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Taxonomic loss and functional reduction over time in the ichthyofauna of the Taquaruçu Reservoir, lower Paranapanema River, Southern Brazil

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We evaluated the fish composition and ecological attributes of the ichthyofauna collected in a limnological zone of the Taquaruçu Reservoir, lower Paranapanema River. Information about the fish community was updated when compared to the previous study (2006). Non-metric multidimensional scaling (NMDS) showed differences in species composition between periods and community weighted means (CWMs) exhibited changes in functional composition over time. Four functional indices were used in the principal coordinate analysis (PcoA) to measure changes in the functional space of species, whereas functional β-diversity inspected differences in the traits composition between the periods. 1,203 individuals were sampled of 43 species, being 16 non-native and 14 new records. Compared to 2006, 27 species were absent, most of them native to Loricariidae and Anostomidae, while Curimatidae and Pimelodidae decreased in abundance. Functional indexes showed a reduction in functional diversity, whereas new species records exhibited functional redundancy. It might have occurred a simplification of the fish community over time, excluding the migratory and specialists species such as the herbivores and detritivores. Accordingly, we concluded that the ichthyofauna of the Taquaruçu Reservoir might have been undergoing a process towards biotic homogenization.

Keywords: Biological invasion, Damming, Homogenization, Long Term Changes, South America.

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Avaliamos a composição de peixes e atributos ecológicos da ictiofauna coletada em uma zona limnológica do reservatório de Taquaruçu, baixo rio Paranapanema. As informações sobre a comunidade de peixes foram atualizadas quando comparadas ao estudo anterior (2006). O escalonamento multidimensional não métrico (NMDS) mostrou diferenças na composição de espécies entre os períodos, e as médias ponderadas da comunidade (CWMs) exibiram mudanças na composição funcional ao longo do tempo. Quatro índices funcionais foram utilizados na análise de coordenadas principais (PcoA) para medir as mudanças no espaço funcional das espécies, enquanto a β-diversidade funcional inspecionou diferenças na composição de traços entre os períodos. Foram amostrados 1,203 indivíduos de 43 espécies, sendo 16 não-nativas e 14 novos registros. Em comparação com 2006, 27 espécies estavam ausentes, a maioria nativa de Loricariidae e Anostomidae, enquanto Curimatidae e Pimelodidae diminuíram em abundância. Os índices funcionais mostraram redução na diversidade funcional, enquanto novos registros de espécies exibiram redundância funcional. Pode ter ocorrido uma simplificação da comunidade de peixes ao longo do tempo, excluindo as espécies migradoras e especialistas como os herbívoros e detritívoros. Dessa forma, concluímos que a ictiofauna do reservatório de Taquaruçu pode estar sofrendo um processo de homogeneização biótica.

Palavras-chave: América do Sul, Barramento, Homogeneização, Invasão biológica, Mudanças de longo prazo.

INTRODUCTION

Studies based on ichthyofauna surveys are relevant to unveil biodiversity patterns (Langeani *et al*., 2007) and the effects of anthropogenic impacts on communities (Orsi, Britton, 2014; Loures, Pompeu, 2019; Ganassin *et al*., 2021). Nevertheless, studies based only on the taxonomic composition of communities may not cover all aspects of biodiversity (Mouchet *et al*., 2010). Currently, the functional facet of communities has been used as a complementary measure of biodiversity (Villéger *et al*., 2017). The use of functional traits (*i.e*., any measurable biological characteristic that might influence the environmental fitness of species) has become key information to disentangle the aspects of functional ecology (Villéger *et al*., 2017; Pimiento *et al*., 2020). Thus, the investigation of species organized in a multidimensional functional space can be a useful approach (Villéger *et al*., 2008), resulting in a reliable source to evaluate biodiversity patterns and mechanisms (Mouillot *et al*., 2013). This approach also provides a powerful tool when it comes to change and loss of biodiversity due to human activities (Toussaint *et al*., 2018; McLean *et al*., 2019), as well as the dynamics of native and non-native species (Olden *et al*., 2006; Pool *et al*., 2010). Hence, functional diversity indexes can be used to compare biodiversity patterns across spatial and temporal scales (Mouchet *et al*., 2010; Pimiento *et al*., 2020).

The upper Paraná River basin is known to be exploited by hydropower (Agostinho *et al*., 2007), regardless of its importance for hydrological and ichthyofaunistic aspects

(Langeani *et al*., 2007). The biotic-abiotic interactions in reservoirs are classified in distinct temporal phases (Agostinho *et al*., 1999), and these interactions may act as an environmental filter on the composition and structure of fish communities (Orsi, Britton, 2014; Smith *et al*., 2018). Reservoirs might select fish individuals with biological characteristics suitable for such environments (Oliveira *et al*., 2018), where some species may be non-natives (Olden *et al*., 2006; Pool *et al*., 2010). Thus, a taxonomic and/or functional simplification of the ichthyofauna may occur, as non-adapted native species, such as dourado *Salminus brasiliensis* (Cuvier, 1816) and pintado *Pseudoplatystoma corruscans* (Spix & Agassiz, 1829) decline and/or disappear over time (Arantes *et al*., 2019). Therefore, reservoirs should become faunistically similar due to a biotic homogenization process (Daga *et al*., 2020; Magalhães *et al*., 2020). In this sense, studies on the structure and composition of ichthyofauna in reservoirs across time are essential to understand the impact of human activity on fish communities (Loures, Pompeu, 2019; Ganassin *et al*., 2021).

The Paranapanema River, one of the major tributaries of the upper Paraná River (Agostinho *et al*., 2007), is heavily fragmented by dams into a cascade of 11 reservoirs (Duke Energy, 2008), and it is as well highly impacted by invasive species (Garcia *et al*., 2018; Pelicice *et al*., 2018; Jarduli *et al*., 2020). Biological invasions in this basin are mainly influenced by the flooding of a natural barrier by the Itaipu Reservoir (*e.g*., Sete Quedas Falls) (Júlio Junior *et al*., 2009). Also, stocking programs (Agostinho *et al*., 2007), aquaculture escapes (Casimiro *et al*., 2018), sporting angling and aquarium dumping (Langeani *et al*., 2007; Jarduli *et al*., 2020) have all negatively affects this area (Garcia *et al*., 2018; Pelicice *et al*., 2018). The Taquaruçu Reservoir is the penultimate one in a series of reservoirs in the lower Paranapanema River (Duke Energy, 2008). This reservoir belongs to the portion of the basin with the largest amount of non-native species, such as the South American silver croaker *Plagioscion squamosissimus* (Heckel, 1840) and the armored catfish *Loricariichthys platymetopon* Isbrücker & Nijssen, 1979 (Garcia *et al*., 2018), and it is known to be under additional anthropogenic activities like deforestation and discharge of human effluents (Vidotto-Magnoni *et al*., 2015).

The ichthyofauna of the Taquaruçu Reservoir was widely investigated more than ten years ago (data ranging from 1993 to 2000) (Britto, Carvalho, 2006). Based on knowledge about the dynamics in reservoirs and its implications to the ichthyofauna, we aimed here to update the previous information on the ichthyofauna (*i.e*., Britto, Carvalho, 2006), and to elucidate changes overtime in the taxonomic and functional composition of the fish community. Our hypotheses were coined after the damming period, as follows: (1) The taxonomic and functional composition of the fish community changed between the distinct time-periods analyzed; (2) Generalist species that are functionally similar, mostly non-natives, are favored over specialist native species between the distinct time-periods.

MATERIAL AND METHODS

Study area. The Paranapanema River rises in the Atlantic Plateau of the "Serra de Paranapiacaba", municipality of Capão Bonito, in the São Paulo State, Southeastern Brazil (Sampaio, 1944). It runs through approximately 930 km until it flows into the upper Paraná River (Sampaio, 1944). Extending from the Southeast of SP to the North of the Paraná State, about 330 km from its main channel define the borders between these Brazilian states (Maack, 1981). The lower Paranapanema River is the portion of the basin that begins after Salto Grande Falls (currently flooded by the Salto Grande Reservoir), covering in extension (from upstream to downstream) the reservoirs of Salto Grande, Canoas II, Canoas I, Capivara, Taquaruçu (our study area), and Rosana (Duke Energy, 2008).

The hydroelectric power plant "Escola Politécnica" (Taquaruçu Dam) was built in 1989 and started to operate in 1991. The Taquaruçu Reservoir is characterized by a run-of-river regime, a length of 80 km, a surface area of 105.5 km^2, and a maximum depth of 18 m (Britto, Carvalho, 2006). This reservoir has few tributaries, and among them, the most important ones are located on the left bank, following: the Capim, Centenário, and Tenente rivers; and on the right bank: the Anhumas River. Nonetheless, a large part of those tributaries is undergoing several impacts due to anthropogenic activities, such as riparian forest deforestation, land use (agriculture and pasture), urbanization, and discharge of domestic and industrial effluents (Vidotto-Magnoni *et al*., 2015).

Samplings sites. Samplings were performed from September 2018 to September 2019 at four sites in the reservoir transitional zone: site 1 (22°39'15.0"S 51°40'42.0"W); site 2 (22°39'37.0"S 51°37'53.8"W); site 3 (22°41'24.7"S 51°34'50.5"W); site 4 (22°41'10.8"S 51°32'20.9"W) (Fig. 1). The transitional zone was determined according to Ward *et al.* (1999) to survey species that inhabit lacustrine and fluvial zones. Following the approach used by Britto, Carvalho (2006), our samplings were standardized and carried out quarterly, where fish were caught using gill-nets (30 to 120 mm between opposed knots), which were set for 24 h and checked every 12 h.

Fish were anesthetized and euthanized by overexposure to 1g/ml clove oil, fixed with 10% formalin, and further transferred to 70% alcohol. The fishes identification were carried out using specific literature (Ota *et al*., 2018), and with the help of a specialist (Dr. Fernando C. Jerep, Museu de Zoologia da Universidade Estadual de Londrina, MZUEL). Further, a collection of voucher specimens was deposited at MZUEL. As for the previous data (Britto, Carvalho, 2006), all species captured in the reservoir transitional zone and their abundances were selected. Subsequently, species were organized according to Fricke *et al.* (2021).

Functional traits. Ten functional traits were selected to cover the largest spectrum possible of the fish community functional space. Hence, traits selected here were associated with habitat occupation, feeding habits, life-history, and reproductive strategy (Villéger *et al*., 2017).

For habitat occupation, we used the following range of adult maximum body size: small size (≤ 200 mm), medium size (≥ 200 – 400 ≤ mm), and large size (≥ 400 mm) (Ota *et al*., 2018). Regarding the water column position, the following classification was utilized: benthonic, demersal, and pelagic (Graça, Pavanelli, 2007). Classification in trophic guilds was used as feeding habit traits (*i.e*., detritivore, herbivore, insectivore, invertivore, omnivore, and piscivore) (Hahn *et al*., 2002; Vidotto-Magnoni, 2009). As traits associated with life-history, our classification followed: periodic, equilibrium, opportunistic, or intermediate (Winemiller, 1995). Finally, for traits related to

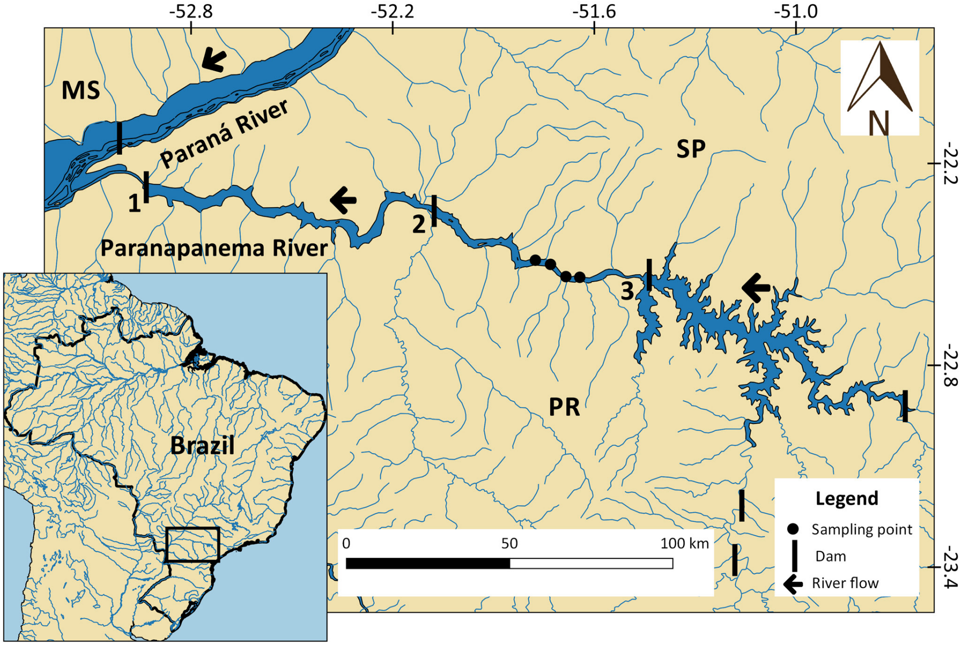

FIGURE 1 | Location of the samplings points in the Taquaruçu Reservoir, lower Paranapanema River (transitional zone, 2020). Hydroelectric power plants: 1– Rosana; 2– Taquaruçu; 3– Capivara. MS = Mato Grosso do Sul State; PR = Paraná State; SP = São Paulo State.

reproductive strategies, we utilized: migratory behavior (non-migratory, short-distance migratory, long-distance migratory); fertilization (internal or external); parental care (parental care or non-parental care) (Agostinho *et al.*, 2003); spawning (single or multiple); oocyte diameter (mm), and fecundity (number of oocytes matured/gonad mature) (Vazzoler, 1996; Orsi, 2010; Froese, Pauly, 2020).

Functional indexes. The distribution of species and their abundance in the functional space characterize functional diversity (Mouillot *et al.*, 2013). Here, we evaluated functional diversity based on four indexes: richness, evenness, divergence, and dispersion. Functional richness (FRic) was defined as the position occupied by species in the functional space (Villéger *et al.*, 2008), while functional evenness (FEve) was based on the uniformity of their abundance in this same space (Mouillot *et al.*, 2013). Functional divergence (FDiv) was calculated as the proportional abundance that was concentrated in species occupying the extremes of the functional space, in the same way as functional dispersion (FDis) was calculated by weighting the average distance of abundance for the extreme traits in this same space (Mouillot *et al.*, 2013).

Statistical analyses. Non-metric multidimensional scaling (NMDS) ordination was employed to elucidate the differences in species composition between the time-periods (*i.e.*, 2006 and 2020). Based on a matrix of distances (*e.g.*, Jaccard method), we verified the degree of similarity between the periods following the species composition data. Thus, in our functional space, we plotted our species composition based on the first two dimensions of the NMDS (final stress level = 0.181). NMDS was run using the function "metaMDS" in the Vegan package (version 2.4–1; Oksanen *et al*., 2019). Also, to test for significant differences between the groupings of the NMDS, we utilized permutational analysis of variance (PERMANOVA) (Anderson, 2008) using 999 permutations and the function "adonis" in the Vegan package (Oksanen *et al*., 2019).

We used the community-weighted mean (CWM) to characterize the functional structure of fish community calculated by each time-period. The CWMs were calculated as the abundance-weighted mean of trait values in the community, which shows an advantage to face the absolute increase or decrease in trait composition (McLean *et al*., 2019). As a result, the proportions of categorical and continuous trait values can be determined (McLean *et al*., 2019). For species with no trait data available, we have completed the dataset using the closest phylogenetic equivalent at the genus level (Penone *et al*., 2014). We assessed changes in the functional structure of the fish community by estimating and comparing the four indexes described above (*i.e*., richness, evenness, divergence, and dispersion) (Mouillot *et al*., 2013). When plotted in a two-dimensional functional space, this approach enables the visualization of potential changes in different components of the community's functional structure, where the axis represents the qualitative traits extracted from a principal coordinates analysis (PCoA) (Mouillot *et al*., 2013). To verify significant differences in the functional diversity indices between the periods was used a one-tailed test ($p < 0.05$) proposed by Swenson (2014). We also used functional dissimilarity indexes to assess the changes in the functional β-diversity based on its functional turnover and functional nestedness-resultant components. Hence, in our study, functional β-diversity measured the functional trait composition differences between two distinct periods in time (*i.e*., 2006 and 2020 datasets) (Mouillot *et al*., 2013; Villéger *et al*., 2013).

The multidimensional functional spaces were computed based on a dissimilarity matrix using a principal coordinates analysis (PCoA, a generalization of the principal component analysis (PCA)), which produces a Euclidean space encompassing the two first PCoA axis minus one (Maire *et al*., 2015). This distance matrix was computed using Gower's distance (Gower, 1971), allowing thus quantitative and qualitative variables to be mixed while giving them equal weights. Also, we compared the mean squared deviation of the functional spaces. Following the approach devised by Maire *et al.* (2015), a PCoA was run using this functional distance matrix, and the best functional dendrogram was obtained based on the procedure implemented by Mouchet *et al.* (2008): using the multidimensional functional spaces from two to seven dimensions, and corresponding to the axis obtained after running the PCoA. Finally, we retained the species coordinates on the first three PCoA axis as the values of the traits (10 traits) describing our fish functional strategies (Villéger *et al*., 2011; Mouillot *et al*., 2013). We performed analyses on the functional structure of community using a set of functions: "*quality_funct_space*", "*plot_funct_space*", "*multidimFD*", "*multidimFbetaD*" (Mouillot *et al*., 2013; Villéger *et al*., 2013). All these functions are available from (http://villeger.sebastien.free.fr/Rscripts.html), and analyses were carried out using the R Programming software version 3.5.3 (R Development Core Team, 2020).

RESULTS

We had 1,203 individuals captured belonging to five orders, 17 families, and 43 species. Out of the 43 species, 16 were non-natives to the upper Paraná River basin (Tab. 1). The families showing the greatest richness were: Pimelodidae (seven species), followed by Anostomidae, Cichlidae, and Serrasalmidae (five species each); whereas the most abundant families were Characidae (n = 338), Loricariidae (n = 195), and Sciaenidae (n = 136). Out of the fish composition data obtained by Britto, Carvalho (2006), 27 species were not captured, being most of them native species of Loricariidae (*e.g.*, nine species) and Anostomidae (*e.g.*, six species). Also, 14 species in our results (*i.e.*, mostly non-native species from different families) were new records to the reservoir transitional zone (Tab. 1). The families with a decrease in abundance were Loricariidae, Anostomidae, Curimatidae, and Pimelodidae; whereas Characidae, Cichlidae, and Parodontidae have displayed an increase in abundance (Tab. 1).

TABLE 1 | Ichthyofauna and functional traits of the Taquaruçu Reservoir, lower Paranapanema River (the transitional zone between 2006 and 2020). * = non-native species to the upper Paraná River basin; # = species only recorded in 2006; + = species only recorded in 2020; n = abundance; SI = size (mm); WP = water column position; TG = trophic guild; LH = life-history; MB = migratory behavior; FE = fertilization; PC = parental care; SP = spawning; OD = oocyte diameter (mm); FC = fecundity (number of oocytes matured/gonad mature). SM = small; MD = medium; LA = large; BE = benthonic; DE = demersal; PE = pelagic; DET = detritivore; HER = herbivore; INS = insectivore; INV = invertivore; OMN = omnivore; PIS = piscivore; E = equilibrium; O = opportunistic; P = periodic; NM = non-migratory; SDM = short-distance migratory; LDM = long-distance migratory; EF = external fertilization; IF = internal fertilization; PC = parental care; NPC = non-parental care; MU = Multiple; SI = single. P&DII 1092 = field number, MZUEL voucher uncataloged.

Family/Species	n		Functional traits										Vouchers
	2006	2020	SI	WP	TG	LH	MB	FE	PC	SP	OD	FC	
Erythrinidae													
Hoplias malabaricus (Bloch, 1794)	35	20	LA	DE	PIS	E	NM	EF	PC	MU	1.3085	43972.96	MZUEL 20741
Hoplias sp.+	0	20	LA	DE	PIS	E	NM	EF	PC	MU	1.3085	43972.96	MZUEL 20761
Parodontidae													
Apareiodon affinis (Steindachner, 1879)	13	44	SM	DE	DET	P	SDM	EF	NPC	SI	0.8900	4345.82	MZUEL 20770
Cynodontidae													
Rhaphiodon vulpinus Spix & Agassiz, 1829#	5	0	LA	PE	PIS	P	LDM	EF	NPC	SI	0.9800	215841	-
Serrasalmidae													
Metynnis lippincottianus (Cope, 1870)*	4	33	SM	PE	HER	P	SDM	EF	NPC	MU	1.0783	11990.53	MZUEL 20737
Myloplus levis (Eigenmann & McAtee, 1907)*+	0	1	ME	PE	HER	P	SDM	EF	NPC	SI	2.3260	7000	MZUEL 20783
Myloplus tiete (Eigenmann & Norris, 1900)#	26	0	ME	PE	HER	P	SDM	EF	NPC	SI	2.3260	7000	-
Serrasalmus maculatus Kner, 1858	41	21	ME	PE	PIS	E	NM	EF	PC	MU	1.4078	34177.77	MZUEL 20743
Serrasalmus marginatus Valenciennes, 1837*	67	40	ME	PE	PIS	EP	NM	EF	PC	MU	1.2339	68082.19	MZUEL 20744
Anostomidae													
Leporellus vittatus (Valenciennes, 1850)#	10	0	SM	BE	INS	P	SDM	EF	NPC	SI	1.0300	12745.39	-
Leporinus amblyrhynchus Garavello & Britski, 1987#	2	0	SM	DE	INS	P	SDM	EF	NPC	MU	1.0300	12745.39	-

➡

TABLE 1 | (Continued)

Family/Species	n		Functional traits										Vouchers
	2006	2020	SI	WP	TG	LH	MB	FE	PC	SP	OD	FC	
Leporinus friderici (Bloch, 1794)	42	1	LA	DE	OMN	P	SDM	EF	NPC	SI	0.6870	244593.6	MZUEL 20788
Leporinus lacustris Amaral Campos, 1945#	1	0	SM	BE	HER	P	SDM	EF	NPC	MU	1.1717	62038.11	-
Leporinus octofasciatus Steindachner, 1915	6	1	ME	DE	OMN	P	SDM	EF	NPC	MU	1.0400	13308.99	MZUEL 20792
Leporinus paranensis Garavello & Britski, 1987#	3	0	LA	DE	OMN	P	SDM	EF	NPC	SI	0.8900	130527.35	-
Megaleporinus obtusidens (Valenciennes, 1837)	2	5	LA	DE	INS	P	LDM	EF	NPC	SI	0.6751	846826.4	MZUEL 20745
Schizodon altoparanae Garavello & Britski, 1990#	3	0	ME	DE	HER	P	SDM	EF	NPC	MU	0.7545	541605.3	-
Schizodon borellii (Boulenger, 1900)*#	10	0	LA	DE	HER	P	LDM	EF	NPC	MU	0.8807	541605.3	-
Schizodon intermedius Garavello & Britski, 1990	50	11	SM	DE	HER	P	SDM	EF	NPC	SI	1.0200	632157.6	MZUEL 20797
Schizodon nasutus Kner, 1858	83	32	LA	DE	HER	P	SDM	EF	NPC	MU	1.2657	265214.6	MZUEL 20758
Curimatidae													
Cyphocharax modestus (Fernández-Yépez, 1948)	16	1	SM	DE	DET	P	SDM	EF	NPC	MU	0.6800	15948.4	MZUEL 20793
Cyphocharax naegelii (Steindachner, 1881)#	8	0	SM	DE	DET	P	SDM	EF	NPC	SI	0.5600	4787.25	-
Prochilodus lineatus (Valenciennes, 1837)#	5	0	LA	DE	DET	P	LDM	EF	NPC	SI	0.9800	1280722	-
Steindachnerina brevipinna (Eigenmann & Eigenmann, 1889)*+	0	17	SM	DE	DET	P	SDM	EF	NPC	SI	0.4874	56353.49	MZUEL 20776
Steindachnerina insculpta (Fernández-Yépez, 1948)	253	7	SM	DE	DET	P	SDM	EF	NPC	SI	0.4637	33503.14	MZUEL 20746
Triportheidae													
Triportheus nematurus (Kner, 1858)*+	0	1	SM	PE	INS	P	SDM	EF	NPC	MU	0.9700	10953.4	MZUEL 20756
Acestrorhynchidae													
Acestrorhynchus lacustris (Lütken, 1875)	90	33	ME	PE	PIS	P	NM	EF	NPC	MU	0.7248	25993.55	MZUEL 20777
Characidae													
Astyanax lacustris (Lütken ,1875)	84	99	SM	PE	INS	P	SDM	EF	PC	MU	0.6800	7442.77	MZUEL 20753
Moenkhausia intermedia Eigenmann, 1908	23	100	SM	PE	INS	OP	NM	EF	NPC	SI	0.7100	18949.21	MZUEL 20790
Roeboides descalvadensis Fowler, 1932*	12	139	SM	PE	INS	P	NM	EF	NPC	MU	0.9200	280	MZUEL 20772
Sternopygidae													
Eigenmannia virescens (Valenciennes, 1836)#	7	0	ME	BE	INS	E	NM	EF	PC	MU	1.9000	531.96	-
Gymnotidae													
Gymnotus inaequilabiatus (Valenciennes, 1839)*+	0	13	LA	BE	INS	E	NM	EF	PC	MU	1.7491	10360.15	MZUEL 20748
Rhamphichthyidae													
Rhamphichthys hahni (Meinken, 1937)*+	0	1	LA	BE	INS	E	NM	EF	NPC	MU	3.0000	1085	MZUEL 20759
Rhamphichthys sp.#	2	0	LA	BE	INS	E	NM	EF	NPC	MU	3.0000	1085	-
Loricariidae													
Hypostomus ancistroides (Ihering, 1911)#	11	0	ME	BE	DET	E	NM	EF	PC	MU	3.2900	420.45	MZUEL 20778
Hypostomus margaritifer (Regan, 1908)#	1	0	ME	BE	DET	E	NM	EF	PC	MU	3.3325	1326.387	-
Hypostomus regani (Ihering, 1905)#	9	0	ME	BE	DET	E	NM	EF	PC	MU	3.3325	1326.387	-
Hypostomus sp.	2	13	ME	BE	DET	E	NM	EF	PC	MU	3.2900	420.45	MZUEL 20749
Hypostomus sp2.#	5	0	ME	BE	DET	E	NM	EF	PC	MU	3.2900	420.45	-

TABLE 1 | (Continued)

Family/Species	n		Functional traits										Vouchers
	2006	2020	SI	WP	TG	LH	MB	FE	PC	SP	OD	FC	
Hypostomus sp4.#	15	0	ME	BE	DET	E	NM	EF	PC	MU	3.2900	420.45	-
Hypostomus sp6.#	34	0	ME	BE	DET	E	NM	EF	PC	MU	3.2900	420.45	-
Loricaria sp.#	19	0	ME	BE	DET	E	NM	EF	PC	SI	4.2800	429.2	-
Loricariichthys platymetopon Isbrücker & Nijssen, 1979*	175	170	ME	BE	DET	E	NM	EF	PC	MU	2.3200	1451	MZUEL 20738
Megalancistrus parananus (Peters, 1881)#	1	0	LA	BE	DET	E	NM	EF	PC	SI	4.2900	13022	-
Proloricaria prolixa (Isbrücker & Nijssen, 1978)	13	12	ME	BE	DET	E	NM	EF	PC	SI	4.2800	429.2	MZUEL 20728
Rhinelepis aspera Spix & Agassiz, 1829#	50	0	LA	BE	DET	P	LDM	EF	NPC	SI	1.3200	181200	-
Auchenipteridae													
Auchenipterus nuchalis (Spix & Agassiz, 1829)*#	53	0	ME	DE	INS	P	NM	IF	NPC	MU	1.3200	2466	-
Auchenipterus osteomystax (Miranda Ribeiro, 1918)*+	0	40	ME	DE	INS	P	NM	IF	PNC	MU	1.3200	2466	MZUEL 20739
Tatia neivai (Ihering, 1930)+	0	1	SM	DE	INV	P	SDM	IF	PC	SI	1.6700	297.24	MZUEL 20794
Trachelyopterus galeatus (Linnaeus, 1766)*	96	38	ME	DE	OMN	P	NM	IF	NPC	MU	1.9000	750	MZUEL 20755
Doradidae													
Ossancora eigenmanni (Boulenger, 1895)*+	0	5	SM	BE	0	P	NM	EF	NPC	MU	0.9000	22400.1	MZUEL 20779
Pterodoras granulosus (Valenciennes, 1821)*#	8	0	LA	DE	PIS	P	LDM	EF	NPC	MU	1.0600	296000	-
Trachydoras paraguayensis (Eigenmann & Ward, 1907)*	43	9	P1	BE	INV	P	NM	EF	NPC	MU	0.9000	22400.1	MZUEL 20767
Pimelodidae													
Iheringichthys labrosus (Lütken, 1874)	81	16	ME	DE	INV	P	SDM	EF	NPC	MU	1.1200	10954.81	MZUEL 20747
Pimelodella gracilis (Valenciennes, 1835)+	0	4	ME	DE	INS	P	SDM	EF	NPC	MU	0.6400	10955	MZUEL 20789
Pimelodella sp.#	6	0	ME	DE	INS	P	SDM	EF	NPC	MU	0.6400	10955	-
Pimelodus maculatus Lacepède, 1803	87	34	LA	DE	OMN	P	LDM	EF	NPC	SI	0.5860	76184.2	MZUEL 20768
Pimelodus ornatus Kner, 1858*	5	1	LA	DE	OMN	P	SDM	EF	NPC	SI	0.3952	54677.58	MZUEL 20765
Pimelodus sp.+	0	1	LA	DE	OMN	P	LDM	EF	NPC	SI	0.5860	76184.2	P&DII 1092
Pinirampus pirinampu (Spix & Agassiz, 1829)	13	1	LA	DE	PIS	P	LDM	EF	NPC	SI	1.1800	189858.2	MZUEL 20740
Sorubim lima (Bloch & Schneider, 1801)*+	0	1	LA	DE	PIS	P	LDM	EF	NPC	SI	1.5400	1200000	MZUEL 20769
Zungaro jahu (Ihering, 1898)#	4	0	LA	DE	PIS	P	LDM	EF	NPC	SI	1.6000	862405	-
Cichlidae													
Cichla cf. *kelberi* Kullander & Ferreira, 2006*+	0	10	LA	DE	PIS	E	NM	EF	PC	MU	1.6087	15694.12	MZUEL 20760
Crenicichla britskii Kullander, 1982	19	10	SM	DE	INS	E	NM	EF	PC	SI	2.0500	955.46	MZUEL 20752
Crenicichla jaguarensis Haseman, 1911#	0	1	SM	DE	INS	E	NM	EF	PC	SI	2.0500	955.46	MZUEL 20784
Crenicichla niederleinii (Holmberg, 1891)#	11	0	SM	DE	INS	E	NM	EF	PC	SI	2.9200	562.91	-
Crenicichla sp.	17	57	SM	DE	INS	E	NM	EF	PC	SI	2.0500	955.46	MZUEL 20764
Geophagus iporangensis Haseman, 1911+	0	3	SM	DE	INS	E	NM	EF	PC	MU	1.7800	1539	MZUEL 20785
Sciaenidae													
Plagioscion squamosissimus (Heckel, 1840)*	131	136	LA	PE	PIS	P	SDM	EF	NPC	MU	0.5300	108314.1	MZUEL 20742

NMDS evidenced a clustering of three groups (*i.e.*, species occurring in both years, species captured exclusively in 2006, and species captured exclusively in 2020), indicating divergences in the fish community over time (Fig. 2). The PERMANOVA confirmed that the species composition in 2006 was significantly distinct from that in 2020 ($R^2 = 0.22$, $P = 0.01$). The CWMs demonstrated a change in six out of ten traits between the datasets of 2006 and 2020, following: size, water column position, trophic guild, migratory behavior, oocyte diameter, and fecundity (Tab. 2). All the functional indexes calculated showed a decreased between 2006 and 2020 datasets (Fig. 3). Changes in functional β-diversity between 2006 and 2020 datasets were observed as well, where the turnover component was almost the total value of total functional β-diversity (Fig. 4).

The results of one-tailed test showed a significant difference in each functional diversity index between the two time-periods. FRic ($t = 80.253$; $P = 0.007$), FDiv ($t = 28.903$; $P = 0.02$), FEve ($t = 33.508$; $P = 0.01$) and FDis ($t = 31.17$; $P = 0.02$) showed decreasing trends along of the two time-periods (2006 to 2020) indicating the loss of several functional traits and change in the abundance of species with restricted to specific groups functional traits.

TABLE 2 | Functional composition by community-weighted means (CWMs), and changes in the ichthyofauna of the Taquaruçu Reservoir, lower Paranapanema River (the transitional zone between 2006 and 2020).

Year	Size (mm)	Water column position	Trophic guild	Life-History	Migratory behavior	Fertili-zation	Parental care	Spawning	Oocyte diameter (mm)	Fecundity (n.oocytes)
2006	Medium	Demersal	Detritivore	Periodic	Short-Distance migratory	External	Non parental care	Multiple	2.0128	17882.09
2020	Small	Pelagic	Piscivore	Periodic	Non-Migratory	External	Non parental care	Multiple	1.4783	27474.19

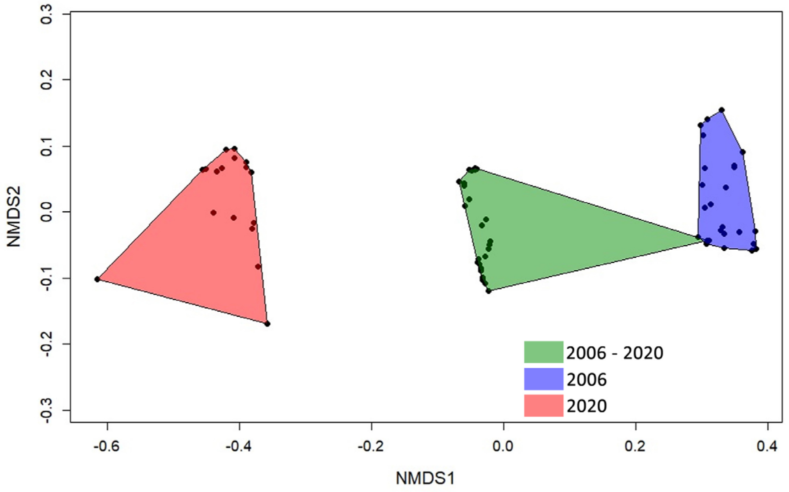

FIGURE 2 | Non-metric multidimensional scaling (NMDS) of the ichthyofauna composition of the Taquaruçu Reservoir, lower Paranapanema River (the transitional zone between 2006 and 2020).

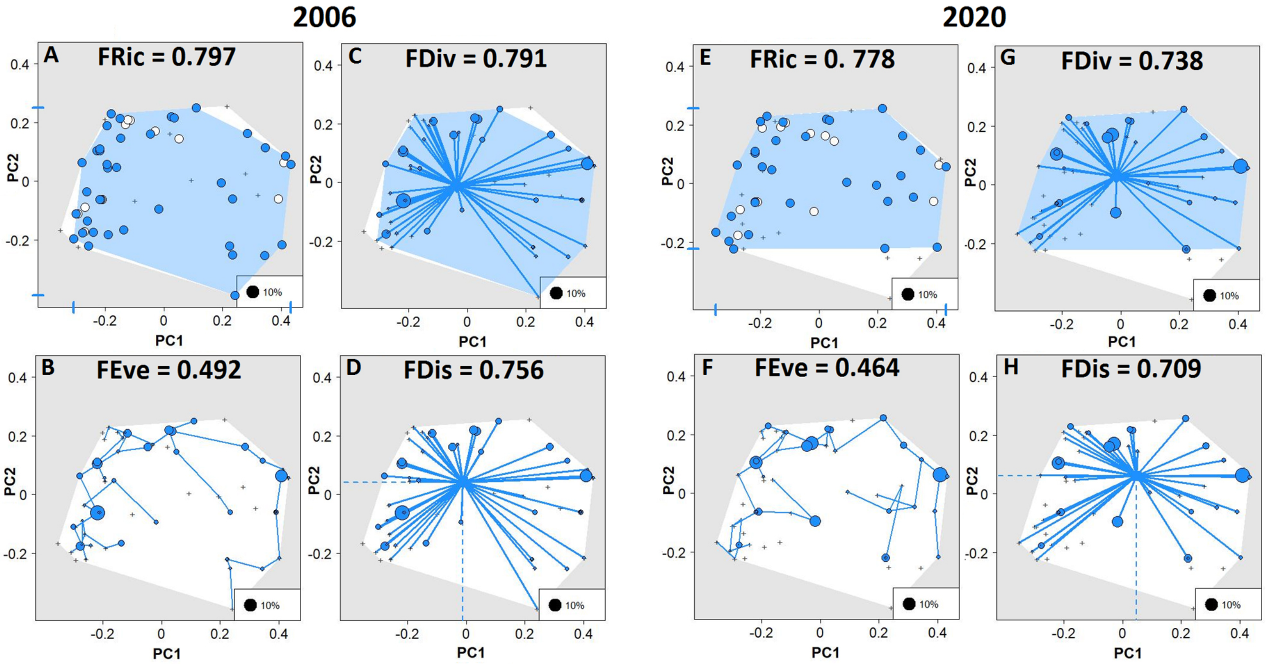

FIGURE 3 | Two-dimensional functional space (PCoA) of the ichthyofauna of the Taquaruçu Reservoir, lower Paranapanema River (transitional zone between 2006 and 2020). **A**, **B**, **C**, **D** = 2006. **E**, **F**, **G**, **H** = 2020. FRic = Functional richness; FEve = Functional evenness; FDiv = Functional divergence; FDis = Functional dispersion.

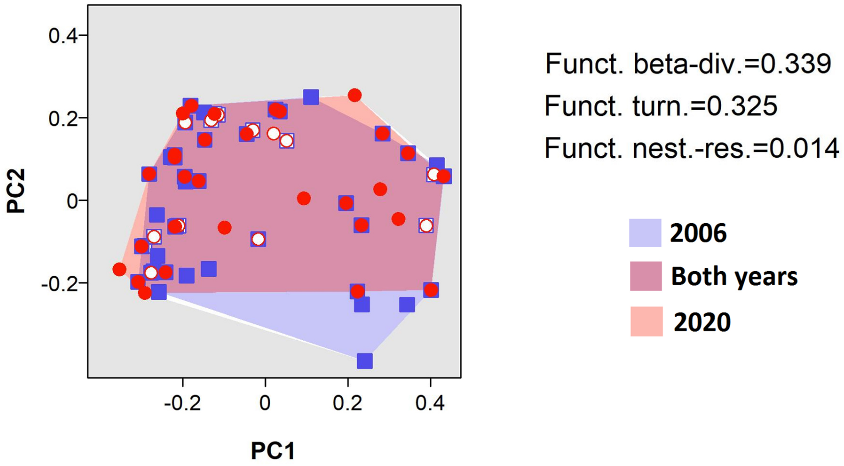

FIGURE 4 | Two-dimensional functional space (PCoA) of the functional β-diversity of the ichthyofauna of the Taquaruçu Reservoir, lower Paranapanema River (the transitional zone between 2006 and 2020).

DISCUSSION

We observed the absence of several native species that were registered in 2006, especially from the Loricariidae and Anostomidae families, and the reduction in the abundance of Curimatidae and Pimelodidae families. On the other hand, 14 species were new records for this current study. However, most of them are non-native to the lower Paranapanema River. Statistical analysis provided indications that there was a significant taxonomic discrepancy between the time-periods. In this sense, the CWMs of traits demonstrated that six out of ten traits considered here had changed over time, a fact corroborated by the decrease in all functional indexes between the time-periods. Finally, the β-functional diversity showed that the new species were functionally redundant.

Changes in the functional composition of the fish community might be related to rearrangements in the ichthyofauna between the time-periods of 2006 and 2020, which have acted predominantly in the loss of richness in Loricariidae and Anostomidae, and it has also decreased the abundance in Curimatidae and Pimelodidae. Most of the species pertaining to the Anostomidae and Pimelodidae in the upper Paraná River display medium to large body size (Graça, Pavanelli, 2007; Ota *et al*., 2018), and migratory behavior (Agostinho *et al*., 2003). As shown in previous studies (*e.g*., Agostinho *et al*., 2007; Hoeinghaus *et al*., 2009), large migratory fish in the upper Paraná River have been harmed, after the damming, by the blocking of movements and the disconnection of critical habitats to life cycles. Besides, the dam's water level control neutralizes seasonal floods, which restrains the connection with the marginal lagoons utilized by early life stages to hide, develop, feed, and grow, thus leading to population depletion (Agostinho *et al*., 2004; Arantes *et al*., 2019). In this sense, several studies have pointed out a graduate occupation of the reservoirs by opportunistic species of smaller body size (Alvim, Peret, 2004; Lima *et al*., 2016; Arantes *et al*., 2019).

Changes in body size and position in the water column due to anthropogenic impacts have been registered in marine ecosystems (*e.g*., continental shelves of the Atlantic Ocean), where smaller and pelagic fish with short life cycles are favored due to reply faster to environmental changes (McLean *et al*., 2019). In the Paraná River, damming has caused changes in the composition of ichthyofauna, varying from pelagic to benthopelagic habitat usage (Oliveira *et al*., 2018), whereas we have found a different pattern (from demersal to pelagic usage of habitat). One could find an explanation for this change in the fish feeding habits, based on the fact that much of Anostomidae species feed on plant material and Pimelodidae species show predator/omnivore feeding, both favored by their sub-terminal mouths (Graça, Pavanelli, 2007), and demersal behavior in the bottom (Vidotto-Magnoni, 2009). Since the previous study was performed few years after the dam has closed (Britto, Carvalho, 2006), species belonging to Anostomidae may have been favored by the trophic upsurge period in the early years of the reservoir, where the increase in transparency and carriage of organic matter from terrestrial floods facilitated primary production (Agostinho *et al*., 1999). However, these individuals were probably overcome by smaller and pelagic fish (except in the case of the large pelagic invasive *P. squamosissimus*) due to changes in the availability of food as the reservoir aged (Cunha-Santino *et al*., 2013; Arantes *et al*., 2019), as well as specialized feeding habits that precluded the use of different resources (Luz-Agostinho *et al*., 2006). On the other hand, for the Pimelodidae individuals, this may have occurred mildly due to their wide feeding capacity (Vidotto-Magnoni, 2009).

Back to the study done by Britto, Carvalho (2006), the short-distance migratory behavior of fish was dominantly represented by Anostomidae and Pimelodidae. Species of both groups can carry out short-distance migration that might allow them to accomplish their life cycles in reservoirs (Agostinho *et al*., 2003; Orsi, 2010). However, the short-distance migrator species have been replaced by non-migrators ones, which may be related to the damming (Agostinho *et al*., 2004; Cunha-Santino *et al*., 2013). This scenario was also seen in the Colorado River, North America, where the decline by damming of native migrant species provided unoccupied niches to sedentary non-native species occupation (besides other environmental factors) (Olden *et al*., 2006; Pool *et al*., 2010). Our results partially corroborate with this trend since we could demonstrate an increase in native and non-native sedentary species belonging to the families: Characidae (*e.g*., native tetra *Moenkhausia intermedia* Eigenmann, 1908; and the non-native saicanga *Roeboides descalvadensis* Fowler, 1932), Parodontidae [*e.g*., native jackknife *Apareiodon affinis* (Steindachner, 1879)], and Cichlidae (*e.g*., native jacundá *Crenicichla* sp.; and the non-native peacock bass *Cichla* cf. *kelberi* Kullander & Ferreira, 2006).

The reduction of the oocyte diameter and the increased fecundity are believed to be guided by environmental forces selecting periodic life-history species (Winemiller, 1995). Therefore, our results denoted a decline of migratory species of this kind. In this way, changes in trait composition might be associated with the loss of Loricariidae species. A previous study in the Paraná River (Suzuki *et al*., 2000) have shown that species of Loricariidae have large oocytes (> 4.0 mm), while in the Paranapanema River, it was found that they had the largest oocyte diameters among the entire ichthyofauna (> 3.0 mm) (Orsi, 2010). For both studies, this group presented lower fecundity and possibly, an equilibrium trait concerning Life-History (Winemiller, 1995). However, in our study, we did not find changes in the composition of life-history traits. In this sense, it should be noted that there are intermediate characteristics between periodic and equilibrium extremes of life-history, where the opportunistic species fit, which produce oocytes varying in size (*e.g*., medium to small oocytes) and medium to large offsprings (Winemiller, 1995). Therefore, we could explain the changes in trait composition here without having changes in life-history because the decrease in oocyte diameter and lower fecundity (Loricariidae), together with the increase in little oocytes and larger offsprings (probably influenced by the non-native opportunistic species) were captured in abundance weighted means (CWMs) (McLean *et al*., 2019).

During the early years of the damming, piscivores species are favored by the increase of preys (Lima *et al*., 2016), whereas the rise of the detritivores species occurs later due to high sedimentation during the process of the reservoir aging (Cunha-Santino *et al*., 2013). However, we have observed an opposite pattern. In the reservoirs of the Iguaçu (Delariva *et al*., 2013), and Tietê rivers (Smith *et al*., 2018), detritivores species became more abundant when food resources were largely available. Hence, the higher representation of detritivores of Loricariidae and Curimatidae [*e.g*., the saguiru *Steindachnerina insculpta* (Fernández-Yépez, 1948)] in the study carried out by Britto, Carvalho (2006) may be associated again with the early stage of the reservoir, which contributed to the concentration of organic matter in the bottom (Agostinho *et al*., 2007). Thus, as found here to Anostomidae, the decreasing of richness in Loricariidae and abundance in Curimatidae, most likely, occurred due to the trophic dynamics in the reservoir (Cunha-Santino *et al*., 2013), and fish inefficiency in exploring other food resources since detritivores are also specialists (Luz-Agostinho *et al*., 2006; Smith *et al*., 2018). Nevertheless, the detritivores may have also been harmed over time by the low carriage of organic material in the reservoir sediment due to the deforestation in the surrounding areas (Vidotto-Magnoni *et al*., 2015), or the dam's water level control (Alvim, Peret, 2004). Besides, benthonic detritivore species (Loricariidae) may have been suffered from low concentrations of oxygen in the bottom of the reservoir (Arantes *et al*., 2019), while the detritivores species, in general, may have been experienced the effects of the run-of-river regime over time, which might have had minor sedimentation due to short-time water retention and small flooded perimeter (Nogueira *et al*., 2012). Likewise, the increase of piscivores species was most likely modulated by the progressive niche occupation left by rheophilic predators (*e.g*., Pimelodidae) (Olden *et al*., 2006; Pool *et al*., 2010). Thus, sedentary species such as *Cichla* cf. *kelberi*, which were introduced by human-mediated activity (*e.g*., sporting angling) (Langeani *et al*., 2007; Jarduli *et al*., 2020), probably increased their occupancy.

The functional turnover showed that changes in trait composition were mostly driven by non-native species, a pattern that has been observed in distinct reservoirs of the upper Paraná River (*e.g*., Orsi, Britton, 2014; Loures, Pompeu, 2019; Daga *et al*., 2020), and others Brazilian watersheds (Arantes *et al*., 2019; Magalhães *et al*., 2020; Ganassin *et al*., 2021). Previously, a global freshwater review found that, in general, non-native species increase the functional richness of fish communities, in some cases beyond 100% (Toussaint *et al*., 2018). However, the functional turnover did not increase or re-establish ecological functions since there was a decrease in all functional indexes analyzed. Consequently, taxonomic turnover was mediated by trait-environment relationships, where species presented functional redundancy (Villéger *et al*., 2010; Pimiento *et al*., 2020). The FRic and FEve indexes decreased over time, meaning that the functional space has been reduced (Villéger *et al*., 2008; Mouchet *et al*., 2010), and the uniformity of traits was modified (Mouillot *et al*., 2013). This finding was supported by the decrease in FDiv index over time, which have indicated that dominant species became functionally closer while the extremes decreased (Mouillot *et al*., 2013), meaning that species having extreme traits (*e.g*., largest oocyte diameters) in the functional space became less represented. Hence, the FDis index decrease over time demonstrated that species had been found closer to the center of functional space, where similar characteristics should remain (Villéger *et al*., 2008). This functional scenario might be justified by the type of environment studied since large watersheds that historically had richer fauna with many ecological functions should become less susceptible to gain traits when non-natives species become established (Toussaint *et al*., 2018).

The decrease in the FRic index, even with the introduction of non-native species, was verified in previous studies such as in the estuarine fish community in Mexico (Villéger *et al*., 2010) and in the Paraná River (Oliveira *et al*., 2018), once the species were functionally redundant. Additionally, a decline of specialized species was observed, that is, species with extreme traits such as herbivory (Villéger *et al*., 2010), and migratory behavior (Oliveira *et al*., 2018) have diminished. Thus, the taxonomic and trait composition of fishes under environmental impacts might substantially change across time, yet the fish communities seem to converge to the same characteristics, showing a functional simplification effect that should drive biotic homogenization

(McLean *et al*., 2019; Magalhães *et al*., 2020). Thus, our results here might enhance and show that the loss of a significant portion of the taxonomic and functional composition in the Taquaruçu Reservoir should probably drive the fish community towards biotic homogenization, an environmental panorama that is most likely subjected to the damming (Loures, Pompeu, 2019; Daga *et al*., 2020; Ganassin *et al*., 2021), and biological invasions (Magalhães *et al*., 2020).

The implications of the environmental scenario found here is quite worrying since fish participate in the nutrient cycle, are considered ecosystem engineers, and control food chains (Villeger *et al*., 2017; Arantes *et al*., 2019). Particularly, the Anostomidae, Curimatidae, and Loricariidae families play an important role in food chains since they promote the flow of nutrients and matter from lower to upper food chain levels (Alvim, Peret, 2004; Luz-Agostinho *et al*., 2006). Thus, herbivores and detritivores species are responsible for mediating most of the flow of matter and energy in large watersheds from South America (Bowen, 1984; Arantes *et al*., 2019). On the other hand, predators as Pimelodidae species have a relevant position in food chains by promoting the moderation of food chain levels below (Agostinho *et al*., 2007). In addition, fish are known to perform several ecosystem services (Villeger *et al*., 2017; Arantes *et al*., 2019), as the importance of families such as Anostomidae, Curimatidae, and Pimelodidae in fisheries resources (Hoeinghaus *et al*., 2009), and Loricariidae in fishkeeping (Graça, Pavanelli, 2007).

In conclusion, we identified a substantial loss or decreased over time in fish species (*i.e*., 2006 to 2020), that have reduced their functional space in the Taquaruçu Reservoir. This scenario might compromise the ecological relationships and ecosystem services in this reservoir. Our results emphasized that reservoirs play an important "filtering" role in structuring fish communities, which should result in a selection of suitable traits driving assemblages to a simplification of characteristics (*i.e*., traits) and, most likely, to biotic homogenization influenced by non-native species. Here, our results reinforced the impacts of damming in fish communities, especially on migratory and specialist species. Hence, we showed that after thirty years have passed the damming, we could find relevant changes in the fish communities, demonstrating that there is a pressing need for continuous monitoring of the reservoirs. We encourage the practice of this approach for successful biological and ecological assessments and management of Brazilian freshwater ecosystems, as well as increasing knowledge on the dynamics in reservoirs, recognizing thus local and regional environmental issues.

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ETHICAL STATEMENT

Fish were anesthetized and euthanized by overexposure to 1g/ml clove oil, fixed with 10% formalin, and further transferred to 70% alcohol. The Animal Ethics Committee authorized the field sampling (CEUA N° 24310.2017.78; collection license Nº 16578).

COMPETING INTERESTS

The authors declare no competing interests.

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