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Small hydropower dam alters the taxonomic composition of benthic macroinvertebrate assemblages in a neotropical river

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Abstract

Hydropower dams substantially modify lotic ecosystems. Most studies regarding their ecological impacts are based on large dams and provide little information about the far more abundant effects of small hydropower dams. Our aim was to characterize the ecological effects of a small hydropower dam and run-of-the-river reservoir on the structure of benthic macroinvertebrate assemblages in the Pandeiros River located in the neotropical savanna of Brazil. We tested the hypothesis that benthic macroinvertebrate assemblages in sites directly affected by the dam and reservoir would show a different taxonomic structure compared with those in free-flowing sites. We expected to find sensitive native species associated with the free-flowing sites, whereas resistant and non-native invasive taxa were expected in impounded sites. We also explored associations between the presence of native and non-native invasive taxa to each habitat type. We found that the structure of benthic macroinvertebrate assemblages was significantly different between free-flowing and impounded sites. Also, we found that the dam and reservoir facilitated colonization of non-native invasive species (*Corbicula fluminea* and *Melanoides tuberculata*) because only in those sites they were found in high abundance, in contrast to the free-flowing sites. Although the environmental conditions imposed by the impoundment altered the structure of benthic macroinvertebrate assemblages, the effects were limited to sites closest to the dam. Our results highlight the necessity of understanding physical habitat changes caused by the presence and management of run-of-the-river dams and reservoirs.

KEYWORDS

Corbicula fluminea, invasive non-native species, lotic ecosystem, *Melanoides tuberculata*, run-of-the-river dam

1 | INTRODUCTION

At the dawn of the XXI century, hydropower is the most common renewable energy source in the world, accounting for 16% of worldwide total electricity generation and representing more than 64% of the Brazilian electricity source (Empresa de Pesquisa Energética, 2016). Given the rising demand for renewable energy sources, hydropower dams and reservoirs are an increasingly common sight on river systems globally (Anderson, Moggridge, Warren, & Shucksmith, 2015), providing relatively low-cost energy sources and reducing the dependency on fossil fuels (Couto & Olden, 2018).

Despite the economic improvements brought by hydropower dams and reservoirs, their construction results in substantially negative ecological impacts on the lotic ecosystems in which they are built, such as (a) dams and reservoirs homogenize naturally variable flow regimes depending on their size and operations (Dynesius & Nilsson, 1994; Hughes, Wildman, & Gregory, 2005; Junk, Bayley, & Sparks, 1989; Poff, Olden, Merritt, & Pepin, 2007); (b) dams markedly reduce the longitudinal flux of sediments (Stanford & Ward, 2001; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980) and wood (Wohl et al., 2019); (c) dams and their reservoirs reduce connectivity with river floodplains (Junk et al., 1989; Ward & Stanford, 1995) and fragment river segments and ecological processes (Fausch, Torgersen, Baxter, & Li, 2002; Pompeu, Agostinho, & Pelicice, 2012); and (d) dams and their reservoirs substantially alter local habitats by reducing current velocities, increasing water depth and altering water temperature (Roni et al., 2002; Roni, Hanson, & Beechie, 2008). (e) Therefore, dams and reservoirs change local taxonomic structure and composition depending on their size and operations, including the increased prevalence of non-native invasive species (Hughes, Rinne, & Calamusso, 2005; Johnson, Olden, & Vander Zanden, 2008; Linares, Callisto, & Marques, 2017; Terra & Araujo, 2011; White, 2014). Importantly, studies on these ecological impacts are mainly based on large dams (e.g., Agostinho, Pelicice, & Gomes, 2008; Horsák, Bojková, Zahrádková, Omesová, & Helešic, 2009; Martins et al., 2015), whereas information about the ecological consequences of small hydropower dams is largely lacking (e.g., Anderson, Moggridge, Shucksmith, & Warren, 2017; Mbaka & Wanjiru Mwaniki, 2015; Obruca & Hauer, 2016; Wang, Chen, Liu, & Zhu, 2016).

Small hydropower dams are defined by Brazilian environmental law as having capacities up to 30,000 kW and reservoir areas up to 13 km^2 (Agência Nacional de Energia Elétrica, 2017). Small hydropower dams have lower construction costs and are easier to license (Fearnside, 2014). Most sites suitable for the construction of large hydroelectric dams are already occupied by existing impoundments, and public support for new large dams is waning because of their high socio-economic costs (Couto & Olden, 2018). Therefore, small dams have been the focus of construction projects in recent decades and can be found in most river systems in the world (Abbasi & Abbasi, 2011; Almeida, Oliveira, Mugnai, Nessimian, & Baptista, 2009). Studies characterizing the effects of small dams on lotic ecosystems are essential for improving management strategies and for predicting and mitigating ecological impacts (Hastings, Meiners, Colombo, & Thomas, 2016).

Among the many taxa used as bioindicators of ecological impacts, benthic macroinvertebrates are some of the most ubiquitous and widely used because of their ability to respond predictably to modifications in lotic environments (Bonada, Prat, Resh, & Statzner, 2006; Ferreira et al., 2017; Klemm et al., 2003). Additionally, the structure of benthic macroinvertebrate assemblages strongly correlates with ecosystem condition at local and regional scales (Ferreira et al., 2014; Ligeiro et al., 2013; Macedo et al., 2016). Adequate assessments targeting such assemblages can thus provide information on the effect of anthropogenic disturbances on lotic ecosystems (Libório & Tanaka, 2016) and improve ecological management of small hydropower dams (Linares, Callisto, & Marques, 2018).

Therefore, the objective of this study was to characterize and understand the ecological effects of a small run-of-the-river hydropower dam and reservoir on the taxonomic and functional structure of benthic macroinvertebrate assemblages in a neotropical savanna river. In particular, we were interested in its effects on macroinvertebrate species composition, species richness, prevalence of non-native invasive species, and functional feeding groups (FFGs). To do so, we tested the hypothesis that benthic macroinvertebrate assemblages in sites directly affected by the dam and reservoir would differ in multiple ways from those in nearby free-flowing sites. We also sought to determine indicator taxa for the different site types. The general goal of our study was to provide insights regarding the effects of small dams on various components of aquatic biodiversity (Hughes & Noss, 1992). Those insights should improve our ability to predict impacts of such dams in natural habitats elsewhere.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted in the Pandeiros River, Minas Gerais state, Brazil. The Pandeiros River, with an approximate length of 145 km, is an important left bank tributary of the São Francisco River. Its floodplains are among the top priority areas for conservation in the neotropical savanna, considered by state law to be of "Special Biological Importance" because of their unique nature in the state and high biodiversity (Drummond, Martins, Machado, Sebaio, & Antonini, 2005). An Area of Environmental Protection covers almost 4,000 km^2, the largest unit for sustainable use in Minas Gerais, and covers the entire Pandeiros River Basin in the municipalities of Januária, Bonito de Minas, and Cônego Marinho (Lopes, D'Angelo Neto, Leite, Moraes, & Capurucho, 2010). The objective of the Area of Environmental Protection-Pandeiros is to protect the Pandeiros wetlands and the biological diversity in the surrounding area because the wetlands are considered the nursery of most migratory fishes of the São Francisco River Basin (Santos, Silva, Barros, & Dergam, 2015).

The Pandeiros dam was installed in 1957, and its reservoir has an area of 280 ha, with a free-crest dam height of 10.3 m (Fonseca, Grossi, Fiorini, & Prado, 2008). The powerhouse was deactivated in 2007, and since then, all economic activities of the dam and reservoir

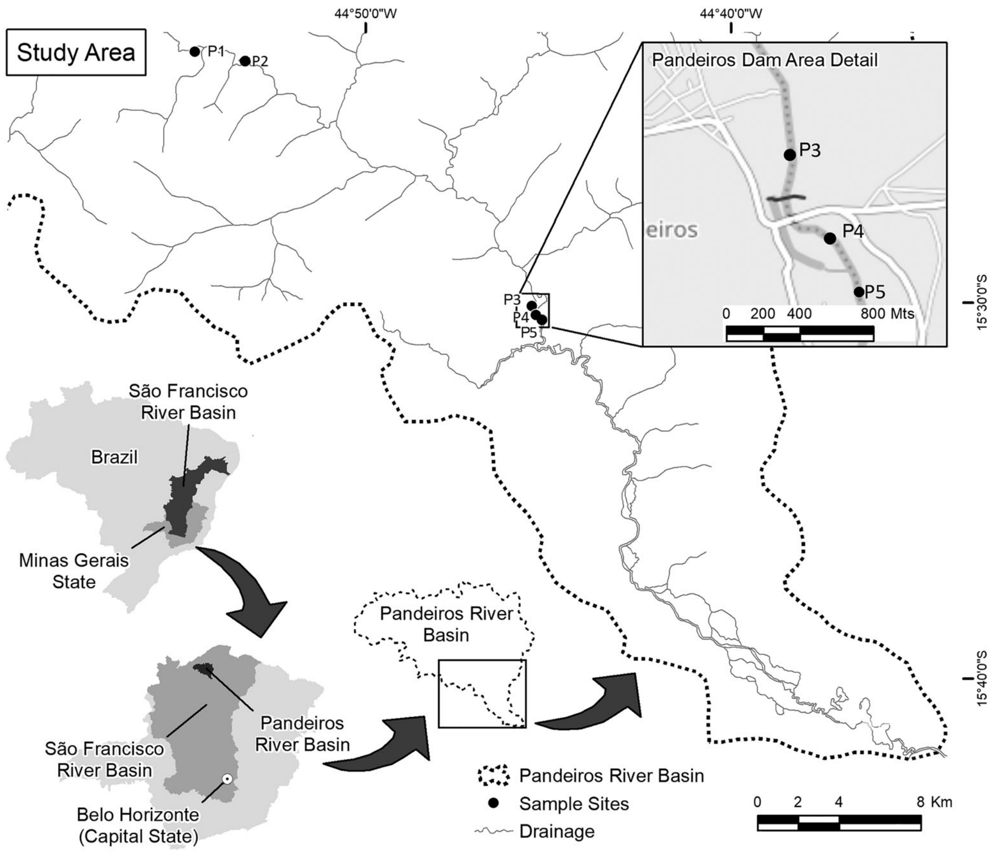

FIGURE 1 Locations of the Pandeiros River sampling sites

have ceased, leading to the filling of the reservoir with sand and fine sediments. The dam is slated for removal when flows are believed sufficient to remove the sediments currently residing in its reservoir. Unlike in the United States, where hundreds of small dams have been removed (Hughes, 2013), this is believed to be the first dam removal in Brazil and in South America.

We sampled five sites (P1 to P5) in the main channel (Figure 1), aiming to represent the diversity of environmental conditions related to the presence of the dam in the Pandeiros River. P1 and P2 are free-flowing sites 20 and 12 km upriver from the dam, respectively, characterized by sandy bottom substrate, wide channel (>5 m), shallow water depth (<1 m), and natural riparian vegetation. These two sites were so distant to guarantee that they had no direct influence from the dam or its reservoir. The remaining sites are what we considered to be dam influenced. P3 is located in the mouth of the reservoir, 500 m upriver from the dam, characterized by sandy bottom substrate, shallow water depth (<2 m), wider channel (>10 m), and no riparian vegetation along one of its margins, because it is next to a human settlement. P4 is located 50 m downriver from the dam and is characterized by sandy sediment in a rocky matrix, deeper water depth (>3 m), narrower channel (<5 m), and natural riparian vegetation on both margins. P5 is located 500 m downriver from the dam, below a series of small cascades, and is characterized by sandy bottom substrate with macrophyte beds, shallow water depth (<1 m), wide channel (>5 m), and a mix of natural riparian vegetation and deforested areas. Similar upstream–downstream study designs are used for assessing point sources in temperate (Hughes & Gammon, 1987; Yoder, Rankin, Gordon, Hersha, & Boucher, in press) and other tropical rivers (Callisto, Goulart, Barbosa, & Rocha, 2005; Feio et al., 2015; Moreno & Callisto, 2006; Terra & Araujo, 2011).

The Pandeiros River is a sand-bedded river in a sandy river basin. In a previous study (Linares et al., 2018), substrate samples were taken to estimate granulometry of these five sampling sites. P1 sediment was predominantly (97.9%) very fine sand (grains 0.06–0.25 mm). P2 sediment was also mostly very fine sand (67.4%) but also had a sizable portion (31.8%) of fine sand (0.25–0.5 mm). P3, on the other hand, was mostly fine sand (64.1%) with a sizable portion (34.1%) of very fine sand. P4 showed a more balanced composition between fine sand (39.8%) and very fine sand (59.3%). P5 substrate composition was more similar to the free-flowing sites with sediment consisting of very fine sand (75.5%) and fine sand (24.0%).

2.2 | Benthic macroinvertebrate sampling

We sampled the macroinvertebrate assemblages six times to cover both the dry (September 2015, April 2016, and June 2016) and the rainy (December 2015, January 2016, and February 2016) seasons. At each site, we sampled four randomly selected stations for 30 s using a kicknet (30-cm opening, 0.09 m^2 of area, and 500-μm mesh), over a total area of 0.36 m^2 per visit. Organisms from each subsample were stored in plastic bags, fixed in 10% formalin, and then washed through a sieve (0.5-mm mesh) in the laboratory.

We identified all sampled macroinvertebrates under a stereomicroscope through use of taxonomic keys (Hamada, Nessimian, & Querino, 2014; Merritt & Cummins, 1996; Mugnai, Nessimian, & Baptista, 2010). Non-native invasive *Corbicula fluminea* (Corbiculidae, Bivalvia) and *Melanoides tuberculata* (Thiaridae, Gastropoda) individuals were identified to species. The other taxa were identified to family (other Insecta) or subclass (Annelida), a taxonomic resolution that requires less laboratory time without compromising the performance of the indices tested (Silva, Herlihy, Hughes, & Callisto, 2017; Whittier & Van Sickle, 2010). The specimens were fixed in 70% alcohol and deposited in the Reference Collection of Benthic Macroinvertebrates, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Brazil.

To assess the ecological condition of each site, we combined the subsamples for each site visit and calculated taxonomic richness and a macroinvertebrate multimetric index (MMI). The MMI is the sum of seven-scaled assemblage metrics: Ephemeroptera richness, % Gastropoda individuals, Shannon–Wiener diversity index, % sensitive taxa richness, % scraper individuals, temporarily attached taxa richness, and gill respiration taxa richness (Silva et al., 2017).

2.3 | FFGs metrics

To assess the functional composition of the benthic macroinvertebrate assemblages of each site, we assessed FFGs and a series of metrics derived from them. The macroinvertebrate taxa were classified as gathering collectors, filtering collectors, shredders, scrapers, or predators following specialized literature (Cummins, Merritt, & Andrade, 2005; Ramirez & Guitiérrez, 2014; Tomanova, Goitia, & Helešic, 2006). We estimated dry-mass biomass instead of abundance to calculate the FFGs because it presents a more accurate picture of the functional structure of the benthic macroinvertebrate assemblages (Jiang, Xiong, Xie, & Chen, 2011; Rivera-Usme, Pinilla, Rangel-Churio, Castro, & Camacho-Pinzón, 2015). To do so, each individual of each taxon, up to 50, was photographed in a stereomicroscope (model Leica M80) equipped with a digital camera (model Leica IC 80 HD). Each photographed specimen's length was measured using Motic Image Plus 2.0 software. The dry-mass biomass (mg/m^2) of each sampled taxon was estimated through use of length-mass equations (Benke, Huryn, Smock, & Wallace, 1999; Johnston & Cunjak, 1999; Miserendino, 2001; Smock, 1980; Stoffels, Karbe, & Paterson, 2003).

To assess the functional condition of the benthic macroinvertebrate assemblages of each site, we calculated three indicators described by Cummins et al. (2005). (a) We scored an autotrophy to heterotrophy index, calculated as the proportion of scrapers to shredders and total collectors. (b) We determined a surrogate for the amount of fine organic sediment (FPOM) transported in the water column from that in the bed sediment, calculated as the proportion of filtering collectors to gathering collectors. (c) We determined a surrogate for substrate stability, estimated as the proportion of scrapers and filtering collectors, which require stable substrates such as large rock and wood, to shredders and gathering collectors, which are often found in unstable sand substrates.

2.4 | Data analyses

To test for temporal differences in macroinvertebrate structure and composition among sites, we ran a generalized linear model with a Gaussian error structure for taxonomic richness and the MMI and then tested model significance with an analysis of deviance (F test). Because these tests failed to detect significant temporal differences, we pooled all six visits for each site.

To test if benthic macroinvertebrate assemblages in sites affected by the dam showed a different taxonomic compositional profile than those in free-flowing sites, we ran a permutational multivariate analysis of variance pairwise contrasts analysis. To further characterize the taxonomic structure of each site, we calculated taxonomic richness and the MMI. We then ran a one-way analysis of variance followed by a post hoc Tukey's honest significant difference test to determine whether differences in the richness and MMI values differed significantly between sites. To check for data normality and homoscedasticity, we ran a Shapiro–Wilk test and a Bartlett test, respectively. To identify whether there were significant associations between taxa and each sampling site, we used an indicator value analysis (Dufrene & Legendre, 1997). To test if benthic macroinvertebrate assemblages in sites affected by the dam showed a functional profile different than those in free-flowing sites, we ran a Kruskal–Wallis analysis followed by a post hoc pairwise Dunn test. We chose this nonparametric analytical protocol because the FFG data did not fit normality. All statistical analyses were performed in R software, version 3.2.3 (R Core Team, 2015), using the “FSA,” “labdsv,” and “vegan” packages.

TABLE 1 Permutational multivariate analysis of variance pairwise contrasts comparing the taxonomic composition of benthic macroinvertebrate assemblages of Pandeiros River sites

Pair	F model	R^2	p value	p adjusted
P1 versus P2	2.492308	.199507	.0285	.285
P1 versus P3	10.65832	.515934	.0018	**.018**
P1 versus P4	3.478075	.258054	.0013	**.013**
P1 versus P5	5.242375	.343934	.0021	**.021**
P2 versus P3	12.12239	.547969	.0022	**.022**
P2 versus P4	3.019066	.231896	.003	**.030**
P2 versus P5	2.52958	.201889	.0081	.081
P3 versus P4	9.526482	.487875	.002	**.020**
P3 versus P5	14.51928	.592158	.0028	**.028**
P4 versus P5	4.22215	.296871	.0034	**.034**

Note. Bold values are significantly different.

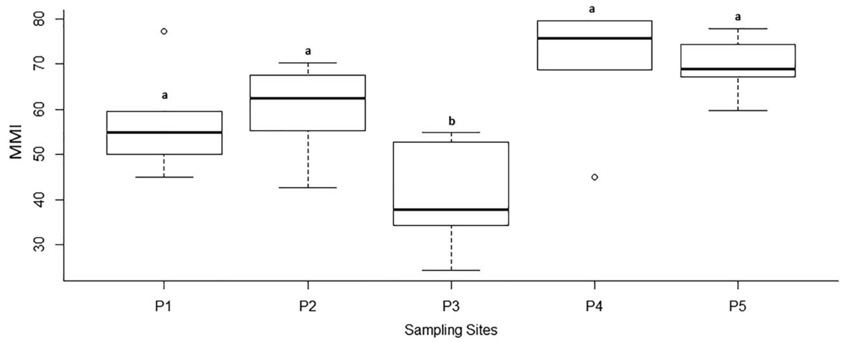

FIGURE 2 Macroinvertebrate multimetric index (MMI) scores at Pandeiros River sampling sites. Bold horizontal lines = medians; box = 25th and 75th percentiles; vertical lines = ranges; and circles = outliers calculated from six site visits. Same letters indicate lack of significant difference

3 | RESULTS

We collected a total of 34,851 benthic macroinvertebrates and 68 taxa (Data S1). Regarding taxonomic composition between assemblages (Table 1), we found that the two free-flowing sites (P1 and P2) were not significantly different from each other. Two of the dam-influenced sites (P3 and P4) showed significantly different taxonomic composition from all other sampling sites, including from each other. P5, further downstream, showed taxonomic composition significantly different from P1, but not P2.

Taxonomic richness and MMI differed in their abilities to assess the dam and reservoir effect. The MMI score for P3 was significantly lower than those of all other sites and that of P4 was significantly higher than those of all sites but P5 (Figure 2). The MMI scores for the sites downstream of the dam (P4 and P5) tended to be higher than all other sites, associated with the occurrence of rocks in P4 and macrophytes in P5. Taxonomic richness was highest at the dam-influenced sites (P3, P4, and P5) and significantly higher at P4 than the two upstream sites (P1 and P2; Figure 3).

Indicator value analysis (Table 2) demonstrated that P1 and P2 were consistently associated only with native and sensitive taxa, Helicopsychidae (Trichoptera) and Empididae (Diptera), respectively. In contrast, P3 and P4 were both associated with the presence of the non-native invasive species *M. tuberculata* and *C. fluminea*, respectively, as well as other resistant taxa, primarily native Gastropoda such as Ampulariidae, Planorbidae, Physidae (P3), and Hydrobiidae (P4). Similar to the free-flowing sites, P5 was primarily associated with native and sensitive taxa, such as Elmidae, Leptohyphidae, and Leptophlebiidae.

The FFG indicators demonstrated the effects of the dam and reservoir on the functioning of benthic macroinvertebrate assemblages. The autotrophy/heterotrophy index (Figure 4) showed that P3 had significantly more autotrophy or less heterotrophy than the other four sites. P4 also showed higher values for this index, but they were insignificantly different from P1 and P5. The other sampling sites (P1, P2, and P5) did not show significant differences between each other for this index. The transported/sedimented FPOM index scores were highest for P4 but differed significantly only from P2 and P5 (Figure 5). The other sampling sites (P1, P2, P3, and P5) did not show significant differences among each other for this index. For the substrate stability index, P3 had the highest values and differed significantly from the other sites except for P4 (Figure 6). P4 also showed relatively high values for this index, with significant differences from P2 and P5, but not P1. The other sites (P1, P2, and P5) did not show significant differences in the sediment stability index between each other.

4 | DISCUSSION

We found that the species composition of two out of the three dam-influenced sites was significantly different from the free-flowing sites (Table 1), which is in accordance with our expectations. More interestingly, whereas native and sensitive taxa were associated with relatively undisturbed sites, non-native invasive and resistant taxa were prevalent at dam-influenced sites. We also found that the functioning of benthic macroinvertebrate assemblages in those two sites was significantly different from the free-flowing sites.

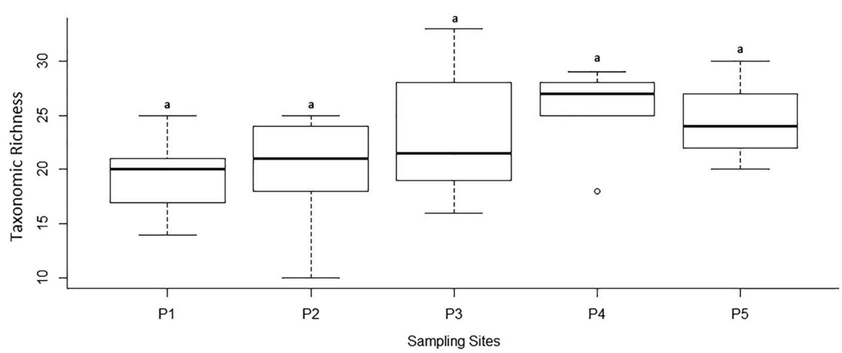

FIGURE 3 Taxonomic richness at Pandeiros River sampling sites. Bold horizontal lines = medians; boxes = 25th and 75th percentiles; vertical lines = ranges; and circles = outliers calculated from six site visits. Same letters indicate lack of significant difference

TABLE 2 Benthic macroinvertebrate indicator taxa for each Pandeiros River site

Site	Taxa	IndVal	*p*
P1	Coenagrionidae	0.67391	.0003
	Helicopsychidae	0.51874	.0198
P2	Empididae	0.59649	.0108
P3	*Melanoides tuberculata*	0.96219	.0001
	Ampulariidae	0.83333	.0003
	Physidae	0.66667	.0026
	Planorbidae	0.64762	.0033
	Hirudinea	0.47325	.015
P4	Gyrinidae	0.67708	.0037
	Hydrobiidae	0.67619	.0021
	Calopterigidae	0.61728	.0008
	Corbicula fluminea	0.58333	.0045
	Caenidae	0.55556	.0082
	Pleidae	0.5	.0071
P5	Simuliidae	0.78652	.0005
	Elmidae	0.68646	.0002
	Naucoridae	0.64141	.0009
	Leptohyphidae	0.57383	.0006
	Pyralidae	0.52294	.0099
	Leptophlebiidae	0.47393	.0105

Despite being a small, run-of-river reservoir with negligible water residence time (Fonseca et al., 2008), the assemblage structure in the reservoir was significantly different from all other sites, displaying significantly lower MMI values and correlated only with resistant taxa or non-native invasive species. The differences in the structure of the benthic macroinvertebrate assemblages likely resulted from alterations in the physical habitat of the lotic ecosystem caused by the presence of the dam (Chester & Norris, 2006; Kloehn, Beechie, Morley, Coe, & Duda, 2008; Van Looy, Tormos, & Souchon, 2014). Therefore, at a local level, small hydropower reservoirs can be very disruptive to lotic ecosystems.

The extent of the dam's influence on sites downstream from the dam was highly localized. Site P4, less than 50 m downstream of the dam, showed significant differences from the free-flowing sites for all tested taxonomic indicators. However, site P5, only 500 m downstream from the dam, tended to be very similar to the free-flowing sites. It exhibited no significant differences in assemblage structure from one of the free-flowing sites, P2, which had similar substrate composition. The differences with the other, P1, can be attributed to normal longitudinal variation in the lotic ecosystem due to the distance of these sites. We believe this means that the effects of the Pandeiros dam are local, because they were not detected by our indicators only 500 m downstream from the direct influence of the dam. This quick recovery downstream from a dam may explain the results of some studies that did not show any significant negative impact of small hydropower dams (Anderson et al., 2015; Mbaka & Wanjiru Mwaniki, 2015). It also suggests that the impacts of a single small hydropower dam on benthic macroinvertebrate assemblages are locally significant and limited in spatial extent. It is important to highlight that isolated small run-of-river dams, such as Pandeiros dam, are rare, as most of these small dams are built as part of sequential impoundment systems (Abbasi & Abbasi, 2011; Almeida et al., 2009). Our results suggest that in these conditions, the local impacts of small dams may add to cause significant changes to river systems as a whole. Future studies using other aquatic assemblages or chains of small dams may corroborate or alter our findings.

The association of flowing-water site P1 with Helicopsychidae (Trichoptera), a sensitive scraper taxon, indicates the presence of epibenthic algae banks (Cummins et al., 2005), characteristic of free-flowing habitats in the Pandeiros River main channel (Fonseca et al., 2008). Conversely, the non-native invasive species, *M. tuberculata* (Gastropoda) and *C. fluminea* (Bivalvia), were strongly associated with dam-influenced sites P3 and P4, respectively. Non-native invasive taxa tend to be most abundant in habitats that are heavily altered by human activities (Johnson et al., 2008; Linares et al., 2017; Molozzi et al., 2011; White, 2014). Site P5, located 500 m downriver of the dam and after a cascade, was associated with the filter-feeding Simuliidae (Diptera), a characteristic taxon of habitats near waterfalls (Ramirez & Guitiérrez, 2014). Also, the association with sensitive taxa, such as Elmidae (Coleoptera),

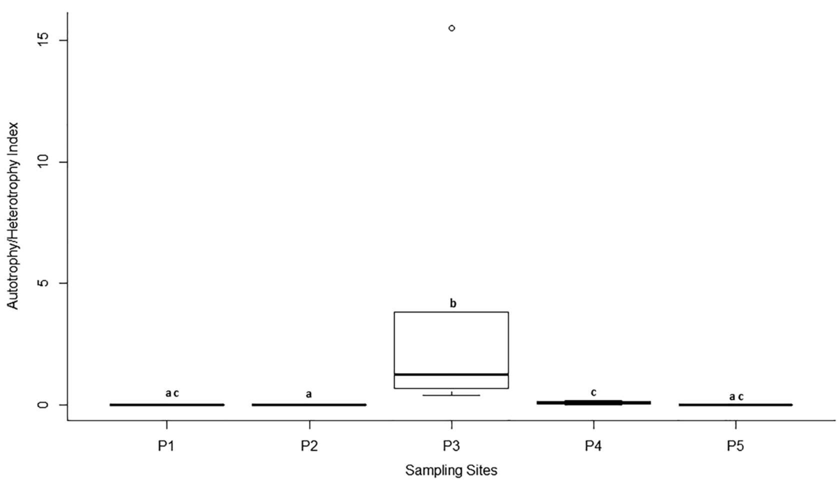

FIGURE 4 Autotrophy/heterotrophy index at Pandeiros River sampling sites. Bold horizontal lines = medians; boxes = 25th and 75th percentiles; vertical lines = ranges; and circles = outliers calculated from six site visits. Same letters indicate lack of significant difference

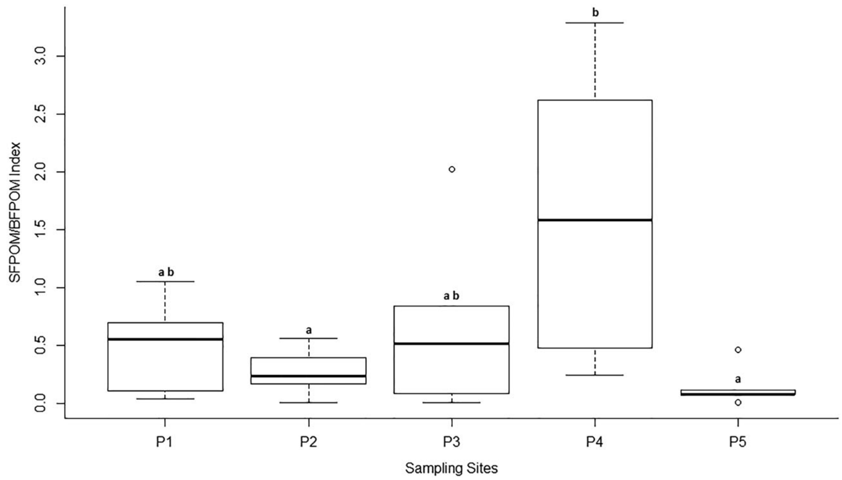

FIGURE 5 Transported/sedimented FPOM index at Pandeiros River sampling sites. Bold horizontal lines = medians; boxes = 25th and 75th percentiles; vertical lines = ranges; and circles = outliers calculated from six site visits. Same letters indicate lack of significant difference

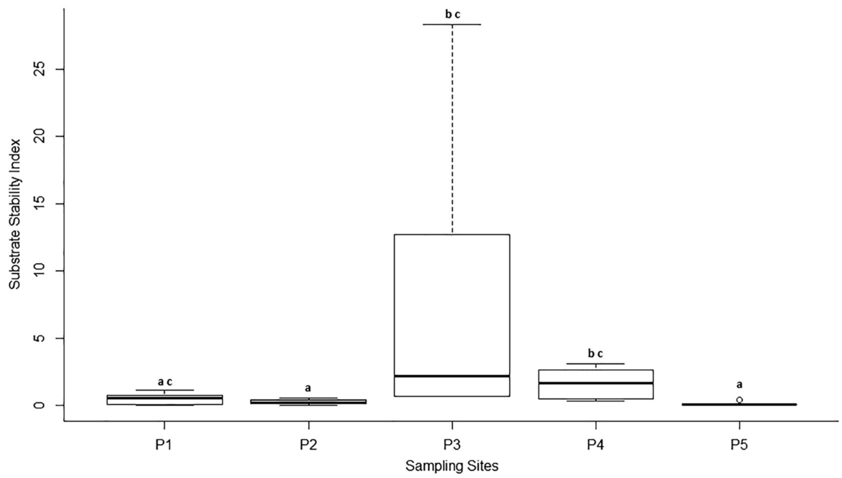

FIGURE 6 Sediment stability index at Pandeiros River sampling sites. Bold horizontal lines = medians; boxes = 25th and 75th percentiles; vertical lines = ranges; and circles = outliers calculated from six site visits. Same letters indicate lack of significant difference

Leptohyphidae (Ephemeroptera), and Leptophlebiidae (Ephemeroptera), indicates that this site has conditions approximating those of free-flowing sites (Wang et al., 2016).

The presence of non-native invasive species is another consequence of the dam and reservoir. Both *C. fluminea* and *M. tuberculata* are common in the São Francisco Basin (Fernandez, Thiengo, & Simone, 2003; Rodrigues, Pires-Junior, Coutinho, & Martins-Silva, 2007). However, in the main stem Pandeiros River, they were only found in great numbers at the two sites directly affected by the dam. This indicates that the dam is acting as a refuge for these species, facilitating their colonization and persistence in the Pandeiros River (Johnson et al., 2008; Linares et al., 2018; Oliveira, Calheiros, Jacobi, & Hamilton, 2011), leading to larger populations of both.

MMI values indicate that P3 had significantly lower ecological condition than the other four sites, meaning that the reservoir is very disruptive to benthic macroinvertebrate assemblages. This result is similar to a previous study of the Pandeiros River (Linares et al., 2018), in that only the reservoir showed significant differences in benthic macroinvertebrate assemblage complexity. During some visits, taxonomic richness was highest at the reservoir site (P3), and richness (Figure 3) tended to be a more variable indicator than the MMI (Figure 2). Others have also reported that taxonomic richness may be a misleading indicator of disturbance compared with the MMI (Hawkins, Mykrä, Oksanen, & Vander Laan, 2014; Hughes & Noss, 1992; Karr, 1981; Klemm et al., 2003).

The FFG indices also suggest that the effects of the dam and reservoir are significant but spatially limited. The autotrophy/heterotrophy index values suggest that the benthic macroinvertebrate assemblages in sites directly affected by the dam (P3 and P4) have different energetic pathways compared with the free-flowing sites (P1 and P2). This is likely a result of the high densities of *C. fluminea* and *M. tuberculata* in the former two sites, because invasive species frequently alter the trophic structure of communities in sites where they are established (Linares et al., 2017; Marchi et al., 2011; Simberloff et al., 2013). Similarly, the significantly higher values of the transported/sedimented FPOM index in P4 probably are related to a significantly higher density of the powerful filter-feeding *C. fluminea*. Previous studies in the Pandeiros River found similar results using thermodynamics-based ecological indicators, suggesting that the invasive species bring new energetic pathways and interactions to the invaded assemblages, increasing their complexity (Linares et al., 2018). The substrate stability index also showed a similar pattern, with P3 and P4 results significantly different from the other sites. It implies that the dam and reservoir interfere with the sediment and wood dynamics of the Pandeiros River. Dams, even small run-of-river ones, interfere with the downstream sediment and wood flow of rivers by retaining larger particles in their reservoirs (Anderson et al., 2015; Hauer et al., 2018; Wohl et al., 2019). The higher substrate stability in P3 can be explained by the retention of large objects, such as logs and large boulders, that increase the substrate stability for benthic macroinvertebrate assemblages, especially in a river with mostly sandy substrate such as the Pandeiros (Rezende, dos Santos, & Gonçalves Júnior, 2012). The results in P4, on the other hand, are most likely derived from a shallow rocky matrix (Linares et al., 2018), and the reduced sediment transport caused by the dam yields more exposed coarse substrate and consequently increases the stable substrate available for benthic macroinvertebrate assemblages.

5 | CONCLUSIONS

Small hydropower dams can substantially disrupt benthic macroinvertebrate assemblage structure, composition, and function close to the dam. These local impacts can significantly affect benthic macroinvetebrate assemblages regionally, especially in the context that these dams are usually built in sequential impoundment systems. We also suggest on the basis of our results that such dams and reservoirs can serve as stepping stones for further non-native invasive species propagation elsewhere in a river basin.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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