



Fish defaunation in reservoirs of the Lower Paranapanema River basin, Brazil

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Abstract: Until now no study has used a defaunation index to quantify the decline of Neotropical freshwater fishes in environments fragmented by dams and reservoirs. So, we applied this index to 143 native fish in five reservoirs in the Lower Paranapanema River, that is situated in one of the Brazilian aquatic environments most impacted by anthropic degradation. Fish species were classified according to their functional groups, which were selected according to the biological characteristics that may reflect in defaunation events. The biggest reservoir in area with more tributaries and forest cover showed lowest defaunation index. The functional groups of fishes more affected by defaunation included species characterized by periphytivores, invertivores and algivores, non-migratory habit, with external fertilization, and parental care. Although reservoirs have different characteristics, this method can be tested in any other hydrographic basin. The results suggested continued conservation efforts to preserve the integrity of tributaries and the native fishes in reservoirs and pointed out the importance of maintaining native vegetation cover and fish restocking programs in the reservoirs with the highest defaunation values. Our finding can be use as the first data source for future studies using this defaunation index.

Keywords: *anthropogenic impact; functional group; fish fauna loss; impoundment; land use.*

Defaunação de peixes em reservatórios do baixo rio Paranapanema, Brasil

Resumo: Até o momento nenhum estudo utilizou um índice de defaunação para quantificar o declínio de peixes neotropicais de água doce em ambientes fragmentados por barragens e reservatórios. Dessa forma, testamos esse índice em 143 espécies nativas em cinco reservatórios do baixo rio Paranapanema, que está localizado em um dos ambientes aquáticos brasileiros mais impactados pela degradação antrópica. As espécies de peixes foram classificadas de acordo com seus grupos funcionais selecionados de acordo com as características biológicas que podem influenciar nos eventos de defaunação. O maior reservatório em área, com mais tributários e maior cobertura florestal apresentou menor índice de defaunação. Os grupos funcionais mais afetados pela defaunação incluíram espécies caracterizadas por hábito alimentar perifítico, invertívoro e algívoro, hábito não migratório, com fertilização externa e cuidado parental. Embora os reservatórios tenham características diferentes, esse método pode ser testado em qualquer outra bacia hidrográfica. Os resultados sugerem esforços contínuos para preservar a integridade dos tributários e dos peixes nativos nos reservatórios e apontam a importância de manter a cobertura vegetal nativa e programas de estocagem nos reservatórios com maiores valores de defaunação. Nossos dados podem ser utilizados como a primeira base de dados para futuros estudos que utilizem o índice de defaunação.

Palavras-chave: *impacto antropogênico; grupo funcional; perda de ictiofauna; represamento; uso da terra.*

Introduction

The conversion of natural landscapes by fragmentation, habitat loss, direct exploitation, the wide spread of invasive species, hunting and water pollution are the principal anthropogenic drivers of defaunation (Young et al. 2016, Galetti et al. 2021). The main predictors of defaunation at the local scale include quantity of landscape-scale native vegetation cover and rate of habitat conversion (e.g., into agricultural and urban areas). The diversity and composition of the fish assemblages may be changed by interference with hydrography, limnology and land use (Fausch et al. 1990, Orsi & Britton 2014, Ganassin et al. 2021), and these changes are intensified in succession of cascading reservoirs (Agostinho et al. 2007a). The replacement of native vegetation with agriculture increases sediment input (Ryan & Emmett 2002, Wantzen & Mol 2013) and nutrients, which interferes with fish fauna reproduction, feeding, and recruitment (Roy et al. 2003). Among the main services offered by fish is the interaction in the dynamics of the food chain and the cycling of nutrients, which enable the resilience of the ecosystem (Holmlund & Hammer 1999) and trophic effects (Bauer & Hoye 2014), also affected in the defaunation process. The simplification of habitats promoted by reservoirs removes or changes native species environments, creates others favorable to non-native species and to native sedentary species with low economic value and no fishing relevance (Agostinho et al. 2007a), reduces fish access to nursery and feeding grounds (Winemiller et al. 2016) and affecting the composition of the native fish fauna, which is directly related to the conservation of environments free of dams and reservoirs (Marques et al. 2018). Reservoirs also act as an environmental filter for specific functional traits, such as those related to reproduction, feeding and habitat use (Muniz et al. 2021).

The combined result of human actions leads to the impoverishment of the local source of vertebrate fauna, i.e., defaunation (Terborgh 2008). The defaunation index is meant to estimate the loss of species and populations or functional extinction of ecological communities and the decline in the abundance of individuals on a global or local scale (Dirzo & Miranda 1990, Dirzo et al. 2014). This index has been extensively used for mammals such as to compare ecological communities over large zoogeographical regions (Giacomini & Galetti 2013), examine the integrity of site-specific faunas and demonstrate how defaunation is changing the historical configuration of assemblages (Bogoni et al. 2018) and the influence of land use on defaunation (Pereira et al. 2021).

Beside extensive studies have assessed the threat of degraded environments and their impacts on species populations of Neotropical freshwater fish fauna (Meffe & Sheldon 1990, Casatti et al. 2009, Casatti et al. 2012, Cohen et al. 2016, Kopf et al. 2016) a quantitative value such as an index has not been used to estimate the decline, even though it is known that populations of freshwater species are more affected than terrestrial ecosystems (McLellan et al. 2014, Turak et al. 2017, Albert et al. 2021). We aimed to evaluate the fish fauna loss in the habitats fragmented by cascading reservoirs, what allows to compare isolated environments resulting from the blockage of fish movements (Agostinho et al. 2007a, Pelicice et al. 2018), thereby assigning a defaunation value for each reservoir. For this study, we chose the Lower Paranapanema River basin as the model. We also investigated comprehending patterns of defaunation for different functional groups of fishes enables us to understand the extent to which an ecosystem is modified (i.e., dams

and land use change), and how its components are threatened is also critical to determine conservation strategies.

Material and Methods

1. Study area

The Paranapanema River is an important, extensively exploited tributary of the Upper Paraná River basin (Maack 2017, Jarduli et al. 2020), which is characterized by high human occupation and intense anthropogenic activities, making this basin the most exploited and fragmented in the Southeast and South regions of Brazil (Agostinho et al. 2007b, Agostinho et al. 2016, ANA 2016). The Paranapanema River basin has an area of 106.500 km² and covers 247 municipalities, with around 2.3% of the Brazilian population concentrated in this river basin (five million inhabitants) (ANA 2016). There are currently 11 hydroelectric plants (HEPs) in operation on the main river channel. The Paranapanema River basin is divided into three regions: Upper Paranapanema, Middle Paranapanema and Lower Paranapanema River basins, and they are quite different from each other because they have distinct geomorphological characteristics (Sampaio 1944).

In the Lower Paranapanema River basin, anthropic actions have extensively modified the habitat in this basin as well. The construction of cascade reservoirs changed the hydrographic and limnological characteristics of the basin (Nogueira et al. 2006, Poff et al. 2007, Pelicice et al. 2014), and urban and agricultural/livestock expansion changed land use by the removal of native vegetation (ANA 2016), altering natural habitats (Young et al. 2016). For this study, the sections disconnected by hydroelectric plants were delimited in the drainage area of the five HEPs installed in the Lower Paranapanema River (Figure 1): HEP Rosana (year of completion: 1987), HEP Escola Politécnica - Taquaruçu (1994), HEP Escola Engenharia Mackenzie - Capivara (1977), HEP Canoas I (1999) and HEP Canoas II (1999) (CTG Brasil 2020), the main characteristics of each reservoir area described in Table 1.

2. Data collection and functional groups

A list of native fish fauna in the Lower Paranapanema River basin was confirmed by an extensive search of the available scientific literature. Searches were done in online databases, like Google Scholar, Scielo, Web of Science, Scopus and Eschmeyer's Catalog of Fishes, private libraries and cross-references searches using the keyword 'Paranapanema', combined with the keywords 'fish', 'survey', 'ichthyofauna', 'fish fauna', and 'diversity', and included species descriptions, inventories and ecological studies between 1995 to 2018, presented in the supplementary material (Table S1). The species surveyed in this study were assumed to exist in the Lower Paranapanema River basin, and the list of the presence/absence of species present in each reservoir is presented in the supplementary material, Table S2.

Functional groups were selected according to the biological characteristics of the fish that may reflect defaunation events, and for which information was available in the literature (Table S3), FishBase data (www.fishbase.org) and from specialists. For some species, there is a lack of basic information on their biology and ecology, which supports the choice of these functional groups. The species were categorized according to trophic guild (algivores, periphytivores, insectivores, invertivores, detritivores, herbivores, omnivores or piscivores),

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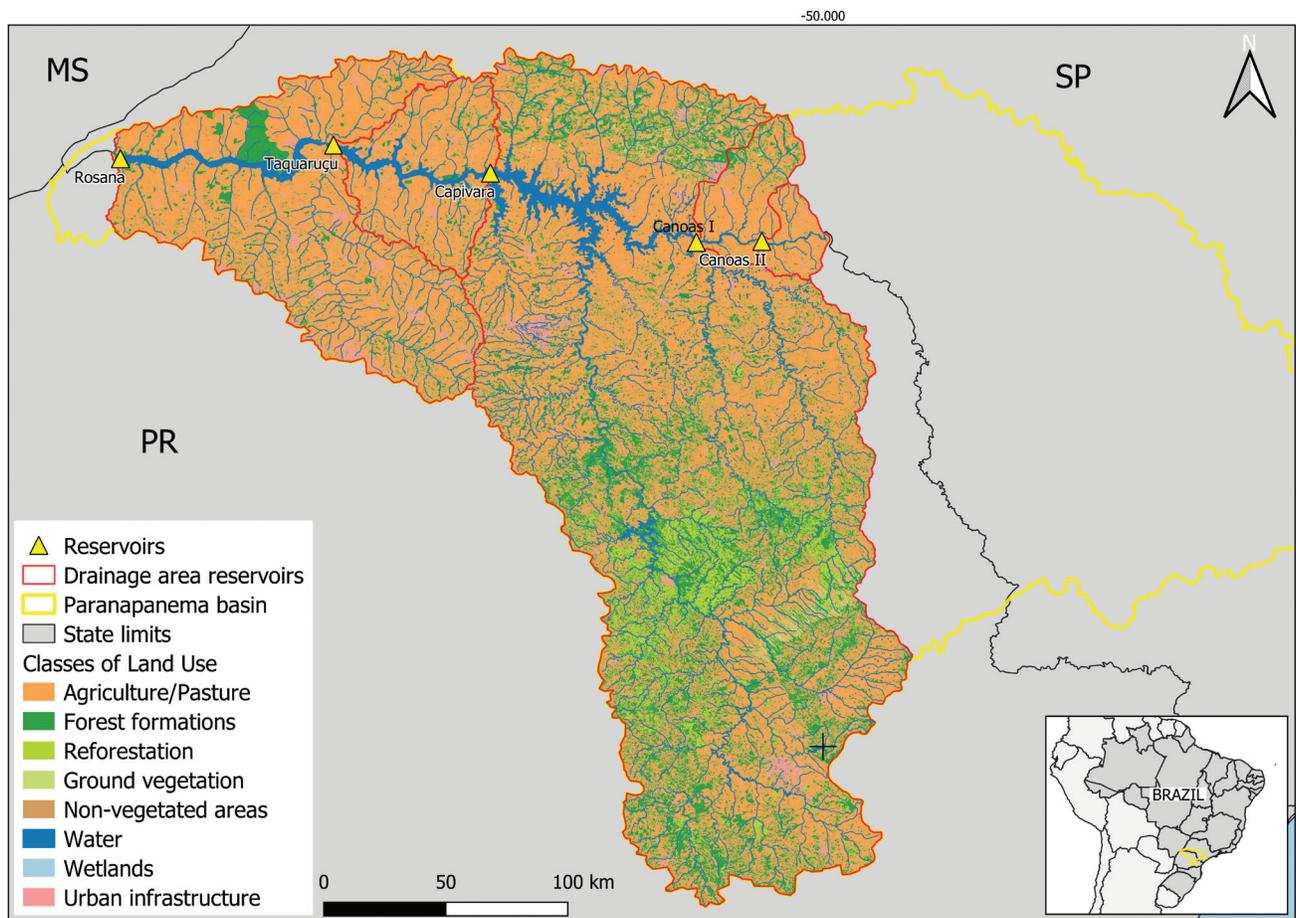


Figure 1. Land use in the Lower Paranapanema River basin, southern Brazil, SP – state of São Paulo, PR – state of Paraná, MS – state of Mato Grosso do Sul.

Table 1. Main features of reservoir of Rosana, Taquaruçu, Capivara, Canoas I and Canoas II reservoirs in the Lower Paranapanema River basin, states of São Paulo and Paraná, southern Brazil.

Hydroelectric plant	Perimeter (km)	Drainage area (km ²)	Main tributaries	Type
Rosana	433	99,000	Pirapó and Pirapozinho	Run-of-the-river
Taquaruçu	301	88,000	Anhumas, Centenário, Tenente, Capim and Santo Inácio	Run-of-the-river
Capivara	1550	84,500	Tibagi, Capivara, Cinzas and Vermelho	Accumulation
Canoas I	120,3	40,920	Pari and Queixada	Run-of-the-river
Canoas II	98,8	39,556	Alambari	Run-of-the-river

Adapted: Duke Energy (2008); CTG Brasil (2020).

migratory behavior (migratory or non-migratory), fertilization (external or internal) and parental care or not (Table S3).

3. Hydrographic variables and land use

The hydrographic basins were delimited in the drainage area of the Rosana, Taquaruçu, Capivara, Canoas I, and Canoas II reservoirs. Four Shuttle Radar Topographic Mission (SRTM) images were used, which are radar images with spatial resolution of 90 m × 90 m from EMBRAPA (Brazilian Agricultural Research Corporation) (Miranda 2005) to obtain altimetric data. The images were imported to the QGIS 3.4 software and the delimitation was performed automatically

using the TauDEM extension. For the drainage network, secondary data were used in shapefile format provided by ANA (Water and Sanitation National Agency).

For the determination of land use in the study area, we used images from the OLI/Landsat-8 sensor acquired on the United States Geological Survey (USGS) website and processed in the ESRI ArcGIS 10.5 software (ArcGIS trial license). The method used was traditional pixel-based classification. The classes of classification were interpreted and associated with land use and land cover classes: agriculture/pasture, forest cover, reforestation, ground vegetation, non-vegetated areas, water, wetlands and urban infrastructure (Figure 1 and Table S4).

4. Defaunation index and variables

The method we used was previously applied to mammalian defaunation (Bogoni et al. 2018, Benítez-López et al. 2019, Wen et al. 2020), but modifications were made for the freshwater environment scenario. The defaunation index (or D_i) (Giacomini & Galetti 2013) was estimated for the entire fish assemblage (i.e., total defaunation per site) and each functional guild/group using the matrix of presence and absence compiled (Table S2). The defaunation index is a weighted measure of dissimilarity between a focal assemblage and a reference assemblage (for example, historical baseline). Our reference assemblage was all the species mentioned in Table S2 and the focal assemblage was the species present in each reservoir, based on the method Giacomini & Galetti (2013) described.

This index ranges from 0 (completely intact) to 1 (completely defaunated), being based on the Bray-Curtis dissimilarity index with a value of importance for the species. In the analysis, we examined levels of defaunation in terms of the species importance value (ω), defined as an intrinsic feature, the body size, and the data for each of the 143 species were from FishBase (Froese & Pauly 2021) (Table S5). In representing ω , we assigned adult body sizes (Vazzoler 1996) elevated to the power of $3/4$ to account for the metabolic allometry of different species as a function of body size (Brown et al. 2004; Giacomini & Galetti 2013).

Body size is a proxy of vulnerability to extinction and conservation concern (Giacomini & Galetti, 2013), with implications on life history, ecological interactions (Brown et al. 2004) and conservation (Hansen & Galetti 2009). Defaunation is calculated using the following formula: $\sum_{k=1}^S \omega k (N_{k,r} - N_{k,f}) / \sum_{k=1}^S \omega k (N_{k,r} + N_{k,f})$. Where r is the reference fish assemblage, f is the focal assemblage, S is the total number of species,

ωk is the importance of species k in terms of its functional influence on defaunation, and N is the occurrence (presence = 1, absence = 0) of species k in the reference and focal assemblage.

5. Statistical analysis

The beta diversity is the change in species composition along a spatial or environmental gradient (Magurran 2011). This analysis was used to understand the structure of the fish communities in the reservoirs, which species are replaced or more easily lost than others, and if environments with a higher defaunation index share these species with reservoirs with a lower defaunation index. We used the analysis of beta diversity components as implemented in the “Betapart package” v.1.5.4 – “R-project” (Baselga et al. 2021). The total dissimilarity for all reservoirs, the turnover (Simpson’s index, β_{sim}), and nestedness (the difference between the Sorensen and Simpson indices, β_{sne}) components were determined by the package computations. The input data table consists of the presence and absence of fish species for each reservoir (Table S2). Cluster and dissimilarity matrices of turnover and nestedness were also performed using the “Betapart package”.

Results

Considering all fish faunas from the Lower Paranapanema River basin, the average defaunation value found was $D_i = 0.24$. Canoas I ($D_i = 0.50$) and Canoas II ($D_i = 0.47$) reservoirs had the highest defaunation values. On the other hand, Capivara Reservoir had the lowest defaunation index $D_i = 0.02$, while Rosana Reservoir had $D_i = 0.24$ and Taquaruçu $D_i = 0.30$ (Figure 2).

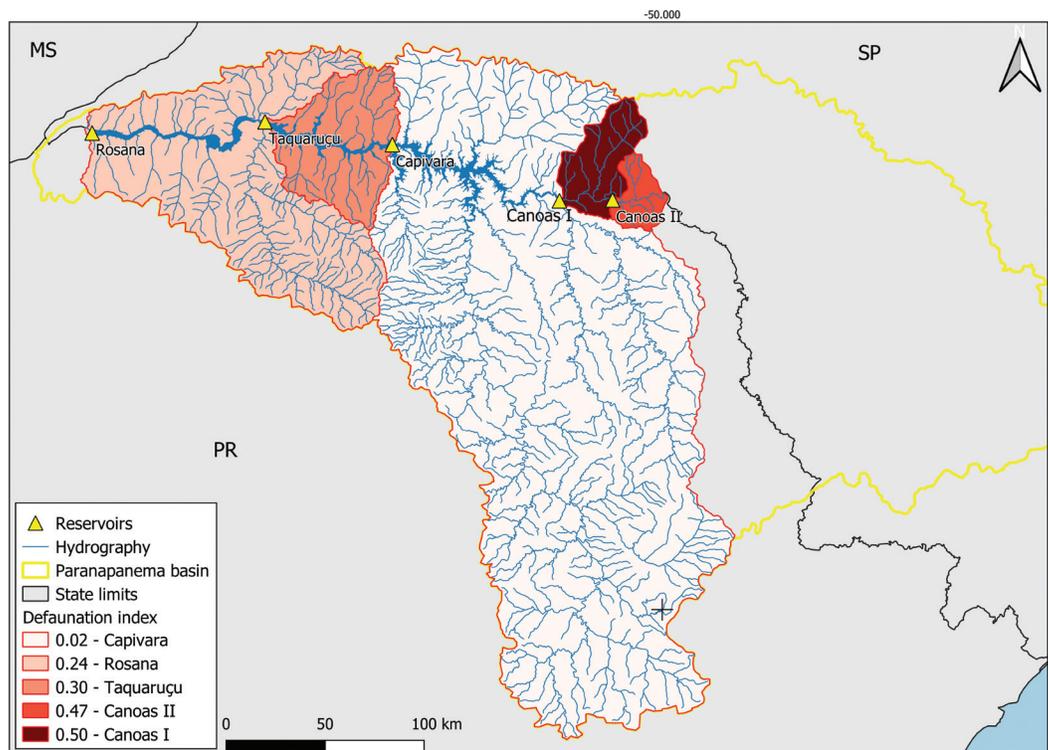


Figure 2. Defaunation index of Rosana, Taquaruçu, Capivara, Canoas I and Canoas II reservoirs in the Lower Paranapanema River, states of São Paulo (SP) and Paraná (PR), southern Brazil, MS – state of Mato Grosso do Sul.

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In evaluating feeding habit, the periphytivores were most related to defaunation ($D_i = 0.63$), followed by invertivores ($D_i = 0.48$), while the least affected groups were piscivores ($D_i = 0.19$) and herbivores ($D_i = 0.08$) (Figure 3). For the Rosana Reservoir, the highest defaunation value was found in the algivore functional group ($D_i = 0.44$), and the least affected group was that of herbivores ($D_i = 0.12$) (Figure 3). In the Taquaruçu Reservoir, the highest defaunation values were in the functional groups periphytivores ($D_i = 0.76$) and invertivores ($D_i = 0.55$). In this reservoir, herbivores had the lowest defaunation values ($D_i = 0.05$; Figure 3). Capivara Reservoir had the lowest defaunation values in all the scenarios analyzed (Figure 2; Figure 3). In this reservoir, algivores, periphytivores, herbivores,

omnivores and piscivores showed no defaunation ($D_i = 0.00$), and invertivores had the highest value ($D_i = 0.10$) (Figure 3). Canoas I Reservoir showed maximum defaunation values ($D_i = 1.00$) for the functional groups algivores and periphytivores and lower defaunation values for the herbivore and piscivore groups ($D_i = 0.18$) (Figure 3). In the Canoas II Reservoir, the periphytivores showed the highest defaunation value ($D_i = 1.00$), and the lowest value was found in the herbivores ($D_i = 0.05$) (Figure 3).

In relation to reproductive strategies, those most related to defaunation had a non-migratory habit ($D_i = 0.31$), practiced external fertilization ($D_i = 0.26$) and showed parental care behavior ($D_i = 0.30$) (Figure 3). Capivara Reservoir had the lowest defaunation values in all

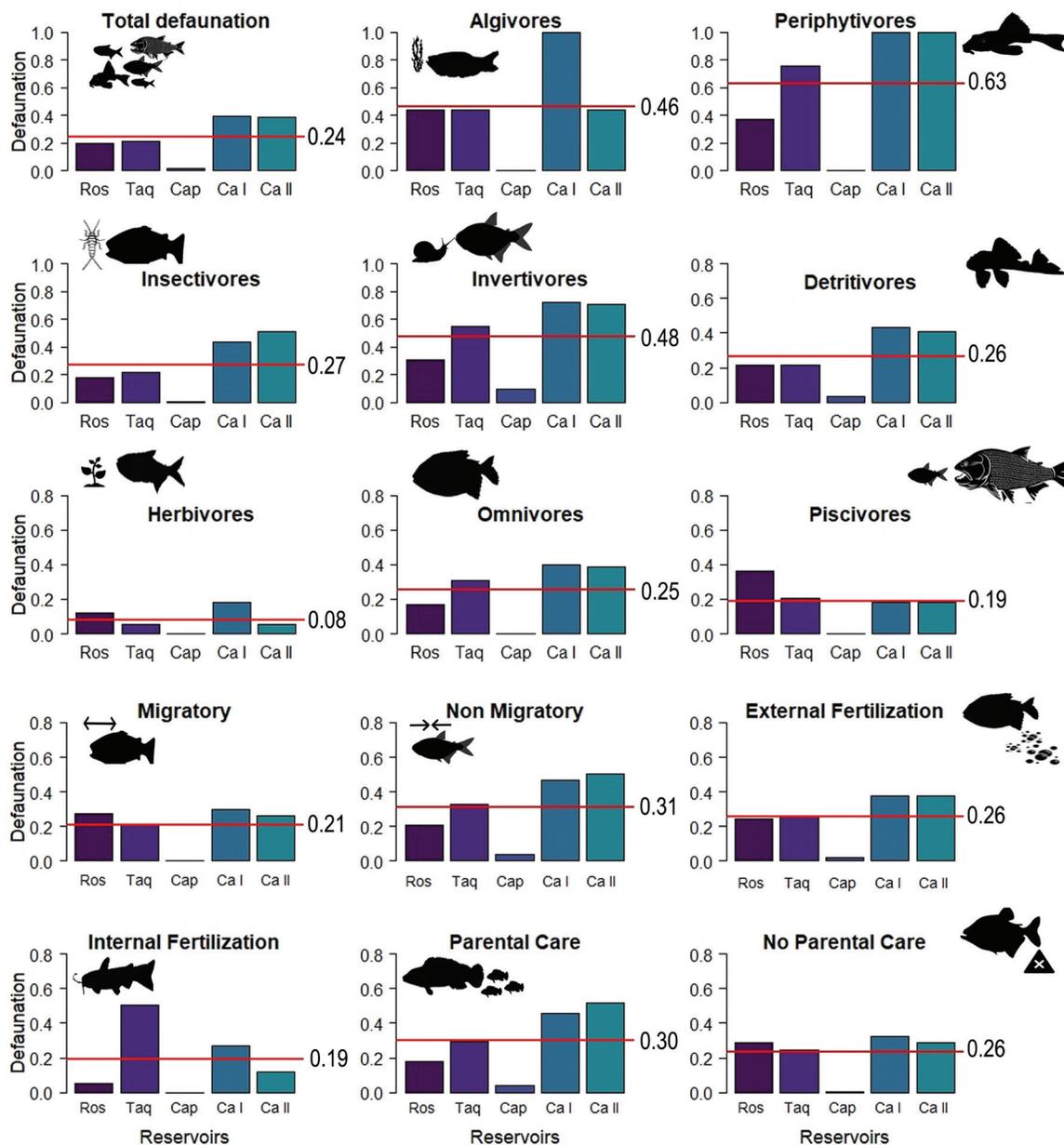


Figure 3. Defaunation index of functional groups; total defaunation, feeding habit (algivores, periphytivores, insectivores, invertivores, detritivores, herbivores, omnivores, piscivores), reproductive strategies (migratory, non-migratory, external fertilization, internal fertilization, parental care, no parental care). Reservoirs: Ros: Rosana; Taq: Taquaruçu; Cap: Capivara; Ca I: Canoas I; Ca II: Canoas II in the Lower Paranapanema River, states of São Paulo and Paraná, southern Brazil. The red line represents the mean values.

functional groups, where migratory and internal fertilization behaviors did not show defaunation ($D_i = 0.00$). The highest defaunation values were found in Taquaruçu Reservoir for internal fertilization ($D_i = 0.51$), Canoas I Reservoir for migratory habit ($D_i = 0.30$), external fertilization ($D_i = 0.38$) and no parental care ($D_i = 0.33$), and Canoas II Reservoir for non-migratory habit ($D_i = 0.50$) and parental care ($D_i = 0.52$).

Capivara Reservoir had the lowest defaunation index, largest reservoir area and more area with forest cover for land use (31.57%) and Canoas II Reservoir had the highest defaunation values,

smaller reservoir area and smallest area occupied by forest (5.73%) (Table S4).

The mean dissimilarity ($\beta s\text{OR}$) between reservoirs was 0.51, with a mean nestedness ($\beta s\text{ne}$) of 0.33 and turnover ($\beta s\text{im}$) of 0.17 (Figure 4). Cluster analysis indicated that the reservoirs had high nesting, where Capivara Reservoir and Canoas I Reservoir showed 48% nestedness with Capivara Reservoir and where Canoas II Reservoir showed 45% nestedness with Capivara Reservoir; high turnover indicated in the cluster analysis was Canoas II Reservoir with Rosana Reservoir, namely 20% (Table 2).

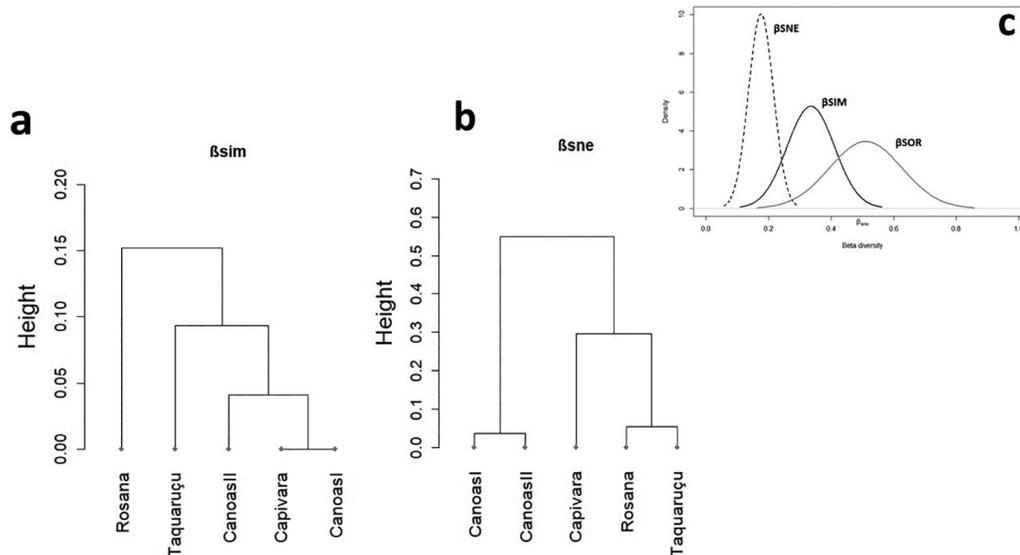


Figure 4. Cluster of turnover ($\beta s\text{im}$) (a) and nestedness ($\beta s\text{ne}$) (b) of fish species in Rosana, Taquaruçu, Capivara, Canoas I and Canoas II reservoirs in the Lower Paranapanema River, states of São Paulo and Paraná, southern Brazil. These clusters result from Beta diversity analysis (Betapart/R-project), and the index was calculated from a matrix of presence and absence of fish species in each reservoir. (c) Graphic representations of total turnover ($\beta s\text{im}$), nestedness ($\beta s\text{ne}$) and total beta diversity ($\beta s\text{OR}$).

Table 2. Pairwise index matrix of turnover ($\beta s\text{im}$) and nestedness ($\beta s\text{ne}$) components of fish species in Rosana, Taquaruçu, Capivara, Canoas I and Canoas II reservoirs in the Lower Paranapanema River, states of São Paulo and Paraná, southern Brazil.

	Reservoirs			
	Rosana	Taquaruçu	Capivara	Canoas I
Turnover ($\beta s\text{im}$)				
Taquaruçu	0.1500000			
Capivara	0.06593407	0.02500000		
Canoas I	0.18367347	0.12244898	0	
Canoas II	0.20754717	0.13207547	0	0.08163265
Nestedness ($\beta s\text{ne}$)				
Taquaruçu	0.05467836			
Capivara	0.20130731	0.26911765		
Canoas I	0.24489796	0.21088435	0.48421053	
Canoas II	0.20911950	0.17619520	0.45360825	0.03601441
Beta diversity ($\beta s\text{OR}$)				
Taquaruçu	0.2046784			
Capivara	0.2672414	0.2941176		
Canoas I	0.4285714	0.3333333	0.4842105	
Canoas II	0.4166667	0.3082707	0.4536082	0.1176471

Discussion

This is the first study to calculate the defaunation index for Neotropical freshwater fish assemblages based on information of occurrence in reference and focal assemblage, total number of species and the importance of species; and how functional groups are affected by defaunation.

Canoas I and Canoas II reservoirs, the two smallest reservoirs in the drainage area of the lower region of the Paranapanema River and the ones with the absence of representative tributaries (Pelicice & Agostinho 2008, Orsi et al. 2016), were the most affected by the defaunation. Before establishing the Canoas system in 1998, the free lotic stretch between Capivara Reservoir and the Salto Grande Dam comprised the richest in this region (Britto et al. 1997). According to our beta-diversity results, the communities of Canoas I and Canoas II reservoirs are nested in the least defaunated reservoirs (Capivara), where all species present in the most defaunated reservoirs also occurred in the least defaunated. Therefore, the species occurring in the smallest reservoirs were more easily lost than others, which was intensified in a reservoir cascades.

Capivara Reservoir showed lower defaunation indices, it is the largest reservoir with more number of tributaries in the Lower Paranapanema River basin and it is the most preserved. This result corroborates the fact that the largest and most representative tributary of the Paranapanema River, the Tibagi River, shelters much of the fish fauna of the Paranapanema River basin (Hoffmann et al. 2005, Jarduli et al. 2020). Therefore, the conservation of environments free of dams and reservoirs is directly related to fish diversity conservation. Marques et al. (2018) recorded 79 species in Porto Primavera Reservoir, a large reservoir with a length of 270 km in the Paraná River mainstem. They reported the importance of riverside stretches upstream of the reservoir, and Garcia et al. (2019) recorded 63 species in a stretch of 110 km in the Congonhas River, which has lotic features and directly flows into reservoirs. In the Neotropical region, the fragmentation and the simplification of habitats promoted by reservoirs is the main human interference in natural hydrological regimes (Agostinho et al. 2007a). Small species that depend on small-order lotic environments, such as algivores, periphytivores, insectivores, and invertivores, suffer more decline due to environmental changes (Agostinho et al. 2008), and the quality of lotic environments is associated with the degree of urbanization of its surroundings (Helms et al. 2005).

Environmental changes affect groups that are more sensitive to large-scale changes, such as small ones, and dependent on small-order lotic environments, such as periphytivores and algivores (Agostinho et al. 2008). In our study, these functional groups were most affected by the defaunation in the basin, probably because of the extensive loss of integrity of lotic environments, including that caused by urbanization (Peressin & Cetra 2014). Alga and periphyton colonize substrate-submerged rocks and logs and represents a vital resource dependent on organic matter from riparian vegetation (Angermeier & Karr 1983). These functional groups were represented by six species of small loricariids and one small lebiasinid that inhabit small-order streams, necessary to maintain short food chains of Neotropical rivers (Casatti et al. 2005, Zuanon & Ferreira 2008). Several species present in dammed environments can indirectly use this food resource associated with the macrophytes that colonize reservoir margins (Hahn et al. 2008, Algarte et al. 2017). Insectivores and invertivores were also affected, and invertivores displayed the second highest defaunation index. The

predominance of insectivorous species may have been associated with the great taxonomic and functional diversity of this group and the spatial heterogeneity that favors colonization by invertebrates (Araújo-Lima et al. 1995). Environmental changes, such as marginal vegetation loss, can influence the abundance and richness of invertebrates and reduce this trophic group (Luiz et al. 1998). Although there is extensive colonization by insects and aquatic invertebrates in reservoirs (Jorcín & Nogueira 2008), animals that support the food chain of various small fish species that occur along the banks of reservoirs (Casatti 2002, Gido et al. 2002, Ferrareze et al. 2015), damming can cause spatial-temporal changes in these communities, associated with the discontinuity of the aquatic system (dos Santos et al. 2016). The piscivore group's defaunation values were low but were above the average in two reservoirs (Rosana and Taquaruçu). This group is the top predator species in the food chain and usually occurs as a small number of species. The elimination of one or a few of them will spread throughout the food chain, interfering with the control of organisms of lower trophic levels and consequently affecting the top-down mechanism (Pelicice et al. 2005, Ticiani & Delariva 2020).

The migratory species did not show defaunation in the largest reservoir (Capivara), in agreement with the fact that the largest and most representative tributaries of the Paranapanema River, the Tibagi, Congonhas rivers and others, harbor a large part of the fish fauna in this basin (Jarduli et al. 2020), as they preserve lotic conditions that favor migratory species (Shibatta et al. 2007). Another factor to be considered, which is directly related to the availability of suitable areas, is the good biotopes for reproduction and recruitment, with spawning areas and nursery grounds (Orsi et al. 2016), which do not occur in smaller systems (Agostinho et al. 2004). These environments, which are still favorable for migratory species, may be affected as new dams are built in tributaries, increasing the defaunation of fish. It is important to emphasize that the decrease in populations of migratory species due to the interruption of their routes by dams has been widely recorded throughout the Upper Paraná River basin (Agostinho et al. 2002, Pelicice et al. 2014, Marques et al. 2018), although our results did not detect high levels of defaunation for the migratory functional group. Non-migrators had higher defaunation rates than did migrators, the negative pressure exerted on migratory populations is higher in a succession of cascading reservoirs, and it is in tributaries without dams that they seek favorable environmental conditions for reproduction (Agostinho et al. 2004, Pelicice et al. 2014, Garcia et al. 2019).

Species with external fertilization and parental care were more affected by defaunation, mainly in the small reservoirs (Canoas I and Canoas II). The lack of representative tributaries and the considerable variation in the water level caused by the dam's operation exposes the nests built on the banks and the eggs adhered to some bank substrate, reducing the recruitment success (Agostinho et al. 2004). Internal fecundation seems to be a successful strategy in the first years after the formation of a reservoir, but in older reservoirs species with more elaborate reproductive strategies have greater occupation success, like cichlids with complex mating choice, nest-building and parental care and small-sized opportunistic characids that colonize shallow shores (Agostinho et al. 2016). Among the reservoirs analyzed, Canoas I and Canoas II reservoirs are the newest, which may be related to the fact that species with parental care have not yet established themselves, which occurs in older reservoirs (Agostinho et al. 2007a).

The area with the highest percentage of land use for agriculture/pasture showed the highest defaunation levels (Canoas II), while the reservoir with the highest percentage of forest cover (Capivara) had the lowest defaunation index. Therefore, environments with less anthropic disturbance uphold the integrity of the fish fauna, either by preserving areas of development and initial growth of fish larvae, maintaining the routes of migratory species (Antonio et al. 2007), or making it difficult to establish non-native species (Nordheimer & Jeschke 2018). Pristine forest fragments can be a constant source of species to impact streams for maintaining the local, regional and functional structure of fish assemblages (Zeni et al. 2019). Freshwater fish were also affected by the removal of native vegetation, which promotes the siltation that most affects the assemblages (Rabeni & Smale 1995). Sensitive and specialized species decrease to the detriment of tolerant and opportunistic fishes (Casatti et al. 2012) and there is an increase in non-native and sediment-tolerant species introduced by humans (Sutherland et al. 2002).

It is worth mentioning that our matrices were built on the basis of presence/absence data and not abundance or biomass. The authors of the method, Giacomini & Galetti (2013), proposed primarily quantitative density data, because they are able to detect many levels of depletion in species density, but it can be used with occurrence, depending on practical limitations and data availability. Therefore, perhaps some groups may not appear to be depleted at first, but they may fall into two situations: 1) data of presence and absence come from old surveys; 2) the species is currently present, but the population is small and declining. In this way, we highlight that the index has limitations in terms of a complete understanding of the general overview of fish defaunation in the basin, with the central focus being to portray the current scenario and to determine whether defaunation has occurred in local or chronic events in view of the factors analyzed. Another limiting factor was the lack of basic information about the biology of several species, which prevented some newly described ones from entering the analysis, and the lack of data before establishing the reservoirs. Even though the information obtained through the review analysis there are no replicas and there is no control area (no affected by the events studies), did not allow us to perform a deeper statistical analysis, go thru a hypothesis test and performed an analysis examining the effect of landscape characteristics (i.e., land use, reservoir size and tributary number) and the trends of each predictive variable in explaining the defaunation levels recorded in the reservoirs. Even with these limitations, the index was useful to indicate impoverishment and for the future analysis this study can be use as the first defaunation index data source from Lower Paranapanema River. It also highlights the importance of analyzing other variables contributing to defaunation or the synergistic combination of them, such as invasive species, water pollution, physical modification, direct exploitation, climate change (Young et al. 2016), conservation status, economic or social value and number of tributaries, and their support capacity before establishment of the hydroelectric plants, since these areas can be used to mitigate the impact on the fish fauna and support the recruitment development of species.

Mitigation measures must be adapted to the characteristics of the reservoirs, in the reservoirs with the highest defaunation values, we suggest maintaining native vegetation cover in land

use and fish restocking programs. In reservoirs with satisfactory environmental conditions, we suggest further conservation efforts to maintain integrity in tributaries and the native fishes. Regarding species permanence, non-migratory and migratory species persist in the reservoirs as long as they have sufficient tributaries to be used as migratory routes. In reservoirs without or with few habitats for reproduction and early stages of development, populations tend to decrease or disappear if measures are not taken for their recovery. It is noteworthy that these measures must have technical-scientific monitoring to obtain valid results. Although the reservoirs analyzed have different characteristics, this method can be tested in any other hydrographic basin in South America. The context and scenario in which the Paranapanema River basin is located are not exclusive to the Upper Paraná River or other Brazilian river basins.

Supplementary Material

The following online material is available for this article:

Table S1. Studies between 1995 to 2018 that investigated fish diversity in the Rosana, Taquaruçu, Capivara, Canoas I and Canoas II reservoirs in the Lower Paranapanema River basin, states of São Paulo and Paraná, southern Brazil.

Table S2. Native fish fauna present in the Rosana, Taquaruçu, Capivara, Canoas I and Canoas II reservoirs in the Lower Paranapanema River, states of São Paulo and Paraná, southern Brazil. Taxonomic classification followed Fricke, Eschmeyer and Fong 2022.

Table S3. References consulted for classification of functional groups: feeding habit, reproductive strategies, fertilization and parental care, of the species from the Lower Paranapanema River, states of São Paulo and Paraná, southern Brazil.

Table S4. Percentage of land use in watersheds that flow into the Rosana, Taquaruçu, Capivara, Canoas I and Canoas II reservoirs in the Lower Paranapanema River, states of São Paulo and Paraná, southern Brazil.

Table S5. References consulted for maximum length of species from the Lower Paranapanema River, states of São Paulo and Paraná, southern Brazil.

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Ana Carolina Vizintim Fernandes Barros: conceived the ideas; designed the methodology and prepared figures and tables; wrote the paper, prepared the manuscript for submission.

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Diego Azevedo Zoccal Garcia: conceived the ideas, wrote the paper; reviewed and revised drafts of the paper.

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Mário Luís Orsi: reviewed and revised drafts of the paper; gave final approval and secured the funding to support the work.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

We declare that the procedures used in this study have no conflict with the Brazilian Laws regarding the use of vertebrates in scientific research.

Data Availability

Our data was compiled from published literature. <https://doi.org/10.48331/scielodata.2BM7QW>

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