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Taxonomic and functional distinctness of the fish assemblages differing among different types of reservoirs in south-eastern Brazil

Tailan Moretti Mattos  | Dandhara Rossi Carvalho  |
Augusto de Salles Guerra-Júnior  | Francisco Gerson Araújo 

Universidade Federal Rural do Rio de Janeiro,
Departamento de Biologia Animal, ICBS,
Laboratório de Ecologia de Peixes, Seropédica,
Brazil

Correspondence

Francisco Gerson Araújo, Universidade Federal Rural do Rio de Janeiro, Departamento de Biologia Animal, ICBS, Laboratório de Ecologia de Peixes, BR 465, Km6, Seropédica, RJ 23897-030, Brazil.
Email: gersonufrj@gmail.com

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Abstract

The dynamics of fish assemblages in reservoirs depend on factors such as the morphology of the catchment, habitat structure, and the uses of the reservoir. In the Paraíba do Sul (PSR) basin in southeastern Brazil, there are several types of reservoirs, some on the main channel, some are cascade reservoirs originated from a diversion of the waters of the PSR, and others are isolated reservoirs from tributaries. This study aimed to evaluate the influences of these three types of reservoirs on the taxonomic and functional distinctness of the fish assemblages. It was hypothesized that reservoirs on the main channel (more inflowing waters and habitat availability) have higher taxonomic and functional distinctness compared to cascade reservoirs, which in turn, have greater distinctness than isolated reservoirs. In addition, we expect assemblage structure to differ among these types of reservoirs because of the close relationship with local environmental conditions and habitat structure. Thirty measurements (26 quantitative and 4 categorical) from 34 fish species representing functional traits associated with locomotion, feeding, life strategy, and habitat use were taken. Fish assemblages differed among the three types of reservoirs, which was probably associated with different environmental and local habitat conditions. Higher taxonomic and functional distinctness were found for the isolated reservoirs, and lower for reservoirs on the main channel. This suggests that the fish fauna in this latter type of reservoir were probably composed of phylogenetically close and morphologically similar species. It is likely that limitation of the available resources induces fish to partition the available niches to coexist, favoring assemblages with species adapted to different functions. Our results demonstrate that assessing fish functional and taxonomic distinctness can be used to advance understanding of fish communities from reservoirs in Neotropical regions.

KEYWORDS

dams, freshwater fishes, functional diversity, taxonomic distinction, tropics

1 | INTRODUCTION

Hydrological changes in rivers have been widely experienced with practices worldwide with approximately two-thirds of the world's

great rivers being impacted by reservoirs (Liermann, Nilsson, Robertson, & Ng, 2012; Winemiller et al., 2016). More than half a million reservoirs, with an area of over 1 ha, currently exist globally, covering an area of 258,570 km² (Downing et al., 2006). Many countries, among

them Brazil, have built reservoirs blocking rivers for hydropower as their primary energy production option (Gibson, Wilman, & Laurance, 2017). The use of hydroelectric power for energy generation in Brazil represents 70% in terms of electricity consumption, whereas the world average is around 16% (von Sperling, 2012). Energy production, employment generation, and substitution of diesel-based thermoelectric generation by hydroelectric generation are some of the advantages. Although reservoirs favor regional economic development, they also bring serious and irreversible alterations to the natural hydrologic regime of rivers, affecting habitat quality and the dynamics of the biota (Agostinho, Gomes, Santos, Ortega, & Pelicice, 2016).

Hydroelectrical generation is relatively new, and it is growing faster (Winemiller et al., 2016). Although there are many large electric power projects ranging from 1,000 to 14,000 MW of installed power in large rivers across the Brazilian territory, small power plants ("small hydro") have also been increasing especially on medium and small-sized rivers. Most "small hydro" are in fact run-of-river hydroelectricity plants with little or no water storage, are believed to reduce the impact on the environment. However, further research concluded that small hydro, similarly to large hydro, is known to cause adverse environmental impacts (Premalatha, Abbasi, Abbasi, Abbasi, and Abbasi (2014).

Reservoirs transform the physical and biological characteristics of rivers, changing the dynamics of flows and the availability of nutrients (Agostinho et al., 2016). Due to the effect of a dam, a new lentic ecosystem is created, with physical and chemical conditions different from those observed in the original environment. The intensity of these changes reflects the local biota, morphometric and hydrological characteristics of the reservoir, dam operation, and interactions with other uses of the basin, including other reservoirs (Agostinho et al., 2016). The main impact is the change from lotic to lentic water, which influences aquatic fauna, including fish (Agostinho, Pelicice, & Gomes, 2008). Other natural river conditions are affected by dams such as flood pulses, flow regime and sediment transport (Ferrareze, Casatti, & Nogueira, 2014; Hoeinghaus, Winemiller, & Agostinho, 2008; Nilsson, Reidy, Dynesius, & Revenga, 2005; Poff, Olden, Merritt, & Pepin, 2007). These changes result in direct impacts, such as habitat losses, but also indirect effects, such as biotic homogenization, favoring generalist over specialist species and facilitating invasion by non-native species, increasing the risk of endemic species extinction rates (Liermann et al., 2012; Winemiller et al., 2016).

Large dams block movements that enable migratory fish species to complete their life cycles. These large dams reduce flood pulses, impairing fish access to marginal lagoons, and other flooded habitats that are essential nursery areas (Winemiller et al., 2016). Furthermore, "small hydro" are one of the renewable energy options which were erroneously believed to be clean. While large storage reservoirs accumulate water and can vary the water level unpredictably, in small hydro this variation is more discrete (Baumgartner, Piana, Baumgartner, & Gomes, 2020). For this reason, small hydro (usually run-of-the-river reservoirs) are commonly presumed to be less harmful than storage reservoirs. However, the fish assemblages within run-

of-the-river reservoirs are less stable than those from the large storage reservoirs because they limit the direct (movement and reproduction of fish) and indirect (primary production and nutrient input) benefits for fish brought from the temporal environmental heterogeneity (Baumgartner et al., 2020).

The structure of fish assemblages in reservoirs undergo remarkable changes. Changes in the composition and abundance are direct consequences of impoundment with the proliferation of some species and/or even local extinction of others species that are unable to withstand drastic changes in environmental conditions (Agostinho et al., 2016). Fishes with migratory behavior decline or even disappear (Hoeinghaus et al., 2008; Petesse & Petrere Jr, 2012), while opportunistic and non-native species tend to dominate assemblages (Pelicice & Agostinho, 2009; Vitule, Skóra, & Abilhoa, 2012). Changes in species composition can also result from colonization by lacustrine species that take advantage of the availability of new niches (Yu, He, & Housavanh, 2019). Vacant niches are filled with non-native species when eurytopic native species are absent from the river reaches connected to the reservoirs, resulting in the impoverishment of native species richness although species richness can be maintained (Liew, Tan, & Yeo, 2016). Assemblages in reservoirs are usually dominated by small-sized sedentary species and non-native fishes (García, Britton, Vidotto-Magnoni, & Orsi, 2018; Santos et al., 2017). In addition, species richness, and fish abundance are influenced by new physicochemical variables that change at different spatial and temporal scales.

Species richness is commonly used as an explanatory variable for ecosystem function because it is easy to measure and sometimes correlates with functional diversity (Rosenfeld, Mall, & British, 2002). However, species composition and richness are poor predictors of the structure and function of the communities (Azevedo et al., 2017). Classifying species into groups based on taxonomic relationship and functional similarity have been shown to be an effective approach to study the influences of anthropogenic and environmental disturbances on ecosystems (Leibold & Chase, 2019). Assemblages formed of groups of taxonomically close and functionally related species are less diverse than others with a similar species number but taxonomically distant (Clarke & Warwick, 1998). To analyze these aspects of biodiversity, Warwick and Clarke (1995) proposed the taxonomic distinctness index. The taxonomic distinctness ($\Delta+$) is the average path (or branch length) between species through a taxonomic hierarchy or phylogenetic tree. This approach has overcome problems of species richness measurements and has several desirable properties as an indicator of biodiversity, one of which is the independence of the sampling effort (Clarke & Warwick, 1998). Taxonomic distinctness does not measure the number of species per se but rather the taxonomic relatedness of species in a community (Clarke & Warwick, 1998, 1999; Leonard, Clarke, Somerfield, & Warwick, 2006). Average taxonomic distinctness [AvTD] and its variation [VarTD] are useful tools to detect the changes in taxonomic structure and to explore ecological alterations (Warwick & Clarke, 2001). The average taxonomic path length between two randomly chosen species from the community and its variance can correlate with the anthropogenic impacts and stress (Warwick & Clarke, 1995, 2001).

Based on the taxonomic distinctness, Somerfield, Clarke, Warwick, and Dulvy (2008) proposed a new index that expresses the similarity between species in terms of functional characteristics. While it makes sense to think of trees when considering taxonomic information, such as a fixed hierarchical set of levels, there is nothing fixed about the levels of functional similarity between species, which are likely to be much more continuous. For this, the hierarchy was disregarded and only functional attributes were used, so the mean functional distinctness ($X+$) was defined by Somerfield et al. (2008) as the average similarity of attributes among species. A trait-based approach to functional distinctness is attractive because functional traits can, in principle, be directly linked to ecosystem processes (Laureto & Cianciaruso, 2015; Stuart-Smith et al., 2013).

Environments with high habitat and resource availability are expected to have complex systems, reflecting positively on the taxonomic and functional distinctness. The colonization process and the organization of assemblages in reservoirs arranged in series on the same river, with unidirectional interactions from upstream to downstream, show distinct patterns (Agostinho et al., 2008; Petesse & Petere Jr, 2012). The morphological, physiochemical, and biological characteristics combined with anthropogenic hydraulic management and water uses in cascade reservoirs, make these systems extremely complex (Thornton, Kimmel, & Payne, 1990). Furthermore, downstream reservoirs are affected by the characteristics of the reservoirs further upstream. On the other hand, spatially isolated reservoirs with small areas and restricted habitat availability tend to be less complex with comparatively low species richness and low taxonomic and functional distinctness (Leibold & Chase, 2019; Warwick & Clarke, 1995).

This study aimed to evaluate the taxonomic and functional distinctness in three types of reservoirs associated with the Paraíba do Sul River basin: 1) reservoirs on the main channel; 2) cascade reservoirs; 3) reservoirs on isolated tributaries. It was hypothesized that reservoirs built on the main river channel (higher inflowing waters and habitat availability) have a higher taxonomic and functional distinctness when compared to cascade reservoirs, which in turn, display higher distinctness than isolated reservoirs. We also expect different fish community structure among the three types of reservoirs associated with different environmental variables and habitat structure. In addition, a greater fish species richness and abundance is expected in reservoirs on the main river channel, compared to cascade and isolated reservoirs that have more limited habitat heterogeneity.

2 | MATERIAL AND METHODS

2.1 | Study area

Eight reservoirs associated with the Paraíba do Sul River (PSR) basin in south-eastern Brazil were studied (Figure 1). Three reservoirs on the main channel of the PSR (Santa Branca, PSR 1; Funil, PSR 2; and Ilha dos Pombos, PSR 3); three are cascade reservoirs receiving waters diverted from the PSR main channel (Santana, CAS 1; Vigário, CAS 2;

and Pereira Passos, CAS 3); and two are isolated reservoirs (Tocos, ISO 1 and Lajes, ISO 2) that receive water from small streams. The reservoirs are located along a gradient of altitude, and have different environmental features (Table 1) such as the date of construction, surface area, retention time, trophic state, and volume of discharge (Uehara, Albieri, & Araújo, 2015).

2.2 | Sampling design

Fish sampling was conducted during the dry (July–August) and wet (January–February) seasons of 2012 and 2013 in all reservoirs, except in reservoir PSR 2 that was sampled in dry and wet seasons of 2010 and 2011. An additional survey was carried out in all reservoirs in the dry season of 2017, when fish were used to take measurements to calculate the functional traits. Three locations (upper, middle, and lower) randomly chosen in each reservoir zone were sampled to cover the different reservoir areas. A standardized fish sampling unit was defined as a set of three gillnets (25×2.0 m; stretched-mesh size 25, 50, and 75 mm between opposite knots) operating over 12 hr. The nets were set in the afternoon and retrieved in the following morning. Catch per Unit Effort (CPUE) was defined as the total number of individuals captured per 150 m^2 per 12 h. During each sampling occasion, the largest reservoirs (PSR 1, PSR 2 and ISO 2) were sampled using 18 sampling units. In the intermediate reservoirs (PSR 3, CAS 1, CAS 2), 9 sampling units were used, and in CAS 3 and ISO 1, the smallest reservoirs, only 6 sampling units were used on each occasion. We averaged the fish catches for all samples for each campaign and for each reservoir. In total, our sampling design comprised 24 samples (3 sampling occasions \times 8 reservoirs).

Concurrently with fish sampling, the following environmental variables were measured: pH, conductivity ($\text{mS} \cdot \text{cm}^{-1}$), dissolved oxygen ($\text{mg} \cdot \text{L}^{-1}$), total dissolved solids ($\text{mg} \cdot \text{L}^{-1}$), temperature ($^{\circ} \text{C}$), oxidation-reduction potential (mV), and turbidity (NTU). These environmental variables were measured using a multiprobe Horiba W-21 (Horiba Co., Shanghai). Transparency (in cm) was measured using a Secchi Disk, and depth (in meters) was measured with a Speedtech Model SM-5 digital echo sounder.

2.3 | Functional attributes

A total of 30 functional attributes associated with locomotion, feeding, life strategy, and habitat use were measured (Figure 2; Table S1). These attributes (26 quantitative and four categorical) were chosen because they are proxies of one or more functional roles derived for fish (Pease et al., 2012; Winemiller et al., 2015). Only adult individuals were used, that is, those with a length equal to or larger than the first maturity size (L_{50}) and at least five individuals were analyzed for each species.

Attributes were measured following Pease et al. (2012). All length measurements were taken using a digital caliper with 0.1 mm precision. Quantitative functional attributes allow the characterization of

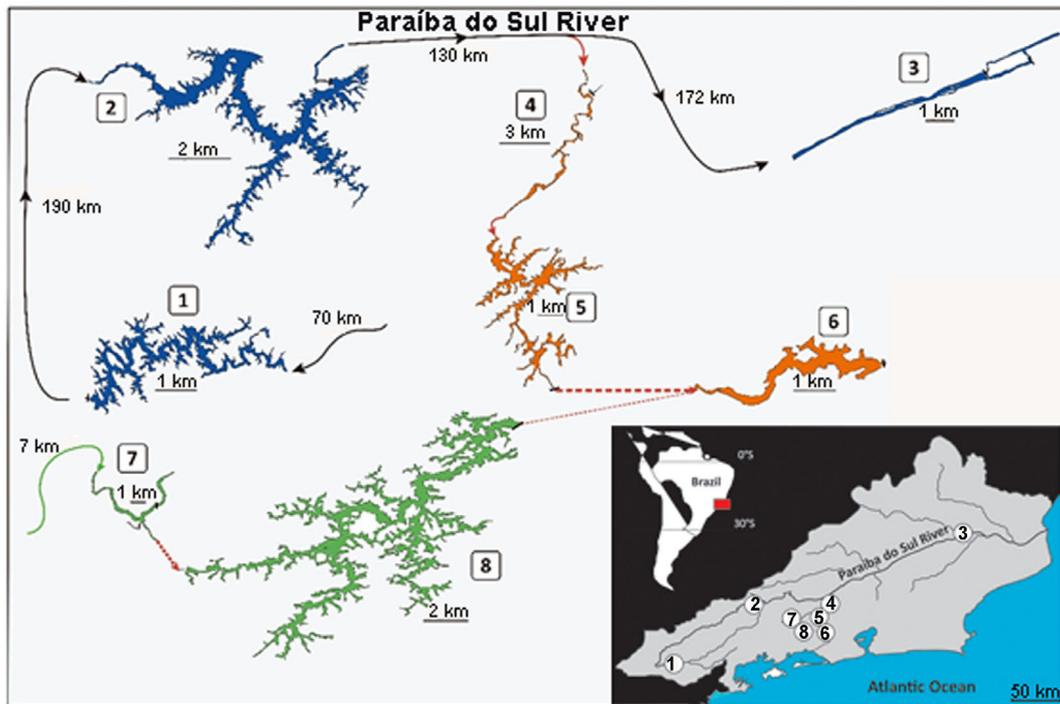


FIGURE 1 Schematic map of the study area showing the eight reservoirs along the Paraíba do Sul River basin: (a) Reservoirs in the main channel (blue) PSR 1–3, (b) Cascade reservoirs (orange): CAS 4–6; and Isolated reservoirs (green): ISO 7–8 [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Key environmental features of the eight reservoirs studied

Reservoir	PSR 1	PSR 2	PSR 3	CAS 1	CAS 2	CAS 3	ISO 1	ISO 2
Start operation	1959	1969	1924	1952	1952	1962	1913	1908
Energy production (MW)	58	121	164	-	380	100	-	132
Area (km ²)	27.2	40.0	4.3	5.9	3.8	1.4	1.2	30.7
Volume (hm ³)	307.3	890.0	6.7	6.1	11.7	4.1	1.9	450.4
Change in water level	S	S	D/S	D	D	D	S	S
Retention time (days)	63	30	0.2	1	2	1.2	1.6	300
Trophic state	M	E	E	H	E	E	M	M
Volume of inflowing water (m ³ /s)	90	192	700	160	160	180	13	12

Note: Change in water level: S, seasonal; D, daily. Trophic state: M, mesotrophic; E, eutrophic; H, hypertrophic.

multiple niche dimensions (Pease et al., 2012) and enable the use of multidimensional methods to estimate functional diversity (Leibold & Chase, 2019). Secondary information (i.e., published data) was only used to complement functional attributes of poorly studied species, for example, oocyte counts and diameter.

To remove the effects of the body size on attributes, we used the procedure applied by Winemiller et al. (2015), with each fish measurement being divided by the total length (TL), and subsequently the average for each functional attribute for each species was calculated. Absolute values were used for the number of gills rakers, oocyte count, and oocyte diameter. The following categorical variables were used: feeding habits (detritivores, invertivores, omnivores, carnivores), position in the water column (surface, mid-water, bottom) mouth

position (superior; terminal; sub-terminal; ventral) and the maximum body size for the species (small, medium, large).

2.4 | Analyses

2.4.1 | Environmental variables

Environmental variables were compared among the reservoirs (fixed factors) with the years (3 years) as random factors. A Permutational Multivariate Analysis of Variance (PERMANOVA) on a Euclidean distance matrix with a type I (sequential) sum of squares were used to calculate *p*-values. In addition, a principal component analysis (PCA)

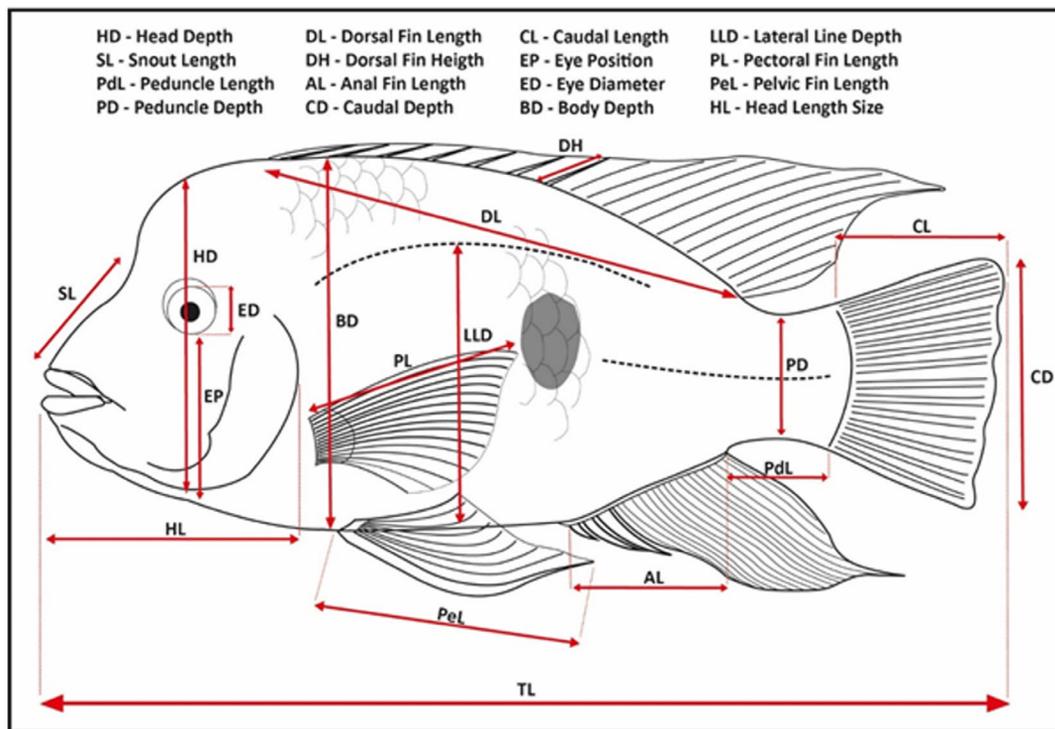


FIGURE 2 Measurements used to calculate the traits for each fish species [Color figure can be viewed at wileyonlinelibrary.com]

was applied to environmental data to identify groups of reservoirs based on environmental variables. Because environmental data have different units of measurements, they were transformed to standard z-scores before analysis with multivariate analysis. Variables that were redundant ($r > 0.80$) were removed from this analysis. We averaged the environmental variables of all samples for each reservoir.

2.4.2 | Community structure

To evaluate differences in the structure of fish communities between the reservoirs, a non-metric Multidimensional Scaling (nMDS) analysis was applied to a Bray-Curtis distance matrix on the numerical abundance of square-root transformed data. A Permutational Multivariate Analysis of Variance (PERMANOVA) on a Bray-Curtis distance matrix with a type I (sequential) sum of squares was used to calculate p -values to compare assemblages structure, species richness, and abundance among the three types of reservoirs. In addition, a Similarity Percentage Analysis (SIMPER) was used to determine the species that most contributed to the within-group average similarity for the different reservoirs.

2.4.3 | Taxonomic and functional distinctness

Taxonomic Distinctness indices ($\Delta+$) were calculated based on Clarke and Warwick (1998) and Warwick and Clarke (2001). The

species were placed in a taxonomic hierarchy, according to Nelson, Grande, and Wilson (2016), from the lowest to the highest level, that is, species, genus, family, order, and subseries. The average taxonomic distinctness ($\Delta+$) is the mean number of steps to reach a taxonomic level common to two species and the calculations were performed across all possible pairs of species in a cluster (Clarke & Warwick, 1998). As standardization, the shortest to longest paths in the phylogenetic tree ranged from zero to 100 according to the number of steps, assuming that the steps have equal lengths.

The average Functional Distinctness ($X+$) is the mean functional dissimilarity between species in the samples. This index was calculated using both, the species abundance matrix and the functional attributes matrix (Sommerfeld et al., 2008). It describes how the taxonomic relationship between species can be enhanced by incorporating functional relationships between species and considering how it can be used to derive functional indices. These indices and the 95% confidence interval funnel curves were obtained using the TAXDTEST routine. A conceptual diagram was prepared to explain how the matrices were built and how the analysis associated with taxonomic and functional distinctness were performed (Figure 3) The PERMANOVA, MDS, SIMPER, PCA, and TAXDEST analyses were performed using the PRIMER6 software ver. 6.1.3 + PERMANOVA ver. 1.0.3. We also compared the mean values of the taxonomic ($\Delta+$) and functional ($X+$) distinctness among the three types of reservoirs (fixed factors). A non-parametric Kruskal-Wallis test was applied to compare the indices among the reservoirs using the STATISTICA software version 10.0 (StatSoft, 2011).

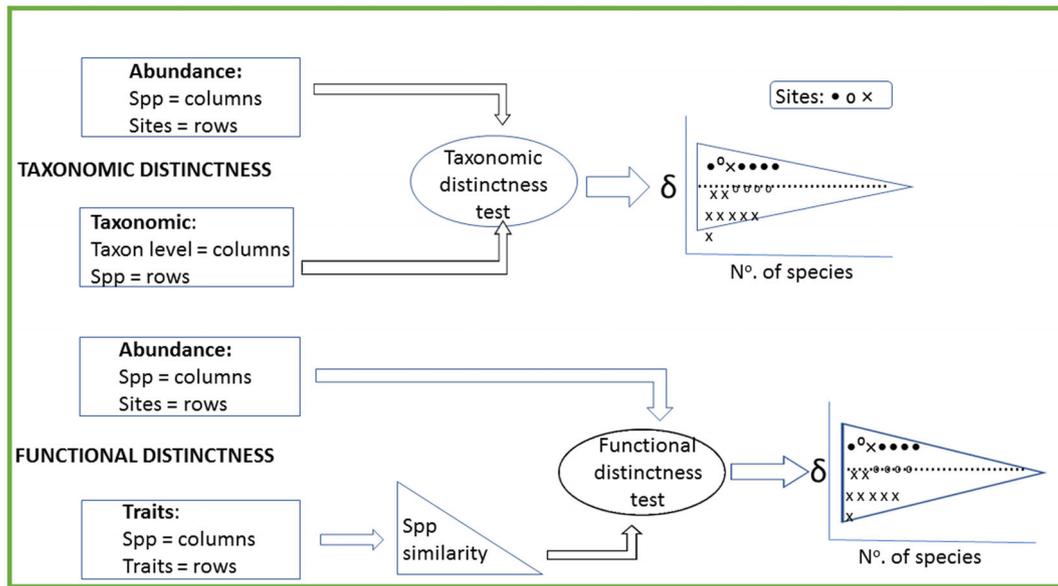


FIGURE 3 Conceptual diagram, explaining how the matrices were built and how the analysis related to taxonomic and functional distinctness were performed [Color figure can be viewed at wileyonlinelibrary.com]

3 | RESULTS

3.1 | Environmental variables

The pH, conductivity, dissolved oxygen (DO), total dissolved solids (TDS), water temperature, oxide-reduction potential (ORP), and transparency showed significant differences ($p < 0.001$) between the three types of reservoirs (Table 2). Conductivity and TDS were significantly higher in the cascade reservoirs compared with the reservoirs on the main river, which in turn, had higher values than the isolated reservoirs.

Water temperature was significantly higher in the cascade reservoirs compared to the reservoirs on the main channel and the isolated reservoirs. Overall, transparency and pH were higher in reservoirs on the main channel, followed by the isolated reservoirs, which in turn were higher than the cascade reservoirs. Dissolved oxygen and the ORP were higher in the isolated reservoirs, followed by the reservoirs on the main channel and than the cascade reservoirs (Table 2). Turbidity and mean depth of the site did not differ significantly between the three types of reservoirs.

A well-defined pattern in the distribution of the reservoir samples was detected by the PCA based on the environmental variables, with the first axis explaining 34.4% of the total variance and the second axis explaining 25.1% (Figure 4). The first axis was negatively associated to transparency, retention time and reservoir area, variables with high values in ISO 2, and to a lesser extent in PSR 1. The second axis discriminated the reservoirs based on high conductivity for example, cascade reservoirs and PSR 2 and PSR 3, in contrast to those with high turbidity (ISO 1). Cascade reservoirs (CAS 1, CAS 2, CAS 3) grouped closely and were characterized by higher conductivity, lower transparency, smaller area, and shorter retention time compared to other reservoirs.

3.2 | Species composition

In total, 34 species of Actinopterygii in four orders, 15 families and 29 genera were identified in the eight reservoirs (Tables 3 and S2). Characiformes, Siluriformes, and Cichliformes had the highest number of species with 11, 11, and 8 species, respectively. The order Cichliformes had four non-native species (ENN). Seven non-native species were recorded in the eight reservoirs, accounting for 20.5% of the total number of species. Of these seven non-native species, four belong to the order Cichliformes (see Table S2).

The total number of recorded species was higher in the reservoirs on the main channel of the PSR and in the cascade reservoirs, which comprised 30 species compared to isolated reservoirs that had only 22 species (Tables 3 and S2). When analyzed separately, the highest number of species was recorded in the CAS 2 (23 species). On the other hand, ISO 1 had the lowest richness, with only 9 species recorded. The mean number of species was lowest in ISO 1 (6.3 ± 1.2 species/sample) and highest in PSR 3 (15.4 ± 3.1 species/sample), whereas fish abundance was highest in ISO 2 (394.0 ± 271.5 individuals/sample) and lowest in CAS 1 (56.3 ± 16.0 individuals/sample) (Table 4).

Differences in fish community structure among reservoirs were clearly identified by nMDS, with each type of reservoir clustering separately (Figure 5). The most conspicuous were the isolated reservoirs that displayed a clear separation of the two other types of reservoirs. Significant differences were found in the assemblage structure among the three types of reservoirs according to PERMANOVA (Pseudo-F = 4.5, $p = 0.001$).

The three types of reservoirs had samples with high (> 45%) within-group average similarity, indicating high consistency in the species composition. The characin *Astyanax cf. bimaculatus* (Linnaeus,

TABLE 2 Mean ± s.d. and PERMANOVA comparisons for environmental variables among the eight reservoirs

Local	pH	Cond	OD	TDS	Temp	ORP	Turb	Transp	Depth
PSR1	6.8 ± 0.1	0.04 ± 0.01	7.0 ± 0.9	0.02 ± 0.01	20.9 ± 0.3	358 ± 15.3	0.02 ± 0.01	4.0 ± 0.7	6.3 ± 1.4
PSR2	8.3 ± 0.6	0.10 ± 0.01	7.7 ± 0.6	0.06 ± 0.02	20.7 ± 0.3	259 ± 36.0	12.2 ± 0.91	2.6 ± 0.7	5.4 ± 2.8
PSR3	7.4 ± 0.5	0.08 ± 0.02	7.4 ± 0.5	0.05 ± 0.01	21.3 ± 0.1	311 ± 32.3	0.80 ± 0.61	3.1 ± 0.3	2.9 ± 1.0
CAS1	6.5 ± 0.2	0.11 ± 0.04	6.1 ± 0.8	0.07 ± 0.02	21.8 ± 0.1	277 ± 52.0	91.5 ± 0.71	1.0 ± 0.1	3.2 ± 1.7
CAS2	6.7 ± 0.2	0.11 ± 0.03	5.8 ± 1.2	0.07 ± 0.02	22.6 ± 0.5	336 ± 10.9	8.95 ± 11.2	1.5 ± 0.1	4.1 ± 1.9
CAS 3	7.4 ± 0.3	0.11 ± 0.04	6.4 ± 0.9	0.07 ± 0.03	21.9 ± 0.2	255 ± 42.1	11.94 ± 2.4	2.0 ± 0.1	3.9 ± 1.3
ISO1	6.6 ± 0.3	0.02 ± 0.01	8.6 ± 1.2	0.01 ± 0.01	18.3 ± 0.6	340 ± 20.9	32.50 ± 53.9	1.5 ± 0.6	2.1 ± 1.2
ISO2	7.2 ± 0.2	0.03 ± 0.01	6.4 ± 0.7	0.02 ± 0.01	23.4 ± 1.2	341 ± 15.9	0.38 ± 0.52	4.1 ± 1.1	10.0 ± 7.7
Pseudo-F	8.3***	131.4***	12.1***	131.6***	5.6**	7.2**	1.9*	25.0***	2.1*
Comparisons	PSR > ISO = CAS	CAS > PSR > ISO	ISO = PSR > CAS	CAS > PSR > CAS	ISO > PSR = ISO	CAS > PSR = CAS	CAS = ISO = PSR	PSR = ISO > CAS	ISO = PSR = CAS

Note: ***, $p < 0.0001$; **, $p < 0.001$; and *, $p < 0.01$. Maximum and minimum values indicated in bold.

Abbreviations: Cond, conductivity (ms. cm^{-1}); DO, dissolved oxygen (mg. L^{-1}); TDS, total dissolved solids (mg. L^{-1}); Temp, temperature ($^{\circ}\text{C}$); ORP, oxide-reduction potential (mV); Turb, turbidity (NTU); Transp, water transparency (m); Depth, mean depth (m) of the site. Reservoirs: PSR1-3, reservoirs on the main channel of the PSR; CAS1-3, cascade reservoirs; ISO1-2, isolated reservoirs.

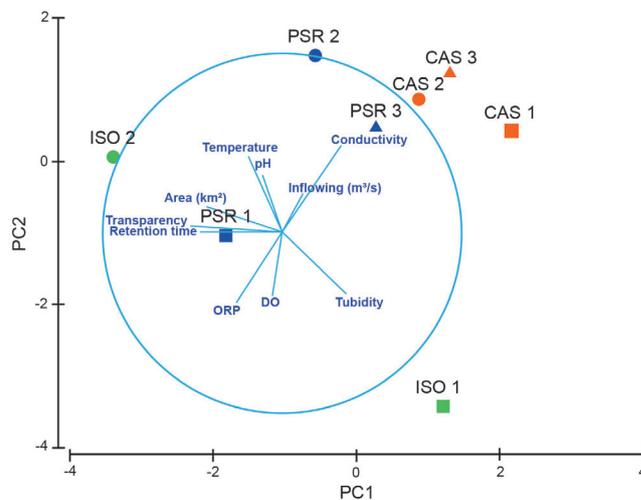


FIGURE 4 Ordination diagram of the first two axes of Principal Component Analysis on the environmental variables. DO, dissolved oxygen; ORP, oxide-reduction potential. Reservoirs: PSR1-3, reservoirs on the main PSR; CAS1-3, cascade reservoirs; ISO1-2, isolated reservoirs [Color figure can be viewed at wileyonlinelibrary.com]

1758) was the most widely distributed species among the reservoirs, with high contribution to the average similarity in all reservoirs except CAS 3 and ISO 1 (Tables 5 and S3). The catfish *Pimelodus maculatus* Lacepède, 1803 contributed significantly to the average similarity of the PSR 1, PSR 2 as well as CAS 3. The armored catfish *Loricariichthys castaneus* (Castelnau, 1855) contributed significantly to the average similarity of ISO 2, CAS 1, and CAS 3. The sciaenids *Pachyurus adspersus* Steindachner, 1879 (native) and *Plagioscion squamosissimus* (Heckel, 1840) (non-native) contributed significantly to the average similarity of CAS 2 and CAS 3 (Table S3). Considering each type of reservoirs, *H. littorale* in the reservoirs on the main channel, *H. affinis*, *P. fur* and *L. castaneus* in cascade reservoirs, and *H. malabaricus*, *T. striatulus*, and *R. quelen* in isolated reservoirs, contributed significantly to within-group average similarity according to the SIMPER analysis (Table 5).

3.3 | Taxonomic and functional distinctness

The species richness did not differ between the reservoirs, except for ISO 2, which had significantly lower richness compared to the other reservoirs ($F = 6.9$; $p < 0.001$). High $\text{TD}\Delta+$ and $\text{FDX}+$ values were observed in all reservoirs, with most samples located within the 95% confidence limit (Figure 6a,b). ISO 1 reservoir, even with the smallest number of species, displayed high $\text{TD}\Delta+$ and the highest $\text{DFX}+$ among all samples, being high taxonomical and functionally distinct (Figure 6a,b).

The reservoir with the largest species richness (PSR 3) did not display the highest $\text{TD}\Delta+$ and $\text{FDX}+$, indicating that the fish fauna was composed of phylogenetically and morphologically similar species. In contrast, PSR 1 and PSR 2 reservoirs, although built on the main

channel of the PSR, displayed low taxonomic and functional distinctness when compared to the other reservoirs.

The elliptical diagrams showed that the variation in taxonomic distinctness had an inverse trend in relation to the average taxonomical distinctness. In contrast, the variation in functional distinctness increased directly with functional taxonomic distinctness (Figure 6c,d).

A trend for greater taxonomic distinctness was observed in the isolated reservoirs (ISO 2 and ISO 1) compared to PSR and cascade reservoirs (Figure 7a). This pattern also coincided with the functional

distinctness, which was lower in the reservoirs on the main channel, and higher in the isolated reservoirs (Figure 7b).

4 | DISCUSSION

The fish assemblage structure changed among the three types of reservoirs as shown in the nMDS ordination and SIMPER analyses. The physicochemical variables may have a role in controlling these changes of fish species, especially the higher conductivity in the cascade reservoirs and the lower conductivity in the isolated reservoirs, whereas dissolved oxygen and ORP were comparatively higher in the isolated reservoirs than in the cascade reservoirs. Such differences in environmental conditions could be associated with differences in assemblage structure between reservoirs. The association between occurrences of *L. castaneus* and high conductivity within cascade

TABLE 3 Number of taxonomic categories found in the three types of reservoirs

System	Species	Genus	Family	Order
Main channel	30	27	15	4
Cascade	30	26	14	4
Isolate	22	19	10	4

TABLE 4 Mean and standard deviation (s.d.) for the number of individuals and number of species per sample in the eight reservoirs

Reservoir	Individuals		Species	
	Mean	s.d.	Mean	s.d.
PSR 1	154.7	44.6	12.0	2.6
PSR 2	311.0	226.2	13.3	1.2
PSR 3	184.0	137.7	15.4	3.1
CAS 1	56.3	16.0	14.0	1.0
CAS 2	83.3	29.0	15.0	2.6
CAS 3	152.7	117.4	10.3	2.5
ISO 1	69.0	81.4	6.3	1.2
ISO 2	394.0	271.5	15.3	2.1

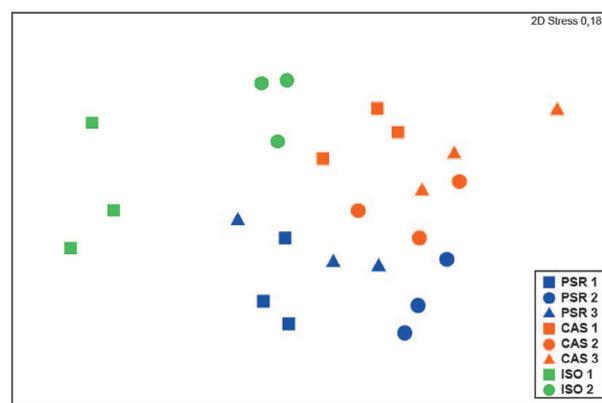


FIGURE 5 Ordination diagram from nMDS analysis on numerical abundance of fish species with samples coded by the reservoirs [Color figure can be viewed at wileyonlinelibrary.com]

Reservoir	PSR (43.6)		CAS (46.1)		ISO (35.8)	
	Av. ab.	Av. Sim.	Av. ab.	Av. Sim	Av. ab.	Av. Sim
<i>A.cf. bimaculatus</i>	7.3	11.3	3.9	8.5	3.9	2.2
<i>H littorale</i>	2.0	2.2				
<i>P. maculatus</i>	5.6	10.1	2.2	4.4	-	-
<i>P. squamosissimus</i>	3.3	2.3	2.8	6.5	-	-
<i>H. affinis</i>	-	-	2.2	3.8	-	-
<i>P. fur</i>			2.3	2.4		
<i>L. castaneus</i>	-	-	3.4	6.7	4.2	2.2
<i>H. malabaricus;</i>	-	-	-	-	1.8	4.2
<i>T. striatulus;</i>	-	-	-	-	2.4	1.3
<i>R. quelen</i>					2.6	3.7
<i>G. brasiliensis</i>	2.0	2.0	-	-	4.3	8.1
<i>O. hepsetus</i>	2.4	2.4	-	-	2.1	5.9

TABLE 5 Species that contributed most to within-group average similarity (%) for types of reservoirs reservoir, according to SIMPER analyses

Abbreviations: AS, average similarity per reservoir in brackets. Av.Ab., average abundance; Av.Sim, average similarity.

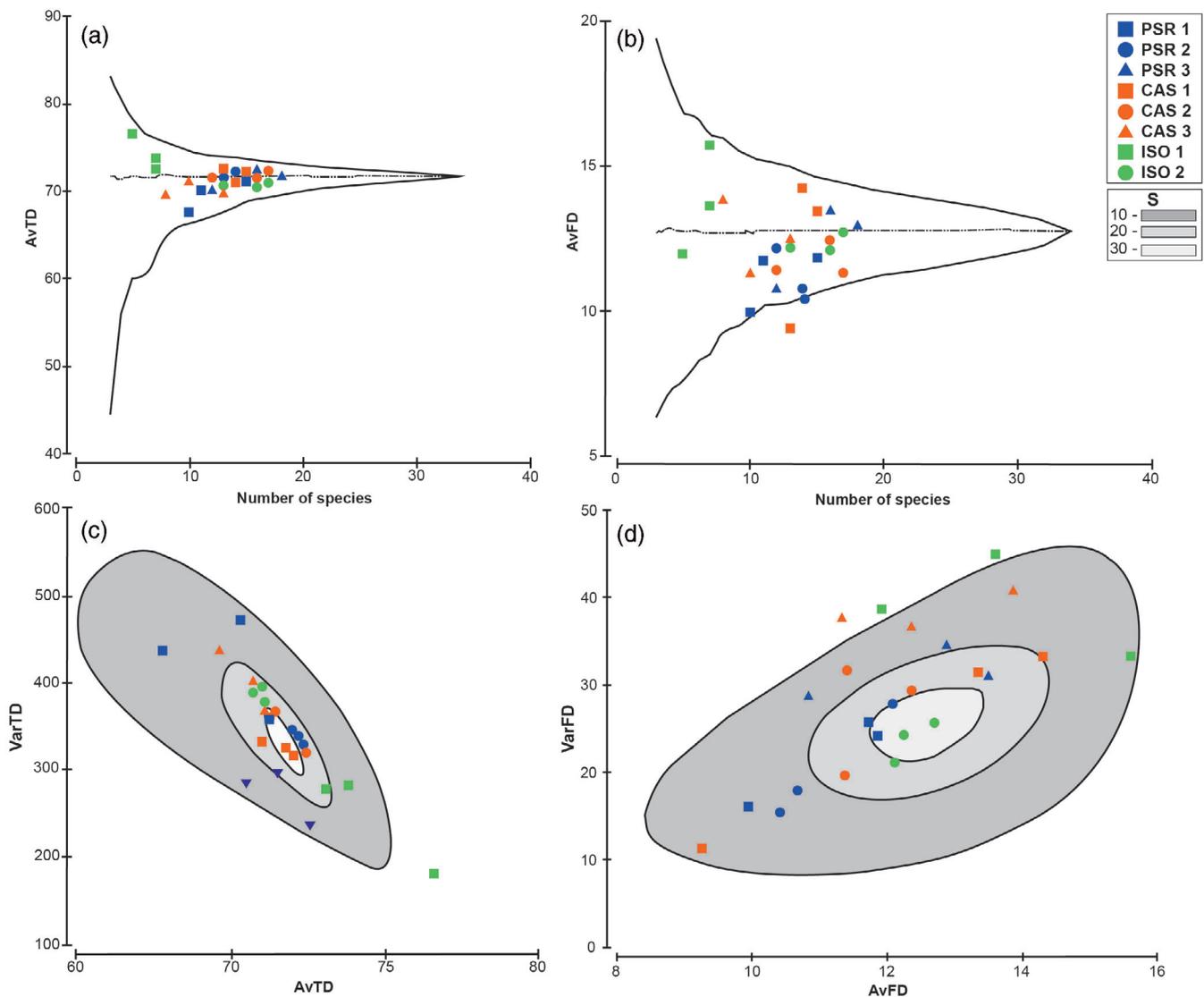


FIGURE 6 Dispersion diagram of species richness against average taxonomic distinctness $\Delta+$ (a), and average functional distinctness $X+$ (b); Variation of taxonomic distinctness versus average taxonomic distinctness (c); and, Variation of the functional distinctness against the average functional distinctness (d) [Color figure can be viewed at wileyonlinelibrary.com]

reservoir, especially CAS3 was reported by Uehara et al. (2015) and confirmed in this study. Another remarkable difference was observed for the volume of inflowing water that was lower in the isolated reservoirs compared to the other two types of reservoirs. High occurrences of *P. maculatus* and *P. squamosissimus* were observed in the reservoirs with a high volume of inflowing water, including the reservoirs on the main channel and the cascade reservoirs. Many studies confirm the importance of local scale variables for the composition and structure of fish communities in reservoirs (Agostinho et al., 2016; Oliveira, Baumgartner, Gomes, Dias, & Agostinho, 2018). Local factors such as flooded area, retention time, volume of inflowing water, and habitat availability influence the composition and structure of fish assemblages in reservoirs (Leibold & Chase, 2019).

A relatively low number of species was recorded within the eight reservoirs (34 species) when compared to fish richness of the PSR.

This is probably related to the greater habitat diversity and high structural heterogeneity of the main river. Araújo, Pinto, and Teixeira (2009) recorded 68 species in the main channel of the PSR, twice the number of fish recorded in the present study. The deleterious effect of the dams and other anthropogenic influences on the ichthyofauna of the PSR (Pinto & Araújo, 2007) may have led to extinction or hindered the colonization of some native fish species in the reservoirs. These changes exert strong selective pressures on the pre-existing aquatic communities because not all species can colonize or maintain self-sustaining populations in this new system (Agostinho et al., 2008). Furthermore, several species that occur in the PSR would not have been supported by the new environmental conditions caused by the reservoirs. When a large river is dammed, two main obstacles are formed: the dam, which obliterates the lotic system and prevents / hinders fish movements and the reservoir itself with its new

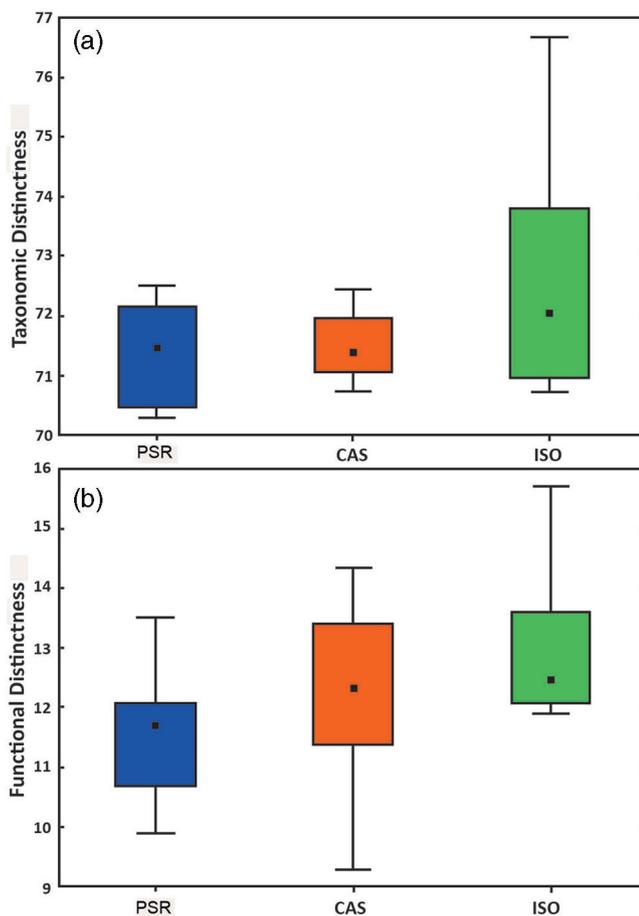


FIGURE 7 Boxplots of taxonomic and functional distinctness in the three types of reservoirs (main channel - PSR, cascade-CAS and isolated-ISO) [Color figure can be viewed at wileyonlinelibrary.com]

configuration, habitat structure, and environmental conditions (Oliveira et al., 2018). In such conditions, species that require running water habitats, such as migratory species, are the most vulnerable. Furthermore, the higher fish richness and abundance in the reservoirs on the main river and in the cascade reservoirs compared to isolated reservoirs are within our expectations for these two community descriptors. Less inflowing water and habitat heterogeneity in the isolated reservoirs may explain these findings. However, one must to keep in mind that 20% of the fish species were non-native, a probable result of the construction of reservoirs.

This study found no evidence to support the hypothesis that reservoirs on the main PSR channel (more water inflow and more habitat availability) had the lowest taxonomic and functional distinctness, indicating that species in environments that receive the highest energy (water flow) tend to support similar functions. PSR 3, a run-of-the-river reservoir with a small surface area, was the only reservoir that followed the expected pattern of high taxonomic and functional distinctness, with most samples located above $DT\Delta+$ and $DFX+$ averages. This reservoir displays environmental features more similar to the lotic conditions, and has a hydroelectric plant that operates on the stranded water model, that is, without water accumulation.

Conversely, the isolated reservoir (ISO 1) that had the highest taxonomic and functional distinctness had the lowest area, reduced water volume, and supported the lowest number of species.

The high taxonomic and functional distinctness in ISO 1 may be associated with the limited habitat and resources availability in this small reservoir, inducing fish to partitioning the niches to coexist. Resource limitation could act as an environmental filter, favoring species adapted to partitioning the resources and functions. According to Rosenfeld et al. (2002), competition is more like to be intense when organisms occupy similar space and time and share the food resources. Dams modify the structure of the fish assemblage, selecting functional traits that reflect species' adaptation to the new environment (Liermann et al., 2012; Oliveira et al., 2018). Therefore, it is likely that the resource limitation in ISO 1 influences the fish composition by selecting species phylogenetically and functionally different, softening the effects of interspecific competition.

The relatively low taxonomic and functional distinctness in the reservoirs on the main channel (e.g., PSR 1 & 2) may be, at least in part, associated with changes in water quality that the PSR basin has experienced in recent decades (Araújo et al., 2009; Uehara et al., 2015). Taxonomic and functional distinctness were more sensitive to anthropogenic impacts than environmental variables (Somerfield et al., 2008; Warwick & Clarke, 2001). In addition, the lentic environment formed after the construction of the reservoir favored generalist species over specialists, jeopardizing endemic species at risk of extinction and resulting in homogenization of the biotic community (Liermann et al., 2012).

Most samples had $DT\Delta+$ and $DFX+$ within 95% of the expected probability. This may have been influenced by the introduction of non-native species (NNS), because 20.5% of recorded species were NNS. In rivers with high number of dams, a false positive effect on the taxonomic richness indices caused by the presence of NNS has been recorded (Canonico, Arthington, McCrary, & Thieme, 2005; Pelicice & Agostinho, 2009). Deleterious effects of NNS have been associated with niche overlap, competition of the native fauna with very competitive non-native species (e.g., tilapias), which can adapt well to the new environment and can feed on different trophic levels (Canonico et al., 2005). The native species are also suffering predation pressure by voracious non-native species such as top carnivorous species of the genus *Cichla* spp. (Pelicice & Agostinho, 2009) or the Sciaenidae *P. squamosissimus* (Barros, Santos, Zanuncio, & Dergam, 2012). In addition, NNS contribute to a potential reduction or local extinction of native species, and they can also give a false idea of quality, as they can increase species richness, taxonomic, and functional distinctness of reservoirs.

Taxonomic and functional distinctness allowed us to evaluate how different the reservoirs were. In this study, these indices were efficient in discriminating the three types of reservoirs, with the highest distinctiveness for the isolated reservoirs. A number of metrics have been developed including taxonomic diversity, phylogenetic diversity, functional roles, and taxonomic and functional distinctness measures ($TD\Delta+$ and $FDX+$) used here. Since these taxonomic distinctness measures are statistically independent of either the sampling

size or richness of samples (Clarke & Warwick, 1998; Warwick & Clarke, 2001) it makes them attractive tools for investigating biodiversity. This study was a first step aiming to help the construction of a tool for linking monitoring, assessment, and management measures. These indices should be viewed as complementary tools in environmental impact assessment, due to their sensitiveness to specific environmental features within the systems being investigated. However, additional studies are required that specifically investigate these indices and the role of hydropower development in the loss of fish biodiversity. The prioritization of management actions considering the different types of reservoirs is a goal to be reached in future research. This goal needs to be institutionalized to ensure maintenance procedures to address objectives that are addressed by the institutions in charge on managing aquatic ecosystems.

We conclude that dams damage lotic systems and pose a major threat to the freshwater species, as reported elsewhere (e.g., Agostinho et al., 2016; Winemiller et al., 2016). Nevertheless, large hydroelectric plants are still the main sources of electricity generation in South America. Many factors other than hydropower (e.g., climate, hydrological conditions, land use, and fishing pressure) can affect fish populations. It is difficult to separate out those caused by hydropower projects that affect fish biodiversity. Even though Brazil has great potential for sustainable energy production (i.e., solar energy, wind power), two-thirds of all power is based on hydroelectric sources (Winemiller et al., 2016). New ways of meeting energy demand using sustainable sources need to be considered.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

ETHICAL APPROVAL

All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

DATA AVAILABILITY STATEMENT

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

ORCID

Tailan Moretti Mattos  <https://orcid.org/0000-0001-6134-3144>

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

Augusto de Salles Guerra-Júnior  <https://orcid.org/0000-0003-4655-0115>

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

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