites are lost or added, i.e., the abundance of all species increases or decreases equally from one site to another (Baselga, 2017). This process is derived from nestedness pattern, analogous to the richness difference component, which implying species eliminations or gains among assemblages (Legendre, 2014).

Beta diversity can be evaluated at multiple spatial scales and patterns of dissimilarity may be different depending on the spatial level analyzed (Crist et al., 2003). Additive partitioning was developed integrating the niche theory with the concepts developed by Whittaker in order to compare the contributions of each component of diversity to gamma diversity across multiple spatial levels (Levins, 1968; Veech et al., 2002). In this approach, revisited by Lande (1996), the diversity is expressed within and between samples using species richness or any diversity measurement (e.g.

Shannon and Simpson indices). This approach provides a direct comparison between spatial and temporal scales, since all components of diversity are measured at the same numerical scale. Gering et al. (2003) detected key spatial scales for the conservation of beetle communities in a deciduous forest, showing this approach provides a very effective tool for biodiversity management and conservancy and an effective approach to understanding multi-scale processes. Based on the observations of Patte (1973) and Nielsen & Müller (2000) it is possible to organize complex systems at hierarchical levels to better understand their processes and identities, as well as to quantify information contained at each level, allowing an integrative concept and a better understanding of community structuring. Once the drivers of species distribution change between scales, it is necessary to study patterns at multiple spatial scales for a more comprehensive understanding of metacommunities (Wiens, 2002; Willis & Whitakker, 2002). Consequently, several studies investigated the distribution of the diversity of stream macroinvertebrates at several scales in hydrologic units, analyzing how the patterns of beta diversity change in these environments (Ligeiro et al., 2010; Hepp & Melo, 2013; Ferreira et al., 2017; Zografou et al., 2017). The patterns obtained reflect processes related to dispersal limitation and environmental filtering, including mass effects and species sorting. Freshwater macroinvertebrates are constantly assessed to test ecological theories and metacommunity structuring. This assemblage presents a high diversity and abundance in aquatic environments, responding quickly to environmental changes, such as flow rate (Newbury, 1988), stream size (Petersen et al., 2004), substrate (Ligeiro et al., 2010) and riparian vegetation (Marklund et al., 2002; Ferreira et al., 2016).

Continental aquatic ecosystems have physical characteristics that support a high biodiversity of macroinvertebrates (Dudgeon et al., 2006). These habitats have longitudinal connections provided by the stream network. Therefore, understanding the role of dispersal on metacommunity dynamics in this environment requires attention to the drainage network (Altermatt, 2013). The branching of the watercourse structure may generate different distribution patterns, depending on the dispersal modes of the organisms (i.e. exclusively or not by the drainage network). Benthic macroinvertebrates of the orders Ephemeroptera and Trichoptera (hereafter ET) can use stream corridors for dispersal, by drift or active swimming (Palmer et al., 1996), and during flying adult stages they may also be able to disperse overland (Bunn & Hughes, 1997; Lancaster & Downes, 2013). These organisms are highly abundant in aquatic ecosystems, including Amazonian streams (Ceneviva-Bastos et al., 2017). On the other side, shrimps (Crustacea: Decapoda) can disperse only through the aquatic pathways, both in adult and larval stages (Hunte, 1979). They are ubiquitous and abundant in tropical streams and constitute an important component of community biomass in tropical freshwater ecosystems (Pringle et al., 1993; Crowl et al., 2001), participating in many ecosystem processes such as processing organic matter, and playing a key role within stream foods webs (Crowl & Covich, 1994; Covich et al. 1999; Crowl et al., 2001). We can fit the dispersal modes of these two groups into the conceptual model proposed by Tonkin et al. (2017) for dispersal pathways in drainage networks. The stream hierarchy model (SHM) assumes minimal dispersal outside the drainage network, so this model applies to organisms with obligatory aquatic dispersal, like shrimps. The headwater model (HWM) represents species specialized in certain types of stream headwaters, but which have good terrestrial dispersal (flight capacity) for at least part of their life cycle, like ET.

Several studies addressed the relative importance of environmental and spatial processes structuring macroinvertebrate metacommunities (De Bie et al., 2012; Heino, 2013), which are related to niche differentiation and dispersal capabilities of the organisms (Leibold et al, 2004). The dispersal capacity of a group determines the importance of this process for the assemblage structuring, both locally and regionally (Beisner et al., 2006; Landeiro et al., 2012). Weaker dispersers usually present a stronger spatial structure and weaker environmental control than organisms with high dispersal capability (Heino, 2011; Soininen et al., 2011; Grönroos et al., 2013). When analyzing an active dispersal community, Shurin et al. (2009) observed a relation between an increased dispersal capacity of the groups and a higher similarity between fragments, i.e., a decrease in beta diversity. In this way, it is expected for macroinvertebrate assemblages to be more spatially structured and to present higher beta diversity at larger spatial extents, when dispersal limitation is more prominent (Baselga, 2010; Dobrovolski et al., 2012). Both environmental filters and dispersal limitation tend to increase species replacement with increasing spatial extent (Soininen et al., 2018). On larger study extents it is also possible to observe nested patterns more clearly, since factors such as local extinctions can be better perceived. At local scale, the spatial structure is usually weaker due to diminished dispersal barriers (leading sometimes to mass effects), and species sorting and biotic interactions are the stronger drivers (Soininen et al., 2011). This can cause a nested pattern of individuals, in which the proportion of the abundance gradients component will be preponderant in the decomposition of beta diversity. So, sites with fewer individuals will be subsets of sites with a larger number of individuals.

Our study intends to evaluate the patterns of beta diversity of aquatic assemblages at two spatial scales in Amazonian streams, as well as to test how environmental and spatial factors affect the beta diversity pattern in freshwater metacommunities with different dispersal modes (shrimps and aquatic insects - ET). For this intent we sampled 15 stream sites in an Amazonian basin, analyzing beta diversity within and between stream sites. We considered the following hypotheses: (i) beta diversity between streams is higher than within streams (between sample units), since at larger spatial extents species sorting is usually stronger considering good dispersers (e.g. ET) and dispersal limitation is usually more prominent considering weak dispersers (e.g. shrimps); (ii) The proportion of abundance gradients is higher within streams and the proportion of balanced variation in abundances is higher between streams, since in small scales the occurrence of mass effects is more evident, whereas in larger scales species sorting is usually more prominent; (iii) Spatial distances will affect the beta diversity pattern of shrimp assemblages since they have a lower dispersal capacity, while ET assemblages are mainly explained by the environmental dissimilarity between stream sites, because they have a good dispersal capacity, sufficient to track the most suitable sites at the region studied.

2. Methods

2.1 Study area

Fifteen streams were sampled within the National Forest (FLONA) of Caxiuanã, northeastern Amazon (Pará state, Brazil). The forest is located on the left bank of the low Anapu River, between the Tocantins and Xingu river basins (Fig. 1). The Anapu River presents its middle and lower portions in low latitude plains, having its mouth at latitude 1 ° 45 'S. Its headwaters are in the Brazilian continental shield in the latitude of 4 ° 30' S, at 200 m asl, and runs south-north. According to the classification defined by Köppen, the climate of the region is type Am, tropical hot and humid, presenting a short period of drought. The region has average annual rainfall between 2000 and 2500 mm, presenting the driest period between the months of September to November and the rainier period from February to April (SUDAM, 1984). The streams in this region are influenced by the tide and the discharge from the Anapu River, which together result in a reduced annual flood pulse (Behling & Costa 2000). The bottom of the streams is usually full of woody debris and leaf litter. The channels are shallow, on average 70 cm deep. The streams of this region are characterized by acidic and oligotrophic waters, with an average pH of 5.5 (Benone et al., 2018).

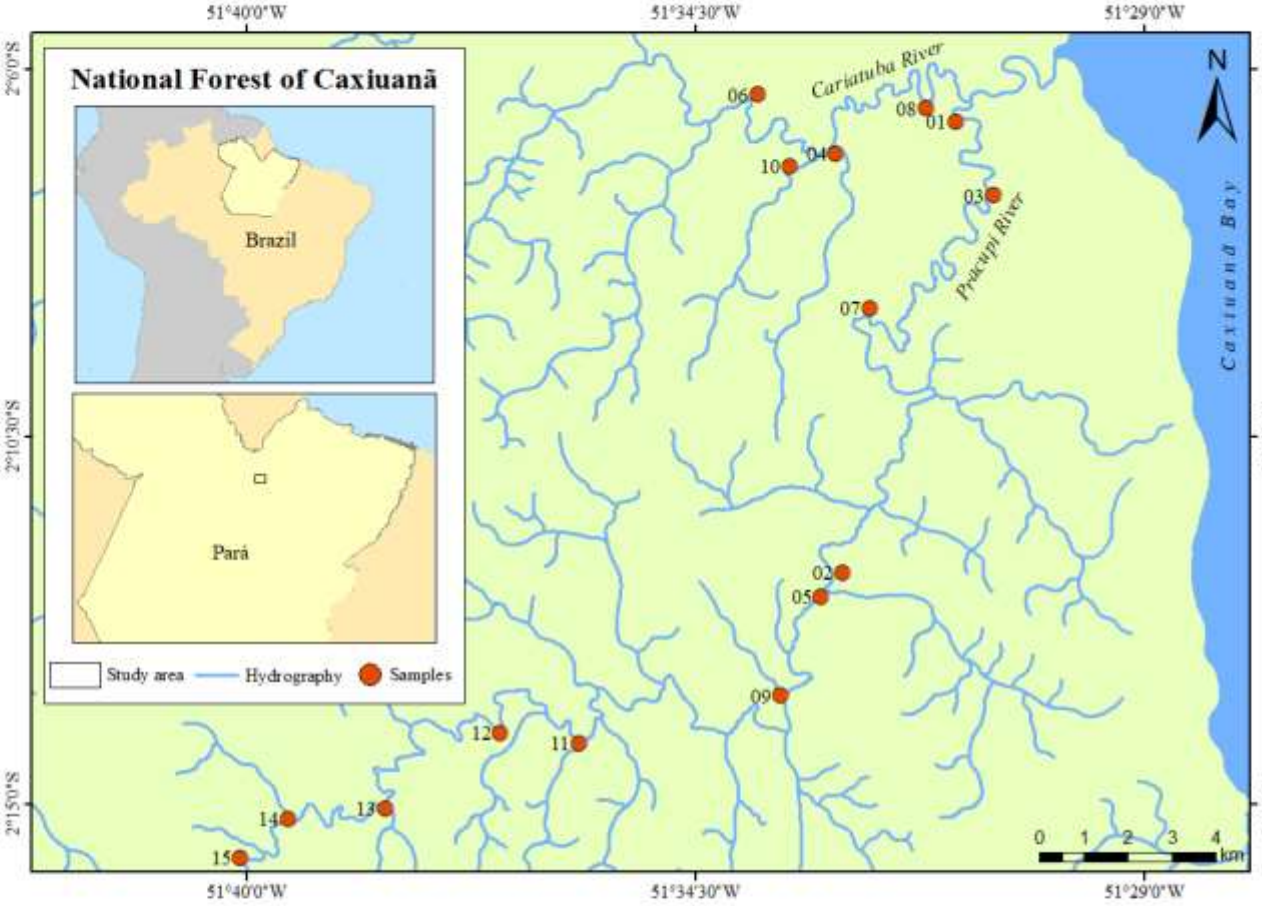

Figure 1 - Location of the lower part of the National Forest of Caxiuanã in the Brazilian state of Pará. Red dots on the map indicate the 15 streams studied.

The Caxiuanã FLONA is composed of 330,000 ha of *terra firme* primary forest (Costa et al., 2007), nearly 85% of its total area, presenting trees with a canopy that reaches 30 m (Costa et al, 1997). Besides *terra firme* forest it is also present the *igapó*, savanna and secondary vegetation (Almeida et al., 1993; Lisboa, 1997). The relief of the Caxiuanã is flat and undulating, and its drainage is branched (Lisboa, 1997).

2.2 Sampling of organisms

Macroinvertebrate collections (shrimps and insects) were carried out in September and October of 2017, during the dry season. In each stream site, we defined a longitudinal reach of 150 meters subdivided into ten sections of fifteen meters. These sections were separated by eleven equidistant transects named "A" (downstream) through "K" (upstream). Each section was subdivided into three segments of five meters each. Only the first two segments of each section were sampled, leaving five meters for the next sampling in order to cause less interference to the local fauna.

The collection effort consisted of two portions of sediment (pooled in a single composite sample) in each segment. It was made using a dip net (*rapiché*) sampler of 18 cm diameter and 250 µm mesh. In the field the individuals were sorted (separating the organisms from the sediment), preserved in alcohol 90% and conditioned in falcon tubes.

In the laboratory, the larvae of aquatic insects (ET) were identified to the genus taxonomic level. The identification was made with the help of the 32x magnification ZEISS® stereomicroscope and based on the dichotomous keys of Pes et al. (2005), Domínguez et al. (2009), Salles (2006), Olifiers et al. (2004), Hamada & Couceiro (2003) and Salles & Domínguez (2012). The specimens were deposited in the Laboratory of Ecology and Conservation (LABECO) of the Federal University of Pará (UFPA). The shrimps were taken to the Emílio Goeldi Museum (MPEG) for identification, going through the same process. The organisms were identified up to the taxonomic level of species based using the dichotomous key of Melo (2003). According to Terlizzi et al., 2009, the information of species level is maintained at genus and family taxonomic levels. Therefore, comparisons of beta diversity patterns between shrimp species and ET genera are reliable.

2.3 Physical habitat measurements

The characteristics of physical habitat of the streams were evaluated by applying an environmental assessment protocol developed by the US Environmental Protection Agency (US-EPA) (Peck et al., 2006) adapted for tropical streams (Callisto et al., 2014). At each transect, and along sections, we measured variables related to resources (food and shelter) important for the organisms studied, including: percentage of roots in the margins (Pct.rm); percentage of small sediment present in the talveg (Pct.sst); average coverage of the riparian vegetation (Ac.rv); number of large wood (0.1 - 0.3m diameter) in the channel (Nlw.1); number of large wood (0.3 - 0.6m diameter) in the channel (Nlw.2); number of large wood (0.6 - 0.8m diameter) in the channel (Nlw.3); average amount of aquatic plants (Aa.ap); average amount of leaf packs (Aa.lp); hanging vegetation used as shelter in the channel (Hv.shelter) and average of large shelter in the channel (Al.shelter).

2.4 Data analysis

The additive partitioning of diversity was used to dissociate, for each macroinvertebrate group, the total taxonomic diversity (γ) into local diversity (α) and difference between sites (β) components, at different spatial scales. This approach gives us a direct comparison between spatial levels, resulting in: $\gamma = \alpha i + \beta i + \beta ii + \beta iii \ldots \beta n$, in which "i, ii, iii ..." corresponding to the different spatial levels considered. The spatial levels we considered were sample units (taken at 5m segments within streams) and stream sites (each sampled reach of 150m). The average richness of the sample units constituted the alpha diversity (α1). β1 was the difference between sample units and β2 was the dissimilarity between stream sites. In this way, the regional gamma diversity was partitioned as: $\gamma = \alpha_1 + \beta_1 + \beta_2$ (Fig. 2). In order to test the relative importance of each beta value generated in the partition and check whether the distributions differed of chance, a null model was used. We used the type 1 null model described by Crist et al. (2003), which consists of randomizing the allocation of individuals among all sample units. The algorithm randomly reorganizes individuals in the samples, preserving the abundance of the original species and the distributions by sample size. This results in an equal total diversity (γ) between the observed and randomized values, and the observed diversities at each hierarchical level are compared with the values of the randomizations. To generate the diversity values expected by chance, the assemblage composition among sites was randomized 9,999 times. The p-value of each component of the partition corresponded to the proportion of simulations that had values higher than the observed diversity. Thus, very low p-values (propexp > obs < 0.025) indicate that the observed diversity is significantly higher than that expected by chance, while very high p-values (propexp > obs > 0.975) indicate an observed diversity significantly lower than expected by chance. The analyses were done using the software Partition version 2.0 (Veech & Crist, 2007).

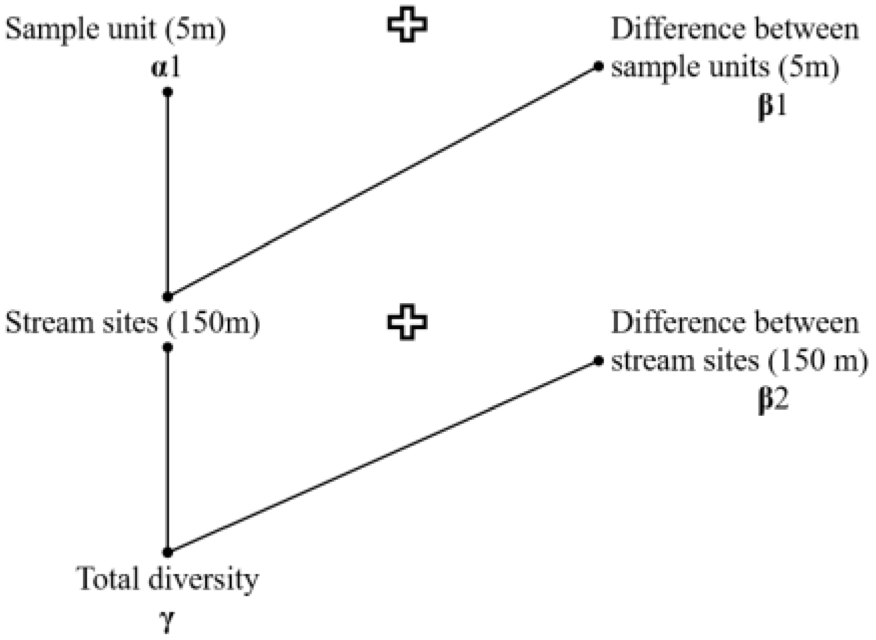

Figure 2 - Representation of the additive partitioning of gamma diversity at all spatial levels considered. Sample units represent the average diversity at the smallest scale (α1), and total diversity (γ) is the total diversity of the studied basin, represented by the sum of all diversity components (γ = α1 + β1 + β2).

We calculated the beta diversity for each spatial level of each group of macroinvertebrates (shrimps and ET) based on the Ruzicka index (Ruzicka, 1958), which considers the composition and the abundance of species, being a quantitative version of the Jaccard index. Total beta diversity was decomposed into balanced variation in abundances (which is equivalent to species replacement when considering the abundances) and abundance gradients (in which is equivalent to richness difference when considering the abundances) components: βtotal = βbal + βgrad (Podani and Schmera, 2013 Carvalho et al., 2012, Baselga, 2017). Thus, βtotal reflects both replacement and loss- gain of specie's abundance between the sites, βbal is the balanced replacement of specie's abundance identities, i.e., the abundances of some species is replaced by the abundances of individuals of different species in another site, and βgrad relates to species loss- gain in abundance differences alone. We calculated the decomposition of beta diversity for the two hierarchical levels. For the lowest level (between sample units) we calculated beta diversity comparing the 20 sample units of each stream, taking the average value for each of the 15 streams, resulting in 15 average values for each component of beta diversity (βtotal, βbal and βgrad). For the highest hierarchical level (stream sites) we used the total abundances present in the 15 streams to generate one decomposition of beta diversity. In this way, we produced dissimilarity matrices based on each component of beta diversity for each macroinvertebrate group in both spatial levels using the 'beta' function in the R package BAT (Cardoso, Rigal, & Carvalho, 2015), program R version 3.2.0.

In order to test the effects of spatial distances and environmental dissimilarity on the variation of beta diversity between sites we used multiple regression of distance matrices (MRM, Lichstein 2007), with each matrix of beta diversity (βtotal, βrepl and βrich) as dependent variables and spatial distances (linear and fluvial) and environmental dissimilarity matrices (one matrix for each of the 12 variables) as predictors. Environmental matrices were generated applying Euclidian distances on standardized data (considering each environmental variable). To represent the spatial distances between sampled sites, we calculated matrices from the geographic coordinates, through two distinct methods: linear and fluvial distances. According to studies carried out by Bilton et al. (2001), a matrix of linear distances is more adequate for the representation of spatial distances for organisms that migrate through the land, like aquatic insects with winged stages. So, we calculated the linear distance matrix using Euclidian distance between the sites. For the shrimps, spatial distances were determined from the dendritic network, i.e., the distance between the sites following the drainage course (fluvial distances) (Landeiro et al., 2011). The shapes of the local drainage system at 1:100.000 scale was used to calculate these distances, being calculated in the ArcGis program.

To test the significance of MRM models and regression coefficients we made 9,999 permutations with response matrix, holding the explanatory matrices constant. Currently there is no model selection implemented for MRM analysis. Therefore, to find the models that best described the dependence of beta diversity on spatial and environmental variables we performed a sort of backward selection. We first performed full models (including all the predictors) and then reduced the number of predictors gradually (each time removing the predictor with worst performance, i.e., lower p value), observing the impact of the model reduction on its coefficient of determination (r^2). When the exclusion generated an expressive relative decrease in the r^2 value, we stopped to exclude predictors. So, we kept the models with fewer predictors and maximized r^2, in this way aiming to respect the principles of explanatory power and parsimony.

In order to better illustrate our analytical process, we made a conceptual scheme describing all the steps we followed to analyze the beta diversity and respond our major questions (Fig 3).

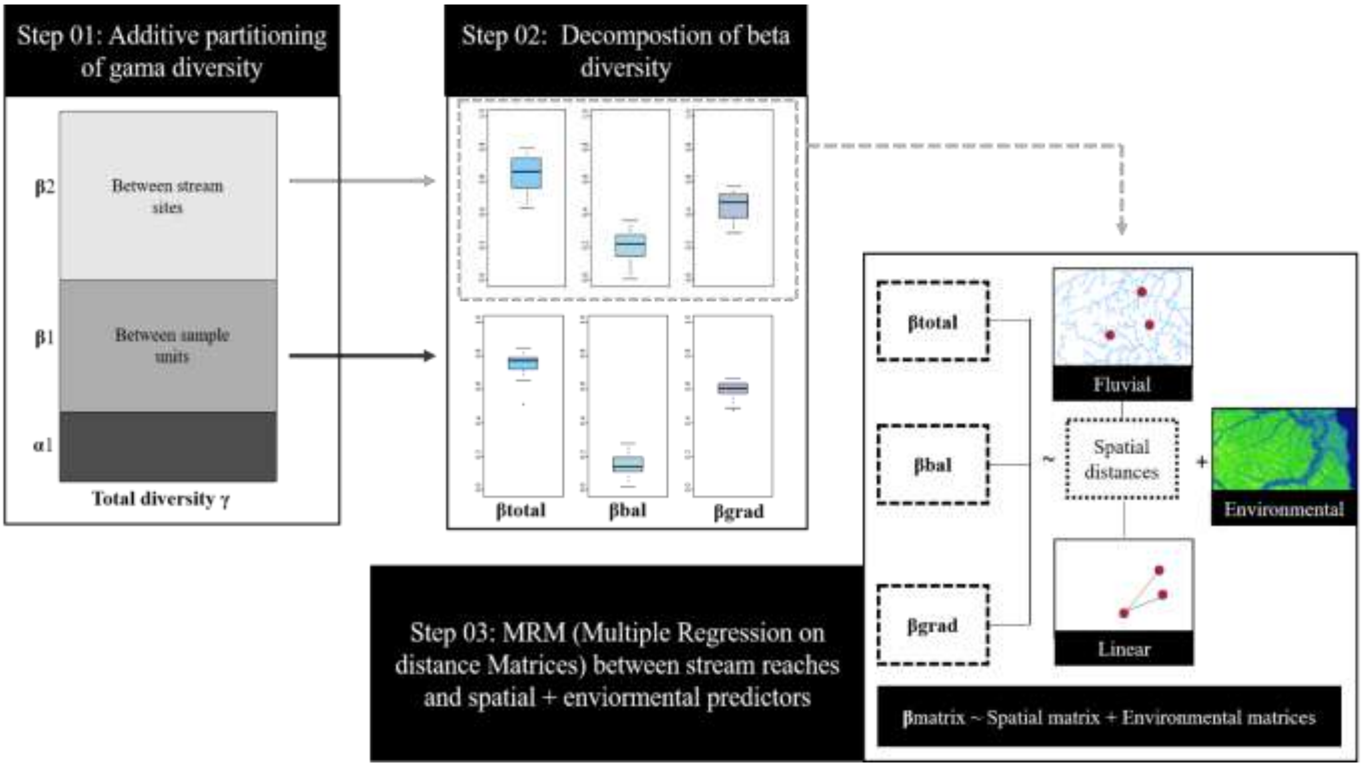

Figure 3 - Conceptual scheme of data analysis

3. Results

Of all the 2432 individuals of macroinvertebrates collected, 1387 were insects of the orders Trichoptera and Ephemeroptera. These were represented by 8 families and 18 genera. The order Decapoda had 1045 individuals, distributed in 3 families, 4 genera and 6 species. The most abundant genus of insect was *Miroculis* sp. (60.12% of specimens), and the least abundant were: *Smicridea* sp., *Ulmeritoides* sp. and *Zelusia* sp. (0.07% of specimens). For the order of decapods, the most abundant taxa were *Palaemon carteri* (Gordon, 1935) (48.55%) and *Euryrhynchus burchelli* (Calman, 1907) (29.34%) (Table 1).

Table 1 - Abundance per macroinvertebrate taxa at 15 stream sites in the FLONA Caxiuanã (Pará, Brazil)

Taxon	*Species/genera*	*Abundance*	*Mean ± SD*
Trichoptera			
Calamoceratidae	*Phylloicus* sp	113	7.5 ± 12.3
Hydropsychidae	*Macronema* sp	89	5.9 ± 5.4
	Smicridea sp	1	0.1 ± 0.2
Leptoceridae	*Oecetis* sp	22	1.5 ± 2.0

	Nectopsyche sp	3	0.2 ± 0.4
	Triplectides sp	26	1.7 ± 4.6
Polycentropodidae	*Cernotina* sp	192	12.8 ± 19.1
Ephemeroptera			
Beatidae	*Aturbina sp*	14	0.9 ± 1.5
	Callibaetis sp	5	0.3 ± 1.0
	Zelusia sp	1	0.1 ± 0.2
Caenidae	*Brasilocaenis sp*	38	2.5 ± 3.6
Euthyplociidae	*Campylocia sp*	17	1.1 ± 2.1
Leptophlebiidae	*Farrodes sp*	13	0.9 ± 1.8
	Homothraulus sp	3	0.2 ± 0.5
	Microphlebia sp	10	0.7 ± 1.3
	Miroculis sp	834	55.6 ± 55.6
	Simothraulopsis sp	5	0.3 ± 0.6
	Ulmeritoides sp	1	0.1 ± 0.2
Decapoda			
Euryrhynchidae	*Euryrhynchus burchelli* (Calman, 1907)	304	20.3 ± 14.5
	Euryrhynchus wrzesniowskii Calman, 1907)	208	13.9 ± 8.2
Palaemonidae	*Palaemon carteri* (Gordon, 1935)	503	33.5 ± 33.2
	Palaemon mercedae (Pereira, 1986)	1	0.1 ± 0.2
	Macrobrachium nattereri (García et al., 1996)	7	0.5 ± 1.0
	Macrobrachium surinamicum (Holthuis, 1948)	18	1.2 ± 2.0
Sergestidae	*Acetis* sp	4	0.3 ± 0.6
Total		**2432**	

According to the additive partition of gamma diversity, the average number of taxa in each sample unit (α1) was similar between the two groups of macroinvertebrates: decapods (1.3) and ET (1.6). In both cases, the alpha diversity was lower than expected by chance (propexp > obs > 0.999). However, when we checked the ratio of α1 to γ the values differed between groups. In shrimps α1 represented 20% of gamma diversity and α1 of ET represented 10% of total richness (Fig 4).

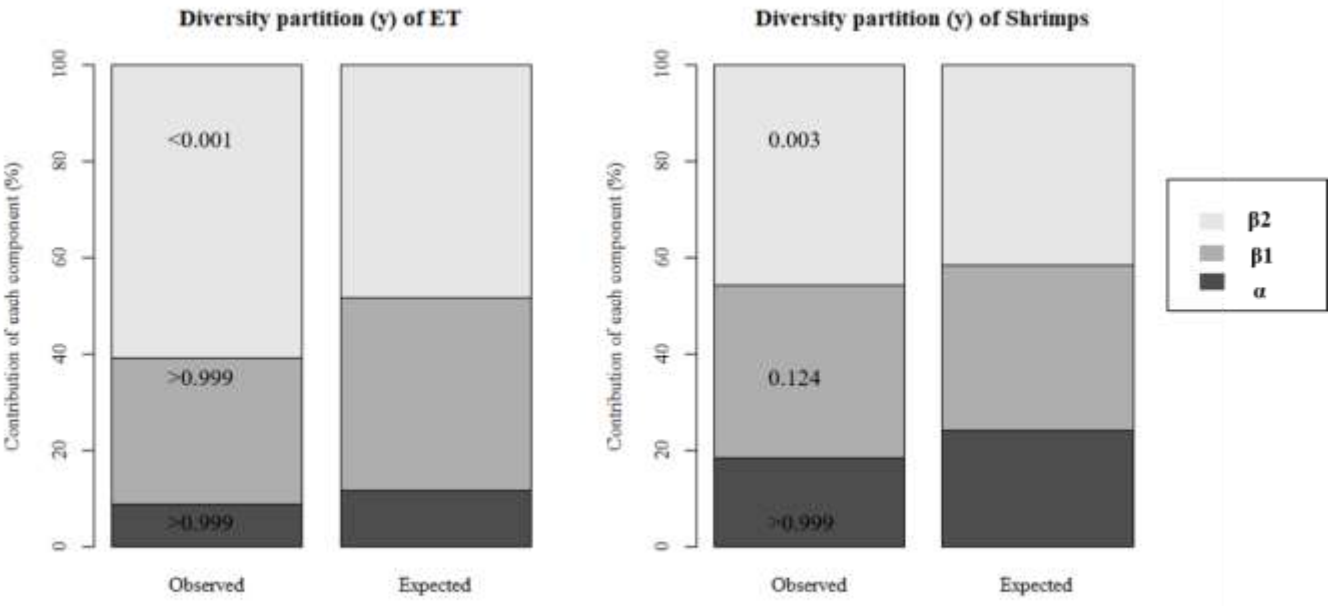

Figure 4 - Observed and expected diversities (alpha and beta) expressed as the percentage of the total richness of ET genera and shrimp species. α1, average number of taxa per sample unit; β1, beta diversity between sample units; β2, beta diversity between streams sites.

The relative contribution of component β1 (difference between sample units) was similar between groups (35% Decapods; 30% ET), and non-significant, so the observed values were not different than expected by chance ($p = 0.124$ for Decapods and $p > 0.999$ for ET). The component β2 (difference between stream reaches) presented a greater contribution to gamma diversity (45.7% Decapods; 60.5% ET), significantly higher than expected by chance ($p = 0.003$ and $p < 0.001$, respectively).

Considering the decomposition of total beta diversity into balanced variation in abundances and abundance gradients components in each of the 15 streams, a very similar pattern was observed for both macroinvertebrate groups. The total beta diversity (Ruzicka index) differed only slightly between macroinvertebrate groups (mean values for ET: 0.724 and shrimps: 0.744; Fig 5). The abundance gradients presented a higher percentage contribution to total beta diversity (ET: 74.3% and shrimps: 79.9%). The average percentage of balanced variation in abundances component also presented little difference between the macroinvertebrate groups (ET: 25.5% and shrimps: 20.1%).

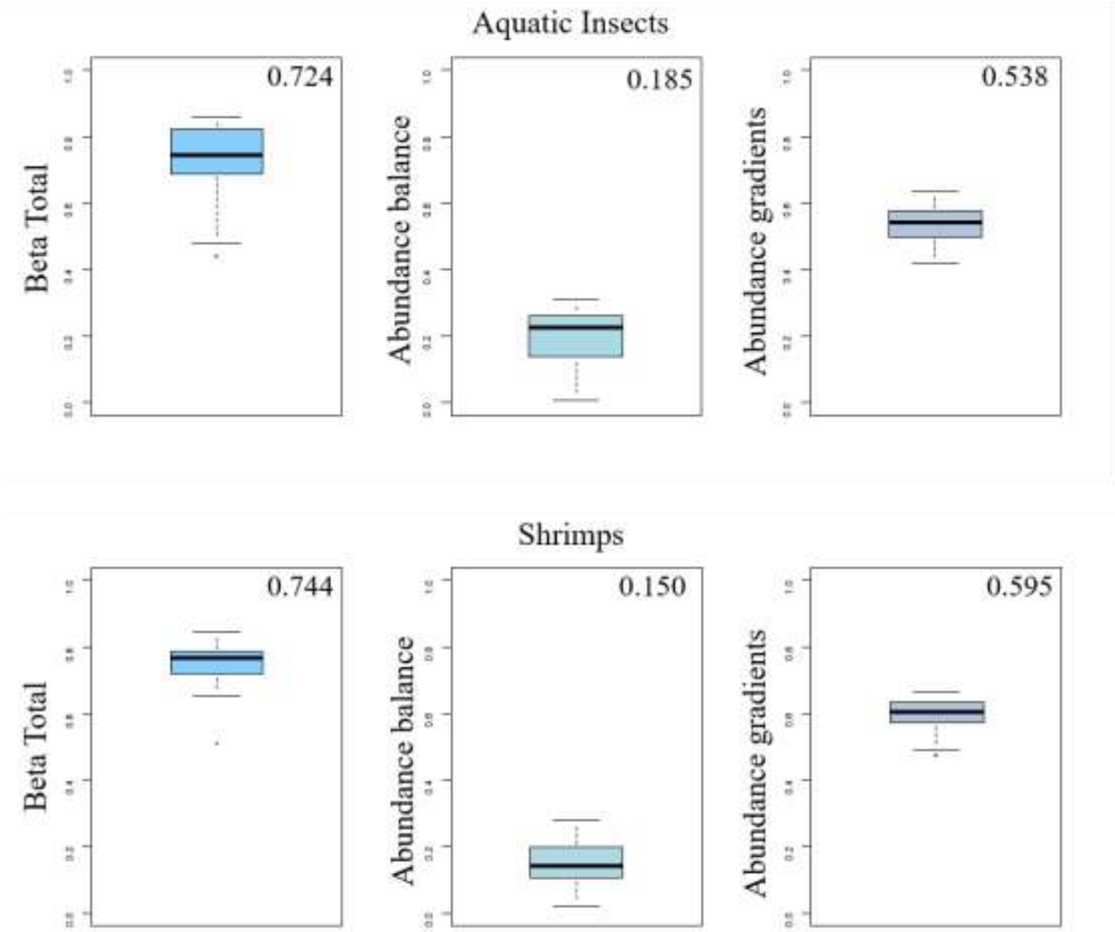

Figure 5 - Boxplots of average values of pairwise dissimilarities (Ruzicka index) between sample units at each stream site for total beta diversity, balanced variation in abundances and abundance gradients of shrimps and aquatic insects (Ephemeroptera and Trichoptera orders). The median value was represented in the horizontal line inside de box, box limits denotes first and third quartiles, whiskers denote minimum and maximum values, and dots indicate outliers. Numbers at the top of the boxes inform the mean of the average values obtained for the mean values of the 15 stream sites.

Concerning the decomposition of beta diversity between the 15 streams we found distinct patterns between groups of organisms. Total beta diversity of shrimps had a lower mean value than total beta diversity of ET (ET: 0.774 and shrimps: 0.614). The percentage contribution of abundance gradients was only slightly higher than species replacement in both groups (ET: 71.9% and shrimps: 62.3%). The percentage contribution of balanced variation in abundances was quite not so similar between groups (ET: 32.1% and shrimps: 37.6% (Fig 6).

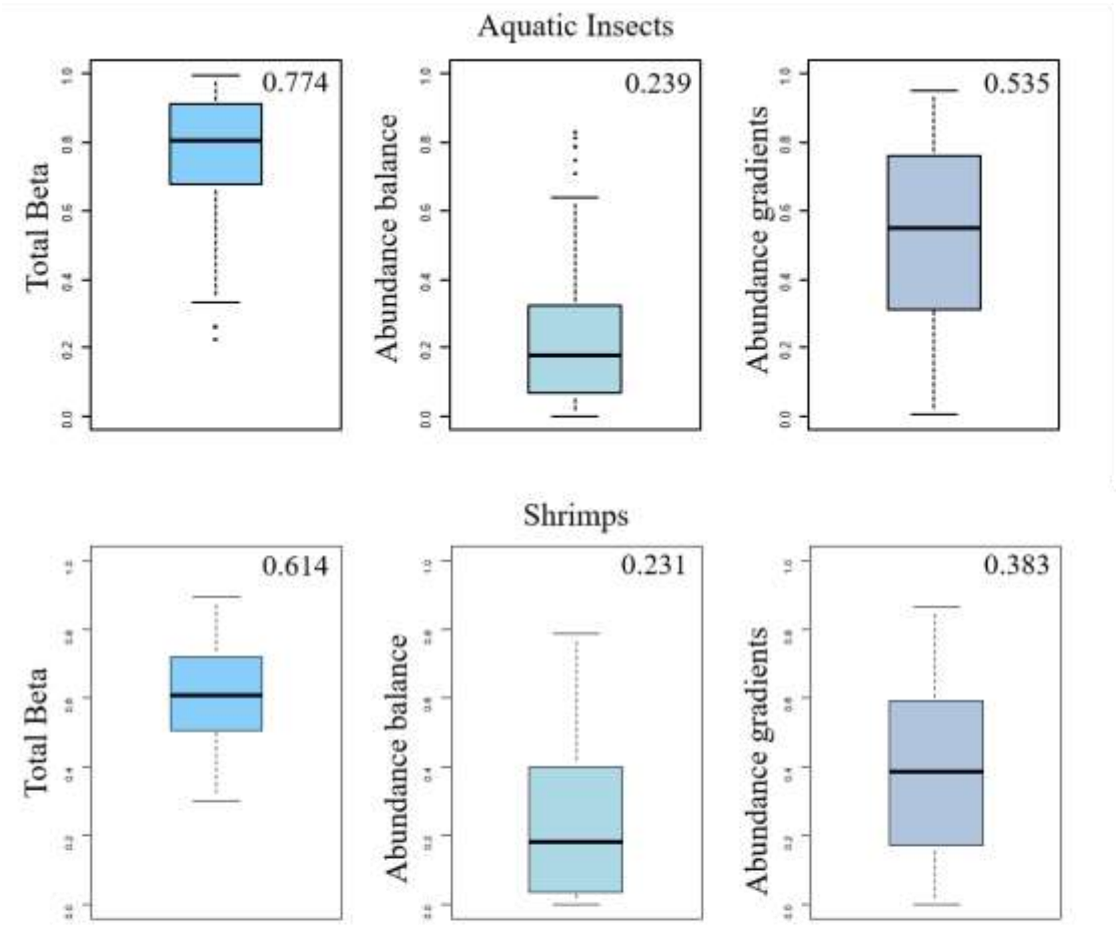

Figure 6 - Boxplots of values of pairwise dissimilarities (Ruzicka index) between stream sites for total beta diversity, balanced variation in abundances and abundance gradients of shrimps and aquatic insects (Ephemeroptera and Trichoptera orders). The median value was represented in the horizontal line inside de box, box limits denotes first and third quartiles, whiskers denote minimum and maximum values, and dots indicate outliers. Numbers at the top of the boxes inform the average of dissimilarity values.

The results of the MRM analyses presented distinct relationships of beta diversity with spatial and environmental components between macroinvertebrate groups. The selected models for ET presented significant environmental effects on the beta matrices and no relationship was found with the linear distances between the sample sites. Furthermore, no predictor was found to explain the relationship between the environmental variables and the βgrad matrix of ET (Table 2). In contrast, when analyzing the shrimp matrices, a mixed pattern was observed; both spatial distances and environmental variables were related with beta diversity. For βtotal and βbal, the spatial component was significant to explain the changes between the assemblages (Table 3).

Table 2 - Results of the MRM (multiple regression of distance matrices) analyses for aquatic insects (Ephemeroptera and Trichoptera orders). Dependent variables were βtotal, βrepl and βrich matrices and independent variables were spatial and environmental distance matrices. r² values were generated for each model and p values for each predictor. We used 9999 permutations for testing statistical significance. Pct.rm: percentage of roots in the margins; Pct.sst: percentage of small sediment present in the talveg; Ac.rv: average coverage of the riparian vegetation; Nlw.1: number of large wood (0.1 - 0.3m diameter) in the channel; Nlw.2: number of large wood (0.3 - 0.6m diameter) in the channel; Nlw.3: number of large wood (0.6 - 0.8m diameter) in the channel; Aa.ap: average amount of aquatic plants; Aa.lp: average amount of leaf packs; Hv.shelter: hanging vegetation used as shelter in the channel and Al.shelter: average of large shelter in the channel.

AQUATIC INSECTS

VARIABLES	**β total**	***p***	**β bal**	***p***	**β grad**	***p***
INTERCEPT	0.702	0.856	0.246	0.223	----	----
LINEAR DISTANCE	----	----	----	----	----	----
PCT.RM	----	----	----	----	----	----
PCT.SST	----	----	-0.078	**0.018**	----	----
AC.RV	----	----	----	----	----	----
NLW.1	0.074	**0.005**	0.07	**0.025**	----	----
NLW.2	----	----	----	----	----	----
NLW.3	----	----	----	----	----	----
AA.AP	0.027	0.354	----	----	----	----
AA.LP	----	----	----	----	----	----
HV.SHELTER	-0.038	0.152	----	----	----	----
AL.SHELTER	----	----	----	----	----	----
Model r²	0.165	**0.039**	0.119	**0.011**	----	----

Table 3 - Results of the MRM (multiple regression of distance matrices) analyses for shrimps. Dependent variables were βtotal, βrepl and βrich matrices and independent variables were spatial and environmental distance matrices. r² values were generated for each model and p values for each predictor. We used 9999 permutations for testing statistical significance. Pct.rm: percentage of roots in the margins; Pct.sst: percentage of small sediment present in the talveg; Ac.rv: average coverage of the riparian vegetation; Nlw.1 :number of large wood (0.1 - 0.3m diameter) in the channel; Nlw.2: number of large wood (0.3 - 0.6m diameter) in the channel; Nlw.3: number of large wood (0.6 - 0.8m diameter) in the channel; Aa.ap: average amount of aquatic plants; Aa.lp: average amount of leaf packs; Hv.shelter: hanging vegetation used as shelter in the channel and Al.shelter: average of large shelter in the channel.

SHRIMPS

Variables	**β total**	***p***	**β bal**	***p***	**β grad**	***p***
INTERCEPT	0.48	0.999	0.19	0.615	0.195	0.998
FLUVIAL DISTANCE	0.00	**0.007**	0.00	**0.001**	----	----
PCT.RM	0.03	**0.039**	----	----	----	----
PCT.SST	0.07	**<0.001**	0.06	**0.038**	----	----
AC.RV	----	----	----	----	----	----
NLW.1	-0.03	**0.042**	----	----	----	----
NLW.2	----	----	----	----	----	----
NLW.3	----	----	----	----	----	----
AA.AP	----	----	----	----	----	----
AA.LP	----	----	-0.07	**0.012**	0.075	**0.018**
HV.SHELTER	----	----	----	----	----	----

AL.SHELTER	----	----	-0.06	**0.044**	0.083	**0.013**
Model r^2	0.227	**0.002**	0.243	**0.002**	0.117	**0.012**

The total beta diversity of ET was affected by the Nlw.1, Aa.ap and Hv.shelter, whereas the balanced variation in abundances component was related to the Pct.sst and Nlw.1. We found relationships between βtotal and βbal with the spatial distances between sites and the Pct.sst. We also found a significant relationship between the total beta diversity and Nlw.1 together with Pct.rm. The components βbal and βgrad were only related to Al.shelter and Aa.lb.

4. Discussion

In general, ecological processes related to the assembly of metacommunities change with the spatial extent considered (Wu & Loucks, 1995, Ligeiro et al., 2010). That is true especially considering the dispersal-related phenomena (Heino & Peckarsky, 2014; Heino et al., 2015a). Processes related to dispersal have been identified as one of the main drivers of beta diversity (Padial et al., 2014), along with environmental heterogeneity (Heino et al., 2015b; Leibold & Chase, 2017). In this study, we first identified the spatial level that contributed mostly to regional diversity. For both macroinvertebrate groups, dissimilarity among stream sites (β2) presented a higher contribution for total diversity of the studied stream basin. This outcome corroborates our first hypothesis, i.e., the higher spatial level (among stream sites) presented greater beta diversity. The higher beta diversity at this level may be associated with both environmental filtering and dispersal limitation, depending of the animal group considered, in agreement with Heino et al. (2015a, 2015b). In insects with winged adults, like ET, it is expected to the individuals to better track the environmental conditions across the region, consequently strengthening the species sorting. In this case, beta diversity mainly reflects habitat heterogeneity among streams in the studied region. In shrimps it is expected the opposite, with dispersal limitation generating beta diversity between streams. We can associate these metacommunity processes with the results of MRMs, which showed the presence of spatial and environmental effects for shrimp and purely environmental for ET. Soininen et al. (2007) also found that total beta diversity increased at larger spatial extents. With the increase in spatial extension there is a possible increase in environmental variation (Jackson, Peres-Neto e Olden, 2001). Therefore, it is possible to relate spatial extension to environmental heterogeneity (e.g. Harrison et al., 1992), resulting in greater strength of species sorting, and greater beta diversity between sites (Heino, 2011). However, the consideration of this pattern should be done with caution at smaller spatial extents as the one we evaluated in this work (more distant streams presenting 20.9km of distance between them). In this study, is more likely to assume that differences in beta diversity observed between sample units and between streams were related to differences in environmental heterogeneity and dispersal processes, with a greater possibility of mass effects in smaller scales (within streams) and greater strength of environmental filters (in ET) and dispersal limitation (in shrimps) between streams.

In our study we found lower values for beta diversity at smaller spatial levels (between sample units, β1), not significantly different from the expected under the null model. On the other hand, differences between stream sites (β2) were high. Ligeiro et al. (2010) also found higher values of beta diversity between stream sites than between riffles / sample units within streams. Hepp & Melo (2013) also followed an additive partitioning approach to evaluate the spatial distribution of benthic macroinvertebrates and found a dependence of the spatial structure with the scale of study. In the other hand, Costa & Melo (2008) showed that environmental differences between microhabitats were more important for the assemblage composition of macroinvertebrates than the spatial location of streams. It was realized that different types of microhabitats located adjacent to each other at the same stream site contained more distinct assemblage compositions than the same type of microhabitats located at different streams. Therefore, it is possible for smaller spatial levels in streams to present high beta diversity due to a high heterogeneity of microhabitats. Accordingly, in our study the lower values of beta diversity found between sample units may be the result of a smaller environmental variation, and also a greater probability of occurrence of mass effects at this scale for both groups

For both groups of organisms, we identified that the mean values of the abundance gradients component contributed mostly to total beta diversity, at both spatial levels (within and between stream sites), in this way only partially corroborating our second hypothesis. This pattern may be the effect of common (widely distributed) and abundant individuals present in our sampling. Most sample units presented species with high abundances, while other sample units had very few species and lower abundances. However, usually the same species were involved as in a nested scheme. This relationship between regional distribution of individuals and their local abundance was reported by Heino (2005) for stream insects, which inferred about relationships between abundance and niche breadth. A pattern of high dissimilarity among assemblages with low species richness (nested pattern) was already described by Chase et al. (2011). It is possible that mass effects at this spatial scale may have promoted homogenization in the assemblage composition between sample units. However, it is still unclear in the literature if any variation in the difference component of beta diversity can be related to an increase or decrease in the spatial scale. As reported by Rádková, 2014, greater importance of the abundance gradients component is expected in cases of nested differences in the quality of the habitats. This pattern has been reported both in comparisons within (Juřičková et al., 2008) and between sites (Hylander et al., 2005; Horsák & Cernohorsky, 2008). Some studies, like Padial et al. (2014) and Leibold & Chase (2017) attribute changes in the values of difference to the frequency of dispersion events and environmental heterogeneity.

Our results showed that the percentage of small sediments present in the talveg and the number of large woods (0.1 - <0.3 m) in the channel significantly influenced most beta diversity components, these two variables being related to βtotal and βbal of ET and shrimps. This partially corroborates the third hypothesis which predicted environmental variables as the main drivers of beta diversity of ET assemblages. The importance of environmental factors structuring aquatic insect assemblages has been described over the years (Ligeiro et al., 2010; Moya et al., 2011; Hepp et al., 2012; Landeiro et al., 2012). Aquatic insects present a high habitat selectivity, which is why they are considered efficient bioindicators in stream assessments (Edegbene & Arimoro, 2012). Insects select habitats based on their suitability for oviposition (e.g. Timm, 1994; Winterbourn, 2003) or due to environmental filters that act on the larvae (Holomuzki & Messier, 1993). The study made by Montag et al. (2019) reports a positive relationship between the amount of wood within stream channels and the composition of insect assemblages in eastern amazon streams. Wright & Flecker (2004) and Pilotto et al. (2016) attribute this to the fact that wood promotes submerged structures that can provide food resources, shelter from predation and nesting sites. Furthermore, the presence of wood contributes to the increase in the structural complexity of the habitat, which has a direct influence on the pattern of distribution of aquatic organisms in aquatic ecosystems (Johnson et al., 2003; Scealy et al., 2007). In turn, the increase in the structural complexity of habitat favors the coexistence of several taxa with different environmental requirements (Barreto, 1999). In agreement with our results, Bryce et al. (2010) also identified the size of the sediment as a structuring factor for assemblages of benthic macroinvertebrates. The absence of relationship between ET beta diversity and spatial distances between stream sites may suggest the absence of dispersal limitation at the studied spatial extent (Heino et al., 2015b).

Both the fluvial distances between sites and the environmental dissimilarities affected the beta diversity of the shrimp assemblages. This result corroborates our third hypothesis which stated that spatial distances would be important explaining the distribution of shrimp assemblages. The relationship found between balanced variation in abundances and total beta diversity with the fluvial distances may be an indication of the life strategy of most of these organisms, which migrate through the stream network during the larval stage. This migration movement confined to the water pathways may generate a strong dispersal limitation (Grönroos et al., 2013), which could be perceived between the studied streams. As our study, Wan et al. (2015) also attributed environmental and spatial predictors as important factors of the distribution of stream macroinvertebrate assemblages. Considering total beta diversity, percentage of roots in the margins, percentage of small sediment present in the talveg and number of large woods in the channel (0.1 - 0.3m) had a significantly relationship with changes in shrimp assemblages. However, in βrepl and βrich we observed average amount of leaf packs and average of large shelter in the channel as the main drivers. These two components are related to the recycling of organic matter in tropical streams, in which shrimps play an important role (Bobeldyk & Ramírez, 2007). Besides of being a food resource, leaf packs in streams also provide shelter against predation (Henderson & Walker, 1986). For βrepl we also found a relationship with percentage of small sediment present in the talveg. The omnivorous habits of decapods make it possible for them to use resources with maximum efficiency (Collins et al., 2007). So, besides using leaves and large woods as food sources or places to find food (i.e. insect larvae, algae and debris), they also use them as shelter against predators and natural disturbances. This leads us to believe that shelter availability, especially leaf packs and the presence of wood in the streams, drives the change in shrimp assemblages between streams.

5. Conclusions

Our results showed that the patterns of beta diversity of ET and shrimp assemblages change with the spatial level analyzed (within and between stream sites). For both macroinvertebrate groups the dissimilarity between stream sites contributed mostly to regional diversity and, at both spatial scales, there was a prevalence of abundance gradients generating beta diversity, which reflects in a nested pattern. In accordance to our predictions, the distribution of ET was explained only by environmental factors, suggesting that dispersal limitation did not occur for these winged dispersants at the spatial extent evaluated. We found a mixed pattern for shrimps, in which both the spatial and the environmental distances explained the variation in beta diversity.

Our findings indicate that the dynamics of aquatic macroinvertebrate assemblages in tropical streams is driven by different predictors when considering groups of organisms with different types of dispersal. We made progress investigating the patterns of beta diversity at small spatial scales, but further studies should make an effort to disentangle the roles of habitat heterogeneity and mass effects to macroinvertebrate beta diversity within stream sites. The use of a hierarchical spatial framework proved to be a very useful approach to identify the scales where biological dissimilarity is more prominent, which is important for both applied and theoretical purposes. The identification of the spatial scale which presents the highest beta values make possible to, as well as to infer about the ecological processes driving patterns of assemblage distribution. Thus, in this study we advanced in the understanding of the generation and maintenance of beta diversity of macroinvertebrates with distinct dispersion capabilities in tropical streams, and the factors that affect the distribution of these assemblages.

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