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PRIMARY RESEARCH PAPER

Beta diversity in stream macroinvertebrate assemblages: among-site and among-microhabitat components

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Abstract The benthic macroinvertebrate community is an important component of stream diversity, because its members are fundamental connectors among the different trophic levels of running waters. In this study, we assessed alpha and beta diversities of benthic macroinvertebrates in three stream sites and four microhabitats: (i) moss in the air-water interface; (ii) submerged roots of terrestrial plants; (iii) leaf litter deposited in pools; (iv) stones in riffles. We constructed rarefaction curves and compared species richness among microhabitats for each stream site. Additionally, we evaluated which factor, stream site, or microhabitat, was most important in determining variation in assemblage structure, i.e., beta diversity. There was no significant difference among microhabitats in terms of taxa richness evaluated by rarefaction curves. Using partial Constrained Correspondence Analysis (pCCA), we found that microhabitat was most important in determining community composition, accounting for 42.02% of the total variation. Stream sites accounted for 22.27%. In accordance with the pCCA, exploratory multivariate methods (ordination and classification) revealed four distinct groups, corresponding to the four microhabitats, independent of stream sites. Our results indicated that differences among environmental conditions are much more important in the determination of stream assemblage structure than are differences in spatial location. Accordingly, adjacent microhabitats in a single stream site harbor macroinvertebrate assemblages more dissimilar than those found in a single microhabitat at different stream sites.

Keywords Riffle · Pool · Moss · Submerged roots · Microhabitat · pCCA

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Introduction

Biological diversity in a region, termed gamma diversity, may be partitioned into two components. The first component is alpha diversity, and includes the diversity of species within sites. Alpha diversity may be measured either as species richness or by

diversity indices. The second component, beta diversity, relates to differentiation of communities along gradients or the rate of species replacement among sites. Beta diversity may be measured in several ways. Koch (1957) suggested the use of the "Index of Biotal Dispersity", an extension of the Jaccard distance index that handles more than two samples. Whittaker (1960) suggested that beta diversity could be measured as the ratio of gamma to alpha diversities. Whittaker's index was widely adopted in the following decades and underwent several adaptations (Harrison et al., 1992; Magurran, 2004). An alternative approach interprets beta diversity as the difference between gamma and alpha diversities (Allan, 1975; Gering & Crist, 2002).

Beta diversity is a measure of biological dissimilarities among environments. Such dissimilarities can be caused mainly by dispersal limitations, usually autocorrelated in space, and by differences in the physical environment. In order to differentiate the influence of spatial variation from those caused by environmental factors, Legendre et al. (2005) suggested the use of partial Constrained Correspondence Analysis (pCCA).

Previous studies have shown that the two main causes affecting beta diversity, difference in environmental conditions and geographical distance, are important factors in stream macroinvertebrate assemblages. Streams provide a multiplicity of microhabitats, each one subjected to a combination of environmental factors. Riffles, submerged roots, pools, and waterfalls are examples of microhabitats commonly found in streams. The specific combination of environmental factors (velocity, depth, availability of organic material, and the type and size of the particles composing the substrate) in each microhabitat is fundamental to the determination of the associated macroinvertebrate assemblage (Beisel et al., 1998; Robson & Chester, 1999; Callisto et al., 2001; Lamouroux et al., 2004). Accordingly, previous studies have related the distributions of taxonomic or functional feeding groups to particular microhabitats. Huamantinco & Nessimian (1999) observed that filter-feeding caddisflies of the genus *Smicridea* (Hydropsychidae) were most abundant in riffles. Wood & Sites (2002) obtained samples from pools, riffles and rootmats, and observed that of the total 75 taxa found, 13 were unique to rootmats.

Despite the relative lack of studies relating the effects of geographical distance to variation of stream macroinvertebrate assemblages, there is clear evidence of its importance in stream macroinvertebrate communities. Historical–biological events affecting a given patch likely affect neighboring areas. For instance, patches within a stream reach may support high abundance of a particular aquatic insect due to the success of a single or a few females in the previous generation (Bunn & Hugues, 1997). Effects of disturbance caused by rupture of debris dams during high-flow events may extend to several areas downstream (Melo & Froehlich, 2004). Accordingly, assemblages are not distributed regularly, even within single homogenous microhabitats. For instance, Downes et al. (2000) found that variation among stream sites in the same river was considerably higher than that observed among rivers. Diniz-Filho et al. (1998) found that differences in composition of aquatic insects among stream sites in the dry season were best explained by pollution. However, geographical distance among stream sites was the best predictor of similarities among stream sites in the rainy season.

We obtained samples from four microhabitats (stones in riffles, submerged roots of terrestrial plants, mosses in the air-water interface zone, and litter deposited in pools) of three stream sites. We compared alpha diversity (species richness) among these four microhabitats. Since different sampling methods were employed in each microhabitat, the comparisons were made using rarefied taxa richness. Our main objective was to relate differences in species composition (i.e., beta diversity) to predictors. Therefore we did not focus on the partition of diversity (species richness) among its alpha and beta components. We used exploratory multivariate analysis, including pCCA, to evaluate which factor, stream site, or microhabitat, better determined differentiation (beta diversity) in community structure.

Methods

Study area and sampling

The streams studied are located in the Rio do Carmo catchment, in the Intervales State Park (24°18′ S, 48°25′ W), São Paulo state, Brazil. The vegetation is

Tropical Ombrophilous Submontane-montane Forest, known as Atlantic Rain Forest. The mean annual precipitation in the area is 2,040 mm. Rainfall is concentrated in the warm period (15–30°C) of September–March with 150–400 mm/mo. The cold period (0–25°C) of April–August receives 60–150 mm/mo. The study comprised samples obtained in three stream sites during the austral summer of 2004. All three streams have forested catchments with well-preserved vegetation, and are free of point pollution. There are no houses or farms in the stream catchments. The streambeds were composed of many types of stones, especially sedimentary stones (Melo & Froehlich, 2001). The first site is a first-order stream with a width of 0.5–1.0 m and a discharge of 0.004 m^3/s. The second stream site is a third-order stream, 3–4 m wide, and with a discharge of 0.076 m^3/s. The third site is a fourth-order stream, 9–11 m wide and with a discharge of 0.493 m^3/s. Geographical distances between sites were less than 6 km. The streams are close to each other and have similar forested catchments. Additionally, the streams were selected based on geological similarity. The single notable differing factor was stream size. A previous study showed that although stream size has an effect on faunal composition, it is of low magnitude (Melo & Froehlich, 2001). Accordingly, most of the differences in taxa composition and abundance among sites can be attributed to differences in stream size and 'natural' inter-site variation. Streams 1, 2 and 3 correspond to streams 1, 6 and 8 in the previous study by Melo & Froehlich (2001), where additional information on the physical characteristics of the streams, their invertebrate assemblages, and a map are provided.

Four microhabitats were sampled within each stream site: (i) stones in riffles, (ii) accumulated leaves in pools, (iii) submerged roots of terrestrial trees, and (iv) attached mosses in the air-water interface of large boulders. In each stream, we obtained 25 sampling units in riffles and 10 sampling units in the remaining microhabitats, resulting in 12 samples and 165 sampling units. Sample units in riffles were individual stones ca 20 cm diameter, sampled using a U-net. The method consists in removing the stone and collecting the dislocated material in the net. Additionally, the stone was carefully examined for attached individuals. Pools were sampled using a rectangular net. Each sampling unit consisted of 1.5–2.0 l of submerged litter. Submerged roots were collected by cutting them with large scissors and retaining the material in a net. Sampling units of roots consisted of 1.0–1.5 l of material. Mosses were collected by scraping boulders with a pocketknife. A volume of ca 250 ml of moss collected from a single boulder corresponded to a sample unit. All sampling units of each sample were collected in a stream reach 50–100 m long.

Material identification

Macroinvertebrates were identified at the lowest possible taxonomic level using taxonomic keys (Dominguez et al., 1992; Merritt & Cummins, 1996; Pes et al., 2005), and then assigned to morphospecies. For consistency in morphospecies determination, we made a reference collection. Characters that usually vary during larval development, such as color and size, were not utilized to distinguish morphospecies. Instead, we defined morphospecies based on shape of body parts, spines, setae, bristles, gills (mainly in Odonata and Ephemeroptera), house architecture (Trichoptera), and ornaments (Elmidae). First-instar larvae of some families were not considered because they lacked diagnostic features. Chironomidae and Acari were not considered. Oligochaeta were included in the analyses but without morphospecies distinction. For simplicity, morphospecies are called taxa hereafter.

Data analyzes

Sampling methodology in each microhabitat varied. Additionally, very different numbers of individuals were sampled in each microhabitat. Species richness is very dependent on sampling effort, precluding a reliable comparison of taxa richness among microhabitats (Gotelli & Colwell, 2001). We used rarefaction to construct individual-based species accumulation curves and compare taxa richness among stream sites and microhabitats.

Sampling units obtained in a given microhabitat and stream site were pooled and designated as a sample. The study thus comprised 12 samples (four microhabitat and three stream sites). Since the sampling methodology varied among microhabitats,

samples used in multivariate analyzes were standardized by dividing the abundance of each taxon in the sample by the total sample abundance. In order to reduce the influence of the most common taxa, relative abundances in each sample were square-root transformed.

We evaluated the resemblance among sites and microhabitat in two ways. First, we obtained a dendrogram of the 12 samples by hierarchical classification using the Unweighted Pair-Group Average Method (UPGMA) and Bray-Curtis (Sørensen quantitative) distance. This allowed us to evaluate whether samples were classified according to site or microhabitat. Second, in order to obtain the relative dispersion of the sample units in relation to site and microhabitat, we obtained an ordination diagram resulting from a Non-Metric Multidimensional Scaling (NMDS) using Bray-Curtis distance. We used in the ordination, data from all sampling units collected in mosses, roots, and pools. Number of individuals in sample units of riffles were too low to be compared to the sample units collected in the other microhabitats. Therefore we decided to combine pairs of sampling units collected sequentially in the field, and obtained 12 composite sample units for each stream site. Since we collected 25 sampling units in each stream site, the last composite sampling unit of each stream site contained three sampling units (numbers 23, 24, and 25). Therefore, the ordination was done using 126 objects: [(10 sampling units × 3 microhabitat × 3 sites) + (12 composite sampling units × 3 sites)]. Data transformation was the same as applied to the 12-sample dataset described above. In order to improve interpretation of the ordination diagram, we plotted the centroid of the sampling units in each of the 12 samples and the convex polygon formed by the external sample units around each centroid.

The relative importance of the two beta diversity components, stream site, and microhabitat, was evaluated by means of partial Constrained Correspondence Analysis (pCCA) applied to the 12-sample dataset. This technique was recommended by Legendre et al. (2005) for the study of beta diversity, particularly in the distinction of geographical and environmental components of variation. This constrained ordination partitions the full variation of the dataset (species composition and relative abundances) into four components: (i) one due to geographic distance, (ii) one due to environmental dissimilarity, (iii) one due to the shared effects of geographic distance and environmental dissimilarity, and (iv) unexplained (residual) variation. The component (iii) above results when explanatory factors (geographic distance and environmental dissimilarity) are correlated (i.e., are non-orthogonal). In our study, all four microhabitats were sampled in all three streams, resulting in an orthogonal design. We were thus able to estimate the independent variance accounted for by components (i) stream sites and (ii) microhabitats. In other words, our sampling design avoided the undetermined component (iii) shared by the two study factors. We were mostly interested in the variation among sites and not in the variation due to distance among sites. Accordingly, we treated sites as a factor (or categorical) variable and used dummy variables to compute the analysis. Similarly, microhabitats were entered as a factor variable in the analysis. The rarefaction, ordination, and classification analyses were done using functions available in the packages "vegan" (Oksanen et al., 2006), "MASS" (Venables & Ripley, 2002) and "cluster" (Maechler et al., 2005) of the program "R" (R Development Core Team, 2006).

Results

The 12 samples contained 20,149 individuals and 191 taxa (Table 1). Taxa richness in samples varied from 53 in riffles of stream site 3, to 80 in submerged roots of stream site 2. Abundance and taxa richness tended to be lowest in riffles. Sampling effort, measured as number of individuals, varied among samples. Accordingly, we calculated rarefied taxa richness expected to occur in 641 individuals, the total abundance obtained in the smallest sample (riffles of stream site 3). Rarefied richness varied from 42.4 (submerged roots of stream site 1) to 60.3 (submerged roots of stream site 2) (Table 1, Fig. 1). Microhabitats presented similar rarefied richness (1-way ANOVA, $F_{3,8} = 0.66$, $P = 0.59$).

The UPGMA analysis revealed that samples were clustered in four distinct groups, each reflecting a specific microhabitat (Fig. 2). The three microhabitats with high availability of organic matter formed a distinct composite group. Samples in riffles were very distinct.

Table 1 Number of individuals, species richness and rarefied species richness in mosses, pools, riffles and submerged roots in three stream sites. Rarefied species richness is the number of species expected to be found in 641 individuals, the size of the smallest sample

Microhabitats	Mosses			Pools			Riffles			Submerged roots		
Streams	1	2	3	1	2	3	1	2	3	1	2	3
Individuals	1053	2168	3288	1154	1396	1428	746	891	641	1783	2524	3077
Species richness	56	65	71	57	74	64	55	57	53	58	80	77
Rarefied species richness	48.6	45.3	44.2	47.4	56.8	45.5	51.1	53.0	53.0	42.4	60.3	48.3
Total individuals		6509			3978			2278			7384	
Total species richness		106			107			94			113	

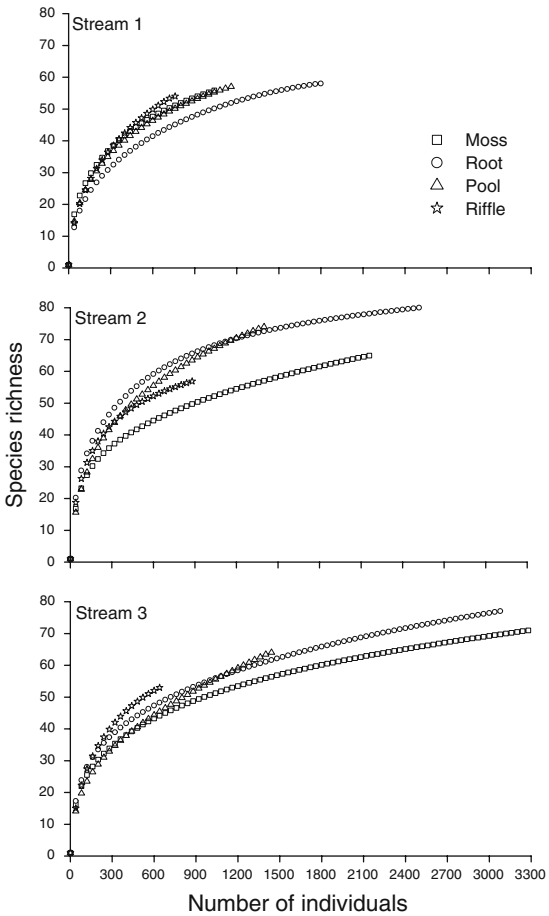

Fig. 1 Rarefaction curves for samples obtained in four microhabitats of three stream sites

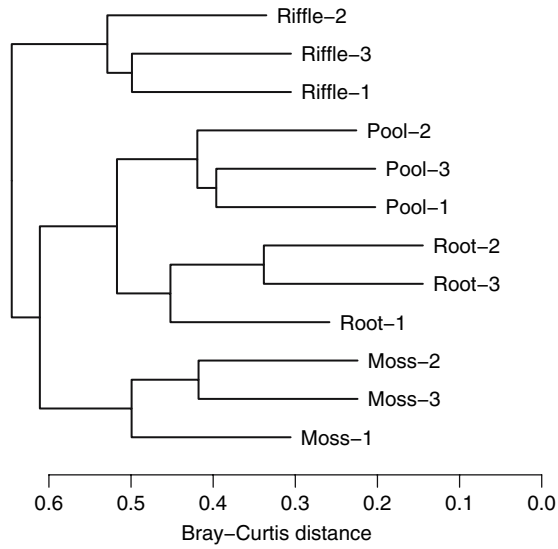

Fig. 2 Classification of samples obtained in four microhabitats and three stream sites using UPGMA linkage and Bray–Curtis distance. Numbers 1–3 correspond to stream sites

The centroids of the sampling units obtained in the NMDS analysis confirmed the four groups reflecting microhabitats revealed in the UPGMA analysis (Fig. 3). Overlap of polygons usually included sampling units of the same microhabitat. The single considerable exception was the overlap between the polygons formed by the scatter of sampling units collected in roots at stream site 1, and those of mosses from the same stream site. Accordingly, the variation of scores of sampling units within groups formed by microhabitats was lower than the variation among groups.

The preponderant importance of microhabitat in determining groups in the UPGMA and NMDS analyses was further confirmed by the partial Constrained Correspondence Analysis (pCCA). According to this last analysis, 42.02% of the total variance in composition and relative abundance of taxa in the 12 samples were explained by microhabitat. Stream site accounted for about half (22.27%) of the variation accounted for by microhabitats. The

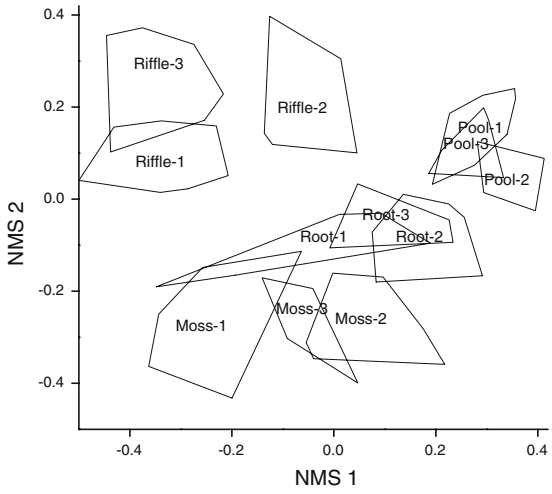

Fig. 3 Non-Metric Multidimensional Scaling of sampling units collected in four microhabitats and three stream sites. Numbers 1–3 designate stream sites. Riffles = Stones in riffles; Pool = Leaves in pools; Moss = Mosses attached to rocks in the air–water interface; Root = Submerged roots of terrestrial plants. Polygons indicate the scatter of sampling units in the ordination space. Labels indicate the centroid of the sampling units belonging to a microhabitat and stream site. Ten sampling units were collected in the root, pool, and moss microhabitats. In riffles, sampling units contained very few individuals, and therefore pairs of them were pooled and used in the ordination, resulting in 12 composite sampling units (see methods for details). Stress = 17.7%

remaining variance, 35.71%, was not explained. This demonstrates that although geographically distant, samples from the same microhabitat are more similar to each other than to samples obtained in different microhabitats of a single stream site.

Discussion

Although some microhabitats produced different taxa richness, the expected richness (by rarefaction curve) for a standardized sampling effort revealed very similar values among microhabitats. This result contrasts with previous studies that showed differences in species richness among microhabitats. For instance, McCulloch (1986) and Boulton & Lake (1992) found that pools harbored a more diversified fauna than those found in riffles. On the other hand, Brown & Brussock (1991) found that riffles were more diverse than pools. This apparent inconsistency might be caused by a sampling artifact. In all three studies cited above, the richest microhabitat was also the one where the largest numbers of individuals were sampled. Accordingly, McCabe & Gotelli (2000) studied colonization of artificial substrates in streams and found that different conclusions are reached when one uses species richness (i.e., sampling effort standardized by individuals) or species density (i.e., standardized effort by area). The authors suggested, therefore, that comparisons should be standardized by individuals (rarefied richness) and not by area, which was reinforced by the observations of Gotelli & Colwell (2001) and by the present study.

Sampling units of riffles and pools were scored on the extremes of the first NMS axis. Perhaps the simplest interpretation is that this first axis represented a gradient of water velocity. On the other hand, it is possible to interpret the second axis as a gradient of availability of coarse organic matter. Our results coincide with those obtained by Huamantinco & Nessimian (1999) in a similar study dealing with caddisflies in sand, stones in riffles, leaves in riffles and leaves in pools. In their study, the first axis separated samples according to water velocity and the second axis according to availability of coarse organic matter.

In the ordination space of the two NMDS axes and in the UPGMA analyses, samples were arranged according to microhabitat, indicating that this factor is more important in structuring macroinvertebrate assemblages than stream sites. Our results confirm previous findings of Wood & Sites (2002), where species composition of similar microhabitats in three different streams were more similar among each other than among the three microhabitats (pools, riffles, and rootmats) in the same stream site. Furthermore, McCulloch (1986) studied the macroinvertebrate assemblage of two stream sites and two microhabitats, and found that similar riffle or pool habitats between streams were more similar to each other than were riffle-pools in the same stream site.

In a previous study of the riffle fauna of the same three stream sites studied here plus seven others, all in the same catchment, Melo & Froehlich (2001) observed that the fauna was distributed according to a gradient of stream size. Similar results were observed in other regions (Baptista et al., 2001; Paavola et al., 2003). The three streams of this study differed in size, and in the study of Melo & Frohelich (2001) they showed relatively distinct faunas. The findings of the

present study indicate that variation due to differences in microhabitat is large enough to override variation caused by stream size.

The arrangement of samples according to microhabitats in the ordination and classification analyses was further confirmed by the pCCA. In this analysis, microhabitats explained 42.02% of the total variation in assemblage structure. Stream sites explained nearly half (22.27%) of the variation explained by microhabitats. In terms of beta diversity, this indicates that faunas in adjacent microhabitats of the same stream site are more differentiated than are faunas of the same microhabitat in different stream sites. As cited above, the three stream sites studied differed in size. Accordingly, part of the variation accounted for by stream sites is likely to be due to differences in stream size. The relative importance of microhabitats in relation to the inter-site variation in the generation of beta diversity should thus have been even higher if the streams were of similar size. At least for the spatial scale and the range of microhabitats studied, environmental factors within a given site are more important in the generation of variance (i.e., beta diversity) than inter-site variation. Our study showed that management practices of biodiversity conservation in stream ecosystems should pay particular attention to maintenance or restoration of physical heterogeneity of the stream channel.

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