

# Heterogenisation of riverine ichthyofauna diversity by small hydropower dams

Dandhara Rossi Carvalho  | Francisco Gerson Araújo 

Laboratório de Ecologia de Peixes,  
Universidade Federal Rural do Rio de  
Janeiro, Seropédica, Brazil

## Correspondence

Francisco Gerson Araújo, Departamento  
de Biologia Animal, Laboratório de  
Ecologia de Peixes, Universidade Federal  
Rural do Rio de Janeiro, BR 465, Km 7,  
Seropédica 23897-030, Brazil.  
Email: [gersonufrj@gmail.com](mailto:gersonufrj@gmail.com)

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## Abstract

Dams modify river physical and chemical attributes. This disruption hampers fish migration, leading to the introduction of non-native species and losses of specialised native species. Small hydropower plants (SHPs) have been suggested for replacing large dams to minimise reservoir size and preserve natural flow regimes. We evaluated the influences of two SHPs on the ichthyofauna in a tropical river, comparing fish taxonomic and functional beta-diversity in three periods. Period-1 preceded SHP construction (Pre-2008), when the river was free-flowing. Period-2 was 1 year after completion of SHP construction (Post-2012). Period-3 was after 10 years of SHP operation (Current-2021). We calculated 10 functional ichthyofaunal attributes based on 12 quantitative morphometric measurements related to habitat use, feeding, and locomotion. The ichthyofaunal composition varied among the periods ( $p = .001$ ) and seasons ( $p = .009$ ), with the highest species richness in the Post period compared to the other two periods ( $p = .002$ ). Abundance significantly decreased over time ( $p = .004$ ). Taxonomic beta-diversity increased in the Post period remaining stable in the Current period. Functional beta-diversity did not change between the Pre and Post periods but significantly increased in the Current period. The turnover component had the greater influence on both taxonomic and functional beta-diversity, with no temporal changes observed in nestedness. The ichthyofauna appears to have undergone heterogenisation and restructuring. Changes include the emergence of more tolerant species (e.g., *Hoplosternum littorale* and *Pimelodus maculatus*), displacement of native and sensitive species (e.g., *Pogonopoma parahybae* and *Steindachneridion parahybae*), and colonisation by a non-native predator (*Plagioscion squamosissimus*). This indicates that small-scale projects such as SHPs harm fish populations by altering habitats and restructuring the ichthyofauna.

## KEYWORDS

dams, environmental changes, freshwater fish, functional traits

## 1 | INTRODUCTION

The severity of anthropogenic threats to freshwater ecosystem biodiversity is increasing worldwide (Spector, 2002). Rivers are

extensively exploited, providing a range of services to the human population, such as water supply, irrigation, and hydroelectric power generation (Ellis et al., 2010; Su et al., 2021). Currently, over half of the major river systems are fragmented by dams globally

(Grill et al., 2019; Nilsson et al., 2005). About two-thirds of the world's large rivers (Fitzgerald et al., 2018; Nilsson et al., 2005) have experienced serious losses in ichthyofauna, with implications for global fish diversity (Liermann et al., 2012). Understanding these human-induced disturbances and the relationships between species distribution and habitat characteristics is often the first step to unravelling the mechanisms that govern biodiversity in these altered ecosystems.

Reservoirs create new ecosystems, altering river physical and chemical characteristics and acting as barriers to fish migrations (Agostinho et al., 2016; Baxter, 1977). These new lentic environments favour the colonisation of non-native species that are more tolerant and capable of establishing in these conditions at the expense of specialised and sensitive native species. This raises the risk of native species extinction because they must adapt to the altered lentic environments (Carvajal-Quintero et al., 2017). Hence, the growing number of dams and reservoirs in tropical rivers poses a significant threat to fish biodiversity (Fitzgerald et al., 2018; Winemiller et al., 2016). To mitigate the impacts of large hydro-power dam construction for electricity generation, small run-of-the-river hydropower plants (SHPs) with reduced reservoir size and flow regime disruption are encouraged (Wang et al., 2022). A global study indicated the existence of 82,891 small dams, and this number could triple with the expansion of this policy (Couto & Olden, 2018). However, little is known about the actual effects of SHPs on the ichthyofauna.

According to Premalatha et al. (2014), SHPs can cause ecosystem problems comparable to those of large hydropower plants, despite generating fewer megawatts (MW). Research on the ecological impacts of small run-of-the-river dams has focused on their effects on ichthyofauna (Cella-Ribeiro et al., 2017; Gibeau et al., 2017; Robson, 2013) and habitat fragmentation, and degradation (Nilsson et al., 2005; Santucci et al., 2005; Simonovi et al., 2021). All three have negative consequences for hydrology and biodiversity (Carvajal-Quintero et al., 2017; Reidy et al., 2012).

Regarding biodiversity, beta-diversity measures spatial variations in the relative abundances of species (Legendre et al., 2005) or in the taxonomic, phylogenetic, or functional relationships among species (Graham & Fine, 2008; Izsak & Price, 2001; Swenson et al., 2011). Taxonomic patterns are the most commonly used, contributing to the understanding of species distribution patterns and assembly structures (Gaston, 2000; Legendre et al., 2005; Pavoine & Bonsall, 2010; Pimm et al., 2014; Toussaint et al., 2016). But relying only on taxonomic approaches has limitations (McGill et al., 2006; Sagouis et al., 2016). An alternative is to incorporate functional diversity, which provides insights into the roles organisms play in ecosystems (Devictor et al., 2010; Pavoine & Bonsall, 2010; Petchey & Gaston, 2002; Villéger et al., 2012). Azevedo et al. (2017) suggested that classifying species into groups based on both taxonomic and functional relationships is preferable for studying anthropogenic impacts and environmental changes on ecosystems. Consequently, beta-diversity can indicate varying levels of anthropogenic influence, which can result in either homogenisation or heterogenisation

processes, leading to either a loss or increase in dissimilarity, respectively (Socolar et al., 2016).

Beta-diversity quantifies variation in species composition (Anderson et al., 2010) along environmental or temporal gradients. Socolar et al. (2016) emphasised the need to consider beta-diversity because of its importance for biodiversity conservation over large areas. Beta-diversity is changed in two ways: turnover, involving species replacement, and nestedness, signifying species loss or gain. To measure these differences effectively, selecting an appropriate dissimilarity metric is crucial. Different dissimilarity components explain these cases differently (Baselga & Orme, 2012). Baselga (2010, 2012) proposed a method to dissect total dissimilarity (e.g., Sørensen or Jaccard indices, and transformations of beta-diversity) into two components: one reflecting dissimilarity from turnover and the other from nestedness.

We evaluated ichthyofauna structure by using taxonomic and functional beta-diversity in the middle upper Paraíba do Sul River, where the Lavrinhas and Queluz SHPs are located. We hypothesised that beta-diversity would increase immediately following dam construction as the system transitioned from lotic to lentic. This shift would lead to the restructuring of the ichthyofauna, with new species adapted to the new environment arriving and previously existing species decreasing. We also hypothesised that beta-diversity would decrease after 10 years as lotic species gradually disappeared because of the SHPs. To test both hypotheses, we used two approaches. (1) We assessed ichthyofaunal structure, abundance, and richness in three periods (pre-construction, immediately after construction, and after 10 years of dam operation). (2) We evaluated the levels of taxonomic and functional homogenisation/heterogenisation in those same three periods.

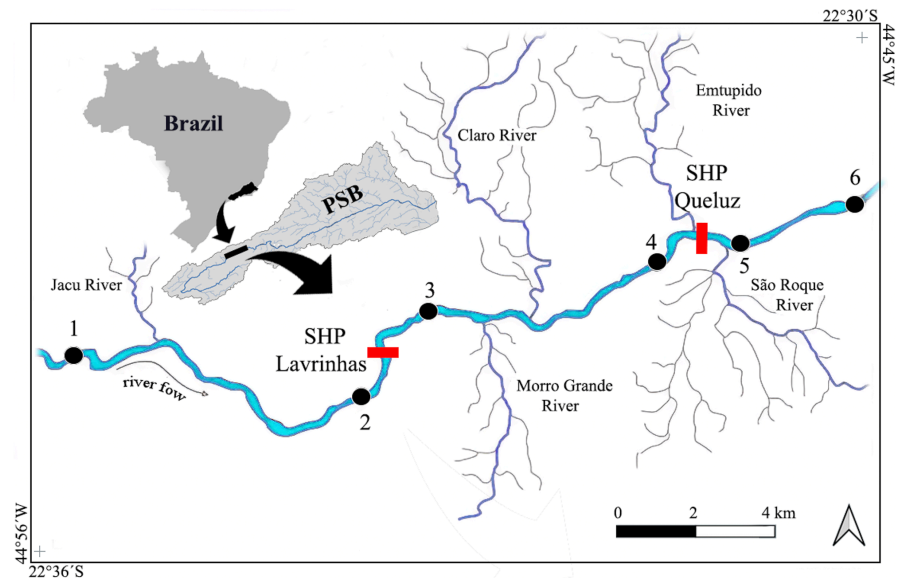
## 2 | METHODS

### 2.1 | Study area

The Paraíba do Sul River is approximately 1100 km long, and its basin drains approximately 55,500 km<sup>2</sup>, spanning parts of Brazil's three most developed states (ANA, 2022; Carvalho & Torres, 2002; Marengo & Lincoln, 2005; Pinto et al., 2009). The basin suffers from deforestation, urban development, large industrial projects, agriculture, and dams (Linde-Arias et al., 2008; Pinto & Araújo, 2007; Terra et al., 2010). In 2011, the Lavrinhas and Queluz SHPs were constructed in the upper-middle river about 8 km apart. Collectively, the SHPs play a pivotal role in meeting both local and regional energy demands, have a capacity of 30 MW each, share a gross head of 13 m, and are equipped with fish ladders with a vertical single-jet slot.

The studied section is about 25 km long (Figure 1; Table 1), occurs at an altitude of 505–475 masl., and has an annual average discharge of 137–380 m<sup>3</sup>/s (ANA, 2022). The predominant climate is hot and humid tropical, with a rainy season from January to April, a dry season from May to August, and a transitional period from September to December. The average annual precipitation is 1360 mm, and

**FIGURE 1** Middle Paraíba do Sul River, showing the locations of the sampled sites (1–6) and the Lavrinhas and Queluz Small Hydropower Plants (SHPs). PSB is the Paraíba do Sul River basin.



**TABLE 1** Location of the six sampling sites along the Paraíba do Sul River.

Site	Geographic coordinates	Description
1	22°34'03" S; 44°55'10" W	Upstream of the Lavrinhas SHP's influence area
2	22°34'16" S; 44°51'49" W	Upstream of the Lavrinhas SHP
3	22°33'48" S; 44°51'38" W	Downstream of the Lavrinhas SHP
4	22°32'41" S; 44°48'02" W	Upstream of the Queluz SHP
5	22°32'46" S; 44°47'23" W	Downstream of the Queluz SHP
6	22°32'17" S; 44°55'53" W	Downstream of the Queluz SHP influence area

the water temperature ranges from 18 to 24°C (Gomes et al., 2021; Moraes & Nery, 2014). In the study reach, the river is braided, featuring islands, rapids, and limited pool areas. The riverbed is predominantly characterised by submerged rocks, creating distinct microhabitats along most of its length. Some sections of the river support abundant aquatic vegetation, which not only serves as shelter but also adds diversity to the shoreline. However, the riparian zone has sparse vegetation cover, with extensive pasture, as well as various buildings. There is direct discharge of untreated sewage along a significant portion of this stretch. These disturbances have substantial impacts on the ecosystem.

We sampled fish and environmental conditions at the six sites during three time periods (Figure 1; Table 1). Period-1 preceded SHP construction (Pre-2008), when the river was free-flowing. Period-2 was 1 year after completing the SHP construction (Post-2012). Period-3 was 10 years after SHP construction (Current-2021). During each of these three periods, we sampled to encompass three distinct seasons: flood (January–March), dry (July–August), and transitional (September–October).

## 2.2 | Environmental assessment

At each site, we measured water temperature (°C), pH, dissolved oxygen (mg/L), and turbidity (NTU) at a depth of approximately 0.5 m. We used a Horiba U50 multiprobe (Horiba Trading Co., Ltd., Shanghai) to

make the measurements. National Water Agency (ANA) discharge and rainfall data were obtained from HidroWeb (<https://www.snirh.gov.br/hidroweb/apresentacao>). We used permutational multivariate analysis of variance (PERMANOVA) and Euclidean distance to make comparisons. We used PERMANOVA with Type I (sequential) sum of squares and conducted 999 permutations to calculate p-values for assessing the significances of periods, seasons, and sites.

## 2.3 | Fish assemblage assessment

Fish sampling involved a total of 54 site visits (6 sites × 3 periods × 3 seasons). We standardised fishing effort during each site visit to ensure we could make meaningful spatial and temporal comparisons. A total of 10 gill nets (25 m × 2 m; mesh sizes of 1.5, 2.0, 2.5, 3.0, 3.5, 4.0, 5.0, 7.0, 9.0, and 10.0 cm between adjacent knots) were deployed at each location to cover various habitats. The nets were set in the early evening and retrieved the following morning, allowing them to fish for approximately 14 h.

### 2.3.1 | Fish assemblage taxonomic structure

We compared fish assemblage structure and its descriptors (number of species and number of individuals) among the three different periods, three seasons and the six sites, nesting sites

within seasons. To ensure the accuracy of our analyses, we applied a square root transformation to the fish data to mitigate the bias introduced by abundant species. Then, we employed permutational multivariate analysis of variance (PERMANOVA) on the Bray–Curtis distance matrix of abundance data. Specifically, we used PERMANOVA with a Type I (sequential) sum of squares and carried out 999 permutations to calculate *p*-values for determining significant differences. Only highly significant values ( $p < .01$ ) were considered to mitigate the risk of committing a Type I error. Additionally, individual-based rarefaction curves (Gotelli & Colwell, 2001) were employed to assess species richness across different periods. Next, we assessed fish assemblage composition patterns via non-metric Multidimensional Scaling (nMDS) on a Bray–Curtis distance matrix. We then used rarefaction and extrapolation curves (Hsieh et al., 2016) to compare species richness among the three periods, and the Indicator Value (IndVal) method

(Dufrene & Legendre, 1997) to identify indicator species for specific periods or seasons. Exclusive and shared effects of environmental variables (water physical and chemical), periods (Pre, Post and Current), seasons, and space (distance among the sites) on fish composition were quantified by variation partitioning (Peres-Neto et al., 2006).

### 2.3.2 | Fish assemblage functional traits

We used fish morphological measurements to calculate functional attributes associated with habitat use, feeding, and locomotion (Manna et al., 2013; Pease et al., 2012; Winemiller et al., 2015). These characteristics are commonly employed in assessing the functional diversity of freshwater fish (Brosse et al., 2021; Leitão et al., 2018). Morphological measurements were collected from species captured

Code	Measurement	Definition
MBS	Maximum body size	Maximum adult length in centimetres (Fishbase)
SL	Standard length	Standard body length (tip of snout to base of caudal fin)
BH	Body height	Maximum body height
HH	Head height	Head height along the vertical axis of the eye
CPH	Caudal peduncle height	Minimum caudal peduncle height
CFH	Caudal fin height	Maximum caudal fin height
ED	Eye diameter	Vertical eye diameter
EP	Eye position	Vertical distance between the center of the eye and the bottom of the body
MH	Mouth height	Vertical distance from the top of the mouth to the bottom of the body
MJL	Maxillary jaw length	Length from snout to corner of mouth
PFL	Pectoral fin length	Length of longest pectoral fin ray
PFP	Pectoral fin position	Vertical distance between upper fin attachment and lower body

TABLE 2 Fish morphological measurements and definitions.

Code	Functional traits	Formula	Ecological relationship
MBS	Maximum body size length	(fishbase)	Metabolism, trophic impact, moving ability, nutrient cycling
BS	Body stretching	$\frac{SL}{BH}$	Hydrodynamism
VEP	Vertical eye position	$\frac{EP}{BH}$	Position of the fish and/or its prey in the water column
RES	Relative eye size	$\frac{ED}{HH}$	Visual acuity
MP	Mouth position	$\frac{MH}{BH}$	Feeding position in the water column
RML	Relative maxillary length	$\frac{MJL}{HH}$	Mouth size and jaw strength
SBD	Side body shape	$\frac{HH}{BH}$	Hydro dynamism and head size
PFP	Vertical position of the pectoral fin	$\frac{PFP}{BH}$	Use of pectoral fins for swimming
PFS	Pectoral fin size	$\frac{PFL}{SL}$	Use of pectoral fins for swimming
PCS	Strangulation of the caudal peduncle	$\frac{CFH}{CPH}$	Flow propulsion efficiency through drag reduction

TABLE 3 Fish functional traits and their ecological relationships.

during the Current period, involving the acquisition of five photographs of five selected adult specimens. In instances where species were rare (<5 individuals), measurements were taken for all available adult individuals. Fish were measured in millimetres (mm), weighed in grams (g), photographed, and then released alive. Species that posed identification challenges were retained for further examination in the laboratory. We relied on values from FISHMORPH, a global freshwater fish database (Brosse et al., 2021), for species exclusively found in the Pre and Post periods and not collected during the Current period.

We recorded 11 morphological measurements (Table 2) by using ImageJ software (Schneider et al., 2012). Images were captured with a metric scale in millimetres (mm) and expressed as biologically meaningful ratios derived from measurements within the same photograph. This approach enabled meaningful comparisons between photographs (Brosse et al., 2021; Toussaint et al., 2016; Villéger et al., 2017). From these measurements, we derived nine functional attributes (Table 3), consisting of nine dimensionless indices. Maximum body size (MBS) was obtained from FishBase (Froese & Pauly, 2022). Some species exhibit unusual morphologies, such as those lacking a caudal fin or having ventral mouths, which can prevent the measurement of morphological traits. To account for these exceptions, we made two adjustments. (1) For species lacking a visible caudal fin (e.g., *Gymnotus carapo*), the caudal peduncle strangulation (PCS) was zero. (2) For species with ventral mouths (e.g., *Hypostomus affinis*), the mouth position (MP) and relative maxillary length (RML) were zero.

### 2.3.3 | Fish assemblage beta-diversity

To compute taxonomic and functional beta-diversity along with turnover (species replacement) and nestedness (species loss), we used presence/absence data for individual species across

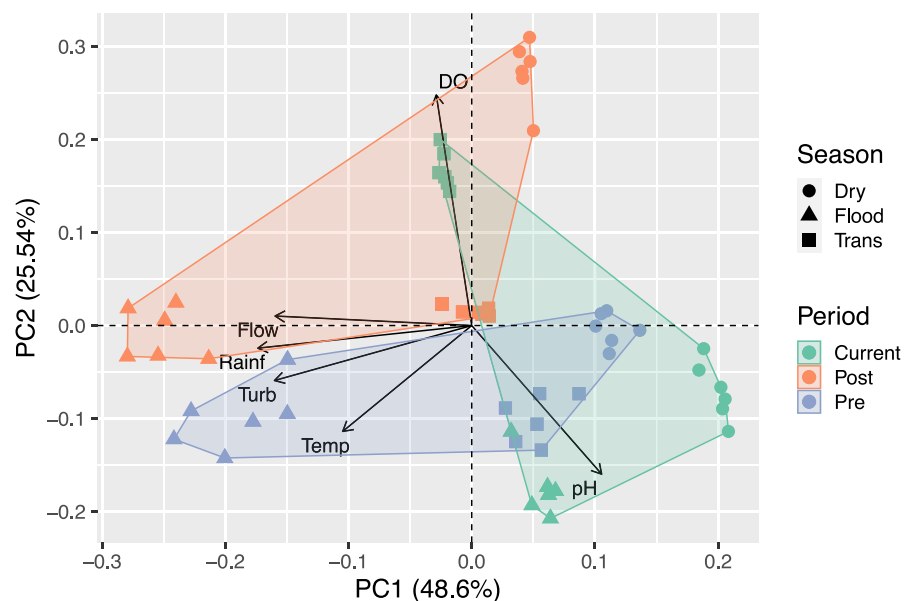
the three time periods (Pre, Post, and Current). Taxonomic beta-diversity and its components were calculated by using the beta.pair function, which generates three distinct distance matrices. (1) Turnover represents the replacement of species by others, driven by factors such as environmental differences or spatial and historical limitations (Baselga, 2010). (2) Nestedness accounts for the loss of species because of factors that result in the ordered disassembly of assemblages (Baselga, 2010; Gaston & Blackburn, 2000). (3) Total dissimilarity, also known as beta-diversity, is the sum of the turnover and nestedness components (Baselga, 2010). We combined the species data matrix with the functional attribute matrix to compute functional beta-diversity and its decomposition into turnover and nestedness components. The species occurrence spreadsheet contained 18 survey visits and a total of 44 species over the three periods. For these analyses, we used the FD (functional diversity) and betapart (beta-diversity partitioning) packages in R version 4.2.1.

## 3 | RESULTS

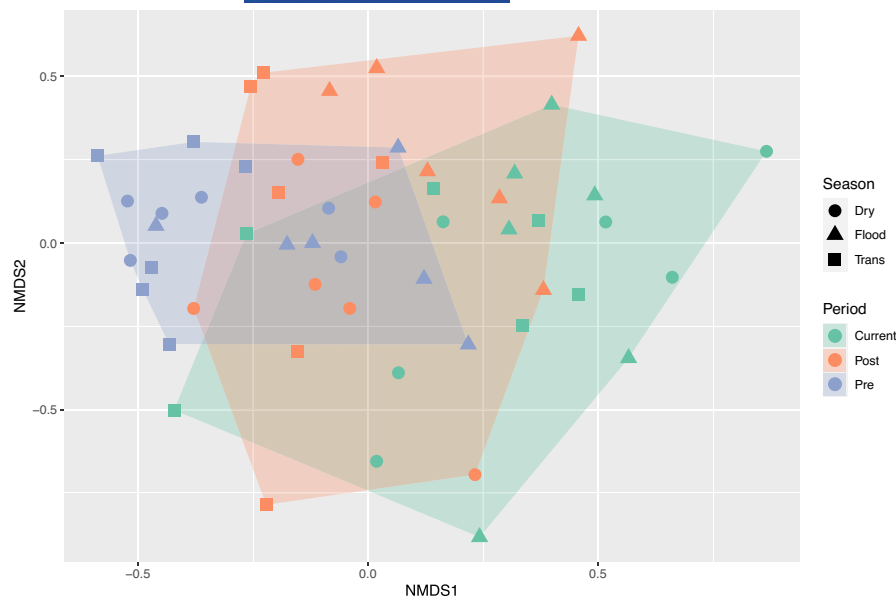
### 3.1 | Environmental variables

There was substantial environmental variability across the three periods and seasons (Table S1). The average water temperature ranged from 19.43 to 25.7°C, dissolved oxygen levels fluctuated between 5.88 and 10.98 mg/L, pH varied from 6.07 to 10.14, turbidity ranged from 12.38 to 124.66 NTU, discharge varied between 142.16 and 379.9 m<sup>3</sup>/second, and monthly accumulated rainfall ranged from 14.4 to 406.1 mm.

The PERMANOVA analysis of the variable set confirmed highly significant differences among periods (Pseudo- $F = 58.93$ ,  $p = .001$ ), seasons (Pseudo- $F = 149.1$ ,  $p = .001$ ), and for the interaction periods versus seasons (Pseudo- $F = 46.04$ ,  $p = .001$ ) but no significant



**FIGURE 2** PCA ordination of environmental data: samples colour coded by period and season. DO, dissolved oxygen; Flow, discharge; Rainf, rainfall; Temp, temperature; Trans, transition; Turb, turbidity.



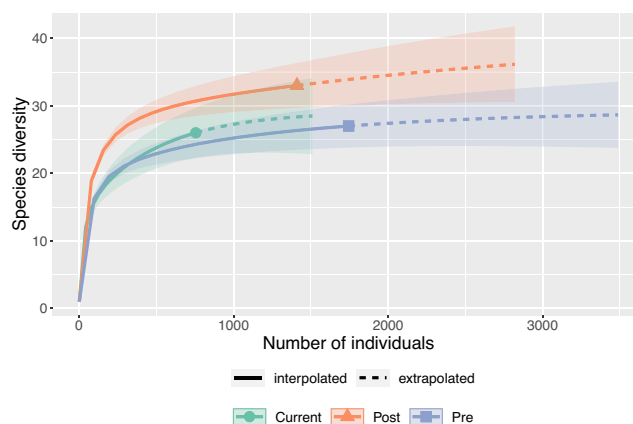
**FIGURE 3** nMDS ordination of fish species abundance: samples coded by periods (Pre, Post, and Current) and seasons.

differences among sites seasonally (Pseudo- $F=0.21$ ,  $p=.955$ ) (Table S2). A temporal and seasonal pattern in the environmental variables emerged from the distribution of samples on the first two axes of the PCA diagram (Figure 2). In terms of associations with PCA axes, rainfall exhibited the most pronounced negative correlation with Axis 1 ( $-0.54$ ), followed by turbidity ( $-0.50$ ) and flow ( $-0.49$ ), with the highest values linked to the Pre and Post periods during the flood season. Dissolved oxygen showed the strongest positive relationship with Axis 2 ( $0.77$ ), associated with the Post and Current periods during the dry and transition seasons, respectively. Notably, during the flood season, the Current period displayed the lowest flow rates, rainfall, and turbidity compared to the other two periods (Figure 2).

### 3.2 | Fish assemblage composition

A total of 3908 individuals were captured, representing 44 species, 17 families, and five orders (Table S3). In the Pre period, 27 species (1744 individuals) were recorded, whereas the Post period featured 33 species (1410 individuals). The Current period revealed 26 species (754 individuals). Notably, 17 species were present in all three periods. Five species were exclusive to the Pre period (two of which are endangered), nine to the Post period, and five to the Current period (Appendix S1).

Significant differences in fish assemblages among the three studied periods were detected through PERMANOVA analysis (Pseudo- $F=6.28$ ,  $p=.001$ ) and for season (Pseudo- $F=2.63$ ,  $p=.009$ ) (Table S4). Conversely, no significant differences were observed among the sites within the seasons (Pseudo- $F=0.90$ ,  $p=.609$ ). A discernible pattern of separation in the structure of fish assemblages emerged among the three evaluated periods, although some samples displayed overlapping characteristics. Notably, the Pre period exhibited a more distinct separation from the Current period, whereas the Post period was positioned between the Pre and Current periods (Figure 3).



**FIGURE 4** INext species rarefaction curves for the three periods (Pre, Post, and Current).

Species and individual numbers were compared across periods, seasons, and sites (nested within seasons). Significant differences were found exclusively for periods (Table S4), affecting both species ( $F=8.65$ ,  $p=.002$ ) and individuals ( $F=7.01$ ,  $p=.004$ ). The Post period exhibited significantly more species per sample than the other two periods, whereas the Pre period had significantly more individuals compared to the Current period. According to the rarefaction curves, species richness was higher during the Post period compared to the other two periods (Figure 4). The IndVal analysis revealed 11 indicator species (Table 4): two for the Pre period and five for the Post period. The Pre and Post periods had three indicator species, and the Post and Current periods had one.

The variation associated with period effects was primarily shared with season (10%) and environmental variables (11%) that also explained exclusively 9% of the fish variation (Figure S1). The spatial effect of the site distribution explained exclusively only 2% of

TABLE 4 Indicator species for periods (Pre, Post, and Current).

	A	B	IndVal	p-Values
Pre				
<i>Harttia loricariformis</i>	.949	.6111	0.762	.005
<i>Rineloricaria lima</i>	.738	.6111	0.672	.005
Post				
<i>Deuterodon intermedius</i>	1.000	.3889	0.624	.005
<i>Prochilodus lineatus</i>	1.000	.2778	0.527	.015
<i>Australoheros facetus</i>	.8876	.2778	0.497	.03
<i>Pimelodella eignemanni</i>	.8376	.2778	0.482	.02
<i>Callichthys callichthys</i>	.8732	.2222	0.441	.03
Pre + Post				
<i>Crenicichla lacustris</i>	.978	.7222	0.84	.005
<i>Pimelodus fur</i>	.8434	.6389	0.734	.025
<i>Psalidodon parahybae</i>	.9643	.5278	0.713	.01
Post + Current				
<i>Plagioscion squamosissimus</i>	1.000	.5833	0.764	.005

Note: A and B reflect the probability of a species being restricted to a specific period and the probability of all samples from a specific period containing that species, respectively.

TABLE 5 Mean and standard deviation of taxonomic and functional beta-diversity across Pre, Post, and Current periods.

Indices	Taxonomic			Functional		
	Pre	Post	Current	Pre	Post	Current
Turnover	0.35 ± 0.19	0.42 ± 0.17	0.45 ± 0.21	0.23 ± 0.23	0.24 ± 0.24	0.36 ± 0.31
Nestedness	0.16 ± 0.14	0.17 ± 0.14	0.16 ± 0.16	0.37 ± 0.27	0.38 ± 0.26	0.39 ± 0.33
β-diversity	0.51 ± 0.12	0.59 ± 0.11	0.61 ± 0.12	0.60 ± 0.28	0.62 ± 0.22	0.75 ± 0.2
t-Test	Turnover	Nestedness	β-diversity	Turnover	Nestedness	β-diversity
Pre, Post	<b>0.003</b>	0.241	<b>0.000</b>	0.7232	0.769	0.521
Pre, Current	<b>0.000</b>	0.919	<b>0.000</b>	<b>0.000</b>	0.559	<b>0.000</b>
Post, Current	0.1462	0.317	0.268	<b>0.000</b>	0.740	<b>0.000</b>

Note: t-Test results (p-values) for period comparisons with significantly different values highlighted in bold.

the fish data. A small fraction was also shared between season and environmental variables (2%).

### 3.3 | Fish assemblage beta-diversity

Taxonomic beta-diversity increased from 0.51 to 0.61 across the three periods, with more from turnover than nestedness (Table 5). Average turnover ranged from 0.35 to 0.45, whereas average nestedness only varied from 0.16 to 0.17. Taxonomic beta-diversity differed significantly only between the Pre versus Post and Pre versus Current periods.

Functional beta-diversity also increased across the three periods, but in this case, more resulted from nestedness than turnover (Table 5). Average nestedness ranged from 0.37 to 0.39, whereas average turnover only varied from 0.23 to 0.36. Functional beta-diversity differed significantly only between the Pre versus Current and Post versus Current periods.

Taxonomic beta-diversity and its turnover component were lower in the Pre period than in Post and Current Periods (Figure S2). In contrast, functional beta-diversity and its turnover component were higher in the Current period than in the Pre and Post (Figure S3). Notably, neither taxonomic nor functional nestedness exhibited significant variation among the three periods.

## 4 | DISCUSSION

Both taxonomic and functional beta-diversity increased within the fish fauna across the study periods, which contradicted our initial hypothesis of a decline in beta-diversity following 10 years of SHP operation. However, increased beta-diversity may not necessarily be desirable. Anthropogenic modifications, such as habitat fragmentation by dams, can increase, decrease, or not change fish assemblage similarity. This depends on the balance between heterogenisation and homogenisation processes at the local level (Petresse & Petreire, 2012;

Socular et al., 2016). Our findings that beta-diversity increased over time indicated a tendency toward greater heterogeneity, characterised by increased dissimilarity, across the three study periods. This increase becomes evident when species that were previously shared among the locations either disappear from the samples partially or entirely. For instance, *Hoplerythrinus unitaeniatus* and *Callichthys callichthys*, which were present in the Pre and Post periods, were not recorded in the Current period. Additionally, new species appeared in some locations but did not become ubiquitous or widespread. This is exemplified by *Deuterodon giton*, *D. hastatus*, *D. intermedius*, and *D. tae-niatus*, which were only observed shortly after the Post period. This period coincided with the emergence of sedentary species adapted to lentic environments, aligning with our expectations.

The preceding processes of beta-diversity heterogenisation can involve either the local gain of species (additive processes) or the local loss of species (subtractive processes). As outlined by Socolar et al. (2016), subtractive heterogenisation entails reduced abundance of many native species, with only a few facing extinction. This pattern appears to apply to species like *Psalidodon parahybae*, *Crenicichla lacustris*, and *Geophagus brasiliensis*, which experienced a significant decrease in abundance over the study periods, ultimately becoming rare in the Current period. In contrast, additive heterogenisation involves the establishment of non-native species, with only a few becoming widespread. This phenomenon is evident in the emergence of *Apareiodon piracicabae* following the establishment of the SHPs. Although this species experienced a slight increase in abundance during the Current period, its frequency of occurrence remained low and unchanged at 11%. This diversification appears to be linked to the SHP and a transition from a flowing lotic environment to one that encompasses lentic sections and physical barriers.

The two types of beta-diversity displayed distinct patterns in relation to their components, namely nestedness and turnover. Turnover exerted a more significant influence on the results, whereas no significant differences were observed in the nestedness component for both types of beta-diversity. In terms of taxonomic beta-diversity, this replacement of species was most pronounced during the Post phase, as species adapted to lentic environments began to colonise. This trend continued with a minor, non-significant increase in the Current period. However, in functional beta-diversity, no distinctions were observed between the Pre and Post periods despite the upward trend; this difference only became evident in the Current period. When comparing these time periods, there was an initial increase in taxonomic dissimilarity during the Post period. However, functional dissimilarity remained relatively consistent, suggesting that the species introduced during the construction of the SHPs might be fulfilling similar ecological roles, potentially leading to competition for resources. Assemblages often exhibit distinct species compositions, but species can share similar in trophic levels (Villéger et al., 2008) and morphological traits (Irz et al., 2007). Notably, a significant increase in functional beta-diversity was observed 10 years after the construction, a trend not concurrently mirrored in taxonomic changes. The ichthyofauna in impounded rivers represents the

outcome of restructuring processes affecting the previous species assemblage (Agostinho et al., 2016). Consequently, the fish assemblage is currently undergoing restructuring with novel interactions between species and the emergence of new functional groups (Agostinho et al., 2008). Our observations reflect a transformation in the ichthyofauna during the study periods, indicating a potential restructuring process because of the dams. These dams serve as environmental filters for fish characteristics, favouring species and functions better suited to the altered environmental conditions.

Following the establishment of SHPs, there was an initial rise in species richness, which was subsequently followed by a decrease after 10 years of operation. In terms of abundance, it is noteworthy that these projects appeared to reduce the fish assemblages by more than half when compared to the Pre period. The rarefaction curves confirmed that the Post period exhibited the highest richness in comparison to the other two periods under study. During the Post period, there was a slight decrease in abundance, and this decrease occurred simultaneously with an increase in richness. It is plausible that these changes were influenced by the introduction of new species, as indicated by new records for *Hypomastycus cope-landii*, *Oligosarcus hepsetus*, *Metynnis maculatus*, and *Hoplosternum littorale*, which experienced a considerable increase in abundance. In the Current period, there was a decrease in the overall number of species, with seven species disappearing from the records, including *Hoplerythrinus unitaeniatus*, *Callichthys callichthys*, *Pimelodella egenmanni*, and *Rineloricaria lima*, which were previously documented in both earlier periods. Additionally, there was a reduction in abundance compared to the Post period. When compared to the Pre period, the difference in the number of species with the Current period was not statistically significant. However, the species composition underwent significant changes despite this minor difference. Furthermore, in the Current period, most species experienced a considerable reduction in abundance, except for non-native species like *Apareiodon piracicabae* and *Plagioscion squamosissimus*. Lenhardt et al. (2009) used the index of biotic integrity (IBI) and confirmed that over a 45-year period in the Serbian Medjuvsje Reservoir, the relative abundance of tolerant species increased, while species intolerant to the conditions created by the reservoir decreased significantly. This observed decrease in both richness and abundance over the years is a consequence of the environmental filtering imposed by damming, resulting in an ecosystem that differs significantly from a natural river system in various aspects.

The appearance of *Plagioscion squamosissimus*, an indicator species of the Post and Current periods, could be a contributing factor to the decline in abundance observed in several other species. This species stands out as one of the primary non-natives introduced and successful inhabitants in numerous Brazilian reservoirs, particularly within the southeastern region of the country. *P. squamosissimus* is an exceptionally voracious predator with the potential to significantly affect the diversity of native fish populations (Agostinho et al., 2016). Interestingly, it was not present during the Pre period. However, it was documented in both the later periods, with its abundance notably increasing in the Current period. The disappearance



of small-sized fish species in various reservoirs within the Rio Grande, Tietê, and Paranapanema River basins has been linked to the presence of this apex predator (Agostinho et al., 2016). Thus, *P. squamosissimus* may indeed be contributing to the decline in abundance observed in native species during the Current period.

All five species exclusively present during the Pre period are native to the Paraíba do Sul River, with two of them, *Pogonopoma parahybae* and *Steindachneridion parahybae*, being listed in the "Red Book of threatened Brazilian fauna." Both species have been adversely affected by dam construction and pollution (Honji et al., 2017). *Steindachneridion parahybae* is a sizable catfish and among the largest species in the Paraíba do Sul River basin. It is endemic to the basin, preferring fast-flowing waters and displaying nocturnal carnivorous behaviour. This species is classified as endangered within this basin and has been regionally extirpated in the state of São Paulo (Garavello, 2005; Honji et al., 2009). *Pogonopoma parahybae*, also endemic to the Paraíba do Sul River basin, has limited biological information available, but occurrences of *P. parahybae* are only noted in lotic stretches; thus, dams and reservoirs pose a significant threat to rheophilic species like *S. parahybae* (Honji et al., 2017).

In summary, our study unveiled a process of heterogenisation within the ichthyofauna subsequent to the construction of Small Hydropower Plants (SHPs) in the middle section of the Paraíba do Sul River. This process is characterised by an increase in both taxonomic and functional dissimilarity, coupled with a documented decline in ichthyofauna abundance. These findings indicate that small-scale projects like SHPs have adverse effects on the ichthyofauna and can act as environmental filters through habitat modifications and the introduction of non-native and generalist species. This, in turn, leads to the restructuring of the ichthyofauna by favouring specific species and ecological functions. Our research represents an initial step in using beta-diversity as a tool for assessing changes in ichthyofauna within altered tropical lotic systems resulting from SHPs in Brazil. We recommend expanding these studies to other basins to gather additional data, with the ultimate goal of proposing biodiversity conservation measures.

#### AUTHOR CONTRIBUTIONS

FGA and DRC conceived and designed the investigation, DRC led most field investigations and data analyses, FGA provided historical data and FGA and DRC wrote the paper.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

#### DATA AVAILABILITY STATEMENT

Data that support the findings of this study are available from the corresponding author upon reasonable request.

#### ORCID

Dandhara Rossi Carvalho  <https://orcid.org/0000-0002-0439-0443>

Francisco Gerson Araújo  <https://orcid.org/0000-0003-4551-1974>

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## SUPPORTING INFORMATION

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

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