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The additive partitioning of macroinvertebrate diversity in tropical reservoirs

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Abstract. Understanding the ways in which diversity changes across spatial scales is important for the conservation of biodiversity. The objectives of the present study were (1) to characterise the diversity of aquatic macroinvertebrates in three Brazilian tropical reservoirs and (2) to determine how the organisms were distributed at different spatial scales, by using a diversity partitioning approach. We compared the diversity-partition results with the null hypothesis that the macroinvertebrate community was uniform across all spatial scales in the study. We expected that differences in environmental variability (sediment characteristics) among the reservoirs and limitations on the dispersal of organisms among reservoirs result in higher biological variability (β diversity). The results of the spatial partitioning analysis of species richness in the reservoirs showed that each Ekman–Birge dredge-sampling unit (α) represented 43.7% of the total variation. β1 diversity (diversity among Ekman–Birge dredge-sampling units) represented 47.2% of the total variation. A partial Mantel test indicated a correlation between the particle-size matrix and the biological matrix. However, the biological matrix was not correlated with the geographical matrix. The partitioning of overall spatial diversity indicated that the distribution of species in the reservoirs was driven by local factors and that diversity was more pronounced at lower hierarchical levels.

Additional keywords: beta diversity, biomonitoring, dendritic areas, invertebrates.

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Introduction

Reservoirs act as barriers, fragmenting rivers and causing significant changes in the composition and abundance of aquatic communities (Horsák *et al.* 2009). These changes in lotic ecosystems result from the formation of lentic ecosystems, and changes in aquatic communities occur in response to changes in water flow and habitat availability (Klemm *et al.* 2003). However, some authors have recognised that local, regional and biogeographical processes can provide an important framework for assessing the composition of biological communities across different scales (Johnson *et al.* 2004; Sandin and Johnson 2004). Local and regional conditions driven by human actions extend beyond the anthropogenic processes themselves. Therefore, identifying the principal factors (e.g. habitat related, geographical, physical or chemical factors) that influence the diversity and abundance of benthic communities is an important issue in community ecology (Puntí *et al.* 2009). Such factors represent the environmental heterogeneity found in ecosystems at multiple spatial scales, and their effects should be reflected in the biological diversity found within ecosystems (Vinson and Hawkins 1998).

Aquatic macroinvertebrate communities respond to multiple environmental gradients, many of which are related to scale (Vinson and Hawkins 1998). Several studies have demonstrated a relationship between the structure of the freshwater benthic community and environmental factors that may be dependent on spatial scales of measurement (Johnson *et al.* 2007; Mykrä *et al.* 2007). Several studies have shown the importance of local-scale factors in determining species richness (Malmqvist *et al.* 1991; Paavola *et al.* 2000). For example, Johnson *et al.* (2004) showed that local-scale variables were better predictors of the characteristics of lake

and stream macroinvertebrate communities than were regional-scale variables. The variation in benthic communities at small scales (habitats) is influenced by substrate type, among other factors (Stendera and Johnson 2005; Costa and Melo 2008). Therefore, understanding the dynamics of macroinvertebrate communities in reservoirs also requires knowledge of the ways in which biological diversity is organised across different spatial scales (Summerville *et al.* 2003).

One interesting approach to understanding the organisation of the diversity of aquatic organisms involves the partitioning of diversity into hierarchical scale-related components, as follows: α (within-site diversity), β (diversity among sites) and gamma (regional diversity) (Whittaker 1960; Allan 1975). An analytical approach using an analysis of additive partitioning of diversity ($\gamma = \alpha + \beta$) (Lande 1996) is a useful method in studies of conservation and restoration. The additive partitioning of diversity breaks down regional diversity into components that can be expressed in the same units and compared over temporal and spatial scales (Crist *et al.* 2003).

In recent years, several studies have discussed additive partitioning analyses and their interpretations. Crist *et al.* (2003) developed a method based on two null models. The first null model examines diversity partitioning on the basis of a randomisation of individuals. In this model, individuals of each species are assumed to be distributed randomly among samples at the lowest hierarchical level. The second null model randomises the sample units to obtain a partitioning of diversity between the sample units at the lowest hierarchical level and the next level up. This approach preserves the patterns of intraspecific aggregation in the data.

In Brazil, several studies have been conducted to evaluate the partitioning of diversity in rivers (Ligeiro *et al.* 2010; Hepp *et al.* 2012; Hepp and Melo 2013), lakes (Flach *et al.* 2012) and wetlands (Ávila *et al.* 2011; Maltchik *et al.* 2012), but additive partitioning analyses have not yet been applied in assessments of biological diversity in reservoirs. The results of such a study could be used in monitoring programs, both in Brazil and in reservoirs in similar regions. Given that the expected richness of taxa in reservoirs is always lower than the expected richness of taxa in rivers (Molozzi *et al.* 2012), an improved understanding of the distribution of benthic organisms in reservoirs may help produce more accurate water-quality assessments of these water bodies.

Additive partitioning enables the simultaneous investigation of β diversity, the local–regional species richness relationship, and the relative importance of diversity at each scale for the total diversity of the region (Stendera and Johnson 2005; Hepp and Melo 2013). Thus, we investigated the partitioning of diversity in different regions of reservoirs across different spatial scales. The objectives of the present study were (1) to characterise the diversity of aquatic macroinvertebrates in three Brazilian tropical reservoirs and (2) to determine how the organisms were distributed at different spatial scales. We compared the results of the diversity partition with the null hypothesis that the macroinvertebrate community was uniform across all spatial scales in the study. We expected that environmental variability (sediment characteristics) among the reservoirs and limitations on the dispersal of organisms would be reflected as a higher amount of biological variability (β diversity).

Materials and methods

Study area

We sampled 35 sites in the littoral zone of the side arms (areas not influenced by the mouths of tributaries) and 55 sites in the littoral zone of the main axis of three reservoirs (Vargem das Flores, Serra Azul and Ibirité) on an affluent of the São Francisco River in Minas Gerais State, south-eastern Brazil (Fig. 1). The reservoirs chosen for the study represent systems under different levels of anthropogenic pressure (Molozzi *et al.* 2011). The elevation of the reservoirs varies from 750 to 800 m (asl). The Vargem das Flores reservoir (19°53′30″S–19°55′25″S and 44°07′22″W–44°10′59″W) was built in the 1970s. The volume of the reservoir is 44 000 000 m^3 and its maximum depth is 18 m (Table 1) (COPASA 2004). The Serra Azul reservoir (19°54′09″S–20°00′52″S and 44°23′16″W–44°30′20″W) is located within an environmentally protected area of 27 200 ha established in 1980. Within this area, 3.2 ha belong to Companhia de Saneamento de Minas Gerais (COPASA 2004), the water company that manages the reservoir (Decree 20.792 1980, on 8 July 1980), and no recreational activities or fishing are allowed. The Ibirité reservoir (19°07′00″S–20°02′30″S and 44°07′3″W–44°05′00″W) was built in the 1960s in the city of Ibirité in the Belo Horizonte metropolitan region. The surrounding area is characterised by multiple types of land use, including operations of petrochemical industry and an urban area from which untreated domestic sewage is discharged into the reservoir (Pinto-Coelho *et al.* 2010).

Macroinvertebrate sampling

Macroinvertebrates were collected with an Ekman–Birge dredge (0.0225 m^2) from as close as possible to the littoral zone at a mean depth of ~4 m. The sampling was conducted during 2008 and 2009. Each year, samples were collected in both the dry season (March and June) and the rainy season (September and December). Sediment was collected with an Eckman–Birge dredge and used to determine granulometric composition and organic matter content according to the methods described by Suguio (1973) and modified by Callisto and Esteves (1996).

Taxonomic identification

The benthic fauna were identified to the family level, except for Chironomidae specimens, which were identified to genus (Merritt and Cummins 1996; Fernández and Domínguez 2001; Mugnai *et al.* 2010). The Chironomid larvae were treated with a 10% solution of lactophenol and identified to genus under a microscope at ×400, by using the Epler (2001) and Trivinho-Strixino (2011) identification keys. We assumed that the unidentifiable species in these families would not affect the results (Melo 2005). Other species were generally identified under a stereomicroscope (×100 magnification).

Data analysis

To evaluate the distribution of communities as a function of sediment characteristics, we performed a redundancy analysis (RDA; Legendre and Legendre 1998). We used taxonomic richness to measure diversity. The null hypothesis that the macroinvertebrate diversity was uniform at all spatial scales was

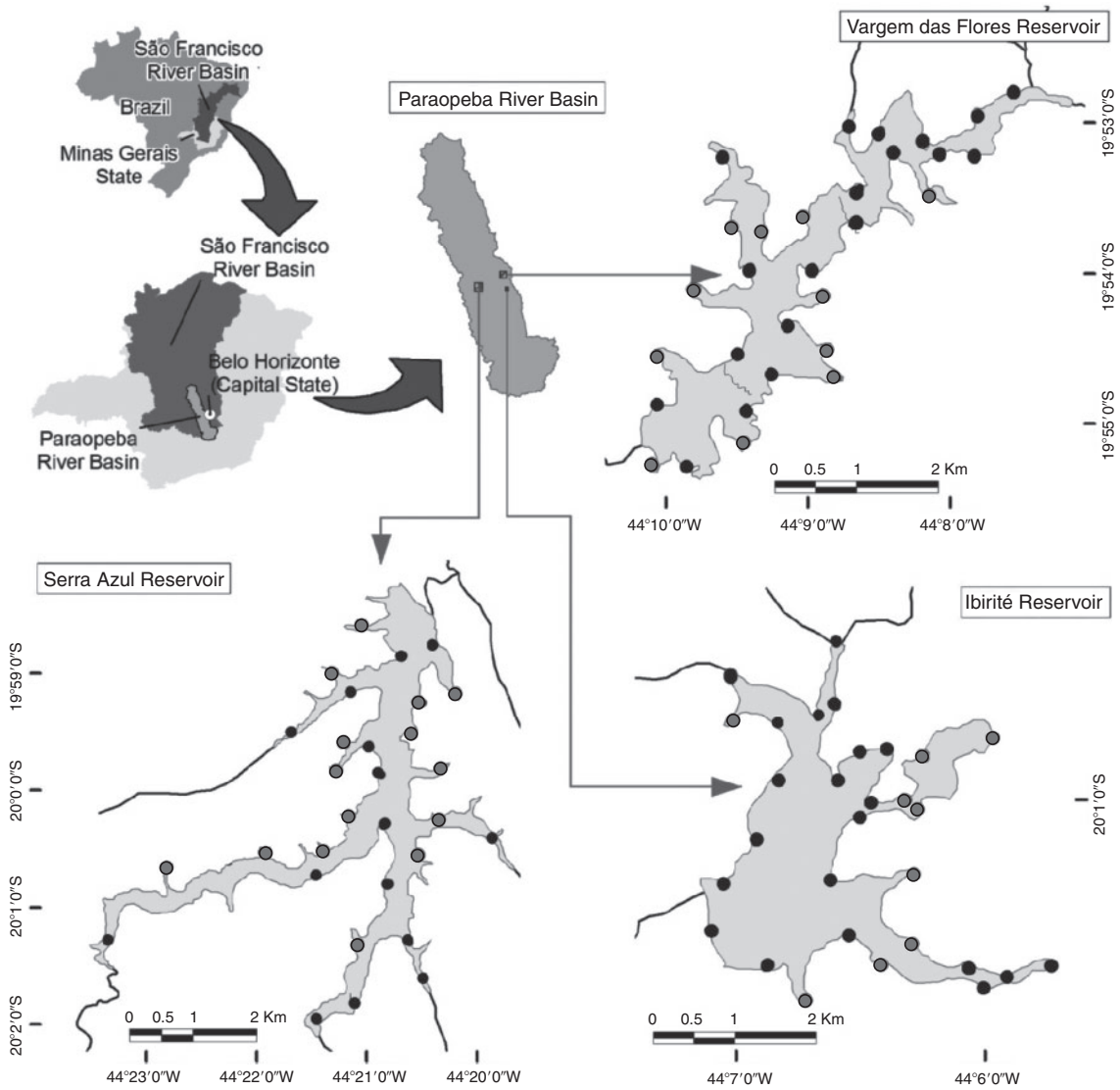

Fig. 1. Location of the 90 sampling sites in the Ibirité, Vargem das Flores and Serra Azul reservoirs in the Paraopeba River, Minas Gerais State, Brazil. Grey points indicate the littoral zone in the side arms (areas not influenced by the mouths of tributaries); and black points indicate the littoral zone in the main axis.

Table 1. Characteristics of the Serra Azul, Vargem das Flores and Ibirité reservoirs
n.a. = not available

Variable	Serra Azul	Vargem das Flores	Ibirité
Construction year	1981	1971	1968
Area (km^2)	7.5	4.9	2.8
Volume (m^3)	88 000 000	37 000 000	15 423 000
Maximum depth (m)	40	18	16
Hydraulic retention time (days)	351	356	n.a.
Fluctuation of reservoir level (m) (2008–09)	5.71	2.54	0.70
Cota spillway (m)	760	837	773

tested by additively partitioning the total diversity. We organised our data according to the following hierarchical levels: within Ekman–Birge dredge sampling units (α), among Ekman–Birge dredge sampling units ($\beta1$), within a region ($\beta2$; side arms and main axis), and among reservoirs ($\beta3$). Thus, the diversity model evaluated in our study was γ (regional diversity) $= \alpha + \beta1 + \beta2 + \beta3$. Average diversity ($\alpha$) was calculated at each level, and the differences among α values were used to express β

diversity (Lande 1996). A significance test was performed by comparing the observed values with those obtained from 10 000 sample-based randomisations (Crist *et al.* 2003). Because it is unlikely that two samples will show the same species composition (including the same abundance), β diversity is affected by sampling variation (Ribeiro *et al.* 2008). The use of sample-based randomisations (Crist *et al.* 2003) preserves the intra-specific aggregation at each scale (Ribeiro *et al.* 2008). The significance test assessed whether the observed values differed from the expected values as a result of chance, by computing the proportion of randomisations in which the statistic (diversity component) produced values higher than the values of observed diversity. High proportions (e.g. >0.975) indicated that the observed values were significantly lower than those expected by chance, whereas low proportions (e.g. <0.025) indicated that the observed values were significantly higher than expected under the null model. We used a partial Mantel analysis to explore the relative importance of local factors (sediment characteristics) and regional factors (dispersal) on the β diversity of the benthic community (Legendre and Legendre 1998). We used Pearson coefficients to identify correlations among the biological matrix (benthic community; Euclidian distance), the environmental matrix (sediment granulometric composition; Euclidian distance) and the geographical-distance matrix (sampling-site geographic coordinates; Euclidian distance). We used a routine in R software (R Development Core Team 2009) written by Ribeiro *et al.* (2008) for the *boot* package (Canty and Ripley 2006).

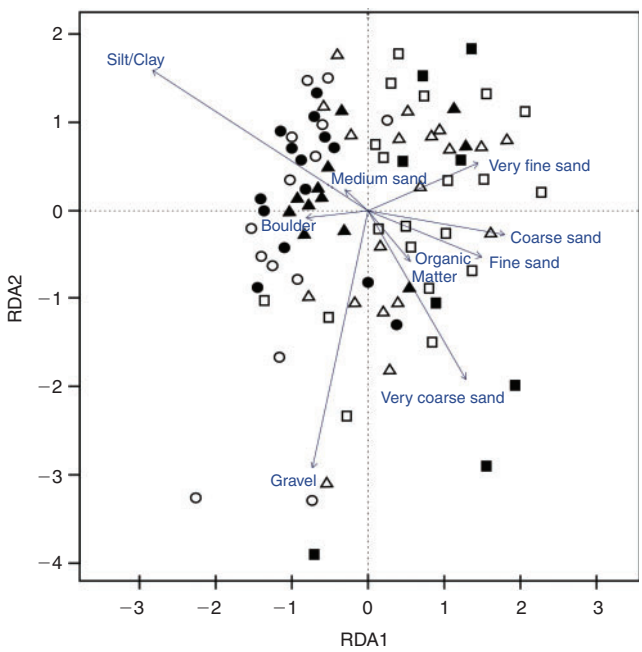

Fig. 2. Redundancy analysis (RDA) of benthic communities and sediments in reservoirs Serra Azul (square), Ibirité (circle), and Vargem das Flores (triangle) in the Paraopeba River Basin, Minas Gerais, Brazil. Open, littoral zone in the main axis; and black, littoral zone in the side arms.

Results

In total, 14 425 individuals belonging to 47 taxa (4 Mollusca, 2 Annelida and 41 Arthropoda) were collected at 90 sites over the two sampling years. The benthic fauna was composed of chaoborids (29.2%), chironomids (26.3%), molluscs (21.0%), oligochaetes (20.8%) and other invertebrates (2.7%). Dipteran larvae were represented by *Chironomus* (8%), *Tanypus* (4%) and *Coelotanypus* (4%). In the Serra Azul reservoir, 1596 aquatic macroinvertebrates were found in the arms and 1101 in the main axis. Twenty-nine taxa were found in each region of the reservoir (Appendix 1). In the Vargem das Flores reservoir, 3615 individuals and 30 taxa were found in the arms, and 1494 individuals and 25 taxa were found in the main axis. In Ibirité, 4249 individuals and 19 taxa were found in the arms, and 2370 individuals and 22 taxa were found in the main axis (see Appendix 1).

The benthic communities were influenced by sediment characteristics (Fig. 2). In the Serra Azul reservoir, the granulometric composition was predominantly sand (coarse sand, fine sand and very fine sand). In the Ibirité reservoir, the sediment was predominantly silt and clay (Table 2). In the Vargem Flores reservoir, the gravel fraction was less than 1% of the total granulometric composition. Silt and clay represented more than 41% of the granulometric composition of the sediments. Furthermore, the influence of sediment characteristics was not dependent on reservoir region (littoral zone of the arms or littoral zone of the main axis).

Table 2. Granulometric composition (%), with mean values (± s.d.) in the Serra Azul, Vargem das Flores and Ibirité reservoirs of the Paraopeba River Basin, Minas Gerais State, Brazil

Sediment fractions are from sediment samples collected with an Ekman–Birge dredge (0.0225 m^2)

Granulometry composition	Reservoir		
	Serra Azul	Vargem das Flores	Ibirité
Gravel	1.34 (± 4.44)	0.81 (± 1.22)	1.78 (± 1.79)
Boulder	0.28 (± 0.54)	1.15 (± 1.79)	1.34 (± 4.44)
Very coarse sand	0.97 (± 1.10)	3.79 (± 2.82)	0.88 (± 0.17)
Coarse sand	17.92 (± 14.76)	2.29 (± 4.19)	0.23 (± 0.15)
Medium sand	0.11 (± 0.14)	22.90 (± 29.76)	25.21 (± 17.06)
Fine sand	58.45 (± 35.23)	3.25 (± 2.34)	0.17 (± 0.14)
Very fine sand	37.22 (± 19.71)	24.35 (± 13.58)	4.56 (± 2.76)
Silt and clay	0.18 (± 0.03)	41.46 (± 34.85)	66.33 (± 20.00)

At the smaller scales (α and β1), the variation in macroinvertebrate composition was 90.9%. The spatial partitioning of species richness in the reservoirs showed that each Ekman–Birge dredge sampling unit (α), on average, had a lower diversity than predicted by the null hypothesis ($Prop_{exp > obs} = 0.999$) (Table 2). However, the β1 diversity values (diversity among Ekman–Birge dredge sampling units) were significantly higher ($Prop_{exp > obs} < 0.001$) than expected from the null model on the basis of the randomisation of sampling units. β2 diversity (species richness among regions within reservoirs) (β2obs: richness average = 1.66) was similar to the richness expected on the basis of the null hypothesis (β2exp richness average = 0.76). All other β-diversity components had higher values than expected under the null model on the basis of the randomisation of sampling units. β3 diversity (among reservoirs) was 4.84 (total variation = 5.7%), which was a lower value than expected under the null hypothesis ($Prop_{exp > obs} = 0.999$) (Table 3).

We found a significant correlation between the benthic-community dissimilarity and the granulometric composition matrix (rM = 0.18, $P = 0.001$). However, no significant correlation was observed between the biological matrix and the geographical distance matrix (rM = 0.04, $P = 0.279$).

Discussion

Additive partitioning is a relatively simple mathematical approach used to describe the relative contributions of diversity components (Crist *et al.* 2003). However, to our knowledge, this approach has not been previously applied to aquatic communities in reservoirs. The partitioning of species richness in the reservoirs in the present study showed that richness at the smallest scale (α; within an Ekman–Birge dredge sampling unit) was lower than that expected under the null model. Previous studies have shown that most of the macroinvertebrate variation at small scales (habitats) is due to substrate type (Costa and Melo 2008; Ligeiro *et al.* 2010; Hepp *et al.* 2012).

The correlation between granulometric composition and dissimilarity of the benthic community supports the hypothesis that substrate characteristics are critical in determining the distribution of aquatic organisms. In contrast to sediment grain size, reservoir region did not appear to contribute significantly to the variability in benthic macroinvertebrates (β diversity). Our results demonstrated the importance of local factors in structuring aquatic communities. With regard to regional factors (location of the reservoirs), the lack of correlation between geographic distance and benthic-community dissimilarity indicated that the dispersal of some benthic taxa is limited (Hepp and Melo 2013).

Granulometric composition of the substrate is a factor because substrate quality in rivers and lakes has been considered to be one of the primary influences on the distribution of benthic macroinvertebrates (Gering *et al.* 2003). Our methods were based on recent observations that certain benthic macroinvertebrate taxa are restricted to a particular type of substrate and that different substrate types host invertebrate communities that differ in biomass, total density and richness (Stendera and Johnson 2005). A more diverse substrate offers greater availability of habitats and microhabitats (on an individual scale), food (directly or adsorbed to sediment particles) and protection (e.g. from currents and predators such as benthic fish) (Gering *et al.* 2003).

Beta diversity increases in rivers with high habitat heterogeneity or environmental heterogeneity (Cornell and Lawton 1992). Water movement, in particular, is considered to be a strong determinant of the composition of the benthic macroinvertebrate communities in rivers (Allan 2004; Johnson *et al.* 2004). Moreover, several studies have demonstrated the importance of other habitat characteristics, such as type of substratum, water chemistry and riparian vegetation, as predictors of macroinvertebrate community composition (e.g. Ormerod *et al.* 1993; Richards *et al.* 1997). In reservoirs in Brazil, Molozzi *et al.* (2012) found that a community composed of Diptera, *Chaoborus*, *Djalmabatista*, *Procladius* and *Polypedilum* was found in sites that had a higher percentage of relatively coarse substrates (gravel, boulders and coarse sand). The same authors found that substrate was a predictor of the distribution of benthic communities in reservoirs that demonstrated maximum values of ecological potential.

The magnitude of β diversity increased only in relation to the scale of β-diversity (β1; among Ekman–Birge dredge sampling units). For the other components, β diversity was lower than expected under the null model. This finding demonstrated that at smaller scales, species are distributed in an aggregated manner. The distribution of larval and adult resources may contribute substantially to these grouping patterns. The distribution pattern is most likely governed by the aggregated distribution of resources at the local scale and by the great variability among sample points at small scales. Thus, the interruption of connectivity among reservoirs and differences in dispersal abilities among species are key factors in determining the α- and β-diversity components of a community (Clarke *et al.* 2008, 2010).

Table 3. Observed and expected total diversity partitioned into α diversity (within an Ekman–Birge dredge sampling unit), β diversity-component 1 (among Ekman–Birge dredge sampling units), β diversity-component 2 (among regions) and β diversity-component 3 (among reservoirs)

Diversity component		Observed	Expected	$Prop_{Exp > Obs}$	%Variation
α	Ekman–Birge dredge-sampling unit	19.23	21.40	0.999	43.7
β1	Among Ekman–Birge dredge-sampling units	20.76	18.59	<0.001	47.2
β2	Among regions	1.66	0.76	0.226	3.8
β3	Among reservoirs	2.33	4.84	0.999	5.3
γ	Regional diversity	44			100

Johnson *et al.* (2004) showed that local-scale variables were better predictors of lake and stream macroinvertebrate communities than were regional-scale variables. These findings were not unexpected because both stream and lake littoral habitats often show high habitat heterogeneity. Given that local variables are more important than regional variables in explaining variability among habitats, species interactions as well as other environmental factors may be important predictors of community composition (Veech *et al.* 2002).

Ávila *et al.* (2011) conducted wetland studies and found that differences among tropical regions were more important than differences among habitat types. A large fraction of the total macroinvertebrate diversity was related to broad spatial scales rather than to habitat type. Nevertheless, the partitioning of the spatial diversity indicated that this effect is more pronounced at lower hierarchical levels in human-constructed reservoirs.

In conclusion, our results showed that local-scale factors are strong determinants of benthic communities in reservoirs. At smaller scales, substrate can help determine the distribution of benthic fauna. However, further studies are needed to support our conclusion that macroinvertebrate variation at small scales is substrate-dependent and to clarify how the scale of sampling influences the diversity of benthic macroinvertebrates in reservoirs. Additional investigations would also be necessary to confirm the hypothesis that macroinvertebrate communities are uniform across all of the spatial scales. In our study, this null hypothesis conflicted with the expectation that environmental variability among reservoirs and the limited dispersal of organisms between reservoirs would be reflected as higher biological variability within reservoirs (β diversity).

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Appendix 1. List of taxa found in the littoral zone of the side arms and the littoral zone of the main axis during 2 years of sampling and relative abundance values (number of larvae collected) for each taxa in the Serra Azul, Vargem das Flores and Ibirité reservoirs of the Paraopeba River Basin, Minas Gerais, Brazil

Taxon	Reservoir					
	Serra Azul		Vargem das Flores		Ibirité	
	Littoral zone arms	Littoral zone on the main axis	Littoral zone arms	Littoral zone on the main axis	Littoral zone arms	Littoral zone on the main axis
Mollusca						
Gatropoda						
Prosobranchia						
Mesogastropoda						
Thiaridae						
Melanoides tuberculatus Müller, 1774	40	30	535	295	1903	189
Planorbiidae						
Biomphalaria straminea Dunker, 1848	1	0	1	0	0	0
Ampullariidae						
Pomacea haustrum Reeve, 1856	0	0	1	6	0	1
Bivalvia						
Corbiculidae						
Corbicula fluminea Müller, 1774	0	0	23	10	1	0
Annelida						
Hirudinea	7	10	55	17	62	26
Oligochaeta	33	51	1003	260	690	958
Insecta						
Ephemeroptera						
Polymirtacyidae	8	7	7	0	3	2
Baetidae	1	1	2	0	0	0
Leptoceridae	0	0	10	4	0	1
Odonata						
Gomphidae	3	0	1	5	0	0
Trichoptera						
Odontoceridae	0	0	1	0	1	0
Hydrophilidae	0	1	0	0	0	0
Philopotamidae	1	0	0	0	0	0
Hydrobiosidae	0	1	0	1	0	0
Coleoptera						
Elmidae	0	1	0	0	7	7
Acari						
Hidracarina	0	0	55	17	0	0
Diptera						
Chaoboridae	864	510	1397	677	558	202
Chaoborus sp.						
Simuliidae	0	0	0	0	2	4
Ceratopogonidae	22	12	6	3	10	13
Tanypodinae						
Labrundinia, Roback, 1987	7	0	0	0	0	0
Coelotanypodini	83	84	126	63	95	67
Coelotanypus Kieffer, 1913						
Pentaneurini						
Ablabesmyia Johhansen, 1905	26	24	4	1	8	3
Procladiini						
Djalmabatista Fittkau, 1908	38	30	17	7	0	0
Procladius Skuse, 1803	52	32	0	2	0	0
Tanypodini						
Tanypus Meigen, 1803	79	66	41	4	187	179
Chironominae						
Chironomini						
Polypedilum						
Dicrotendipes Kieffer, 1913	0	0	0	1	0	6
Beardius Reiss & Sublette, 1985	0	0	1	0	0	0

(*Continued*)

Appendix 1. (Continued)

Taxon	Reservoir					
	Serra Azul		Vargem das Flores		Ibirité	
	Littoral zone arms	Littoral zone on the main axis	Littoral zone arms	Littoral zone on the main axis	Littoral zone arms	Littoral zone on the main axis
Aedokritus Roback, 1958	5	2	213	73	147	30
Chironomus Meigen, 1803	19	8	23	4	380	643
Cladopelma Kieffer, 1921	5	1	2	0	0	0
Cryptochironomus Kieffer, 1918	0	2	1	0	0	0
Fissimentum Cranston & Nolte, 1916	230	155	5	6	0	0
Goeldichironomus Fittkau, 1965	1	0	10	5	11	7
Harnischia Kieffer, 1921	7	3	48	12	13	0
Lauterborniella Lenz, 1941	7	0	0	0	0	0
Paralauterboniella Lenz, 1941	0	1	0	0	0	0
Pelomus Reiss, 1989	4	20	0	0	0	
Polypedilum Kieffer, 1913	35	32	13	9	13	0
Stenochironomus Kieffer, 1919	0	1	0	0	0	0
Zavreliella Kieffer, 1920	10	2	0	0	0	0
Nilothauma Kieffer, 1921	1	0	1	0	0	0
Alotanypus Roback, 1971	0	2	0	0	0	0
Parachironomus Lenz, 1921	0	1	0	0	0	2
Pseudochironomini						
Manoa Fittkau, 1963	1	0	0	0	0	0
Pseudochironomus Mallock, 1915	0	2	0	0	0	0
Tanytarsini						
Tanytarsus van der Wulp, 1984	2	5	10	8	147	30
Cladotanytarsus Kieffer, 1924	0	0	0	0	1	0
Nimbocera Reiss, 1972	4	4	3	4	10	0