



Influences of small hydroelectric power plants on homogenization of the ichthyofauna in a tropical river

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Abstract The native fishes of the Neotropical region have been heavily impacted by the construction of reservoirs that block the rivers in different degrees. Small Hydroelectric Power Plants (SHPP) have been an alternative way to take advantage of small electricity production potential, with low cost. However, there is no basis in the belief that SHPP have less deleterious effects on river habitat than large hydropower plants. The aim of this study was to evaluate eventual changes in the ichthyofauna because of the influences of SHPP in the middle reaches of a tropical river in south-eastern Brazil. The raised hypothesis is that SHPP change the ichthyofauna composition and increase the taxonomic and functional similarities (homogenization). Fish collections were carried out quarterly at six locations along a 20 km stretch of the Paraíba do Sul River, before and after the construction of the SHPP. The fish community structure changed between the two periods, with a decrease in the fish numerical abundance, whereas the species richness did not change. Sensitive species with specialized feeding habits (namely, *Hartia loricariformis*, *Steindachineridium parahybae*, *Hypomasticus mormirops*, *Characidium alipioi*, *Chyphocharax gilbert*, *Corydoras nattereri* and

Pogonopoma parahybae) occurred only before the SHPP, being replaced by several species of Characiformes, among them four of genus *Astyanax* (namely, *A. giton*, *A. hastatus*, *A. taeniatus*, and *A. intemedium*) that are tolerant and omnivores; however, most of functional traits were maintained. The taxonomic dissimilarity increased significantly, whereas the functional dissimilarity did not differ between the two periods. The hypothesis of ichthyofauna homogenization was not confirmed in this study, probably because of the short time period since the SHPP construction.

Keywords Biotic homogenization · β -diversity · Freshwater fish · Reservoirs

Introduction

Hydrological alteration of rivers is a common practice all over the world, with about two thirds of the world's great rivers impacted by dams (Nilsson et al. 2005; Fitzgerald et al. 2018). Most dams were constructed to produce electricity, supply water for human populations and agriculture, and flow control, thus developing local and regional economies. However, dams represent one of the biggest threats to aquatic biodiversity in the world (Johnson et al. 2008; Liermann et al. 2012; Oliveira et al. 2018). The construction of a reservoir is equivalent to the formation of a new ecosystem, changing the lotic physicochemical characteristics and creating lentic conditions (Baxter 1977; Tundisi and Matsumura-Tundisi 2003; Agostinho et al. 2016). The main changes caused

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by reservoirs include loss of terrestrial and aquatic biodiversity, disruption of fish migration, hydrological changes downstream of dams, interference with sediment transport, flooding of agricultural areas, loss of historical and cultural heritage, and social effects due to population relocation (Agostinho et al. 2016).

River fragmentation by anthropogenic activities has developed rapidly, affecting the biodiversity that is sheltered in these freshwater ecosystems (Marchetti et al. 2006; Fuller et al. 2015). The effects of dams on fish include isolation of populations, interruption of routes for fish migration jeopardizing the reproductive process, limiting gene flow and making populations more simplified (Fahrig 2003; Oliveira et al. 2018). Thus, fragmentation can lead to the division of a population into two or more units, which may result in speciation or increase the likelihood of extinction (Lande 1993; Newman 2000) threatening wealth and diversity (Turner 1996; Pimm and Raven 2000). In addition, changes may occur in the abundance of species best adapted to the new environment, modifying the community structure, with the proliferation of small-sized species and reduction or even local extinction of large migratory species.

In Brazil, there is a great potential for the construction of Small Hydroelectric Power Plants (SHPP), that is, those units that produce up to 30 MW, to supply demands of small municipalities, industries and rural areas. Currently, 426 SHPP are in operation in Brazil and 30 are under construction, accounting for 3.66% of national power generation (ANEEL 2019). Most of the SHPP are run-of-river schemes associated with relatively low dams with the amount of water running through the power plant being determined by the water flowing in the river. Thus, these small-scale power plants are believed to minimize impacts on rivers, which support populations of migratory fish species, with low influence on fish assemblage's homogenization/differentiation. However, no evidence exists to justify such a belief. Like large hydropower, SHPP have deleterious effects on the environment that include river habitat affected by the interruption of water flow, barriers to animal movement in the water, water loss from evaporation and wilderness quality of the sacrificed portion of a river (Kibler and Tullós 2013; Bakken et al. 2014; Couto and Olden 2018). The very same aspects of the environment are affected in similar measure, if calculated on per kilowatt basis, when SHPP are used instead of large hydro (Premalatha et al. 2014). In addition, the

new lentic conditions tend to change environmental variables (e.g. dissolved oxygen, temperature, pH and turbidity) and consequently other components of the aquatic biota, thus influencing the fish community (Zhou et al. 2009; Kibler and Tullós 2013).

Biotic homogenization was first reported by McKinney and Lockwood (1999) as the replacement of local biotas by non-native species that constantly replace rare and endemic species with widely distributed species. This definition was expanded by numerous authors (see Olden and Poff 2004a), who had agreed that biotic homogenization should be described as losses of β -diversity or more broadly as the ecological process by which different biotas lose distinction at any level of organization: genetic, taxonomic or functional (Vitule and Pozenato 2012). Therefore, homogenization, whether genetic, taxonomic or functional, is defined as an increase in spatial similarity of a given biological variable over time, and is generally assessed by comparing the average parity similarity of the calculated variable at two distinct times (Olden and Poff 2004a). Changes in the habitat because the construction of hydroelectric plants were associated with the homogenization of the ichthyofauna (Marchetti et al. 2001).

The taxonomic homogenization is defined as “the increase in taxonomic similarity of two or more biotas in a given time interval, i.e. the decline in β -diversity” (Olden and Rooney 2006; Vitule and Pozenato 2012). This type of homogenization can cause the simplification of food chains, and considering that extinctions and invasions that are related to the life history of the species, this phenomenon may be accompanied by functional losses (Olden 2006). Accounting for taxonomic/functional changes in communities is important and relatively easy to achieve (Olden and Poff 2003; Leprieur et al. 2009). However, functional changes may occur in homogenized communities that are largely independent of taxonomic identity. Therefore, a more subtle ecological examination of homogenization is necessary. According to Olden (2006), functional homogenization is the increase of functional similarity of biotas over time, due to the establishment of species with similar roles in the ecosystem and losses of species with unique functional roles. The functional homogenization of interconnected communities may increase vulnerability to large-scale changes or disturbances in the environment (Vitule and Pozenato 2012).

The Paraíba do Sul River (PSR) is one of the most important lotic systems in south-eastern Brazil, draining

more than 50% of the territory of the state of Rio de Janeiro (Carvalho and Torres 2002; Marengo and Lincoln 2005). Its drainage area is one of the most impacted in the country, with different types of activities such as deforested areas destined to agriculture, urban occupation of the banks, large industrial plants and dams (Pfeiffer et al. 1986; Pinto and Araújo 2007; Linde-Arias et al. 2008; Terra et al. 2008). A recent change in this lotic system was the construction of two Small Hydroelectric Plants (SHPP) in the river middle reaches. The SHPP were built in the second half of 2011 in the middle reaches of the PSR, with both having a fish transposition device (fish ladder).

The present study aimed to evaluate the ichthyofauna in the period before and after the construction of these SHPP to assess eventual effects on the fish community (structure, abundance and richness). The hypothesis to be tested is that SHPP change the composition of the ichthyofauna, as well as they change taxonomic and functional β -diversity because the interruption of water flow and creation of the new lentic environment that greatly differs from the lotic conditions. We expect a replacement of sensitive species by species more tolerant and adapted to the new lentic conditions, and an increase in the taxonomic and functional similarity of the ichthyofauna (homogenization). In addition, we examined eventual changes in environmental variables between the two periods and their effects on the fish assemblages.

Materials and methods

Study area

The studied area extends for about 25 km and is comprised in the middle reaches of the Paraíba do Sul River, at an altitude ranging from 470 to 500 m above the sea level (Fig. 1). The Paraíba do Sul River Basin drains an area of approximately 57,000 km² in south-eastern Brazil. The flow in the studied area varies from 250 to 400 m³/s. The predominant climate is tropical hot and humid, with the rainy season in summer (October to March) and the dry season in winter (April to September). The average annual rainfall ranges from 1,250 to 1,500 mm and the temperature ranges from 15 to 31 °C.

This river stretch has a diversified habitat structure, with the presence of islands, rapids and a few

backwaters. The bed is comprised by submerged rocks in almost all extension, forming different microhabitats. The aquatic vegetation is abundant in some stretches, which favour the occurrence of shelters and increase habitat diversification. The margins have little vegetation cover, with large pasture areas nearby. Several canals with untreated sewage discharge into this stretch.

Small Hydroelectric Power Plants (SHPP)

Lavrinhas (44°47'W; 22°33'S) and Queluz (44°52'W; 22°34'S) SHPP were only 8 km apart each other, and each has an installed capacity of 30 MW (Table 1). They are low-fall plants operating on the water line (reduced flooding areas and do not form reservoirs) with a single-jet vertical-slot fish ladder.

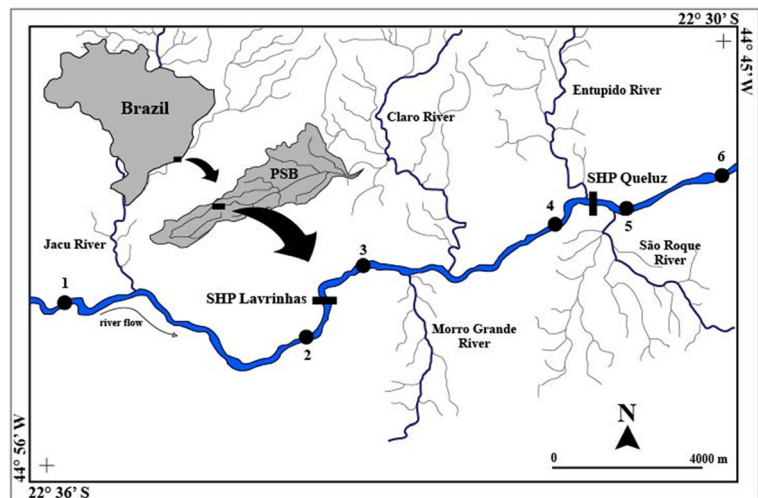
Sampling

Quarterly fish samplings were conducted at six sites in two periods 2008 and 2012/2013 (Fig. 1). The first (before the construction of SHPP) sampling period was carried out in February, May, August and October 2008, and the second (after the construction of SHPP) in October 2012, and January, April and July 2013. The sampling design had a total of 48 samples (six sites \times four seasons \times two periods).

A standardized fishing effort was applied along a stretch of approximately 20 km of the middle reaches of the Paraíba do Sul river in both periods. A total of 12 gill nets (25 \times 2 m; mesh size of 1.5; 2.0; 2.5; 3.0; 3.5; 4.0; 5.0; 7.0; 9.0; 10.0; 11.0 and 12.0 cm between adjacent nodes) were randomly distributed within each site, with a total sampled area of approximately 600 m². The nets were set up at the dusk and retrieved at dawn of the next day, remaining in operation for approximately 14 h. In addition, 10 throws of casting nets (3 m diameter and 2–3 cm mesh size) and 10 try of sieves (80 cm diameter and 1 mm mesh size) were performed. The sampling unit was defined as the sum of the number of fish collected by all fishing equipment at each sampling occasion in a given location.

Concurrently with fish sampling, measurements of the following physicochemical variables were performed at each site: water temperature (°C), pH, dissolved oxygen (mg/l) and turbidity (NTU). The measurements were conducted at approximately 0.5 m below water surface, in a distance of approximately 3 m

Fig. 1 Study area, middle reaches of the Paraíba do Sul River, indicating of the sampled locations (1, 2 ... 6) and the two (Lavrinhas and Queluz) SHPP (bar). The Paraíba do Sul River basin (PSB) also showed



from the margin of the river, using a Horiba U50 multiprobe (Horiba Trading Co. Ltd., Shanghai).

Functional traits

The functional traits (Table 2) were chosen to encompass different roles that influence important functional roles of the ichthyofauna related to life history strategy, energy accumulation, feeding habits and vertical distribution in the water column (Pinto and Araújo 2007; Villéger et al. 2012; Batista et al. 2015; Winemiller et al. 2015; Villéger et al. 2017). The traits information was collected directly from the fish species, from the database of the Laboratory of Fish Ecology,

Table 1 Technical characteristics of the Lavrinhas and Queluz, the two Small Hydroelectric Power Plants in the middle reaches of the Paraíba do Sul River

PCH	Lavrinhas	Queluz
Outflow	215 m ³ /s	217,5 m ³ /s
Maximum water level	498.5 m	484.5 m
Normal downstream water level	484.5 m	471.50 m
Flooded area	0.35 km ²	0.56 km ²
Reservoir area	0.72 km ²	1.54 km ²
Volume	3.37 × 10 ⁶ m ²	8.85 × 10 ⁶ m ²
Retention time	4 horas	11 horas
Mean depth	6 m	7 m
Maximum depth	21 m	17.7 m
Capacity	30 MW	30 MW

Universidade Federal Rural do Rio de Janeiro, and from the FishBase (Froese and Pauly 2019).

β-diversity

β-diversity was calculated based on presence/absence data of individuals of each species in each sample for the period before and after the construction of SHPP. The taxonomic and functional β-diversity and their decomposition of turnover (species substitution) and nestedness (species extinction) were calculated. To calculate taxonomic β-diversity and its decomposition, the beta.pair function (incidence-based paired dissimilarities) was used, which computes three distance matrices representing (i) turnover, (ii) nestedness and (iii) total dissimilarity (Baselga 2010). The species data matrix was combined with the traits matrix to calculate the functional β-diversity. The betapart function (beta-diversity partition) was used to calculate functional β-diversity and its decomposition. The indices were obtained using the R script “multidimFbetaD” supplied by Sébastien Villéger (<http://villegger.sebastien.free.fr>). These analyses were performed in the software R version 3.5.1.

Statistical analysis

A two-way factorial analysis of variance (ANOVA) was used to compare the environmental variables between the two periods and the six sites. Where the

Table 2 Functional traits categories with indication of the rationale for the trait selection

Traits	Categories (Quantitative values)	Rationale
Maximum body size	Small (< 7 cm) Medium (7–15 cm) Large (15–40 cm) Very large (> 40 cm)	Related to individual energy needs and possible impact on food web (Batista et al. 2015). Size also influences growth rate, with large fishes growing slowly than small ones.
Transversal body shape	< 1.0 1.0–2.0 2.0–3.0 > 3.0	It is a measure that reflects the vertical position in the water column and the hydrodynamic capacity of the species (Villéger et al. 2012; Batista et al. 2015).
Feeding habits	Carnivores Detritivores Herbivores Invertivores Omnivores Piscivores	Reflects the trophic structure, based on the fish diet, as well as the distribution of resources and adaptation of the species to the habitat. (Batista et al. 2015).
Vertical distribution	Benthic Benthic/Pelagic	Reflects vertical distribution in the water body and potential impact on the habitat. Critical to determine fish ecological niches.
Sensitivity	Tolerant Sensitive	Reflects species sensitivity to environmental degradation (Pinto and Araújo 2007).

ANOVA showed a significant difference, a “*posteriori*” Tukey HSD test was used to determine which means were significantly different at the 0.05 level. Pairwise correlation coefficients were calculated between the environmental variables to detect eventual co-linearity ($r > 0.7$; Leathwick et al. 2006; Clarke and Gorley 2015), but no significant association was found among these variables. Further, a Permutational Analysis of Variance (PERMANOVA) was used to compare the multivariate environmental data between the periods and sites (fixed factors). A principal component analysis (PCA) was applied on the standardized environmental data to identify temporal and spatial patterns, i.e., groups of samples coded by the periods and localities (sites) according to the environmental variables. Because environmental data have different units of measurements, they were transformed to standard z-scores, i.e., they were converted in the same unit of standard deviation to become dimensionless before submit to multivariate analysis.

The species richness and the number of individuals were compared between the two periods using a one-way ANOVA. ANOVA was performed using the software Statistica version 10.0 (StatSoft Inc. 2011). To assess differences in the composition of the fish communities between the periods, a Principal Coordinate Analysis (PCoA) was applied on a Bray-Curtis distance matrix on the fish data.

Additionally, a Similarity Percentage Analysis (SIMPER) was used to determine the species with the greatest contribution to the within-group similarity in both periods. A permutational multivariate analysis of variance (PERMANOVA) on a Bray-Curtis matrix with a Type I (sequential) sum of squares to calculate p-values was used to compare fish assemblage structure between the two periods. The raw fish data were square-root transformed to reduce the bias of abundant species before all analyses on species on the fish assemblage structure.

A redundancy analysis based on a Euclidean distance matrix (dbRDA) was used to evaluate the influence of environmental variables on the fish assemblage structure in the periods before and after the construction of the SHPP. Further, the relationship between the traits and species were assessed for the two studied periods using principal coordinate analysis (PCoA) on the traits data to show groups of species sharing similar functions. Reference (Clarke and Gorley 2015) was mentioned in the manuscript; however, this was not included in the reference list. As a rule, all mentioned references should be present in the reference list. Please provide the reference details to be inserted in the reference list. These analyses were performed using the software Primer version 6.1.3 + PERMANOVA version 1.0.3 (Anderson et al. 2008).

Results

Environmental variables

Water temperature ranged from 19.7 to 27.4 °C, dissolved oxygen from 5.5 to 12.5 mg/l, pH from 5.7 to 8.1 and turbidity from 13.5 to 171 NTU. None of these environmental variables showed differences between the sites ($P > 0.05$, Fig. S1 in the Supplementary Material). The dissolved oxygen changed significantly between the two periods ($F = 17.67$; $p = 0.001$) with comparatively higher values in the second (after the SHPP) period, whereas the pH ($F = 8.14$; $p = 0.007$) was significantly higher in the first (before the SHPP) period. No significant differences were found for temperature ($F = 0.15$; $p = 0.705$) and turbidity ($F = 1.01$; $p = 0.322$) between the two periods. The PERMANOVA results confirmed the differences between the periods (Pseudo- $F = 5.6$, $P = 0.001$) but no significant differences were found between the sites (Pseudo- $F = 0.3$, $P = 0.9$) or period vs. sites interaction (Pseudo- $F = 0.2$, $P = 0.9$).

A well-defined spatial pattern in the distribution of samples was detected along the first two axes of the Principal Component Analysis on the environmental

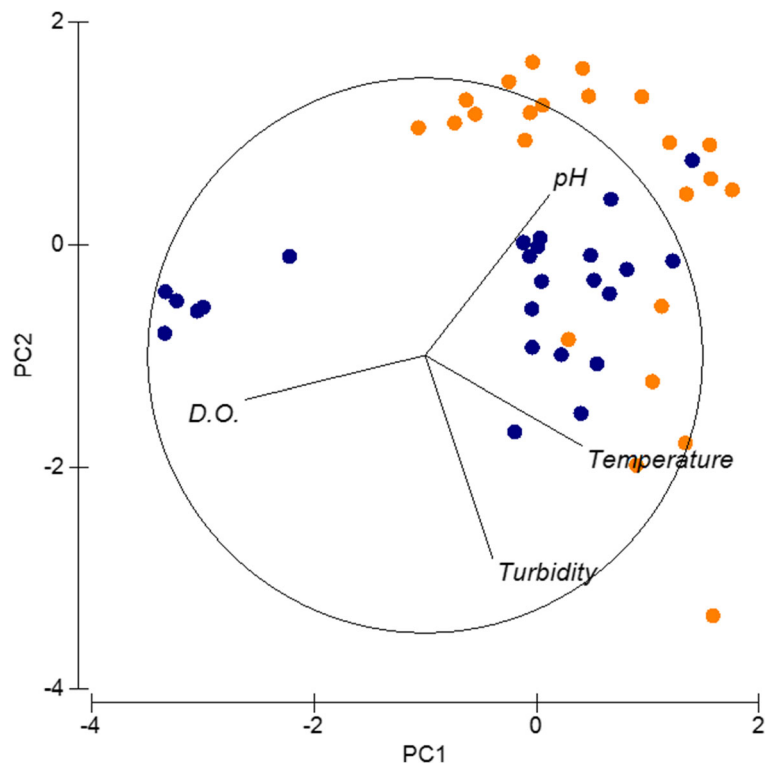
variables (Fig. 2). The axes 1 (45.3%) and 2 (30.1%) explained 75.4% of the data variation. Dissolved oxygen had the highest correlation with the axis 1 (-0.65), followed by temperature (0.57) and pH (0.45). Turbidity was the variable more closely correlated with the axis 2 (-0.73) followed by the pH (0.58). Samples from the first period had higher pH and lower dissolved oxygen compared with samples from the second period.

Species composition

A total of 4662 individuals were sampled, belonging to 43 species, 18 families and seven orders during the two sampling periods. The orders with the highest species richness were the Characiformes (19 species) and Siluriformes (14) species. Thirty-three species (2917 individuals) were recorded in the first period, whereas 34 species (1745 individuals) in the second period (Table S1 in Supplementary Material).

Most species (24 species) occurred in both periods (Table S1 in Supplementary Material). Nine species in four orders were recorded only in the first period, being three Characiformes [*Characidium alipioi* Travassos, 1955, *Cyphocharax gilbert* (Quoy & Gaimard, 1824)

Fig. 2 Ordination diagram of the first two axes of the principal component analysis on the environmental variables with samples coded by the two periods. Before (orange) and after (dark blue)



and *Hypomasticus mormyrops* (Steindachner, 1875)], four Siluriformes [*Corydoras nattereri* (Steindachner, 1876), *Harttia loricariformis* (Steindachner, 1877), *Pogonopoma parahybae* (Steindachner, 1877) and *Steindachneridion parahybae* (Steindachner, 1877)], one Cyprinodontiformes [*Poecilia reticulata* (Peters, 1859)] and one Synbranchiformes [*Synbranchus marmoratus* (Bloch, 1795)]. On the other hand, 10 species in three orders were recorded only in the second period, being eight Characiformes [*Apareiodon piracicabae* (Eigenmann, 1907), *Astyanax giton* (Eigenmann, 1908), *Astyanax hastatus* (Myers, 1928), *Astyanax intermedius* (Eigenmann, 1908), *Astyanax taeniatus* (Jenyns, 1842), *Prochilodus lineatus* (Valenciennes, 1837), *Pseudocorynopoma heterandria* (Eigenmann, 1914), and *Salminus brasiliensis* (Cuvier, 1816)], one Cichliiformes [*Australoheros facetus* (Jenyns, 1842)] and one Siluriformes [*Rhamdia quelen* (Quoy & Gaimard, 1824)]. Thus, these new species from the period after the SHPP are phylogenetically more similar when compared to those unique species from the period before the SHPP.

The species richness did not differ ($F_{1,46} = 0.06$; $p = 0.79$) between the first (13.3 species/sample) and the second (13.1 species/sample) periods according to ANOVA (Fig. 3). The number of individuals was significantly higher ($F_{1,46} = 14.6$; $p = 0.0019$) in the first period (121.5 individuals/sample) compared with those of the second period (72.7 individuals/sample).

Different fish assemblage structures were observed between the two periods according to the PCoA (Fig. 4). These differences were confirmed by the PERMANOVA analysis for comparison of fish assemblage structure between the two periods (Pseudo-F = 8.88 $p = 0.001$).

Similarity Percentage Analysis (SIMPER) showed that both periods presented high within-group average similarity (> 45%), indicating the high consistency of the species composition among the samples. *Hypostomus auroguttatus* (Kner, 1854), *Astyanax* aff. *bimaculatus* and *Pimelodus maculatus* (Lacepède, 1803) were the species that had the largest contribution to the average abundance and average similarity and in both periods. On the other hand, *Astyanax parahybae* (Eigenmann, 1908), *H. loricariformis* and *Rineloricaria lima* (Kner, 1853) contributed to the average similarity only during the first period, whereas *Hoplias malabaricus* (Bloch, 1794), *Plagioscion squamosissimus* (Heckel, 1840) (non-native) and *Hypostomus affinis* (Steindachner, 1877) contributed only to the average similarity in the second period (Table 3).

Environmental influences on the fish community

The first dbRDA axis was negatively correlated with the dissolved oxygen ($r = -0.67$) and turbidity ($r = -0.72$) and positively correlated to the pH ($r = 0.15$). The second dbRDA axis was negatively correlated with the dissolved oxygen ($r = -0.70$) and temperature ($r = -0.12$) and positively with the turbidity ($r = 0.69$) and pH ($r = 0.16$). The dissolved oxygen (D.O.) was the environmental variable that most discriminate the first (comparatively lower D.O.) and second (comparatively higher D.O.) periods (Fig. 5).

Callichthys callichthys (Linnaeus, 1758), *Gymnotus carapo* (Linnaeus, 1758) and *Hoplosternum littorale* (Hancock, 1828) were associated with sites with high turbidity and dissolved oxygen, whereas the non-native

Fig. 3 Mean abundance (Number of individuals/sample) and species richness (species/sample) in the two studied periods. Codes: abundance before, dark yellow; abundance after, dark blue; richness before, light yellow; richness after, light blue

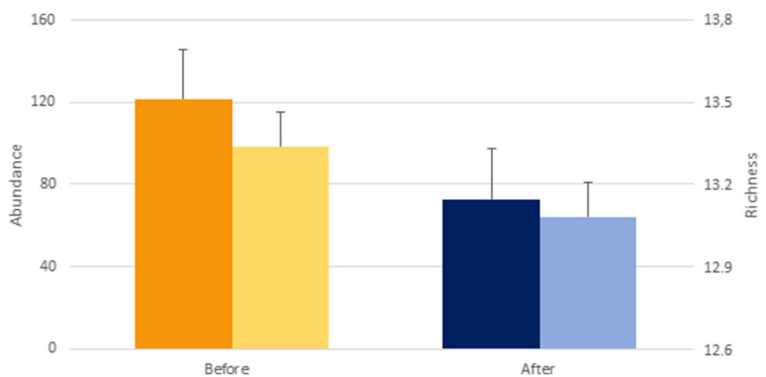
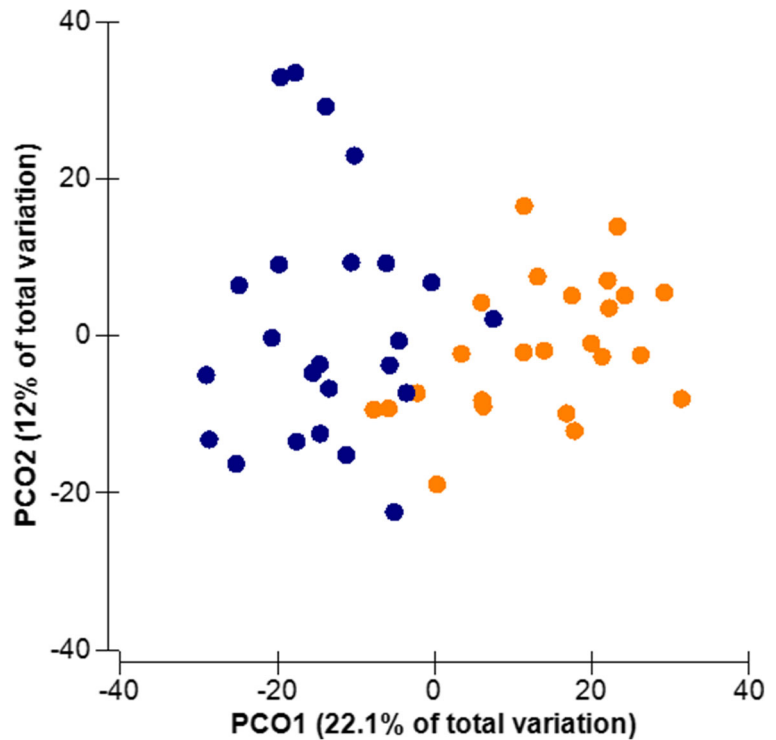


Fig. 4 Ordination diagram of the Principal Coordinate Analysis (PCoA) on the numerical abundance of fish species, with samples coded by the periods before (orange) and after (dark blue) the SHPP



P. squamosissimus was associated to sites with high D.O. *Hypostomus auroguttatus* and *Astyanax* aff.

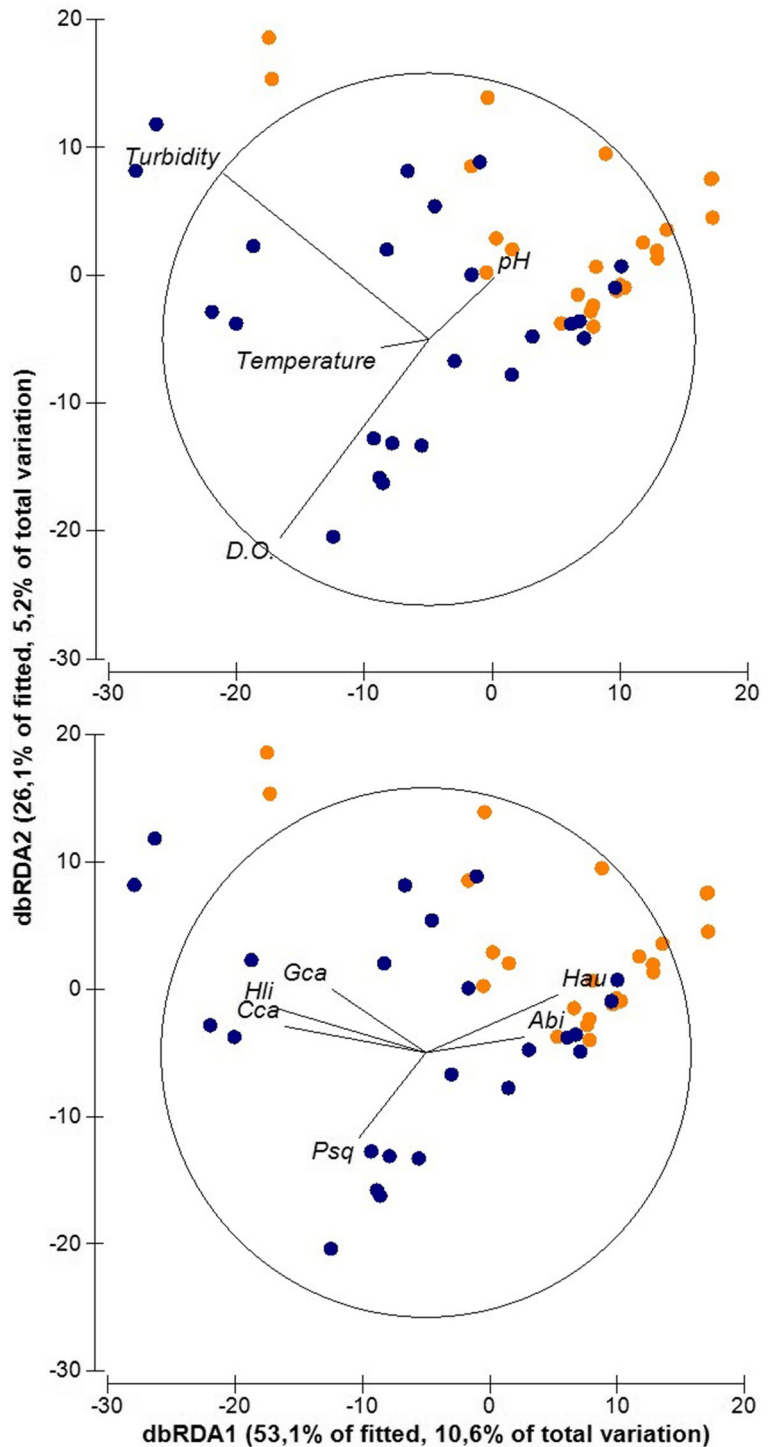
bimaculatus, were associated to sites with low D.O. concentrations and high pH (Fig. 5).

Table 3 Species that most contributed to within-group average similarity in the periods before and after the construction of the SHPP according to similarity percentages analyses (SIMPER)

Average similarity (%)	Before (59.78%)		After (48.24%)	
	Av.Ab	Av.Sim.	Av.Ab	Av.Sim
<i>Hypostomus auroguttatus</i>	5.69	14.86	2.19	5.11
<i>Astyanax</i> aff. <i>bimaculatus</i>	5.12	13.49	3.43	10.73
<i>Pimelodus maculatus</i>	3.01	6.64	2.31	5.92
<i>Pimelodus fur</i>	2.20	3.67	0.86	1.41
<i>Oligosarcus hepsetus</i>	1.55	3.41	2.03	3.84
<i>Hoplosternum littorale</i>	1.66	2.54	2.57	5.25
<i>Crenicichla lacustris</i>	0.94	1.59	1.42	2.70
<i>Gymnotus carapo</i>	0.99	1.45	1.46	2.61
<i>Astyanax paraguayae</i>	1.56	2.73	-	-
<i>Harttia loricariformis</i>	1.10	1.72	-	-
<i>Rineloricaria lima</i>	1.06	1.72	-	-
<i>Hoplias malabaricus</i>	-	-	1.09	2.65
<i>Plagioscion squamosissimus</i> *	-	-	1.00	2.00
<i>Hypostomus affinis</i>	-	-	0.75	1.29

Av.Ab., average abundance (number/sample); Av.Sim., average similarity (%). * non-native species

Fig. 5 Distance-based redundancy analysis (dbRDA) on relationship between fish assemblage structure and the environmental variables. Samples coded by periods and environmental variables (above) and periods and species (below). Period codes: before, orange; after, dark blue. Species code: Abi, *Astyanax aff. bimaculatus*; cca., *Callichthys callichthys*; Gca, *Gymnotus carapo*; Hau, *Hypostomus auruguttatus*; Hli, *Hoplosternum littorale*; Psq, *Plagioscion squamosissimus*



The first two PCoA axes explained 72.9% of the total variance of the traits data (Fig. S2 in Supplementary Material). Before the SHPP, the benthic-pelagic traits were positively associated with the axis 1, being

represented by cichlids and species of the genus *Astyanax*. In contrast, the benthic, detritivores, and fish with < 1 transversal body shape were represented by the Siluriformes species that had negative correlation with

the axis 1. The axis 2 was negatively correlated with sensible species such as *H. loricariformis*, *P. parahybae* and *S. parahybae* in the first period, but disappeared after the construction of the SHPP. The functional group of benthic-pelagic increased after the SHPP because of the appearance of several species of the genus *Astyanax* (e.g., *A. giton*, *A. hastatus*, *A. intermedius* and *A. taeniatus*).

Taxonomic and functional β -diversity

The taxonomic β -diversity increased significantly from the first period (mean = $0.34 \pm 0.10\text{SE}$) to the second period (mean = $0.42 \pm 0.10\text{SE}$), with a higher turnover contribution compared to the nestedness. The turnover and nestedness components also increased between the two periods. The average turnover in the first period (0.24) was higher than the nestedness component (0.10) and contributed 70.59% of the taxonomic β -diversity, whereas the nestedness component contributed 29.41% (Table 4). The mean turnover in the second period (0.30) was higher than the nestedness (0.12), contributing 71.43% of the taxonomic β -diversity, whereas the nestedness contributed with 28.57% (Table 4).

The functional β -diversity and its turnover and nestedness components did not differ significantly between the two periods. The mean turnover in the first period (0.13) was lower than the nestedness (0.21) and contributed 38.24% of the functional β -diversity, whereas the nestedness contributed 61.76% (Table 4). The mean turnover in the second period (0.15) was lower than the nestedness (0.20), contributing 42.86% of the functional β -diversity, whereas the nestedness contributed 57.14% (Table 4).

Discussion

An increase in the ichthyofauna dissimilarity occurred after the construction of the two SHPP in the middle reaches of the Paraíba do Sul River, which was contrary to our expectations of fauna homogenization. In addition, the tendency of increase in the taxonomic dissimilarity was not matched by the functional dissimilarity, which did not vary between the two periods. This suggests that changes in the composition of the ichthyofauna did not lead to additions of functions. Communities can tend to be very dissimilar in terms of species

composition but similar in terms of biological composition regarding trophic levels (Villéger et al. 2008), morphological traits (Irz et al. 2007) or phylogenetic lineages (Bryant et al. 2008). In the present study, the SHPP seems to contribute to changes in species composition (high taxonomic β -diversity) that are functionally similar (low functional β -diversity). Further, this pattern is very unlikely to suggest biotic homogenization.

The high taxonomic β -diversity after the construction of the SHPP had the most contribution of the turnover (71.43%). The predominance of the turnover can suggest that sites present environmental heterogeneity that favour selection by different fish species. Conversely, the comparatively low functional β -diversity that remained unchanged between the two periods had predominant contribution of the nestedness (57.14–61.76%), which can indicate losses of functions because environmental filtering favours certain species traits over others, and only fish with traits with the ability to tolerate the changes between the lotic and the lentic conditions would endure in the new created environment (e.g., generalists or resistant species). The species replacement detected occurred with taxonomically closely related species, i.e., of the new 10 species, eight were of the same order (Characiforms), six of the same family (Characidae) and four belong to the same genus (*Astyanax*). On the other hand, the nine replaced species that occurred only before the SHPP, were taxonomically more distinct, belonging to four orders and nine different genera. This indicates a predominance of species replacement with some loss of function, thus confirming the high contribution of taxonomic turnover and functional nestedness after the construction of the SHPP.

Patterns of increasing taxonomic dissimilarity with unchanged functional dissimilarity were described for 137 European river basins (Villéger et al. 2014), with the loss of functional dissimilarity typically exceeding the loss of taxonomic dissimilarity. Thus, even though the ichthyofauna presents different species, they shared some functional attributes, resulting in a possible functional redundancy. This pattern seems to match our findings, with the fish assemblage of the Paraíba do Sul River being influenced by the SHPPs, that is, a species replacement that theoretically maintains or loses some functions, given the greater contribution of functional nestedness compared to taxonomic nestedness.

Biotic homogenization is a process that occurs over long time period or large spatial scale (Olden and Poff 2004b; Clavero and Gracia-Berthou 2006; Smart et al.

Table 4 Mean and standard error for taxonomic and functional β -diversity for the periods before and after the SHPP. The results of the t-test to compare B-diversity between the two periods were also shown

Indices	Taxonomic			Functional		
	Before	After	t-test (p)	Before	After	t-test (p)
β -diversity	0.34 ± 0.10	0.42 ± 0.10	9.5 (p = 0.001)	0.34 ± 0.18	0.35 ± 0.13	0.59 (p = 0.56)
Turnover	0.24 ± 0.12	0.30 ± 0.13	6.19 (p = 0.001)	0.13 ± 0.12	0.15 ± 0.12	1.53 (p = 0.13)
Nestedness	0.10 ± 0.09	0.12 ± 0.09	t = 2.38 (p = 0.018)	0.21 ± 0.19	0.20 ± 0.16	0.55 (p = 0.58)

2006) and losses of species at local scale because the invasion or introduction of new species may take a long time to occur. The taxonomic homogenization of fish fauna is a temporally and spatially dynamic process; initial local increases in β -diversity through species introduction could be blurred because of scaling to regional and national levels or by the continuous expansion of a reduced number of exotic species (Castaño-Sánchez et al. 2018). We found no evidence of ichthyofauna homogenization, a probable consequence of the short period of operation of the SHPP, the connectivity of the hydrologic systems, and the characteristics of small water accumulating by the dams. In some ways, this kind of enterprise seems to cause less damage to the environment than the complete blocking of the lotic systems and the total isolation of the ichthyofauna and its migratory paths caused by large barrages. However, this belief is questionable (see Kibler and Tullos 2013; Bakken et al. 2014; Premalatha et al. 2014). Although the larger land occupation for large hydropower is explained by the extent of the reservoirs, both SHPP and large dams cause direct impacts on lotic systems, such as habitat loss and changes in river connectivity, but also indirect impacts such as biotic homogenization, favouring generalist species over specialized species and facilitating invasion by non-native species, increasing the risk of extinction of endemic taxa (Liermann et al. 2012; Bakken et al. 2014; Fitzgerald et al. 2018). Whereas large hydropower plants have greater cumulative effects related to total land inundation, potential sediment transport disruption, and potential for reservoir-induced seismicity, SHPP return greater impacts, per megawatt of power generated, with respect to the length of river channel affected, diversity of habitats affected, influence to lands designated as conservation and biodiversity priorities (Kibler and Tullos 2013).

There is an enhanced tendency towards eutrophication of the impounded lake and downstream

sections of the river. The hypolimnic water that is normally used for power generation and then discharged into the river downstream is much cooler than the river water. This generates temperature shocks which stress the river biota (Chari et al. 2005). SHPP have deleterious effect on river habitat affected by the interruption of water flow, barriers to animal movement in the water, water loss from evaporation and wilderness quality of the sacrificed portion of a river (Premalatha et al. 2014). Although this study does not have a more detailed historical database, it is possible that the ichthyofauna homogenization process has already started, although it was not detected with the available information in this short time period. The replacement of specialized and sensitive species by more generalists or resistant species is and indicative of homogenization.

A clear change in the community structure between the two periods was detected by PCoA analysis. Such changes were mainly caused by changes in the rank of numerical contribution of the most frequent species, as well as the replacement of some taxa between the two periods. The habitat structure and environmental changes between the lotic and lentic conditions can lead to an expected change in fish fauna, with species more resistant and pre-adapted to the new lentic conditions being favoured, among them several non-native species (Johnson et al. 2008). In addition, the changes related to the transformation of a lotic into a lentic environment are already sufficient for running water specialists undergo or not to survive in the flooded area, whereas opportunistic and generalist species settle easily. In addition, the obliteration of the lotic system by dams results in harm for several species that cannot overcome this barrier despite the fish ladder. Thus, even when species can migrate up the fish ladder, they can hardly return to the downstream region of the dam (Johnson et al. 2008; Vitule et al. 2012).

Our findings indicated that species richness did not change between the two periods, and that a decreasing in fish abundance occurred. Stability in the species richness did not corroborate other studies that reported decreases in the richness after damming because the loss of environmental heterogeneity is greater in the lotic conditions (Bojsen and Barriga 2002). Alhassan et al. (2015) found a decrease in the fish abundance after the damming of a lotic system in Ghana, and attributed to a decrease of several fish species that were susceptible to oxygen depletion. The formation of the lentic environment favours the prolongation of the retention time and phytoplankton development, consequently increasing oxygen levels. Kishor et al. (2018) reported the dissolved oxygen as an important variable driving a gradient of species distribution. In the present study, decreases in the fish abundance was not related to oxygen levels that increased, whereas the pH decreased after the construction of the SHPP and the temperature and turbidity remained practically unchanged between the two periods.

Studies on biotic homogenization as well as the effects of damming caused by SHPP on species composition, richness and abundance are rare in Brazil. These aspects have not been satisfactorily studied in Neotropical rivers. Habitat homogenization can cause assembly homogenization through loss of native species and addition of non-native species (Scott and Helfman 2001). Special care must be taken when constructing dams, as they are structures that facilitate ichthyofauna homogenization. There is a tendency to increase species homogenization due to the introduction of cosmopolitan species aiming to increase food supply and sport fishing to the detriment of native fauna. The results found in the present work had not yet pointed to the existence of the homogenization process caused by the SHPP influences. However, analyses that consider a longer period after the SHPP are needed to a deep assessment of this issue.

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Conflict of interest The authors declare that they have no conflict of interest.

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