Acta Limnologica Brasiliensia

Publication of the Brazilian Association of Limnology

Original Article
Acta Limnologica Brasiliensia, 2024, vol. 36, e32
https://doi.org/10.1590/S2179-975X10023
ISSN 2179-975X on-line version

Beta diversity of macroinvertebrate assemblages associated with aquatic macrophytes in shallow lakes within a tropical floodplain-dammed river

Diversidade beta de assembleias de macroinvertebrados associados a macrófitas aquáticas em lagos rasos na planície de inundação de um rio tropical represado

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Cite as: Callisto, M. et al. Beta diversity of macroinvertebrate assemblages associated with aquatic macrophytes in shallow lakes within a tropical floodplain-dammed river. *Acta Limnologica Brasiliensia*, 2024, vol. 36, e32. https://doi.org/10.1590/S2179-975X10023

Abstract: Aims: We assessed the beta diversity of macroinvertebrates associated with aquatic macrophytes in a dam-regulated river floodplain. We tested two hypotheses: (1) macroinvertebrates associated with aquatic macrophytes have higher beta diversity (higher turnover and nestedness components) in the downstream areas closer to the São Francisco River compared to upstream sites; (2) closer lakes share a higher similarity of aquatic macroinvertebrates, disregarding their position relative to the dam. **Methods:** We sampled four lakes, including two upstream (L1- natural and L2- regulated by a Small Hydropower Dam - SHD) and two downstream (L3, L4, unregulated) by the SHD. **Results:** We corroborated our first hypothesis because we found a higher turnover of macroinvertebrates associated with aquatic macrophytes close to the São Francisco River (L4 downstream), where higher non-native mollusk species richness occurs, while we found higher nestedness upstream and downstream of the SHD (L1, L2, L3). We corroborated our second hypothesis, as closer lakes are more similar than distant lakes. Finally, these differences were consistent between lakes for emergent, floating leaf, and submerged aquatic macrophytes. **Conclusions:** Aquatic macrophytes are essential habitats for macroinvertebrates in the Pandeiros River basin, with higher beta diversity in the lake closer to the São Francisco River.

Keywords: flood pulse; decommissioning; small hydropower dam; conservation; habitat.

Resumo: Objetivo: O objetivo foi avaliar a diversidade beta de macroinvertebrados associados a macrófitas aquáticas em uma planície de inundação de um rio regulado por hidrelétrica. Testamos duas hipóteses: (1) macroinvertebrados associados a macrófitas aquáticas têm maior diversidade beta (em ambos os componentes *turnover* e *nestedness*) em áreas a jusante próximas ao Rio São Francisco se comparadas a áreas a montante, e (2) lagos próximos são mais similares, independente de sua posição em relação à barragem. **Métodos:** Foram amostrados quatro lagos, sendo dois a montante (L1- natural e L2- regulado pela Pequena Central Hidrelétrica - PCH) e dois a jusante (L3, L4- não regulados pela PCH). **Resultados:** Nossa primeira hipótese foi corroborada porque encontramos maior *turnover* no lago próximo ao Rio São Francisco (L4 a jusante), onde ocorre maior riqueza de espécies não nativas de moluscos, enquanto aninhamento foi mais importante nos lagos a montante e a jusante da PCH (L1, L2, L3). Nossa segunda hipótese também foi corroborada porque lagos mais próximos são mais similares do que lagos distantes. Finalmente, essas diferenças foram consistentes entre lagos para as macrófitas emergentes, com folhas flutuantes e submersas. **Conclusões:** As macrófitas aquáticas são importantes habitats para macroinvertebrados na bacia do Rio Pandeiros, com maior diversidade beta no lago mais próximo ao Rio São Francisco.

Palavras-chave: pulso de inundação; descomissionamento; pequena central hidrelétrica; conservação; habitat.

1. Introduction

Floodplain lakes exhibit wide variations in water level due to many natural factors, such as frequency and intensity of precipitation, flooding topography, evaporation rates, and human uses (Linares et al., 2020a; Petsch et al., 2022). Thus, the natural flood pulses determine the composition and structure of aquatic organism assemblages in these ecosystems (Thomaz, 2022). In floodplains, the cycling of matter and energy flow between terrestrial and aquatic ecosystems sustains high productivity and, consequently, high biodiversity (Pinto et al., 2003; Junk et al., 2014). Therefore, floodplain lakes' ecosystem functioning and diversity patterns depend on water level oscillations and hydrological connectivity to the main river (Junk et al., 1989). In periods of flooding, rivers overflow, and water floods low areas in the floodplain, favoring the dispersion of species among the different aquatic ecosystems. In contrast, in drought periods, isolation between these lakes and the main river channel may occur (Bayley, 1995; Thomaz et al., 2007).

Among the many factors that regulate the biodiversity structure in floodplain ecosystems, the functional groups of aquatic macrophytes are one of the most important (Soares, 2014; Shimabukuro & Henry, 2019). Aquatic macrophyte functional groups (submerged, emerged, and floating) have different physical structures and thus can provide different microhabitat types for macroinvertebrates in floodplain shallow lakes, influencing the abundance and diversity of the aquatic biota (Soares, 2014; Meerhoff & González-Sagrario, 2022). Most shallow lakes depend on their aquatic macrophytes' presence, diversity, and density (Attayde et al., 2022). Therefore, the structure of aquatic macrophyte habitats for aquatic fauna is a key component that influences the spatial distribution of associated macroinvertebrates. On the other hand, in ecosystems poor in macrophytes and homogeneous, the macroinvertebrates biodiversity is lower (Soares, 2014).

Beta diversity represents the dissimilarity in species composition of biotic assemblages (Tuomisto, 2010; Zhang et al., 2019). Beta diversity can be partitioned into turnover (species replacement) and nestedness (sites with lower species richness are subsets of others with higher species richness) components, aiming at explaining how beta diversity is structured across spatial gradients (Baselga, 2010; Cortés-Guzmán & Alcocer, 2022). Therefore, biological communities in lakes subject to the natural flood pulse, being more heterogeneous and less predictable, should show a higher turnover contribution. In contrast, lakes regulated by anthropogenic dams should favor generalists and lose specialist taxa, dominating the nestedness component. Different studies assessed beta diversity within river basins or regions (Gutiérrez-Cánovas et al., 2013), including the beta partitioning of turnover and nestedness components (Krynak et al., 2019) in free-flowing river basins. However, there is a lack of information about how hydropower dams influence the beta diversity of macroinvertebrate assemblages associated with aquatic macrophytes in tropical floodplains. Invasive species, mostly mollusks, often are a common sight in tropical hydropower reservoir cascades along the São Francisco River basin that crosses over 3,500 Km of Brazil due to anthropogenically altered ecological conditions that facilitate their introduction and establishment (Linares et al., 2020b). Besides, the intense navigation in the São Francisco River is also, or even more important, to facilitate the dispersion and colonization of mollusk species (especially *Corbicula fluminea* (Müller, 1774) and *Limnoperna fortunei,* Dunker (1857), Barbosa et al., 2016). This is an important knowledge gap because shallow lakes can be highly affected by climate change, particularly the impact of extreme climatic events (e.g., Epele et al., 2024) such as droughts/floods and storms that may affect water levels and nutrient loading and concentrations through increasing or decreasing runoff from the basins (Thayne et al., 2022).

We assessed the beta diversity of macroinvertebrates associated with aquatic macrophytes in a dam-regulated river floodplain. We investigated two hypotheses. The first was that macroinvertebrates associated with aquatic macrophytes have higher beta diversity among macrophyte banks in the downstream areas closer to the São Francisco River than upstream sites. We predicted that turnover is greater downstream (lakes 3 and 4), where mollusk non-native species are more abundant due to the influence of the São Francisco River. Therefore, this would drive the difference of the assemblages to the other sites because of the additive heterogenization by non-native species (Socolar et al., 2016). We expect some taxa (mainly those mollusks) to contribute more to the observed differences, as can be measured by species contributions to beta diversity (SCBD, Legendre & Cáceres, 2013). The second hypothesis was that closer lakes share greater similarities with aquatic macroinvertebrates, disregarding their position relative to the dam. We predicted closer lakes' total beta diversity, turnover, and nestedness patterns would be more similar. Also, we predict that more distant lakes should contribute more to the total beta diversity compared to closer sites, as can be measured by a larger local contribution to beta diversity (known as LCBD, Legendre & Cáceres, 2013).

2. Material and Methods

2.1. Study area

The Pandeiros River is a tributary on the left bank of the São Francisco River, extending approximately 145 km from its headwaters to the São Francisco River. It is located entirely in the northern region of the Minas Gerais State. The Pandeiros River basin is an Area of Environmental Protection with almost 4000 Km^2, the largest unit for sustainable use in Minas Gerais state. Its floodplains are among the top priority areas for conservation in the neotropical savanna, considered by Minas Gerais state law to be of "Special Biological Importance" because of their unique nature regarding its state and high biodiversity (Drummond et al., 2005). The AEP-Pandeiros was created to protect the Pandeiros wetlands and the biological diversity in the surrounding area, which are the nursery of most migratory fish species of the São Francisco River basin (Lopes et al., 2010).

Pandeiros Small Hydropower Dam (SHD) was installed in 1957 in the municipality of Januária (Figure 1). Its reservoir has an area of 280 hectares with a free-crest dam height of 10.3 meters. Its powerhouse is located about 400 meters downstream of the dam, and when in operation, it turned up to 35 m^3/s, with a power of 4.2 MW (Fonseca et al., 2008). The SHD had its operation suspended in 2007 due to the non-approval of its Operating License and the creation of the EPA downriver, aiming to protect the Pandeiros River wetlands. Since then, the SHD has not carried out bottom discharges, which causes the accumulation of sediments upstream and presents little hydrometric variation. The SHD now acts as a physical barrier to the continuous flow of the Pandeiros River, keeping one of its marginal lakes at a constant water level and having significant, albeit localized, impacts on the structure of Pandeiros River's benthic macroinvertebrate assemblages, including an increased abundance of invasive mollusks (Linares et al., 2018, 2019, 2020b). There is a gap in information about macroinvertebrates associated with aquatic macrophytes in this river basin.

The vegetation cover of the Pandeiros River basin is formed by a mosaic of phytophysiognomies of the Cerrado biome, in addition to areas with deciduous and semi-deciduous forests. The semi-arid climate is predominant in the region, with temperatures fluctuating between 9 °C in winter (June to August) and 45 °C between October and January, in late spring and early summer, respectively. The rainfall regime is irregular, varying between 900 and 1250 mm, with up to 90% of rainfall concentrated in December and January. The lakes have similar water chemical characteristics, including temperature (19.3-27.2 ° C), electrical conductivity (38.2-81.0 µS/cm), different dissolved oxygen levels and pH (5.4-7.8), low turbidity (< 25 NTU) and positive oxi-redox in water and sediment (Table 1).

2.2. Sampling design

To evaluate the influence of the SHD on the macroinvertebrate assemblages associated with

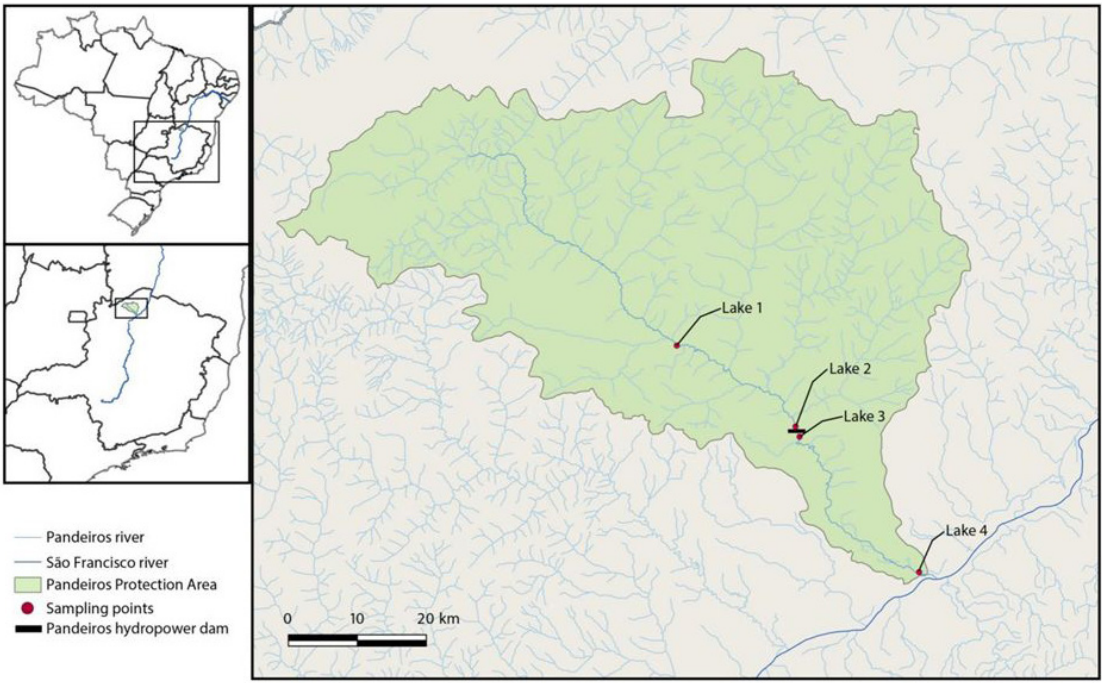

Figure 1. Map of the study area with the location of the four river-floodplain lakes studied along the Pandeiros River, Minas Gerais State, Brazil. Water flows from north to south in the studied river.

Table 1. Abiotic parameters in the three macrophyte habitats (rooted with emerged leaves (HB1), rooted with floating leaves (HB2), and rooted with submerged leaves (HB3) in each river-floodplain lake in the Pandeiros River.

Parameters		Lake 1			Lake 2			Lake 3			Lake 4		
		HB1	HB2	HB3	HB1	HB2	HB3	HB1	HB2	HB3	HB1	HB2	HB3
Temperature	(ºC)	20.2	20.0	19.3	27.2	26.2	26.1	25.7	27.0	21.8	25.1	22.6	23.4
Electrical conductivity	(µS/cm)	38.2	39.9	46.2	70.9	70.8	69.5	81.0	79.3	77.6	64.7	86.9	74.0
Dissolved oxygen	(mg/L)	2.6	2.0	1.4	7.0	7.0	5.9	8.0	6.9	3.0	5.7	5.4	4.8
	(% sat)	30.8	22.8	15.8	93.3	90.3	65.4	101.8	87.0	35.3	72.9	64.8	77.3
Oxi-Redox	(mV)	84.0	74.8	60.3	24.4	145.0	193.7	116.6	8.6	65.3	156.9	-18.0	126.3
pH		6.5	5.4	5.9	7.5	7.6	7.8	6.5	6.6	6.6	6.8	6.5	6.4
Turbidity	(NTU)	13.6	23.7	24.8	12.7	16.7	22.8	7.5	11.6	13.3	9.8	19.6	24.1

aquatic macrophytes, four shallow lakes (depth below 1.5 m) were sampled, two upstream and two downstream from the Pandeiros SHD (Figure 1), three of which are subject to the natural flood pulse (L1, L3, L4) and one regulated (without water level variation due to the SHD presence, L2). The distance between Lake 1 and Lake 4 is 50 Km (L1-L2: 21Km; L1-L3: 23Km; L2-L3: 2Km; L3-L4: 26Km).

Field samplings were carried out in July 2019 during the dry season. The associated macroinvertebrates were collected in three functional groups of macrophytes (HB, habitats): rooted with emerged leaves (HB1), rooted with floating leaves (HB2), and rooted with submerged leaves (HB3). These macrophytes are in the aquatic/terrestrial transition zone (Junk et al., 1989). Four samples of macroinvertebrates associated with each macrophyte functional group were randomized in each macrophyte bank, totaling twelve samples per lake. The size of macrophyte stands was standardized in 10 m^2 each per shallow lake to avoid the expected scaling up in the number of macroinvertebrates with increasing macrophyte surface area (habitat complexity-diversity relationship), avoiding that differences between macrophyte stands could cause differences in observed macroinvertebrate composition.

The macrophytes were collected using a 20 x 20 cm quadrat. In a field laboratory, they were washed on a sieve with a 0.5 mm mesh to separate the associated macroinvertebrates from the organic debris. Macroinvertebrates were sorted and identified up to species (mollusks) and family (insects) level according to Mugnai et al. (2010) benthic taxonomic key, and annelids remained as Hirudinea and Oligochaeta. They are deposited in the Benthic Ecology Laboratory at the Universidade Federal de Minas Gerais (Belo Horizonte, Brazil).

2.3. Data analyses

To evaluate our two hypotheses, we first calculated beta diversity at different spatial scales, and in each scale, we computed Jaccard dissimilarity for presence-absence data (Baselga, 2012). To assess the first hypothesis, the first scale we analyzed was among macrophyte types within each lake, where we considered richness in each macrophyte bank as alpha diversity, the whole lake assemblage as gamma diversity, and their difference in composition as beta diversity. Beta diversity ($beta_{Jac)}$ at each lake was then decomposed into turnover and nestedness for presence-absence data. We also computed the metrics "local contribution to beta diversity" at this scale using abundance data (LCBD, Legendre & Cáceres, 2013). LCBD breaks up diversity into its site-based uniqueness, revealing the lakes that mostly contribute to total beta diversity. Similarly, we also computed the metrics "species contribution to beta diversity" at this scale using abundance data (SCBD, Legendre & Cáceres, 2013). SCBD breaks down diversity into species-level contributions, highlighting the species that primarily drive total beta diversity. To test for differences in multivariate dispersion among macrophyte types and lakes, i.e., beta diversity, we used the *betadisper* function from the vegan package in R (Oksanen et al., 2024). This function assesses the homogeneity of variances by comparing the average distance of each group member to the group centroid in the ordination space. We used Jaccard distances for presence-absence, called an ANOVA to check for significance, and checked for pairwise differences using Tukey. Finally, due to the importance of the Mollusk for the biodiversity of shallow lakes in the Pandeiros floodplain (Linares et al., 2020a), we computed the percentage contribution of each mollusk taxon within each lake.

We followed these analyses by investigating the next spatial scale to the second hypothesis, the differences among lakes in the Pandeiros River floodplain. At this scale, each lake represented the alpha diversity, the pooled diversity of the four lakes was gamma diversity, and the difference was beta diversity. Similar to the previous scale, beta diversity was decomposed into turnover and nestedness for presence-absence data for all pairwise comparisons. We partitioned each macrophyte independently, looking for among-lake patterns that could be happening in a specific life form. We conducted all analyses using R- environment v. 4.3.1 (R Core Team, 2023) using the packages betapart (function *betapair*, Baselga et al., 2023) to compute beta diversity partition and adespatial (function *beta.div*, Dray et al., 2023) to compute LCBD and SCBD values.

3. Results

We collected 5682 macroinvertebrates associated with aquatic macrophytes in the four lakes (Lake 1 = 1793, Lake 2 = 631, Lake 3 = 1384, Lake 4 = 1874) (Data available in https://doi.org/10.48331/scielodata.QDUL1G). Diptera (30.3% of the total abundance, divided into six families), Odonata (11.6%, six families), and Mollusca (51.7%, six families and two non-native species) were the most abundant taxa in all lakes, with Chironomidae (Diptera) being the most abundant family in the three macrophyte habitats (Data available in https://doi.org/10.48331/scielodata.QDUL1G). Besides, in all lakes, Planorbidae and Chironomidae comprised most of the sampled individuals, with 49% (lake 1) to 37% (lake 3) of the sampled assemblages. *Pisidium* C. Pfeiffer, 1821 (Sphaeriidae, Bivalvia) was the dominant mollusk taxon in Lakes 1, 2, and 3, while *Littoridina* (Souleyet, 1852) (Cochliopidae, Gastropoda) dominated at Lake 4. The invasive species *Corbicula fluminea* (Müller, 1774) (Cyrenidae, Bivalvia) was present in Lake 3 (9.4%) and Lake 4 (3.73%), whereas *Melanoides tuberculata* (Müller, 1774) (Thiaridae, Gastropoda) was present in Lake 4 (16.48%).

Regarding the macrophyte type, beta diversity was higher for submerged rooted ($F_{2,45}$=7.55, P < 0.01), compared with rooted with emergent leaves and floating rooted. We found that nestedness was the main incidence partitioning (60% of contribution) in the lake upstream of the Pandeiros SHD (Lake 1); an equal contribution of turnover and nestedness in Lake 2, which is regulated by the SHD; 79% of nestedness contribution in Lake 3 - downstream SHD; while turnover was the main incidence (80%) in Lake 4 - close to the São Francisco River (Figure 2). The local contribution to beta diversity was higher and significant at Lake 4 (LCBD = 0.48, p<0.001), closer to the São Francisco River. The lowest LCBD was at Lake 3 (LCBD = 0.10), downstream of the SHD, while Lakes 1 and 2 had

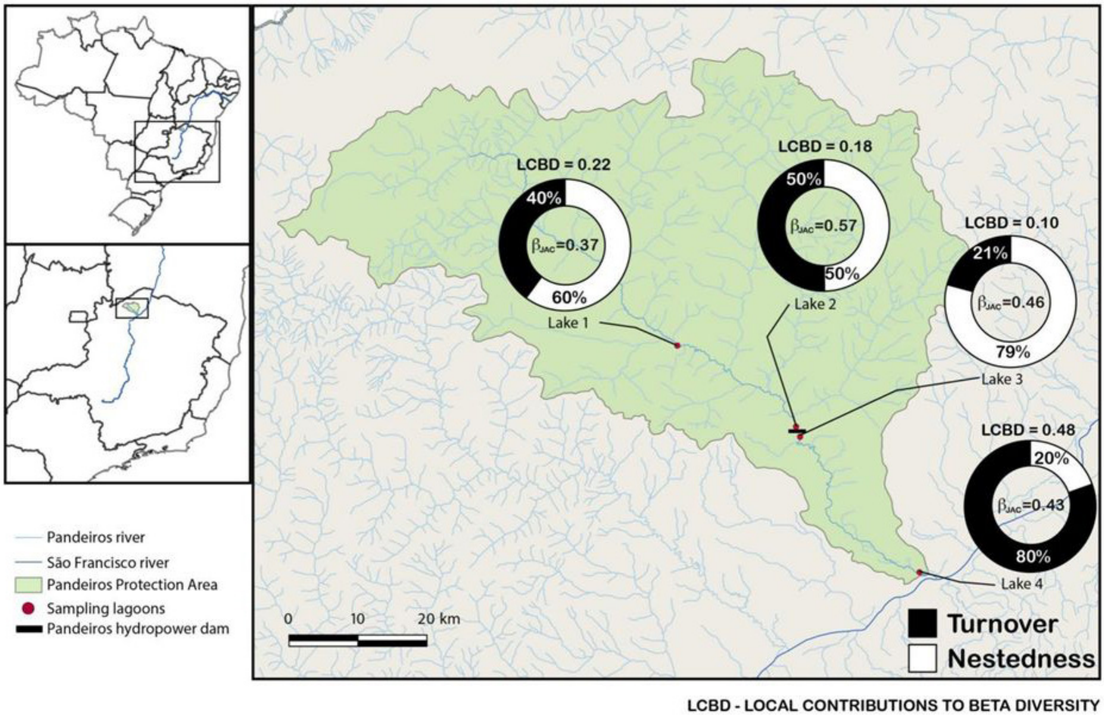

Figure 2. Beta diversity using Jaccard dissimilarity ($ß_{Jac}$) among macrophyte banks within each lake; its incidence partitioning into turnover (black) and nestedness (white) components and Local Contributions to Beta Diversity (LCBD) for each lake in the Pandeiros River (Minas Gerais, Brazil).

similar LCBD values (0.22 and 0.18, respectively); however, such results were not significant. The highest $beta_{Jac}$ value was observed at Lake 2 (0.57), followed by Lake 3 ($beta_{Jac}$ = 0.46), Lake 4 ($beta_{Jac}$ = 0.43), and Lake 1 ($beta_{Jac}$ = 0.37). Beta diversity was highest among the distant lakes (0.59) (L1-L4). Species Contributions to Beta Diversity (SCBD) were highest for the mollusk species. They can be attributed to their functional preferences, including scraper gastropods such as the invasive *Melanoides tuberculata* and the native *Littoridina* at Lake 4, and filtering-collector bivalves, *Pisidium* (native species), the invasive species *Corbicula fluminea* (Figure 3). We found spatial differences between mollusk species in the naturally flooded lake (*Pisidium*, lake 1) and invasive mollusk species present downstream of the SHD at lakes 3 and 4 (Figure 3). We found a lower difference for the turnover component of beta diversity between the closer lakes L2-L3 ($beta_{Jac}$ = 0.27) (Figure 4). Beta diversity was highest among the distant lakes (0.59) (L1-L4). Besides, beta diversity differed between lakes for emergent, floating leaf, and submerged aquatic macrophytes (Figure 5).

4. Discussion

Our first hypothesis that macroinvertebrates associated with aquatic macrophytes have higher beta diversity in the downstream areas closer to the São Francisco River was partially corroborated. Our results evidenced that the predominance of turnover or nestedness depends on the position of the lake in the Pandeiros River continuum, showing that turnover in the closest lake to the São Francisco River may result from the influence of the flood waters of the later on the former river's floodplain, in accordance to our first prediction. Thus, the flood pulse alterations promoted by the reservoir cascade in the lower São Francisco River (Barbosa et al., 1999; Callisto et al., 2005) may cause changes to macroinvertebrate's composition and distribution on the Pandeiros River upstream. This might influence environmental variables, including dissolved oxygen in the water, explaining the composition of macroinvertebrates' patterns. We also found that mollusks, both native and invasive species, were the main ones responsible for the composition differences in the macroinvertebrates associated with aquatic macrophytes, mainly increasing the contribution of turnover on the lakes closer to the São Francisco River may be showing that its flood pulse contribution causes species replacement more often in these lakes. Ecologically, this means there is a greater contribution of the São Francisco River in these lakes, even compared to the dam, which

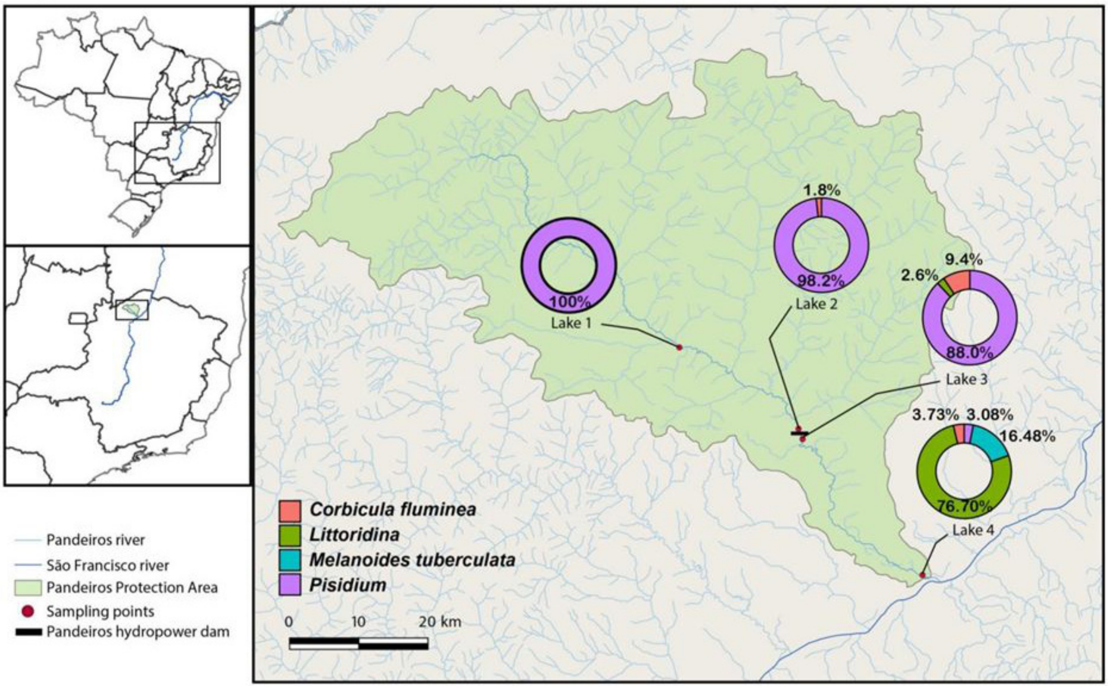

Figure 3. Mollusk assemblage composition and relative abundance in the four floodplain lakes at the Pandeiros River.

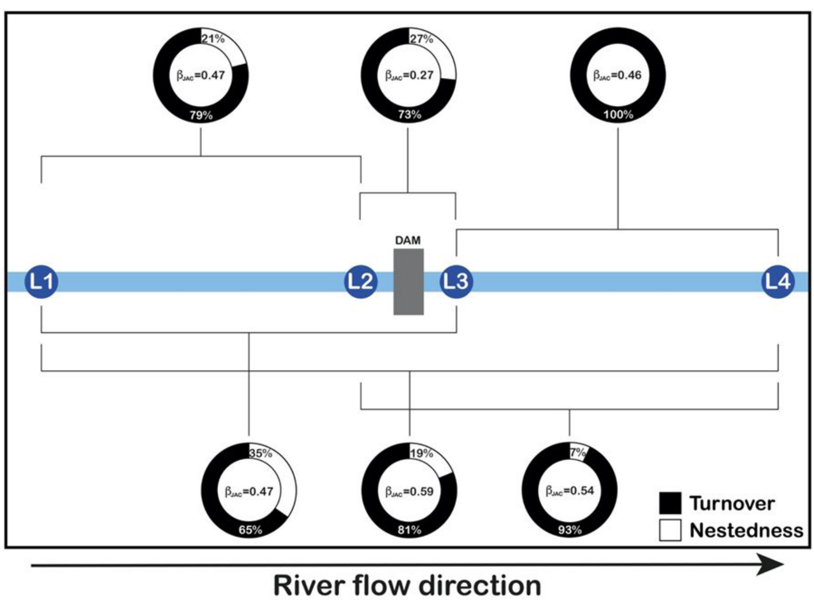

Figure 4. Paired beta diversity and its components turnover (black) and nestedness (white) between the four floodplain lakes at the Pandeiros River (Minas Gerais, Brazil).

should be considered facing the big human changes caused in this watershed.

We corroborated our second hypothesis because closer lakes share a greater similarity of their macroinvertebrate assemblages with each other, disregarding their position relative to the dam. We found that the beta diversity varies between lakes and macrophyte habitats due to scraper gastropods or filtering-collector bivalves. Thus, as scraper gastropods and bivalve filtering collectors use different energy sources feeding on algae and transported FPOM, they change the benthic macroinvertebrate assemblage complexity (as described by eco-exergy and specific eco-exergy

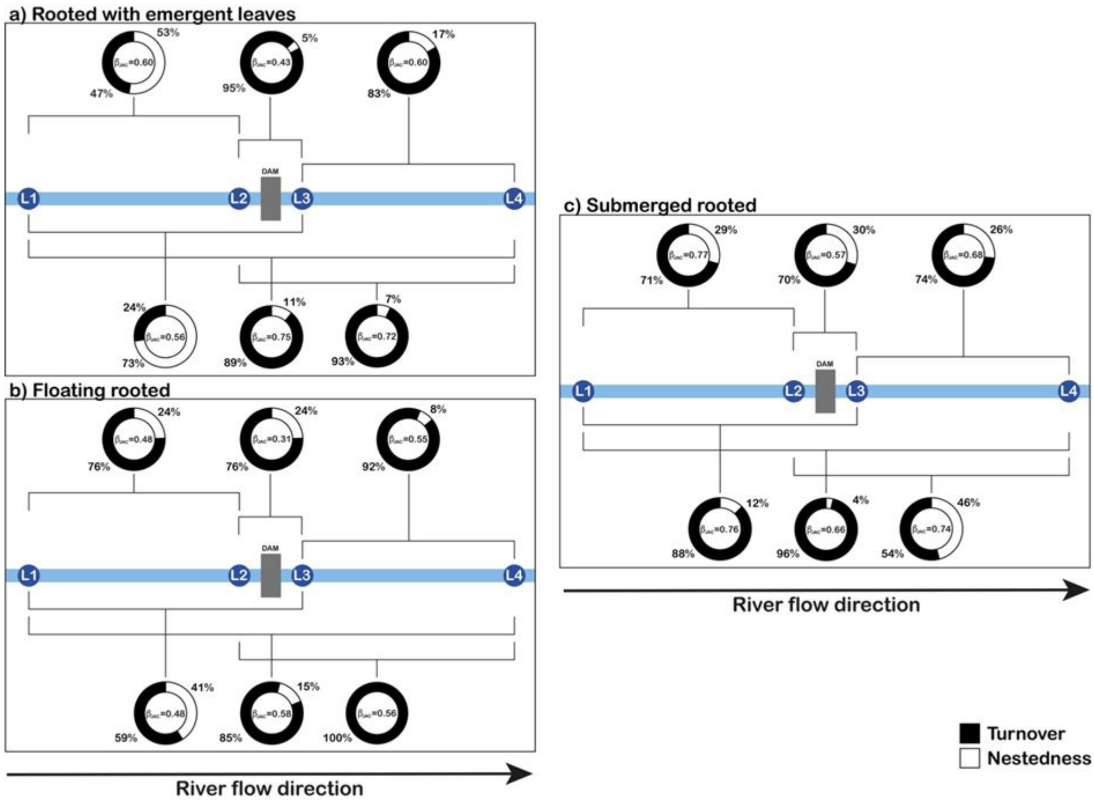

Figure 5. Paired beta diversity and its components turnover (black) and nestedness (white) for rooted with emerged leaves aquatic macrophytes (a) floating rooted aquatic macrophytes, (b) and submerged rooted aquatic macrophytes, (c) in the four floodplain lakes at the Pandeiros River.

indicators; see Linares et al., 2018) and the latter acts as ecosystem engineer (Linares et al., 2017). The invasive mollusk species were not more abundant in the SHP-regulated lake (Lake 2) but at the closest lake to the São Francisco River (Lake 4). The native mollusk genus *Pisidium* dominated 100% of the upstream natural lake (Lake 1). Still, invasive mollusk species were not abundant in the upstream SHP-regulated lake (Lake 2), nor reached more than 20% in the closest lake to the São Francisco River (Lake 4).

Two common invasive mollusk species to the São Francisco River basin were found in the shallow lakes at the Pandeiros River basin: *Corbicula fluminea* and *Melanoides tuberculata*. *Corbicula fluminea* is an invasive species that originated in Asia, often common in neotropical hydropower reservoirs, which causes changes in the taxonomic and functional structures of benthic macroinvertebrate assemblages (Darrigran et al., 2020). This species acts as an ecosystem engineer, altering the sediment compartment's physical habitat, changing other species and ecosystem conditions, taxonomic composition, and benthic species distribution (Linares et al., 2022). Specifically, burrower macroinvertebrates are prejudiced by limiting access to soft substrates (Firmiano et al., 2021) and getting more exposure to fish predators. The tropical hydropower reservoirs, as man-made ecosystems, exhibit altered ecological conditions that facilitate the introduction and establishment of *C. fluminea* (Linares et al., 2020b). Often *C. fluminea* disrupts the environmental linkages between sediment and water column, altering the nutrient cycling by rapidly incorporating plankton from water column food webs into the organic matter decomposition in the sediment compartment, increasing the complexity of benthic macroinvertebrate assemblages but disrupting the native planktonic food webs (Linares et al., 2017, 2018, 2019). *C. fluminea* can also form an altered hard substrate with the accumulation of their alive and dead shells, excluding native benthic taxa adapted to soft substrates (Linares et al., 2022). *Melanoides tuberculata* is a typical scraper feeding on periphytic algae, protozoans, and bacteria colonizing aquatic macrophytes' surfaces (Weir & Salice, 2012). As both invasive species have no natural predators in this region and succeed in colonizing tropical reservoirs, they are common in the neotropics (Santos & Eskinazi-Sant'Anna, 2010).

5. Conclusions

We conclude that aquatic macrophytes are important habitats for macroinvertebrates in the Pandeiros River basin, with higher beta diversity in the lake closer to the São Francisco River. As we identified the mollusk species but insects' identification remains up to family level, we emphasize the importance of the use of higher specific levels of taxonomic resolutions in studies conducted about anthropic disturbances on beta diversity once we could see better effects at species levels (including functional traits of species) than family ones. We assume that our study is limited to a single field sampling in the four shallow lakes. We suggest assessing a possible seasonal (rainy and dry) difference in macrophytes and associated macroinvertebrates along the Pandeiros River basin for further studies.

Acknowledgements

We are grateful for continued funding by Programa Peixe Vivo of the Companhia Energética de Minas Gerais (P&D Aneel-Cemig GT-611) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the MSc scholarship to DR. MC and RS were awarded Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) research productivity grants 304060/2020-8 and 308350/2022-7, respectively. MC is Resident Professor at the Instituto de Estudos Avançados Transdisciplinares (IEAT/UFMG). MSL received a postdoctoral scholarship from the Programa de Apoio à Fixação de Jovens Doutores no Brasil/FAPEMIG (Process BPD-00021-22). We acknowledge SISBIO (No. 106357) and IEF-MG (No. 074/2014 e 018/2019) environmental licenses for field sampling. Colleagues from the Universidade Federal de Minas Gerais (UFMG) and Universidade Federal de Lavras (UFLA) helped with field sampling. Several Laboratório de Ecologia de Bentos ICB/UFMG colleagues helped with sample processing. We acknowledge two anonymous reviewers and the editor, Danielle K. Petsch, for their detailed and constructive comments on an earlier version of this manuscript.

Data availability

All research data analyzed in the research is available in the Dataverse of Acta Limnologica Brasiliensia on SciELO Data. Access is free. It can be accessed in https://doi.org/10.48331/scielodata.QDUL1G.

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Received: 21 November 2023
Accepted: 01 July 2024

Associate Editor: Danielle Katharine Petsch.