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Spatial distribution patterns of fish assemblages in Neotropical reservoirs

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Tese apresentada ao Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais do Departamento de Biologia, Centro de Ciências Biológicas da Universidade Estadual de Maringá, como requisito parcial para obtenção do título de Doutora em Ecologia e Limnologia.
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Isaac Newton

Padrões de distribuição espacial das assembleias de peixes em reservatórios neotropicais

RESUMO

Dada a grande diversidade de espécies de peixes contidas na região Neotropical, bem como a importância desses organismos como elo nas cadeias tróficas aquáticas, se faz necessário conhecer os distintos processos que governam a organização espacial de suas comunidades. Sabe-se que a estrutura das assembleias de peixes varia acentuadamente em relação ao espaço a depender de fatores abióticos, interações bióticas e processos de dispersão. Entretanto, esses fatores determinantes na estruturação das comunidades de peixes variam indiscriminadamente em corpos aquáticos barrados. O curso de grandes rios tem sido alterado devido à construção de reservatórios e o número de empreendimentos em construção ou inventariados vem aumentando significativamente nas últimas décadas. Portanto, avaliar como ocorre a organização espacial das assembleias de peixes nesses ambientes (i.e., barrados), bem como desvendar os preditores associados a essa organização é de extrema importância para fins conservacionistas e implementações de medidas de manejo. Para investigar tais aspectos, na primeira abordagem foram estudadas três cascatas de reservatórios pertencentes a diferentes bacias hidrográficas, para avaliar os efeitos da disposição em série dos reservatórios nos padrões de diversidade, distribuição e riqueza das assembleias de peixes. Na segunda abordagem, foram avaliados 29 reservatórios situados no estado do Paraná com o objetivo de identificar relações entre a organização das guildas tróficas de peixes com preditores ambientais, espaciais e morfológicos. Os resultados encontrados pelas duas abordagens sugerem que, na maioria dos reservatórios estudados, as alterações ambientais provocadas devido à construção de barragens, bem como suas características morfológicas e modos de operação têm efeitos negativos sobre a diversidade, distribuição e abundância das espécies de peixes e exercem influência sobre as diferentes guildas tróficas de peixes.

Palavras-chave: Cascata de reservatórios. Guildas tróficas. Metacomunidades. Organização espacial. Peixes de água doce.

Spatial distribution patterns of fish assemblages in Neotropical reservoirs

ABSTRACT

Given the great diversity of Neotropical fish species, as well as the importance of such organisms as a link within aquatic food chains, it is essential to assess different processes that drive the spatial organization of their communities. It is known that the structure of fish assemblages varies markedly in relation to space, depending on abiotic factors, biotic interactions, and dispersion processes. However, these determining factors in the structuring of fish communities vary indiscriminately in dammed aquatic bodies. The course of large rivers has been altered due to the construction of reservoirs and the number of projects under construction or inventoried has been increasing significantly in recent decades. Therefore, evaluating how the spatial organization of fish assemblages occurs in environments (i.e., dammed), as well as unraveling the predictors associated with this organization is of extremely important for conservation purposes and the implementation of management measures. To investigate such aspects in dammed environments, in the first study three cascades of reservoirs belonging to different hydrographic basins were studied, in which the effects of these reservoirs arranged in series on the patterns of diversity, distribution and richness of the assemblages were evaluated. In the second study, 29 reservoirs located in the state of Paraná were evaluated in order to identify relationships between the organization of fish trophic guilds and environmental, spatial and morphological predictors. The results found suggest that, in most of the studied environments, the environmental changes caused by the construction of dams, as well as their morphological characteristics and modes of operation have negative effects on the diversity, distribution and abundance of fish species and exert an influence on the different fish trophic guilds.

Keywords: Cascade of reservoirs. Trophic guilds. Metacommunities. Spatial organization. Freshwater fish.

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1 INTRODUCTION

Fish are a fundamental link in aquatic food chains, have limited dispersion, interact closely with environmental conditions, in addition to having great economic value as a basis for human food consumption (Petry et al. 2011). Freshwater environments comprise about 1% of the Earth's surface, however, they contain approximately 45% of the planet's fish species (Lévêque et al. 2008). Specifically, the Neotropical region is home to the greatest diversity of freshwater fish species in the world, with estimates of approximately 9,000 species (Birindelli & Sidlauskas 2018). Inserted in this context, Brazil, which has a vast territorial dimension and large hydrographic basins, stands out as the country with the greatest richness of this ichthyofaunistic diversity (Agostinho et al. 2005), with approximately 3,500 species of fish cataloged in its various freshwater environments (Froese & Pauly 2020). Furthermore, it is noteworthy that the country also exhibits an extraordinary rate of endemism, since many species have a geographical distribution limited to the hydrographic systems in which they occur (McAllister et al. 1997). Thus, knowing the processes that govern the organization of these communities through space is essential to help in the conservation of the biodiversity of the Brazilian ichthyofauna (Legendre et al. 2005; Leprieur et al. 2009; Zbinden & Matthews 2017).

The structure of ecological communities varies markedly over space and time, and these variations have many causes and consequences. Typically, communities are assembled by a combination of abiotic factors, biotic interactions, and dispersal processes/capacity (Chase & Leibold 2003; Leibold et al. 2004). Unraveling the relative importance of these factors has been a major challenge for understanding this assemble (Holyak et al. 2005; Hildrew 2009; Mittelbach 2012), as well as for management, conservation and monitoring of biodiversity (Brown et al. 2011; Heino et al. 2013). These studies become even more important in disturbed aquatic systems, as they can help to better understand the dynamics of fish communities and generate useful information for the conservation, restoration and management of rivers that suffer high levels of degradation.

The course of large rivers has been heavily modified by human disturbances (Nilsson et al. 2005; Vorosmarty et al. 2010). Among the main sources of degradation of aquatic environments are the construction of dams (Dudgeon et al. 2006). The construction of large dams severely alters the hydrological regime (Poff et al. 2007), causing the loss of natural environments and changes in limnological conditions and spatial heterogeneity. The changes caused in the continued transfer of matter, energy and nutrients from the river due to dams affect the availability of resources, reproductive success and fish recruitment, with effects on species composition (Ward & Stanford 1983; Agostinho et al. 2004; Luz-Agostinho et al. 2008; Oliveira et al. 2015). In this way, fish assemblages are reorganized along the river course (Pelicice et al. 2018), changing the patterns of diversity in space (Oliveira et al. 2005). This transformation process is even more intense when these reservoirs are arranged in series (cascades), promoting cumulative and synergistic impacts that can propagate throughout the river.

The number of dams has increased significantly in recent decades to meet the energy demands arising from the rapid growth of human population and economy, especially in the Neotropical region (Winemiller et al. 2016). Only a small fraction of rivers in the world remains unchanged (Vorosmarty et al. 2010). For Brazil, recent estimates indicate that 1,027 dams are under construction or have already been inventoried (Zarlf et al. 2015). Given this scenario, it is extremely important to assess how fish assemblages are distributed (e.g., in relation to richness, abundance and trophic organization) in barred environments and which factors predict possible patterns. These aspects were addressed in two approaches, briefly described below.

In the first approach we analyze the effects of three reservoir cascades on the diversity, distribution and abundance of fish assemblages, seeking to identify convergent spatial patterns and inferences about the mechanisms that structure fish metacommunities. In the second approach, we seek to understand the main factors responsible for structuring the trophic guilds of fish, evaluating the relative importance of spatial, morphological and environmental characteristics in different reservoirs.

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2 EFFECTS OF RESERVOIR CASCADES ON DIVERSITY, DISTRIBUTION, AND ABUNDANCE OF FISH ASSEMBLAGES IN THREE NEOTROPICAL BASINS

ABSTRACT

River systems are characterized by the existence of longitudinal processes structuring fish assemblages. However, the construction of dams, many of them built in cascades, are disrupting these processes worldwide. Here, we analyzed the fish assemblages across reservoir cascades in three Brazilian river basins (Iguaçu, Paranapanema, and São Francisco) to identify whether there is a spatial convergent pattern and to infer the mechanisms structuring metacommunities in these Neotropical rivers. Linear models were used to assess the effect of reservoir cascades, and the associated morphological, spatial and environmental variables, on the species richness and diversity along them. We analyzed if reservoir cascades produce similar species distribution patterns using the elements of metacommunity structure framework and beta diversity and its components. Finally, super-organizing maps were used to find common trends in species abundances and the environmental, morphological, and spatial variables along cascades. The negative relationship between species richness and diversity and the position in the cascade indicated diversity declines along cascades. However, the resulting metacommunities varied in each river basin. They conformed a quasi-Gleasonian structure, a Clementsian structure, and a nested structure with stochastic species loss in the Iguaçu, Paranapanema, and São Francisco River basins, respectively. Generally, total beta-diversity (βsor) and species turnover (βsim) between pairs of reservoirs increased along reservoir cascades, especially at the downstream end, whereas nestedness (βsne) depicted distinct trends in each river basin. By contrast, there were general decreases in species abundances along cascades, especially downstream the fourth reservoir, with very few species benefiting from such situation. In general, species present in the downstream reservoirs were subsets of the species present in the upstream reservoirs (particularly in the São Francisco River Basin), while some had singular responses to the environmental gradient and appeared or disappeared at random. Although the cascade has an effect on fish assemblages, reservoir characteristics and operation also influence them. Our study highlights the impact of such structures and shows general patterns of fish assemblages that should help to mitigate the resulting ecological impacts and assist the process of infrastructure planning.

Keywords: Freshwater fish, Tropical reservoirs, Cascading Reservoir Continuum Concept, Serial dams, Serial Discontinuity Concept

2.1 Introduction

A major goal of community ecology is to identify and interpret the patterns of species distribution and abundance (Leibold et al., 2004; Mittelbach, 2012). A comprehension of these patterns will permit us to better understand and model both current and future distributions of species. Environmental conditions, both biotic and abiotic, are the main factors that govern species occurrence and hence communities in terms of species richness and diversity (Jackson et al., 2001; Peres-Neto, 2004). A variety of distributional patterns have been hypothesized in nature (e.g., Elements of metacommunity structure (EMS) approach; Leibold and Mikkelson, 2002) to describe community structure through the analysis of spatial organization. So, the recognition of distributional patterns is the first step to understand the processes structuring ecological communities and the general rules that govern them. Thus, the identification of a non-random spatial organization in communities is an evidence of the action of at least one underlying structuring factor (Oliveira et al., 2005).

In community ecology, the interaction between organisms and the environment is often illustrated by the concept of environmental filtering, as abiotic conditions can act as thresholds precluding species presence (Kraft et al., 2015). Both environmental filtering and biotic interactions influence species assemblages and interact dynamically to drive species distribution patterns, as the strength and direction of biotic interactions can strongly influence and be influenced by the abiotic context (Callaway et al., 2002; Kraft et al., 2015). Environmental gradients partly act as environmental filters that allow or exclude species in local communities depending on the combination of organism traits, abiotic features, and selective forces (Capers et al., 2010; Comte et al., 2016; Daga et al., 2012; Poff, 1997). Therefore, finding similar patterns in independent systems can suggest the existence of fundamental mechanisms driving the organization of the communities (Tisseuil et al., 2012).

River systems are characterized by some predictable environmental gradients caused by the longitudinal variation in abiotic and biotic factors (e.g., temperature, slope, water flow, conductivity), which drive the structure of the environments and communities (Johnson et al., 1995; Vannote et al., 1980). These longitudinal patterns along streams and rivers courses have been described using various conceptual frameworks, such as the continuous river concept, the spiral nutrient concept and the process domain concept (Montgomery, 1999; Vannote et al., 1980; Webster and Patten, 1979), all of them assuming an uninterrupted continuum. The course of rivers, however, has been intensely modified by anthropogenic activities (Grill et al., 2019; Vörösmarty et al., 2010; Zarfl et al., 2015). The construction of large dams alters natural flow regimes, nutrient and sediment fluxes and favors dramatic changes in the former habitats, typically by depleting downstream segments and turning upstream segments into homogeneous uninterrupted lentic habitats (Poff et al., 2007; Santos et al., 2020). Consequently, fish assemblages are reorganized along the river course, changing the biodiversity distribution patterns (Agostinho et al., 2000; Oliveira et al., 2005). The new ecosystem created by damming may have its impacts explained by the serial discontinuity concept (SDC) (Ward and Stanford, 1983). According to this concept, these infrastructures causes discontinuity in physical and biological characteristics, especially in relation to matter, energy, and nutrient dynamics (Granzotti et al., 2018; Santos et al., 2018; Ward and Stanford, 1983). The SDC predicts shifts in biotic and abiotic factors that vary in intensity and direction (upstream or downstream) as a function of the distance to the reservoir. The loss of connectivity by impoundments leads to longitudinal shifts in different variables (e.g., temperature, substrate, nutrients and biodiversity), especially when these impoundments are arranged in cascades, producing decreases of fish diversity in downstream river segments or dams (Ward and Stanford, 1983). Furthermore, due to the discontinuities caused by dams, species appear or disappear from local assemblages, creating turnover and/or nested longitudinal patterns, which change the distribution of fish assemblages (Pelicice et al., 2018).

The impacts and environmental changes caused in river systems are even more intense when reservoirs are built in cascades or series, as they produce cumulative or synergistic impacts that can propagate throughout the river system (Barbosa et al., 1999; Santos et al., 2018). More pronounced biotic and abiotic modifications are common because river systems present interconnected ecological processes but, especially, when the outflow of a reservoir is the only inflow of the downstream one (Santos et al., 2020). In this regard, the cascading reservoir continuum concept (CRCC) was proposed by Barbosa et al. (1999) as a conceptual framework to formalize the ecological processes in systems with dam sequences. This concept highlights the changes that occur in environmental factors, such as water quality, sediment and nutrient fluxes or connectivity of the river segments. Reservoir cascades typically lead to oligotrophication of downstream reservoirs with a direct consequence in the biodiversity and distribution patterns (Barbosa et al., 1999; Ney, 1996; Straškraba, 1994). In addition, decreases in biodiversity and functional changes in the composition of assemblages, especially due to the decreases in habitat heterogeneity, are expected to be frequent (Ward and Stanford, 1983), as it has been already verified in some studies (Loures and Pompeu, 2018; Santos et al., 2016). For example, Santos et al. (2020) found a decrease in the abundance of detritivorous species along the longitudinal gradient of a reservoir cascade due to an intense oligotrophication process. This impoverishment of the biotic community can be expected for other functional groups in reservoir cascades, especially over time, since the change in the trophic state of the reservoirs typically results in a decrease in primary productivity of the system (Barbosa et al., 1999), negatively affecting the secondary productivity and finally the fishes (Hoeinghaus et al., 2009). Nevertheless, the ultimate configuration and extension of the effects may depend on the specificities of the reservoir cascade, such as the morphological/operational (e.g., residence time, volume or depth) and spatial (e.g., cascade position, altitude or distance to source) characteristics of the constituent reservoirs and their interactions with the original matter and sediment fluxes of the river basin (Santos et al., 2018; Straškraba et al., 1993).

In tropical countries, a large expansion of hydroelectric projects is in progress and a myriad of additional dams have been projected to satisfy the energy demands of the rapidly-growing human population and economic development (Lees et al., 2016; Winemiller et al., 2016; Zarfl et al., 2015). Only in Brazil, 1,027 dams, including large and small hydroelectric, are under construction or inventoried (Zarfl et al., 2015). For a future scenario (2030) in which all projects are supposed to be implemented, the number of barred water bodies will likely double, with more than 70% of the plants being installed in streams where there are no impoundments yet (Toffoli, 2015). Modifications in environmental conditions, following reservoir construction, can result in varied effects on the original fish assemblages (Bailly et al., 2016). Therefore, understanding the effects of reservoir cascades on fish assemblages is an urgent need, especially in countries such as Brazil where hydropower represents the main energy source.

In this context, we analyzed the fish assemblages across reservoir cascades in three Brazilian river basins (Iguaçu, Paranapanema, and São Francisco) to identify whether there is a spatial convergent pattern and to infer the mechanisms structuring metacommunities. We hypothesized that reservoir cascades would have a convergent controlling effect on the diversity, distribution, and abundance of fish assemblages in these different river basins. We expected a downstream reduction in species diversity along reservoir cascades and, as a consequence, a nestedness metacommunity structure. We also expected a decrease in the abundance of some species along the cascade, since reservoirs become less productive and consequently would sustain depleted communities. Specifically, we evaluated the three reservoir cascades in three different ways. First, we assess species diversity patterns using richness and diversity indices, and through linear models we tested and disentangled the effects of the environmental, spatial, and morphological characteristics of the reservoir cascades on species diversity. Secondly, to test for the existence of similarities in assemblage structure, we applied the elements of metacommunity structure (EMS) framework to delineate metacommunity types in each reservoir cascade, then we compared the dissimilarities between upstream and downstream reservoirs using beta diversity and performed a DistLM (Distance-based Linear Model) to verify the effects of the environmental, spatial, and morphological characteristics of the reservoir cascades on beta diversity components. Finally, we used super-organizing maps to identify common trends (i.e., clusters) in species abundances and the environmental, morphological, and spatial variables along cascades.

2.2 Methods

2.2.1 Study area

The data used in this study were collected from three large Brazilian basins: Iguaçu River, Paranapanema River, and São Francisco River (Fig. 1). The first two basins are located in the Paraná River basin, which has the second largest drainage area (2.8 · 106 km2) after the Amazon basin (Galves et al., 2009; Stevaux et al., 1997) and is the most impounded Neotropical basin with 72% of its hydraulic potential already exploited

(Souza-Filho et al., 2004; Agostinho et al., 2007). Currently, there are 54 dams built in the basin and an additional ongoing project (AECweb, 2020; ITAIPU, 2020).

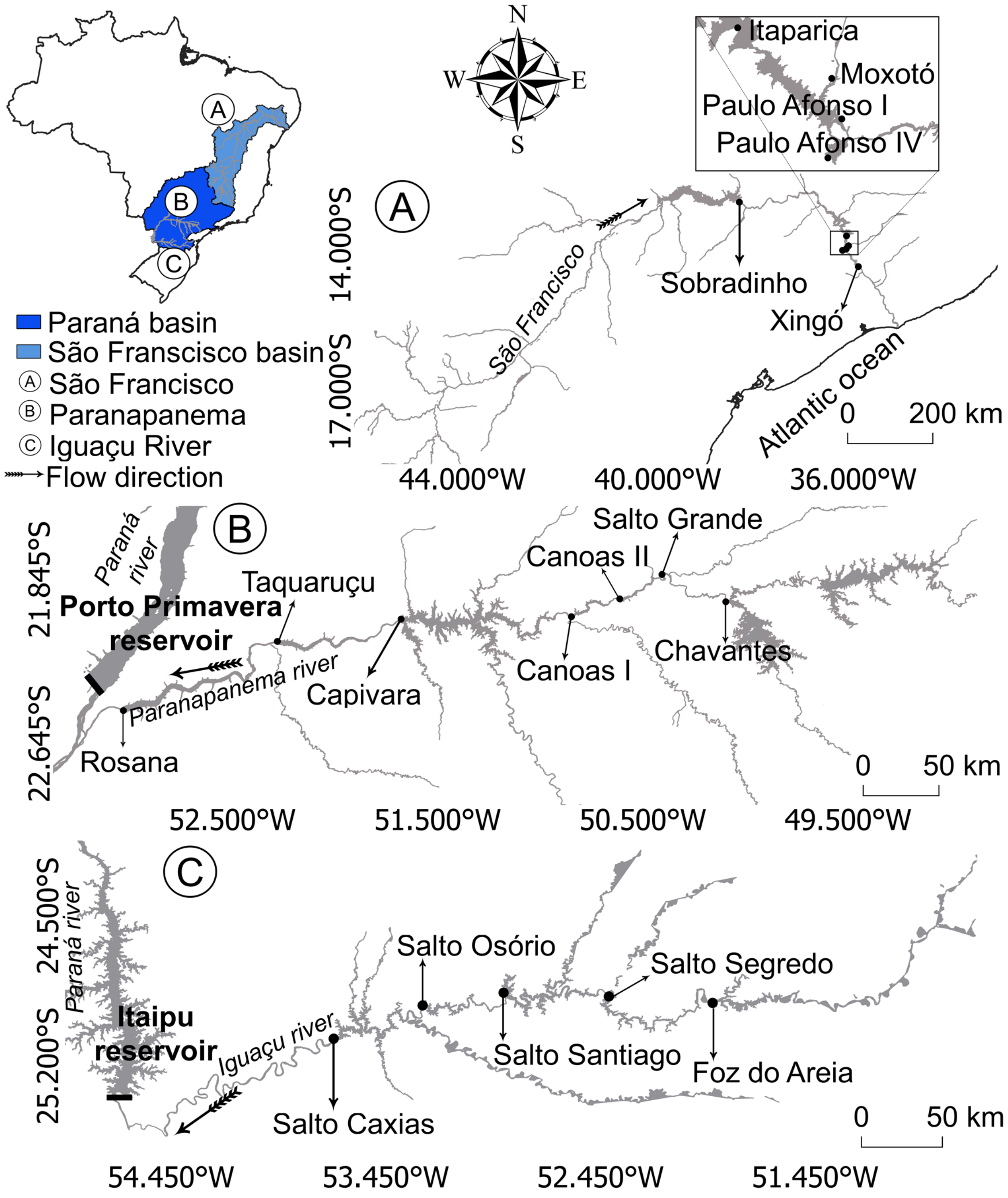

Fig. 1. Location of the hydrographic basins and their respective reservoir cascades in Brazil: A) Iguaçu River basin, B) Paranapanema River basin, and C) São Francisco River basin.

The Iguaçu River basin has an area of approximately 7.2 · 103 km2 and runs 1,060 km westward receiving water from various tributaries until it flows into the Paraná River. The high slope of the Iguaçu River basin, on the third plateau, constituted a major attraction for hydroelectric use, and from 1975 it began to change dramatically with the installation of the first large hydroelectric plant (Foz do Areia). Although there are 12 large reservoirs in the middle/lower and another three in the upper Iguaçu River basin (Daga et al., 2016), in this study we investigated five of them arranged in cascade (Fig. 1). These reservoirs in cascade occupy about 41.0% of the river length and turned the stretch of the great rapids of Iguaçu in a succession of large lakes, representing 655 km2 of flooded area (Barão, 2007).

The Paranapanema River basin is a main tributary of the upper Paraná River basin and has a drainage basin of approximately 106,500 km2 (ANA, 2016). Dozens of hydropower dams were built in the basin during the 20th century and eleven large dams regulate the main channel, affecting the upper, middle and lower reaches of the basin (Pelicice et al., 2018). Here we studied seven of these cascading reservoirs (Fig. 1), which together flood approximately 1,800 km2 of its drainage basin (Agostinho et al., 2008).

The São Francisco River basin, the third largest river basin in Brazil and the 25th longest river in the world, has a drainage area of approximately 636,420 km2, occupies about 8% of the Brazilian territory, and has its hydroelectrical potential highly exploited, reaching a total flooded area of 5856.2 km2. The cascade reservoir complex of the São Francisco River basin is the only complex in Latin America inserted in a semi-arid region known as the Drought Polygon, where marked seasonal variations in water flow occur. Currently, the São Francisco River basin has 28 hydroelectric dams and complexes of dams providing 10.8 GW of installed generation capacity, however, in this study, we investigated six of them arranged in a cascade. There are approximately 117 proposed sites for the development of new small and medium-sized dams, mainly in the upper reaches of the basin to the west and south (O'Hanley et al., 2020).

We studied cascades of 5, 7, and 6 consecutive mainstem reservoirs in each of these three river basins, respectively (Fig. 1). Basic data on these reservoirs are given in Tables S1 and S2. These reservoirs vary in terms of age, area, elevation, and water residence time, but correspond to a very similar regional species pool of fish faunas. Considerable details on the fish assemblages of all of these reservoirs in the Iguaçu (Daga et al., 2015, 2020; Santos et al., 2017), Paranapanema (Pelicice et al., 2018; Santos et al., 2017), and São Francisco (Santos et al., 2017, 2018, 2020) basins are available.

2.2.2 Data collection

2.2.2.1 *Environmental data*

Environmental data were obtained at different periods. For the São Francisco, the surveys in Sobradinho reservoir occurred between October 2006 and July 2009, while the other reservoirs of this system were sampled quarterly between December 2007 and September 2010. The Iguaçu and Paranapanema basins were sampled in July and November 2001. Diverse environmental variables were collected in every reservoir and survey, namely water temperature (°C), conductivity (µS cm^{-1}), dissolved oxygen (mg L^{-1}), turbidity (NTU) and pH were measured from surface water in the field using a multiparameter probe. In addition, water transparency (m) was estimated using Secchi disk. Samples obtained using a Van Dorn bottle (2.5 L) were stored in polyethylene bottles and placed on ice to preserve in low temperatures until analysis. Using the methodology described by Mackereth et al. (1978) and APHA (2005), we obtained the following variables: chlorophyll-*a* (µg L^{-1}; Nusch, 1980) and, nitrate and total phosphorus concentrations (µg L^{-1}; APHA 2005; Mackereth et al., 1978). Limnological conditions have a strong influence on the structure of fish assemblages, as they are related to the productivity and ecological tolerance and fitness (Huston, 1979, 2004; Miranda and Krogman, 2015).

2.2.2.2 *Morphological data*

Following Pelicice et al. (2015) and Santos et al. (2017), we also recorded some variables that are more related to the morphology and functioning of the reservoirs and determined to have potential influence on fish assemblages: reservoir age, area, length, volume, and depth, water residence time, and accumulated volume of upstream reservoirs (Table S2).

2.2.2.3 *Spatial data*

For analyses, as descriptors of the spatial gradient along each cascade, we used the position of the reservoir in the cascade, elevation of each reservoir, and watercourse distance between the reservoir and river source. For position in the cascade, we assigned a value of 1 to the most upstream reservoir, 2 for the reservoir located immediately downstream of the first, and so on. Elevation values were obtained using Google Earth. The hydrologic distance was estimated with a shapefile of the hydrographic network and the Dijkstra algorithm, which measures the smallest distances between two points (Dijkstra, 1959; Loro et al., 2015), using the QNEAT3 complement (Qgis Network Analysis Toolbox; Raffler, 2018), implemented in QGIS 3.0 (QGIS Development Team, 2018).

2.2.2.4 *Biological data*

Our fish dataset was based on 132 sample surveys. For Iguaçu and Paranapanema River basins, each reservoir was sampled twice (in July and November 2001), totaling 10 and 14 surveys, respectively. For São Francisco River basin, samples were taken every two months between November 2006 and September 2009 in the Sobradinho reservoir, and between February 2008 and December 2010 in the other reservoirs (18 months of samples in each of the 6 reservoirs, totaling 108 surveys). In São Francisco surveys, environmental data were always obtained after the biotic data and the months nearest to the fish sampling campaigns were used for analyses.

Fish were caught in the lacustrine region of the reservoirs with gill nets of different mesh sizes (2.4–14 cm between knots for Iguaçu and Paranapanema; 1.2–9 cm between knots for São Francisco), which were exposed for 24 h in each reservoir and revisited at 8:00, 16:00, and 22:00 h. For all basins, we used both species richness and relative abundance. Relative abundance of each species captured was expressed as catch per unit of effort (CPUE; number of individuals in 1000 m^2 of gillnet during 24 h) for each sampling unit. The data used in this study were obtained by Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura of the Universidade Estadual de Maringá (for Iguaçu and Paranapanema) and by Laboratório de Ictiologia e Limnologia of the Universidade Federal Rural de Pernambuco (for São Francisco).

2.2.3 Data analysis

To perform all analyses, the two months of sampling, of both environmental and biotic variables, were used for the Iguaçu and Paranapanema basins. For São Francisco River basin, the sampling of environmental variables and of the fish assemblage were performed at different times in the reservoirs (18 samples for the fish community and 12 for environmental). Thus, it was necessary to impute the values of the environmental variables in the missing months to also obtain 18 months of samples for these variables. Due to the temporal structure of the collected data, we performed the imputation using the *"moving averages"* technique, in which the imputed values are a weighted average of four observations, namely the two previous ones and the two subsequent ones to the absent value. For this analysis we used the *imputeTS* package (Moritz and Bartz-Beielstein, 2017) in *R* software (R Core Team 2020).

2.2.3.1 *Diversity patters along cascades*

To characterize fish diversity in reservoirs, two metrics based on Hill numbers (Hill, 1973) were used: species richness (Hill number of order 0, ${}^{0}D$) and the exponential of Shannon's index (Hill number of order 1, ${}^{1}D$). To test the effects of the cascade position in relation to fish diversity (using the two diversity metrics), we used linear models in the package *stats* in the *R* software (R Core Team, 2019). Models were calculated separately for the two indices and the interaction between basin and cascade position was used to test whether the effect of cascades varied among basins.

In addition, linear modelling was used to evaluate the influence of the morphological, spatial and environmental variables on the diversity indices. In order to reduce the collinearity among predictors, we removed predictors with Pearson's $| r | > 0.6$, as recommended by Dormann et al. (2013); thus, six variables were retained to perform the analyses: altitude, residence time, depth, area, Secchi and total phosphorus. Secondly, we computed variance inflation factors (VIF) on each model (Fox and Monette, 1992); all variables had VIF < 10 indicating no severe multicollinearity in our models. The predictors effects were centered and standardized, so that the regression coefficients would become comparable in magnitude (Schielzeth, 2010). Then, we selected the most parsimonious models (i.e., in relation to the set of predictor variables used) with the lowest Akaike's information criterion corrected (AIC_c) for small sample size with $\Delta AIC_c<2$ (Burnham and Anderson, 2002). When more than one model had $\Delta AIC_c<2$, we retained the predictor variables selected for both. In both diversity indices, all selected predictor variables were evaluated (see Table S3 in Supplementary Information).

2.2.3.2 *Elements of metacommunity structure (EMS) and beta diversity*

To analyze the distribution patterns of the assemblages along each reservoir cascade and verify which idealized metacommunity structure best fitted the species distributions, we used the EMS framework described by Leibold and Mikkelson (2002) and later expanded by Presley et al. (2010). Based on a species-by-site incidence matrix, EMS analysis assesses the coherence, turnover, and boundary clumping of species distributions, looking for the best fit model. The different metacommunity characteristics are evaluated in a hierarchical way: coherence (step 1), turnover (step 2), and boundary clumping (step 3). By ordering the matrix, the species with similar occurrence among sites are closer to one another. Coherence, the first pattern tested, is assessed by counting the number of gaps in species range from the ordinated matrix and by comparing that value to a null model. If the number of gaps is significantly less than those occurring at random (checkerboard distribution), then turnover is evaluated. Turnover is assessed by counting the number of species replacements between sites and comparing that value to the null distribution. A significant negative turnover suggests a nested distribution, whereas a significant positive turnover suggests an evenly spaced, Clementsian or Gleasonian structure (distinguished in the sequence using a boundary clumping analysis). Finally, boundary clumping was evaluated using Morisita's dispersion index and subsequently tested against expected distributions using a chi-squared test. Values significantly greater than one indicate clumped range boundaries (Clementsian), values significantly less than one indicate hyperdispersed range boundaries (evenly spaced) and close to one indicate randomly distributed range boundaries (Gleasonian). Each of these six structures has an analogous quasi-structure (Presley et al., 2010), which is defined by stochastic range turnover. The EMS framework can be viewed as a three-dimensional space, in which communities represent points in space, allowing metacommunities to be qualitatively compared to one another. To perform EMS analyses, we used the "Metacommunity" function of the *metacom* package (Dallas, 2014) in *R* (R Core Team 2019). Due to the environmental gradients that occurs in basins with cascading reservoirs, we used a user-defined incidence matrix of sites-by-species previously ordered according to reservoirs' position for each cascade. The EMS metric interpretations were compared to a fixed-proportional (R1) null model. All null models were based on 9,999 permutations.

Complementarily, we evaluated the correlation (Spearman) between the cascade position (mid-point between reservoirs) and the beta diversity (βsor) and its turnover (βsim) and nestedness (βsne) components for each basin. We used the Baselga (2010) method to calculate and partition the beta diversity based on the Sørensen index and extracted the dissimilarity values between the first reservoir and the downstream ones from the dissimilarity matrices (βsor, βsim and βsne) for the correlation analysis. For this, we use the "beta.pair" function (i.e., to calculate the beta diversity pairwise between the reservoirs) implemented in the *betapart* package in *R* (Baselga and Orme, 2012). Finally, the "cor.test" function was used to calculate and test the significance of the Spearman correlation.

To evaluate the influence of morphological, spatial and environmental variables on beta diversity components and to select the best explanatory model, we applied a

DistLM (Distance-based Linear Model). The variables were selected following a forward variable selection approach using the Akaike's information criterion (AIC_c) as performance criteria and the process stopped when adding any additional variable caused increases in the AIC (Anderson et al., 2008; Blanchet et al., 2008). Prior to model development, the beta diversity components were standardized and the Euclidean distances between surveys were calculated. The morphological, spatial and environmental variables were also standardized, and collinear variables were removed before the forward variable selection (Neter et al., 1996). Distance-based redundancy analysis (dbRDA) was used to examine the influence of predictors on the spatial distribution of samples (Anderson et al., 2008). The "capscale", "rda", and "ordistep" functions (9,999 permutations) were used to perform DistLM and dbRDA, both from the *vegan* package (R Core Team, 2020).

2.2.3.3 *Super-organizing maps*

Super-organizing maps (Kohonen, 1982; Wehrens and Buydens, 2007; Wehrens and Kruisselbrink, 2018) were used to verify the existence of common trends (i.e., clusters) among species abundance (CPUEs) and the environmental, morphological, and spatial variables along the reservoir cascade. Self-organizing maps are a kind of artificial neural networks used for dimensionality reduction and data exploration that do not assume linearity or specific shapes on the analyzed trends and super-organizing maps (hereafter, SOM) are variants that are able to accommodate the existence of multiple surveys per river basin. Both are based on the development and ordination of a series of prototype neurons that minimize their distance to the training samples (in this case the sequences of CPUEs of fish species and the environmental, morphological, and spatial variables along reservoir cascades). The resulting unit neurons are usually ordinated into a bidimensional map and the optimization of the organizing map is conducted to globally preserve the original relationships (topology) of the input data. Therefore, unit neurons that are located near to each other in the map have similar associated samples (in our case trends along reservoir cascades). Unlike standard self-organizing maps, the super-organizing maps involve the development of multiple overlaying self-organizing maps, where each one maps different datasets of equal number of samples but encompassing different input variables or, as in this case, multiple surveys that involved the same sampled variables (e.g., CPUE of a given species). Consequently, the super-organizing map for Iguaçu and Paranapanema included two layers each and that for São Francisco, 18. The input trends along reservoir cascades are assigned to the closest unit neuron across SOM layers (i.e., surveys). Therefore, after the optimization, the resulting map can be used to inspect the existence of gradients within the simplified version of the responses along reservoir cascades or to cluster the resulting prototype sequences (codebooks) to find main trends across surveys, as depicted in Fig. 2.

The development and visualization of the SOMs were performed using the *kohonen R* package (Wehrens and Kruisselbrink, 2018). The input data were arrayed into multilayer datasets, one layer per survey, where rows corresponded to species CPUEs and environmental, morphological, and spatial variables and columns to the ordered sequence of reservoirs from upstream to downstream (Fig. 2-I). Prior to the SOM training, each row corresponding to the CPUEs and the environmental, morphological, and spatial variables along the reservoir cascade was standardized (*z*-score) to remove the effects of different measurement units. The surveys performed in Sobradinho (i.e., the uppermost reservoir of the São Francisco River basin) in 2006 were removed as they became non-informative. A hexagonal lattice was selected and the dimensions of the map (number of unit neurons in the *X* and *Y* dimensions) were not predefined. The selected dimensions were those that simultaneously minimized the quantization and topographic errors (Céréghino and Park, 2009) (Fig. 2-II) and they varied between 1 and 12 provided that there were sufficient data to train the map. SOM convergence can be sensitive to initial conditions; therefore, each SOM was trained 5 times while the number of iterations was set to 1000.

Once the optimal dimensions of the SOMs were determined, we plotted the resulting maps to inspect the existence of common trends and distribution patterns. In addition, we used the resulting SOM codebooks to cluster the input trends. However, unlike standard self-organizing maps were codebooks are arrayed into a single matrix, super-organizing map also render the codebooks as 3D matrices, which limits the applicability of standard clustering approaches used in former studies (e.g., Zhang et al., 2018). To overcome such limitation, we built undirected networks based on the distance matrix among codebooks using the *igraph R* package (Csardi and Nepusz, 2006). The "cluster_louvain" function (Blondel et al., 2008), which implements the multi-level modularity optimization algorithm to find the community structure that maximizes the modularity, was used to cluster the unit neurons (Fig. 2-III). Finally, the sequences of species CPUEs and the environmental, morphological, and spatial variables associated to each cluster were simplified into single trends with confidence intervals to inspect similarities among groups and river basins (Fig. 2-IV).

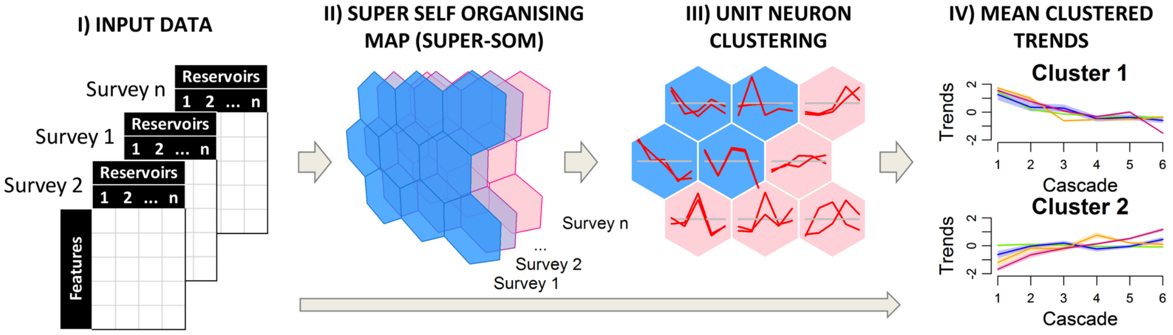

Fig. 2. Flowchart depicting the process followed to find common trends among species abundances (CPUEs) and environmental, morphological, and spatial variables along the reservoir cascades with super-organizing maps.

2.3 Results

2.3.1 Diversity patterns along cascades

The fish diversity of reservoirs showed differences among cascades (see Fig. S4 in Supplementary Information): i) in Iguaçu, the species richness did not vary along the cascade but the exponential of Shannon index (^{1}D) showed a tendency to increase downstream; ii) in Paranapanema, the species richness patterns along the cascade are not so clear, although there is a general downstream reduction in ^{1}D; iii) in São Francisco, there is a clear downstream decline in both diversity indices.

The linear models indicated that the basin and cascade position, as well as the interaction between them, had significant effects on both diversity metrics (Table 1). The most parsimonious linear model included: altitude, residence time, depth, area, Secchi and total phosphorus, respectively (see Table S5 in Supplementary Information). The model parameters indicated a positive relationship between the reservoir diversity (richness and ^{1}D) and morphological characteristics of the reservoir as area and residence time. On the other hand, the variables depth, Secchi (only for richness) and altitude showed negative relationships with the diversity metrics (Table S5).

Table 1 Linear models of fish richness and the exponential of Shannon's index (Hill number of order 1, ^{1}D) with river basin and reservoir cascade position. SS = sum of squares; d.f. = degrees of freedom. *P* values < 0.05 are bolded.

Diversity metrics	**Source of variation**	**SS**	**d.f.**	***F*-value**	***P***

($R^2_{adjusted}$)					
Richness (0.781)	Cascade position	6061.50	1	349.28	**<0.001**
	Basin	1174.90	2	33.85	**<0.001**
	Cascade position × Basin	1457.40	2	41.87	**<0.001**
^1D (0.617)	Cascade position	755.51	1	135.67	**<0.001**
	Basin	426.17	2	38.26	**<0.001**
	Cascade position × Basin	128.37	2	11.53	**<0.001**

2.3.2 Fish metacommunities structure and beta diversity

In the three river basins (Iguaçu, Paranapanema, and São Francisco), the corresponding total observed richness of fish species was 30, 72, and 60, respectively. Although all metacommunities exhibited significant negative coherence, the patterns of species distribution along reservoir cascades varied for each basin. The fish metacommunity of the Iguaçu River basin exhibited a quasi-Gleasonian structure (Fig. 3a). It was also characterized by non-significant positive turnover, and a non-significant Morisita's index larger than one (Table 2). The fish assemblage of Paranapanema River exhibited positive turnover, and a significant Morisita's index larger than one (Table 2), corresponding to a Clementsian structure (Fig. 3b). A Nested structure with stochastic species loss was found for São Francisco River (Fig. 3c), characterized by negative turnover, and non-significant Morisita's index larger than one (Table 2).

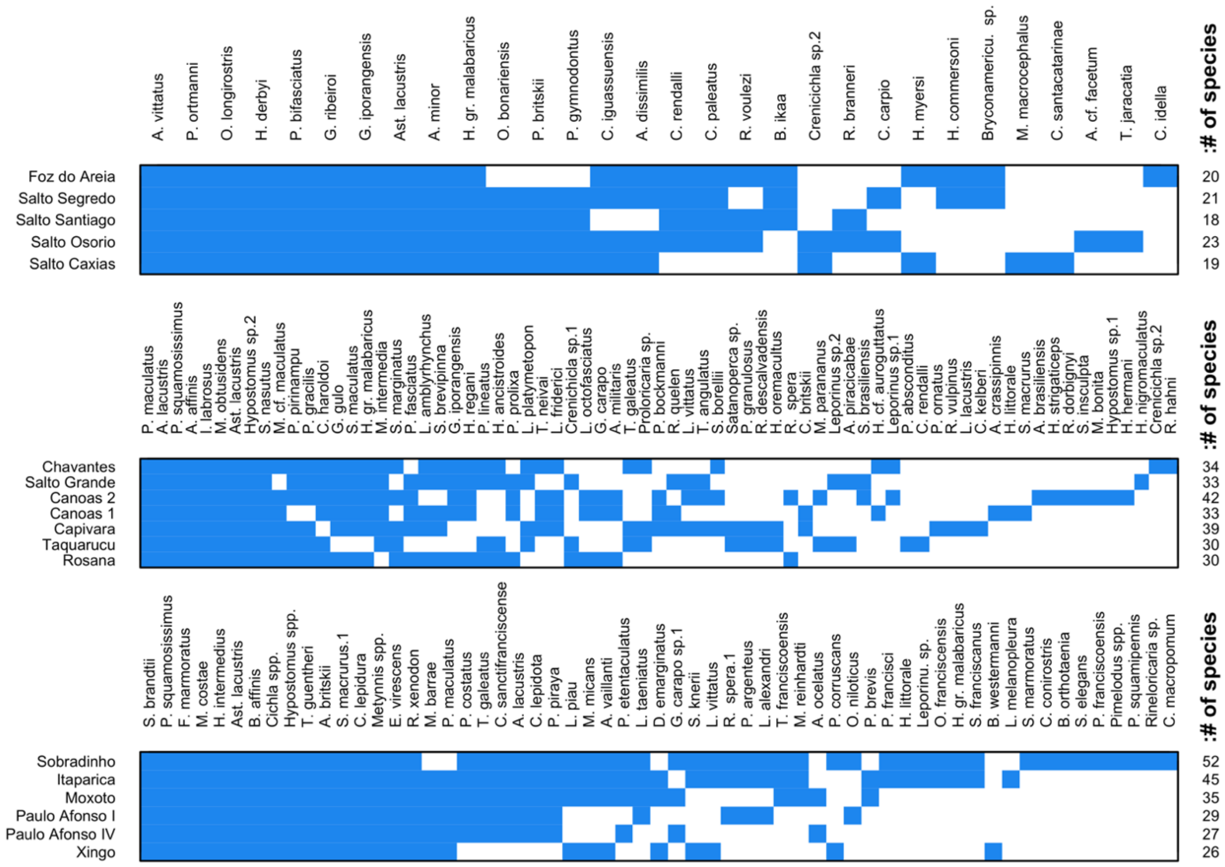

Fig. 3. Species presence (in blue) in the reservoirs of the Iguaçu (uppermost), Paranapanema (central), and São Francisco (lower) river basins. Reservoirs arranged by their longitudinal position are in rows; species are in columns. The total observed species richness is also given.

Table 2 Elements of metacommunity structure (EMS) analysis of the Iguaçu, Paranapanema e São Francisco river basins. SD = standard deviation; EAbs = number of embedded absences. The mean and standard deviation values refer to the simulated communities.

Basin	Coherence					Species turnover					Boundary		Interpretation
	EAbs	z	P	Mean	SD	Rep	z	P	Mean	SD	Morisita's Index	P	
Iguaçu	12	-7.37	<0.01	39.9	3.69	163	1.29	0.19	125.4	29.97	1.19	0.07	Quasi-Gleasonian
Paranapanema	94	-15.65	<0.01	232.1	8.88	2753	3.04	<0.01	2165.7	238.49	1.21	<0.01	Clementsian
São Francisco	39	-12.19	<0.01	127.8	7.28	518	-2.59	<0.01	769.3	96.89	1.08	0.14	Nested stochastic species loss

In Iguaçu and Paranapanema, turnover was the component that had the largest contribution (mean = 0.19 ± 0.08 SD and mean = 0.33 ± 0.09 SD, respectively), while nestedness was the main contributor in São Francisco (mean = 0.15 ± 0.10 SD). Generally, total beta-diversity (βsor) and turnover (βsim) between the first reservoir (i.e., reference) and downstream reservoirs increased along the reservoir cascade in every basin, especially by the end of the cascade, except in the Paranapanema River basin, where βsor and βsim did not vary much along the cascade to markedly decrease in the last downstream pair of reservoirs (Fig. 4). By contrast, nestedness (βsne) depicted distinct trends in each river basin. It was mainly increasing in São Francisco, whereas in Iguaçu and Paranapanema it showed a unimodal trend with the minima at the extremes and in the middle, respectively. However, no significant Spearman correlation was found between any of them and cascade position (see Table S6 in Supplementary Information), but that found for total beta-diversity and nestedness in São Francisco (r_S=1.0, P=0.017).

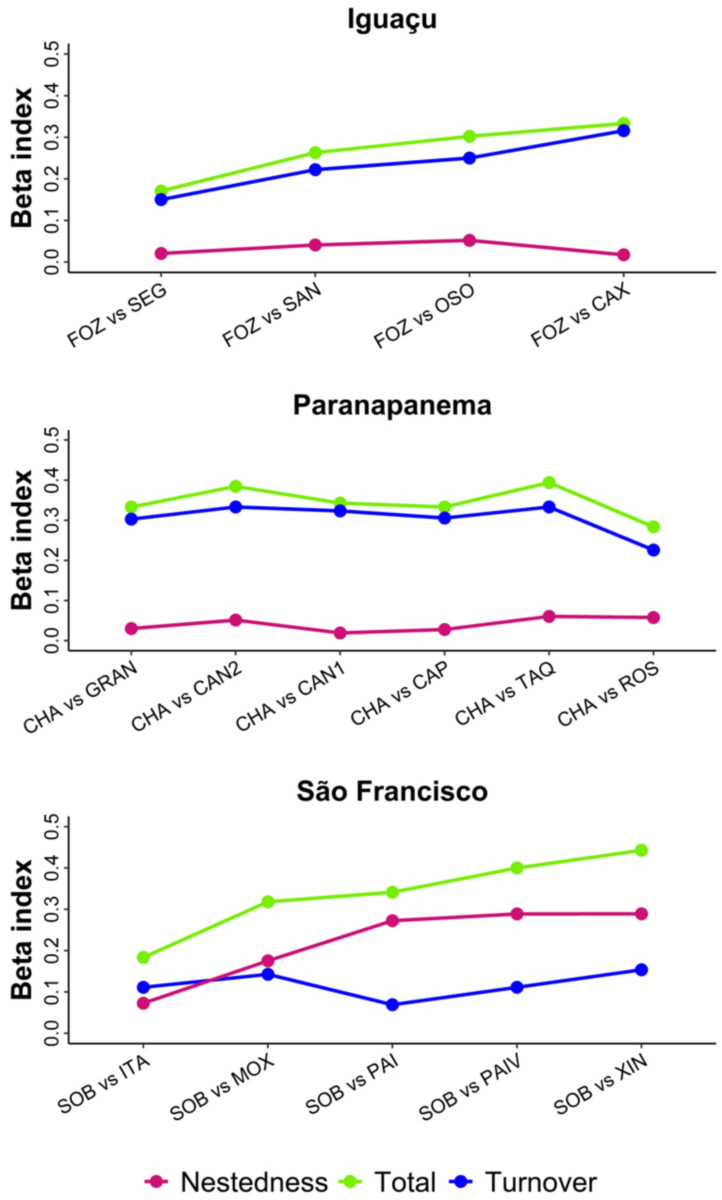

Fig. 4. Total beta diversity and its components (nestedness and turnover) of fish in reservoir along the three cascades (river basins). Each of the reservoirs was compared with the first, most upstream reservoir.

The DistLM for all basins included morphological and environmental variables for total beta-diversity (βsor) and turnover (βsim): area, depth, residence time and nitrate, respectively. For nestedness (βsne), only the morphological variable area was included (see Table S7 in Supplementary Information) (Fig. 5).

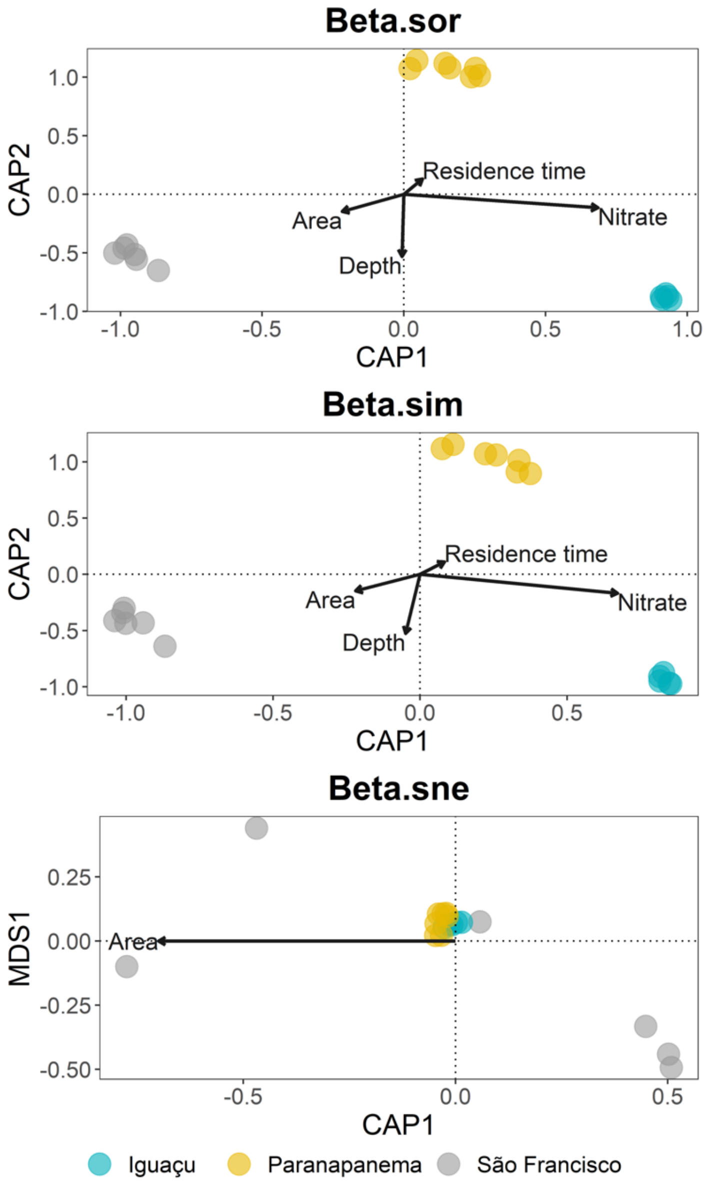

Fig. 5. Distance-based redundancy analysis (dbRDA) with the predictor variables (area, residence time, depth and nitrate) showing the greatest importance for the linear model DistLM.

2.3.3 Abundance patterns along cascades

The optimal SOM dimensions varied for each river basin but the total number of neuron nodes correlated with the number of species collected in each river basin (Fig. 6). The “cluster_louvain” function indicated the existence of three major clusters in each river basin, although the variables assigned to each cluster differed (see Figs. S8 in

Supplementary Information for additional results). The clusters indicated different trends along cascades in each river basin and the uncertainty was higher for Iguaçu and Paranapanema due to the smaller number of surveys, although the largest uncertainty among surveys corresponded to the environmental variables collected in the Iguaçu River basin regardless of the cluster (Fig. 7).

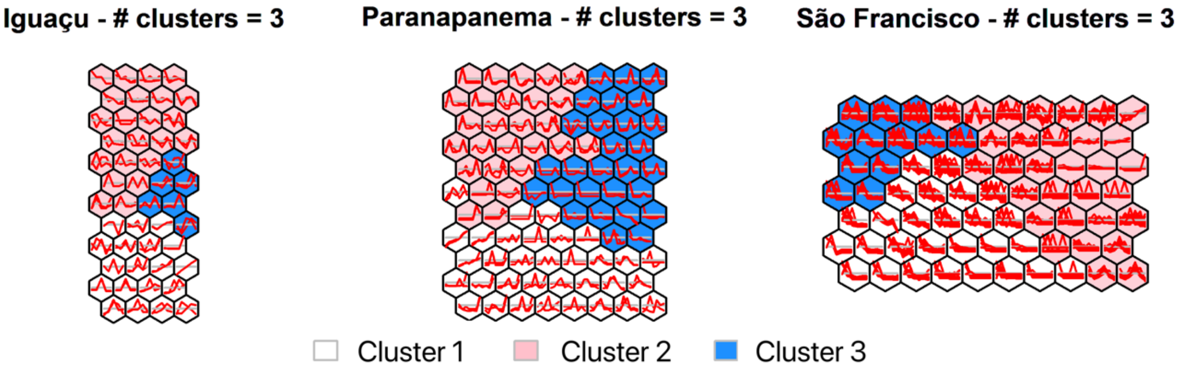

Fig. 6. Depiction of the optimal super-organizing maps obtained for every river basin. Overlaid red lines are the prototype codebooks obtained in every layer of the optimal super-organizing map. The different color patterns highlight the different clusters.

The first cluster of the Iguaçu River basin included most of the spatial variables (67%) and approximately 45% of species and morphological variables, with *Psalidodon bifasciatus* being the most abundant species in this group (Fig. 7). This cluster encompassed flat-to-increasing trends with their maxima in the third reservoir of the cascade (i.e., Salto Santiago). The second cluster included decreasing trends and included most of the remaining variables, including 43% of species. The most characteristic variables of this group were chlorophyll-*a*, total phosphorus, turbidity, water residence time and age, whereas the species experiencing the most pronounced decreases were *Glanidium ribeiroi* and *Hypostomus derbyi*. The last cluster encompassed few species and variables that showed a close-to-unimodal pattern with the maxima around the fourth reservoir such as the invasive *Coptodon rendalli*.

In Paranapanema the species were evenly distributed across clusters (Fig. 7). The first cluster included flat (species and environmental variables) or increasing trends (morphological and spatial variables). By contrast, the second and third clusters encompassed irregular decreasing trends. The second cluster included most of the environmental variables (63%) and no spatial variables, whereas the third cluster encompassed most of the morphological (71%). The most characteristic variables of the second group were chlorophyll-*a*, total phosphorus, and Secchi, and the species that showed the most decreasing trend along the cascade was *Trachelyopterus galeatus*. The most characteristic variables of the third cluster were area, depth, water residence time and volume, whereas the species depicting the strongest decreasing trends were *Hypostomus* spp. and *Plagioscion squamosissimus.*

The first cluster of São Francisco encompassed clearly decreasing trends and 42% of the species and 57% of the morphological variables. The most characteristic variables included in this group were area, volume, total phosphorus concentration, and turbidity. The species experiencing the largest decrease along the cascade was *Triportheus guentheri*, followed by *Curimatella lepidura* and *Tetragonopterus franciscoensis*. The second cluster encompassed the remaining variables that showed flat-to-increasing trends, although the clustered species abundances did not increase. The last cluster only included a few species (17%), less abundant in the uppermost reservoir of the basin (i.e., Sobradinho). The most remarkable species of the last group that showed the largest decreases along the cascade were *Bryconops affinis*, *Acestrorhynchus britskii*, *Moenkhausia costae*, and *Plagioscion squamosissimus*. Specific percentages and the complete list of features assigned to each cluster can be consulted in Tables S9 (Supplementary Information).

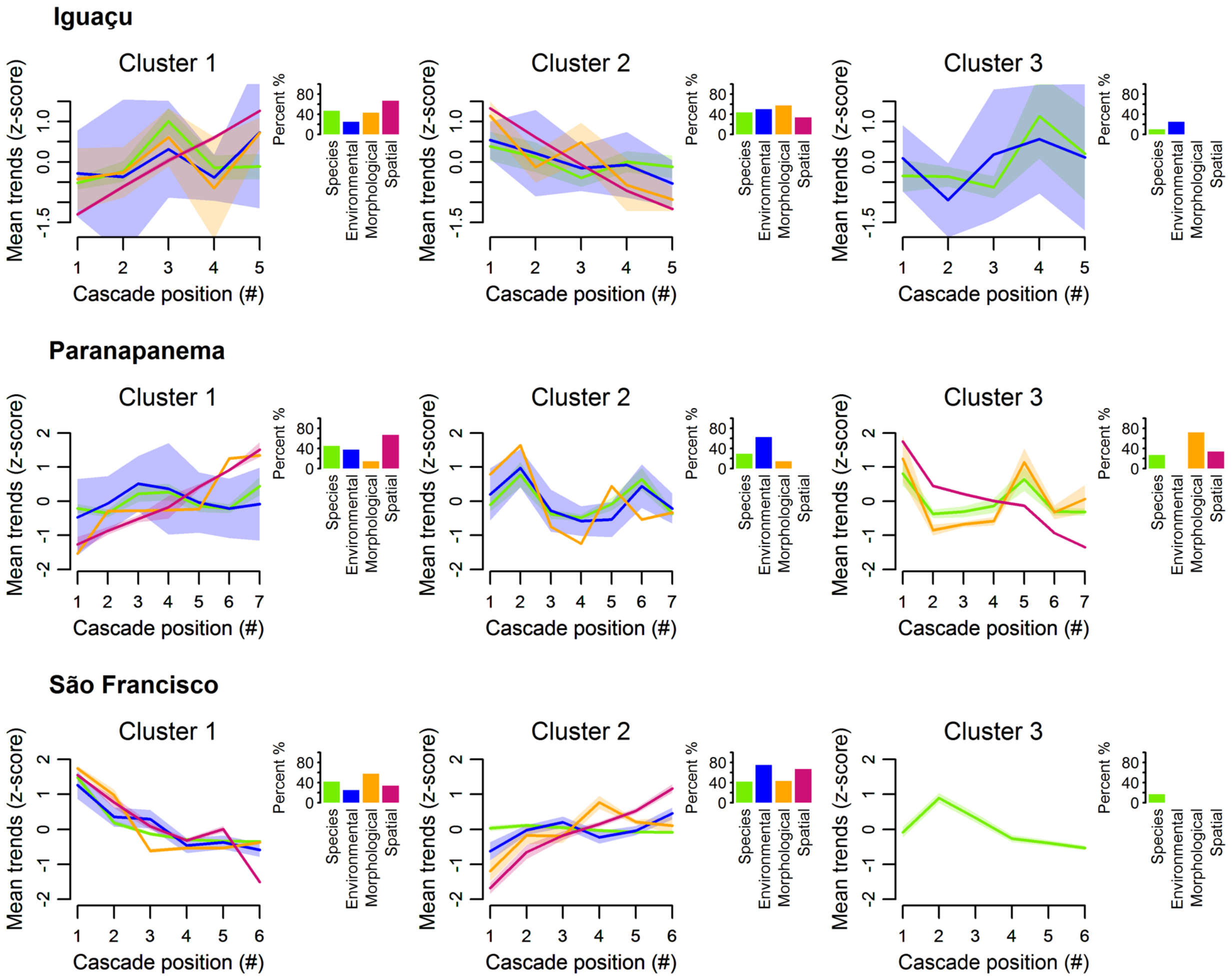

Fig. 7. Line charts depicting the mean values of the original trends assigned to each unit neuron cluster obtained after clustering the prototype codebooks of the super-organizing maps. The shaded areas correspond to 95% confidence intervals. The small bar plots next to the line charts depict the proportion of trends (i.e., species CPUEs and the environmental, morphological, and spatial variables) included in the group.

2.4 Discussion

By evaluating the three basins (Iguaçu, Paranapanema, and São Francisco) together and separately, we confirmed that reservoir cascades have a deleterious effect on the species distribution, diversity and abundance. Along the cascades, it is possible to observe relevant changes and decreases on species diversity, especially richness, and abundance, with major changes in species composition (i.e., beta-diversity) at the downstream end of the cascades and few species being able to sustain higher abundances in these impoverished downstream environments. The linear models showed that both the position in the cascade and the morphological, spatial, and environmental variables (e.g., residence time, depth, area, altitude, total phosphorus and Secchi) influenced diversity reservoir structure. The SOMs highlighted how the abundances of large groups of species (e.g., clusters 1 and 3 of São Francisco and cluster 2 of Iguaçu) decrease along cascades, although there were irregular patterns caused by the local characteristics of each reservoir (Barbosa et al., 1999; Santos et al., 2017, 2018; Straškraba, 1994), especially in Iguaçu and Paranapanema. This is reflected in the analyzed cascades of the Iguaçu and Paranapanema rivers as they exhibited positive turnover with some species individual responses to the reservoir sequence and appearing or disappearing at random prompting different metacommunity structures. The species present in the downstream reservoirs of São Francisco exhibited, on the contrary, a clearer patter as they were, in general, subsets of the species present in the upstream reservoirs. Thus, for São Francisco (i.e., the best sampled basin) the expected pattern of reduction of species richness and formation of subsets in the downstream reservoirs (nestedness pattern) was clearly found, corroborating the main hypothesis of the study.

2.4.1 Diversity patterns along cascades

As hypothesized, reservoirs affected the species diversity along cascades. Although other variables have also an influence (water residence time, area and depth), our hypothesis that the cascade has a controlling effect on species diversity was confirmed, since cascade position had significant effect on both diversity indices. However, these changes patterns in diversity showed differences between basins. For the São Francisco basin, there was a clear decrease in diversity in the downstream direction. On the other hand, the Iguaçu and Paranapanema basins did not present as clear patterns, partly due to the smaller sample size. In general, reservoirs that had lower cascade position (i.e., upstream in the cascade) were those that showed greater species diversity. By contrast, reservoirs with the lowest species diversity were those with the higher cascade position (i.e., downstream position), which contradicts the general pattern observed in numerous studies on natural river systems where species richness is higher in lowland river segments (Bistoni and Hued, 2002; Suvarnaraksha et al., 2012). Nonetheless, some studies carried out in reservoir cascades have shown a reduction in species richness in the downstream direction (Loures and Pompeu, 2019; Pelicice et al., 2018), as also verified by beta diversity, whose values increased along the cascade.

Another characteristic that proved to be important in determining species diversity along reservoir cascades was water residence time, which is closely related to the size of the reservoir and their type of operation (i.e., accumulation or run-of-river). Reservoirs that had higher residence times showed greater species diversity, as also observed by Li et al. (2012) and Santos et al. (2017). The variability of water level fluctuations has to be considered important for biota inhabiting these lowland environments, since they are interfacing aquatic and littoral zones, which provides heterogeneity of physical structure, habitat diversity, trophic resources and shelter (Leira and Cantonati, 2008; Logez et al., 2016). Reservoirs with smaller fluctuations of water level reduce fish access to littoral habitats that are essential nursery areas and feeding grounds, as well as affect the timing and physiological condition for the reproduction of fish (Matthews, 1998; Vazzoler, 1996; Winemiller et al., 2016). Thus, water level variation that could provide better conditions for fish feeding and reproduction is virtually absent in these reservoirs with lower residence time, and this condition seems to result in impoverished fish assemblages. Unfortunately, reservoirs that are located upstream of the studied basins are usually larger (i.e., with larger areas) and have longer water residence times (i.e., accumulation reservoirs). This spatial arrangement adds a confounding element on the effect of reservoir cascades that will require further confirmation in additional river basins. However, observing the best sampled cascade (i.e., São Francisco), this decreasing pattern of diversity was quite clear, which reinforces the conclusions about the negative effects on the ichthyofauna.

2.4.2 Fish metacommunities structure and beta diversity

Our EMS analysis results in conjunction with beta diversity patterns further supported the role of the cascades as major drivers in species composition along the three river basins, as major changes occurred at the downstream end of the cascades, although intrinsic characteristics of each basin and reservoir also influenced community structures along the environmental gradients. The structure of the fish metacommunity along the cascade of the Iguaçu River basin followed a quasi-Gleasonian pattern. This pattern reveals individual species responses to environmental variation and may be linked to the dispersion capacity of each species (Gascón et al., 2016; Presley et al., 2010). This is because the Iguaçu River is known for having large waterfalls along its entire route

(Baumgartner et al., 2012), which favored the appearance of a higher number of endemisms in the basin (Daga et al., 2016). Thus, the evolutionary patterns coupled to the former and current characteristics of the basin have an influence on the actual metacommunity structure, presenting at certain points species capable of thriving in these environments with specifics geomorphological and hydrographical characteristics (Muniz et al., 2020).

On the other hand, the metacommunity structure in the Paranapanema basin showed a Clementsian pattern along the cascade. This structure implies similar responses by species groups to an environmental gradient (Clements, 1916). Pelicice et al. (2018) formerly analyzed the species composition in some reservoirs of this cascade and verified that, although many species seem to be widely distributed in all reservoirs, some are restricted to certain impoundments. A possible explanation for this pattern found in the Paranapanema basin may be due to the preservation of some remnant lotic areas and large tributaries close to some reservoirs, which allow an increase in some groups of species at certain points in the cascade. Several authors have evaluated the importance of tributaries (e.g., Laranjinha River, Cinzas River and Tibagi River) for the maintenance and viability of the ichthyofauna in other river basins and in the Paranapanema River (Dias et al., 2004; Galindo et al., 2020; Orsi et al., 2010). The presence of these environments helps the sustenance of the populations of migratory fish in some reservoirs along the cascade (e.g., Capivara), favoring an increase in species richness and also abundance. This indicates that the former and current characteristics of the basin, at the catchment but also and the local scales, interact with the native community assemblages to permit or preclude the establishment of newcomer species, thus shaping the actual metacommunity structure.

We found a pattern of nested species for São Francisco with loss of species in the upstream-downstream direction. This pattern was expected for the São Francisco River basin, since Santos et al. (2016) already found a nested distribution pattern for the benthic assemblage in this same cascade. Nestedness may arise as a result of environmental conditions of the habitats or species-specific characteristics, such as dispersal ability or tolerance of abiotic conditions (Henriques-Silva et al., 2013). Especially in reservoir cascades, where permanent lentic areas change environmental conditions and decrease hydrological connectivity, intensification of species loss is expected (Santos et al., 2016; Vitorino et al., 2016). This is because these changes caused by reservoirs can affect and eliminate functional groups (Mims and Olden, 2012), as evidenced by the reduction of migratory and invertivorous fish species in this same cascade (Santos et al., 2017) or other examples of reduction in migratory and rheophilic species in Neotropical reservoirs (Agostinho et al., 2008). Santos et al. (2017), who previously evaluated the São Francisco cascade, verified that the differences in the environmental, spatial and morphological characteristics that occur along these reservoirs (i.e., turbidity, area, type of operation, position of the reservoir in the cascade) were highly associated with different functional traits of the ichthyofauna. They found that along the cascade, the reservoirs characteristics act as filters for the presence or absence of the species, thus showing that the functional characteristics of the species were determinant for their occurrence in a certain reservoir along the cascade, since reservoirs change environmental conditions and as a consequence limit species presence.

2.4.3 Abundance patterns along cascades

In contrast to the general patterns observed in natural river basins (Bistoni and Hued, 2002; Suvarnaraksha et al., 2012), the results obtained with the SOMs indicated that in each of the three basins there were mainly both: species that reduce their abundance and species that sustain similar abundance along the cascades. Nonetheless, the number of species able to revert these patterns were limited to a few. These general trends reinforce the conclusions obtained with the linear models of the diversity indices, the structures of metacommunities and the beta diversity decomposition, indicating that reservoir cascades exert an influence on species presence, the resulting species diversity but also on the specific abundances.

Among clusters that exhibited reduction patterns, the main spatial variable selected was elevation (i.e., a proxy for the longitudinal gradient). This result suggests that fish-assemblage composition and abundance depend on the longitudinal position, with some influence of the adjacent reservoir, as verified by the serial discontinuity concept (Ward and Stanford, 1983). In fact, Loures and Pompeu (2018) evaluating a cascade of reservoirs in the Araguari river, found that almost 20% of the fish assemblage structure was explained by the position of the reservoir in the cascade, which emphasizes the importance of the longitudinal gradient for reservoirs cascades. Similarly, other studies have found a reduction in species abundance in a longitudinal gradient of dammed rivers (Agostinho et al., 2016; Orsi and Britton, 2014).

As with the DistLM analysis, we verified a convergence of the selected morphological variables in the clusters of decreasing patterns, such as area and residence time. Loures and Pompeu (2018) also found that the reservoir area is aligned to the species-area hypothesis (MacArthur and Wilson, 1967), which predicts that larger areas encompass a greater number of species and individuals. Thus, fish species abundance in the Neotropics tends to be positively correlated with the reservoir area, since larger areas have higher environmental heterogeneity and hence support larger populations (Bailly et al. 2016; Ortega et al., 2018). The residence time also influences the species abundance patterns, with lower values of abundance found in reservoirs with shorter residence times (due to the inferior stability mentioned in section 4.1). The largest reservoirs (i.e., usually uppermost) have long residence time and tend to have a greater abundance of species (Baumgartner et al., 2020; Li et al., 2012; Santos et al. 2017, 2018). Along the cascade, subsequent reservoirs generally tend to be smaller and have shorter residence times, which is reflected in the lower abundance of species. The residence time has a great influence on the nutrient retention, which influences the heterogeneity and productivity of the reservoir (Soares et al., 2012) and consequently the fish assemblage (Franco et al., 2018; Miranda and Krogman, 2015; Muniz et al., 2019).

Regarding the environmental variables, there was also convergence of turbidity, chlorophyll-*a,* and total phosphorus in the clusters where there was a reduction in species abundance. In general, along the cascades it is expected a decrease in turbidity (directly dependent on the retention time), decreases in phosphorus, nitrate and phosphate concentrations following the decrease in turbidity, an increase in light penetration, a decrease in oxygen concentration, and finally, a decrease in pH (Santos et al., 2020). Thus, limnological and trophic alterations can cause local changes in fish assemblage along reservoir cascades (Pagioro et al., 2005; Santos et al., 2018, 2020).

In addition, it was possible to notice that few groups of fish have a slight increase in their abundance along the cascade, while most of them did not clearly vary or presented a marked decrease or extirpation in the downstream reservoirs. Santos et al. (2017) demonstrated the role of dams as environmental filters, reducing the abundance of migratory and invertivorous species (e.g., *T. guentheri*, *T. galeatus*, *A. britskii* – species selected in clusters with decreasing trend). Along with that, there was an increase in the abundance of sedentary species towards the upstream reservoirs (e.g., *P. bifasciatus* and *A. affinis* – species selected in clusters with increasing trend) (Oliveira et al., 2018). Agostinho et al. (2016), in a synthesis of the impacts of reservoirs on the ichthyofauna, highlighted the dominance of species with trophic plasticity, sedentary lifestyle, parental care, small body size and low market value, which coincides with most of the species included in the clusters with flat trend along the cascades. In addition, due to changes in habitat quantity and quality, impoundments facilitate freshwater invasions by non-native species (Casimiro et al., 2017) and these often become abundant in these areas, as it was the case of *C. rendalli* in the Iguaçu River basin.

2.4.4 Limitation and caveats

As it usually occurs with ecological studies using large space-time scales, we recognize some limitations of our study that must be considered. First, we have sampling inconsistencies along the evaluated reservoir cascades. Two of the three basins analyzed (i.e., Iguaçu and Paranapanema) have only two sampling campaigns while the third basin (São Francisco) has 18. This imbalance in the number of samples may be responsible for a bigger contribution of the São Francisco basin in the found patterns. The second limitation is that for the São Francisco river basin there is a lack of environmental data as they were not measured in every biological survey. Although the data have these limitations, this does not take away the importance of this study, since little is known about the changes that cascading reservoirs cause on diversity, distribution and abundance of fish assemblages and the SOMs, where each basin is analyzed separately, indicated that few species are able to increase their abundances in the downstream reservoirs of the studied cascades.

2.5 Conclusions

The effects of the reservoir cascades on fish diversity, distribution, and abundance using large-scale spatial analyses (i.e., across river basins) was analyzed. Our results demonstrate that the impacts of reservoir cascades in contrasting basins affected fish assemblages, although each reservoir can respond differently due to e.g. environmental settings and operation because the effects seems to be context dependent (i.e., varies depending on the basin and its characteristics). Understanding the effects of reservoir cascades on fish assemblages is important, as its impacts are pervasive and, in many circumstances, can be irreversible (Agostinho et al., 2008). This understanding becomes even more necessary since hundreds of new reservoirs are planned for construction in the coming years (Zarfl et al., 2015). It will become necessary to favor more meaningful assessments of fish assemblage changes in relation to ecosystem functioning and its vulnerability to river fragmentation by dams, especially when constructed in sequence, given the possible amplification of negative effects on the biota.

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SUPPLEMENTARY INFORMATION

APPENDIX S1- Study reservoirs and variables used

Table S1. Mean (± standard deviation) of environmental variables used in this study. IG = Iguaçu; PP = Paranapanema; SF= São Francisco. N = sample size for each reservoir.

Reservoir	River	N	Water Temperature (°C)	Dissolved Oxygen (mg L^{-1})	Turbidity (NTU)	Chlorophyll-a (µg L^{-1})	pH	Conductivity (µS cm^{-1})	Nitrate (µg L^{-1})	Total phosphorus (µg L^{-1})	Secchi (m)
Foz do Areia	IG	2	22.1 ± 5.7	7.00 ± 0.1	10.77 ± 7.8	7.72 ± 9.1	7.66 ± 1.2	43.13 ± 5.5	461.50 ± 84.1	13.10 ± 1.7	1.95 ± 0.0
Salto Segredo	IG	2	22.8 ± 7.3	6.76 ± 0.2	10.57 ± 5.8	3.28 ± 1.7	6.95 ± 0.2	39.59 ± 10.4	558.50 ± 37.5	9.70 ± 4.7	1.33 ± 0.6
Salto Santiago	IG	2	23.0 ± 6.0	7.04 ± 0.1	4.79 ± 3.6	11.22 ± 14.8	7.70 ± 1.3	38.49 ± 1.9	422.50 ± 68.6	11.65 ± 2.1	2.03 ± 1.2
Salto Osório	IG	2	22.6 ± 5.6	7.23 ± 0.2	8.98 ± 0.0	12.01 ± 14.7	7.75 ± 1.4	37.68 ± 1.3	503.00 ± 8.5	6.20 ± 4.0	1.50 ± 0.4
Salto Caxias	IG	2	23.1 ± 4.0	7.04 ± 0.2	2.70 ± 0.3	3.65 ± 3.5	7.11 ± 0.4	37.64 ± 1.6	508.00 ± 50.9	10.45 ± 2.3	2.53 ± 0.2
Chavantes	PP	2	22.4 ± 3.1	7.49 ± 0.4	3.71 ± 4.1	2.82 ± 3.0	6.98 ± 0.4	55.39 ± 1.0	172.50 ± 46.0	7.20 ± 0.8	5.15 ± 1.1
Salto Grande	PP	2	20.3 ± 0.6	7.85 ± 0.0	4.73 ± 0.7	2.74 ± 1.7	7.34 ± 0.1	59.76 ± 1.8	227.00 ± 49.5	14.40 ± 5.8	5.80 ± 0.0
Canoas II	PP	2	26.0 ± 0.7	6.87 ± 0.6	7.42 ± 5.4	4.72 ± 3.7	6.80 ± 0.1	58.99 ± 2.6	200.50 ± 65.8	10.70 ± 2.4	1.18 ± 0.6
Canoas I	PP	2	26.2 ± 0.9	6.60 ± 0.4	9.73 ± 12.0	0.94 ± 0.8	6.89 ± 0.2	57.95 ± 1.7	191.50 ± 55.9	10.25 ± 0.5	1.95 ± 0.6
Capivara	PP	2	25.8 ± 0.3	6.45 ± 0.4	3.41 ± 0.6	3.55 ± 0.2	6.82 ± 0.2	57.64 ± 1.8	293.00 ± 28.3	8.35 ± 4.0	2.20 ± 0.6
Taquaruçu	PP	2	20.0 ± 0.1	7.34 ± 0.6	5.22 ± 2.0	4.16 ± 1.1	7.54 ± 0.4	59.49 ± 3.1	330.50 ± 91.2	8.60 ± 5.8	4.10 ± 0.0
Rosana	PP	2	19.2 ± 0.9	7.33 ± 0.2	4.85 ± 2.3	1.96 ± 2.3	6.96 ± 0.1	59.54 ± 1.0	361.00 ± 76.4	9.90 ± 0.0	2.10 ± 0.2
Sobradinho	SF	18	27.4 ± 1.6	7.66 ± 0.6	14.99 ± 9.1	2.52 ± 1.4	7.84 ± 0.3	63.80 ± 24.9	46.00 ± 39.1	66.50 ± 19.6	1.20 ± 0.6
Itaparica	SF	18	26.5 ± 2.0	7.75 ± 0.4	4.96 ± 2.5	2.83 ± 1.1	7.92 ± 0.3	70.92 ± 17.9	37.50 ± 22.5	59.50 ± 17.0	2.70 ± 1.1
Moxotó	SF	18	26.7 ± 1.9	7.65 ± 0.4	4.40 ± 1.8	2.58 ± 1.0	8.01 ± 0.4	109.4 ± 40.1	45.00 ± 38.2	66.00 ± 17.8	3.00 ± 1.2
Paulo Afonso I	SF	18	26.6 ± 1.6	7.63 ± 0.7	2.60 ± 2.1	1.71 ± 0.8	7.82 ± 0.5	69.00 ± 15.0	65.00 ± 35.7	50.50 ± 19.6	3.25 ± 0.9

Paulo Afonso IV	SF	18	26.3 ± 2.0	7.60 ± 0.4	3.68 ± 1.2	1.93 ± 0.6	7.99 ± 0.4	72.80 ± 17.1	23.50 ± 27.8	50.50 ± 16.4	3.23 ± 1.4
Xingó	SF	18	27.7 ± 1.5	7.55 ± 0.3	3.24 ± 1.3	3.29 ± 1.4	8.08 ± 0.2	73.09 ± 20.2	37.00 ± 29.2	49.00 ± 9.5	3.65 ± 1.2

Table S2. Morphological and spatial characteristics of the studied reservoirs.

Reservoir	River	Position	Elevation (m)	Distance to source (m)	Age (years)	Area (km^2)	Length (km)	Water residence time (days)	Volume (hm3)	Depth (m)	Accumulated volume (hm^3)
Foz do Areia	Iguaçu	1	721	407966.8	34	139	60	102	5779	135	0
Salto Segredo	Iguaçu	2	608	505150.1	22	84.88	70	47	3000	100	5779
Salto Santiago	Iguaçu	3	500	591024.3	35	208	70	50.8	6753	78	8779
Salto Osório	Iguaçu	4	398	656388.9	34	62.9	35	16	1270	43	15532
Salto Caxias	Iguaçu	5	326	746733.7	16	144.2	75	33	900	53	16802
Chavantes	Paranapanema	1	472	307396.1	44	400	40	418	8795	78	0
Salto Grande	Paranapanema	2	381	360560.9	56	12	15	1.5	44	9.2	8795
Canoas II	Paranapanema	3	364	396145.7	22	22.51	30	5.5	140	16.5	8839
Canoas I	Paranapanema	4	350	430385.0	15	30.85	30	3.8	207	26	8979
Capivara	Paranapanema	5	340	543581.1	39	419.3	110	119	10540	52.5	9186
Taquaruçu	Paranapanema	6	284	623807.5	25	80.1	60	10	672	26.5	19726
Rosana	Paranapanema	7	255	738426.8	28	220	90	18.6	1920	26	20398
Sobradinho	São Francisco	1	386	1846463.5	35	4214	200	104.40	34116	30	0
Itaparica	São Francisco	2	302	2306677.0	26	828	180	72	10782	101	34116
Moxotó	São Francisco	3	254	2332949.3	38	93	25	5	1150	50	44898
Paulo Afonso I	São Francisco	4	225	2338464.1	60	4.8	5	31	26	80	46048
Paulo Afonso IV	São Francisco	5	248	2351774.4	36	12.9	5	31	127	80	46074
Xingó	São Francisco	6	141	2403260.7	20	60	50	16	3800	100	46201

Table S3. Model selection table used to choose the best variables (with deltaAICc < 2) to perform the linear model analysis of of fish richness and the exponential of Shannon's index (Hill number of order 1, ${}^{1}D$).

Response variables	**Altitude**	**Area**	**Depth**	**Total phosphorus**	**Residence time**	**Secchi**	**df**	**AIC$_c$**	**delta**	**weight**
Richness	-0.828	1.594	-1.182		1.422	0.433	7	545.7	0.00	0.446
	-1.125	1.531	-1.121	0.371	1.383	0.515	8	545.8	0.18	0.409
	-0.700	1.298	-1.265		1.552		6	548.7	3.01	0.099
	-0.827	1.242	-1.244	0.174	1.546		7	550.4	4.77	0.041
		1.174	-1.596	-0.327	1.808		6	556.9	11.23	0.002
${}^{1}D$	-2.892	4.425	-1.256	1.503	1.892		7	811.1	0.00	0.386
	-3.647	5.180		1.682	1.336		6	812.8	1.76	0.160
	-2.721	4.258	-1.327	1.389	1.986	-0.298	8	813.0	1.96	0.145
	-1.793	4.906	-1.439		1.948		6	813.7	2.65	0.103
	-1.614	4.493	-1.555		2.130	-0.605	7	814.6	3.53	0.066

APPENDIX S2- Additional results

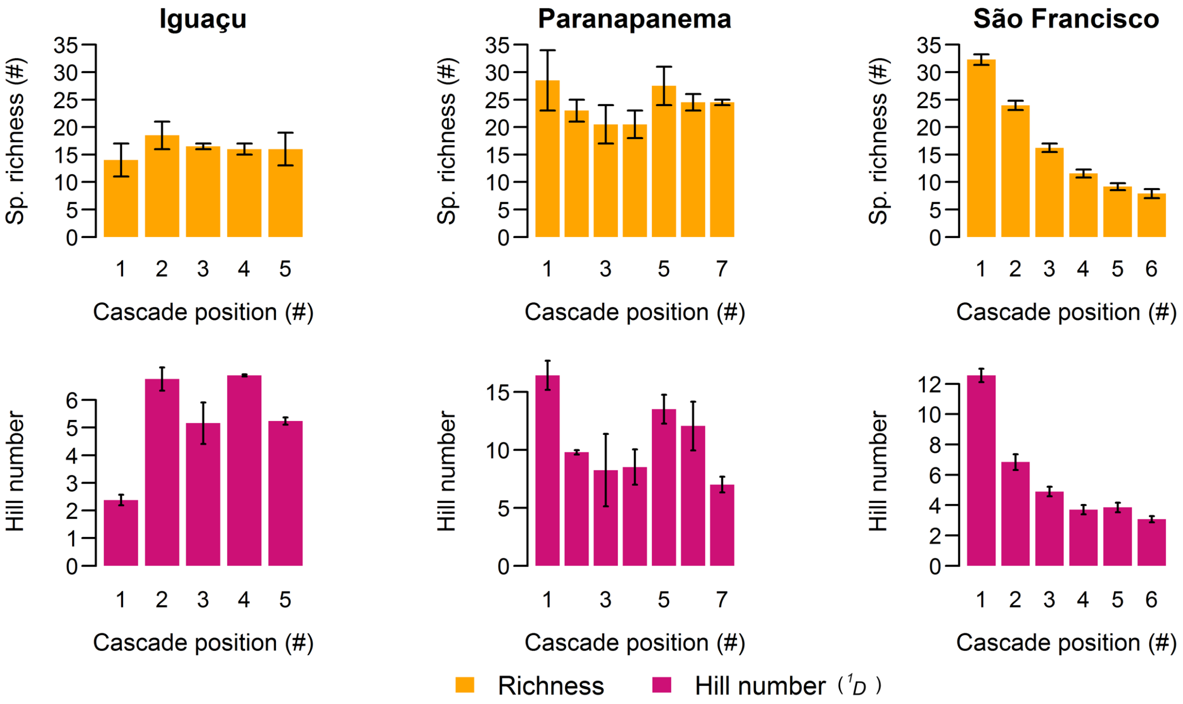

Figure S4. Box plots of diversity metrics (richness and the exponential of Shannon's index (Hill number of order 1, ^1D) along the reservoirs cascades in the three river basins.

Table S5. Results of the linear model analysis with p-value of the permutation for the selected model. *P* values < 0.05 are bolded.

Response variables (R^2 adjusted)	**Predictor variables**	**Estimate**	**SE**	**t-value**	***P*-value**
Richness (0.676)	Intercept	17.57	0.44	39.83	**<0.001**
	Altitude	-2.72	0.82	-3.30	**0.001**
	Residence time	1.98	0.62	3.19	**0.002**
	Depth	-1.33	0.65	-2.03	**0.044**
	Area	4.26	0.75	5.65	**<0.001**
	Secchi	-0.30	0.55	-0.54	0.588
	Total phosphorus	1.39	0.72	1.92	0.057
^1D (0.767)	Intercept	6.30	0.16	39.35	**<0.001**
	Altitude	-1.12	0.30	-3.76	**<0.001**
	Residence time	1.38	0.23	6.12	**<0.001**
	Depth	-1.12	0.24	-4.72	**<0.001**
	Area	1.53	0.27	5.59	**<0.001**
	Secchi	0.51	0.20	2.58	**0.012**
	Total phosphorus	0.37	0.26	1.41	0.160

SE, standard error of the estimate represents the average distance that the observed values fall from the regression line; t-value, t-distributed for generalizes linear mixed models; P-value, probability of a random influence of factor.

Table S6. Spearman's correlation test across components of beta diversity and its components and reservoir cascade position. r_S = Spearman's rank correlation coefficient (rho); βsor = beta diversity; βsim = turnover component; βsne = Nestedness component. *P* values < 0.05 are bolded.

Basin	**Variable**	r_S	***P*-value**
Iguaçu	βsor	1.0	0.083
	βsim	1.0	0.083
	βsne	-0.2	0.916
Paranapanema	βsor	-0.2	0.741
	βsim	-0.2	0.741
	βsne	0.5	0.356
São Francisco	βsor	1.0	**0.017**
	βsim	0.3	0.553
	βsne	1.0	**0.017**

Table S7. Results of of DistLM (Distance-based Linear Model) analysis with p-value of the permutations for the selected models. Pseudo-F = the multivariate analogue of Fisher's ratio, estimates by how much the sum of square deviates from random; d.f. = number of degrees of freedom. *P* values < 0.05 are bolded.

Components (R^2_{adj})	**Predictor variables**	**d.f.**	**Variance**	**Pseudo-F**	***P*-value**
*β*sor (0.663)	Area	1	0.409	3.773	**0.003**
	Depth	1	0.792	7.302	**0.001**
	Nitrate	1	2.095	19.320	**0.001**
	Residence time	1	0.395	3.643	**0.001**
*β*sim (0.718)	Area	1	0.362	3.705	**0.002**
	Depth	1	0.745	7.609	**0.001**
	Nitrate	1	2.065	21.087	**0.001**
	Residence time	1	0.364	3.724	**0.002**
*β*sne (3.265)	Area	1	0.042	9.156	**0.001**

Figures S8. Analysis with super-organising maps (Super-SOM)

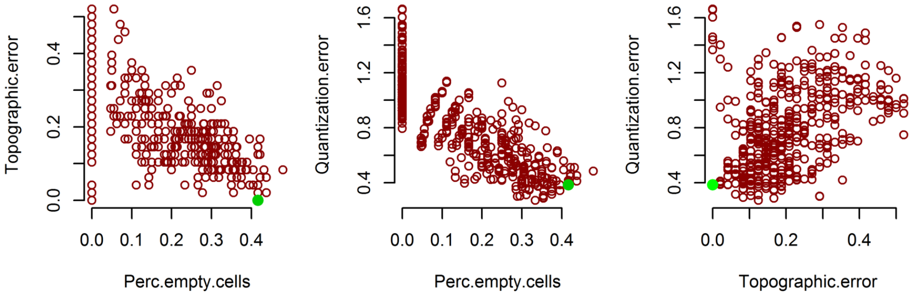

Figure S8a. Relationships of topographic and quantization errors with percentage of empty cells (i.e. unit neuron nodes) obtained during the optimisation of the dimensions (*X*, *Y*) of the super- organising map (Super-SOM) used to scrutinise the ecological trends in the Iguaçu River Basin. The selected Super-SOM rendered the topographic and quantization errors highlighted by the green dot (*X*=5 and *Y*=9). The percentage of empty cells is depicted for illustrative purposes since it was not considered to select the optimal Super-SOM.

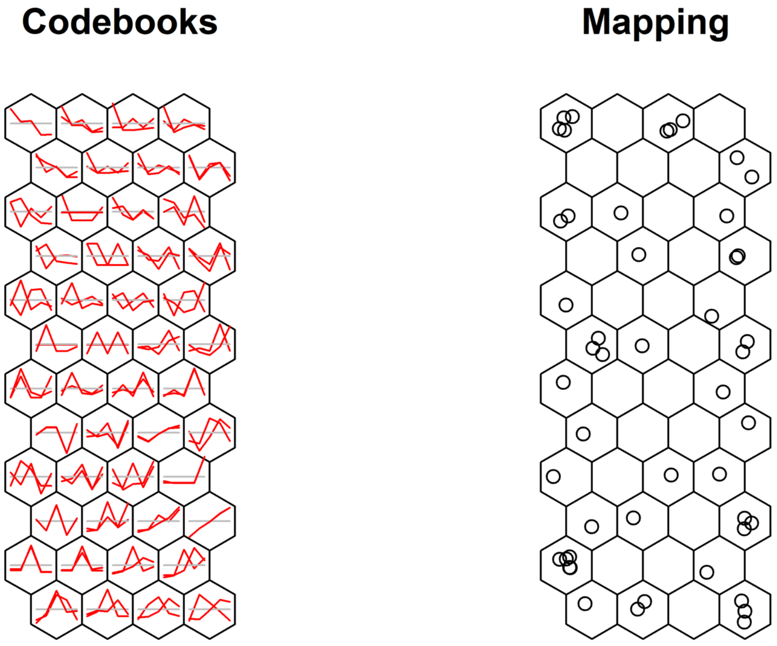

Figure S8b. Overlay of the codebooks of the optimal super-organising map (Super-SOM) summarising the ecological trends in the Iguaçu River Basin (left). Mapping of the species and environmental, morphological, and spatial factors within the optimal Super-SOM (right).

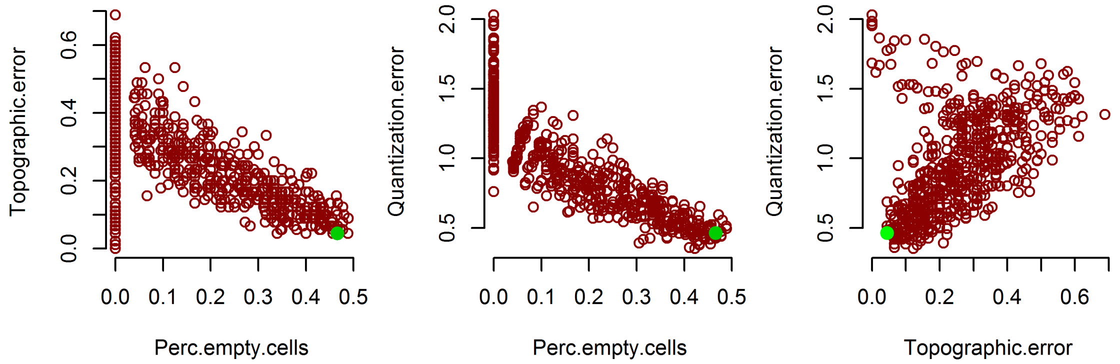

Figure S8c. Relationships of topographic and quantization errors with percentage of empty cells (i.e. unit neuron nodes) obtained during the optimisation of the dimensions (X, Y) of the Super-SOM used to scrutinise the ecological trends in the Paranapanema River Basin. The selected Super-SOM rendered the topographic and quantization errors highlighted by the green dot (*X*=9 and *Y*=10). The percentage of empty cells is depicted for illustrative purposes since it was not considered to select the optimal Super-SOM.

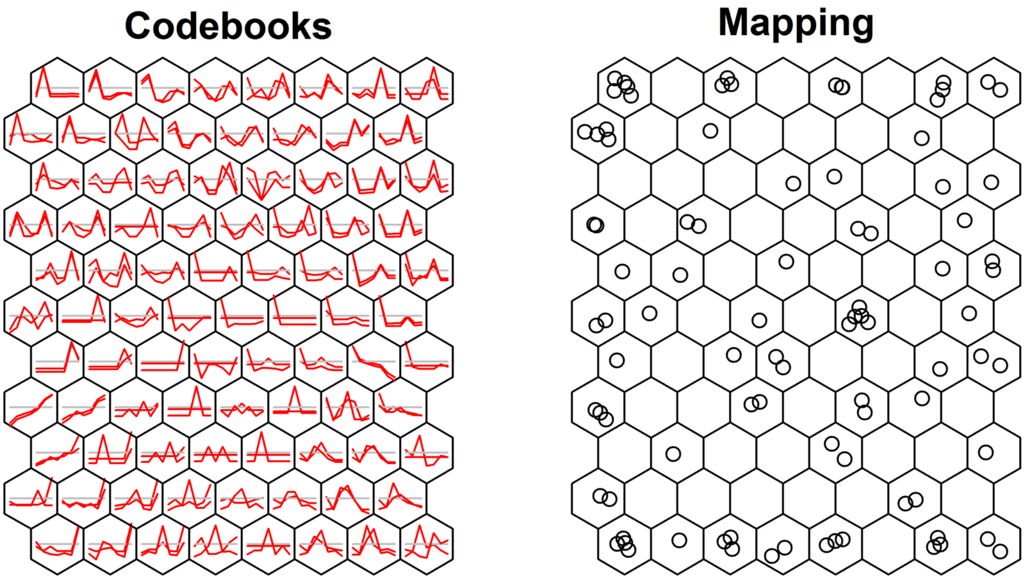

Figure S8d. Overlay of the codebooks of the optimal Super-SOM summarising the ecological trends in the Paranapanema River Basin (Left). Mapping of the species and environmental, morphological, and spatial factors within the optimal Super-SOM (Right).

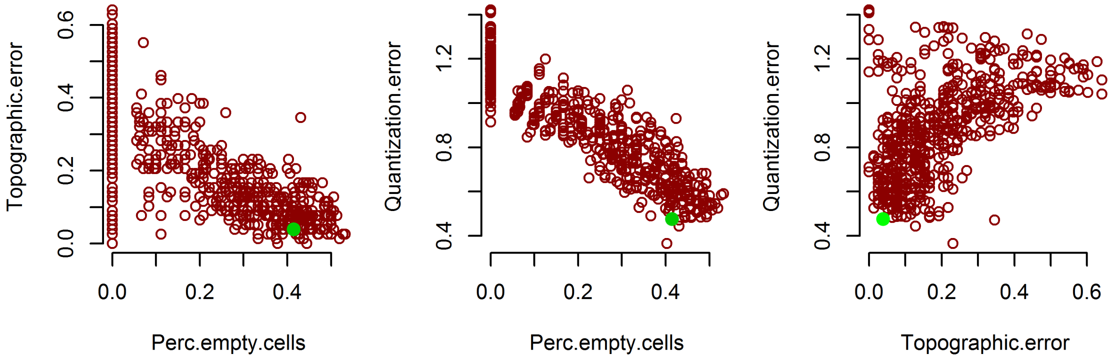

Figure S8e. Relationships of topographic and quantization errors with percentage of empty cells (i.e., unit neuron nodes) obtained during the optimisation of the dimensions (X, Y) of the Super-SOM used to scrutinise the ecological trends in the São Francisco River Basin. The selected Super-SOM rendered the topographic and quantization errors highlighted by the green dot (*X*=8 and *Y*=8). The percentage of empty cells is depicted for illustrative purposes since it was not considered to select the optimal Super-SOM.

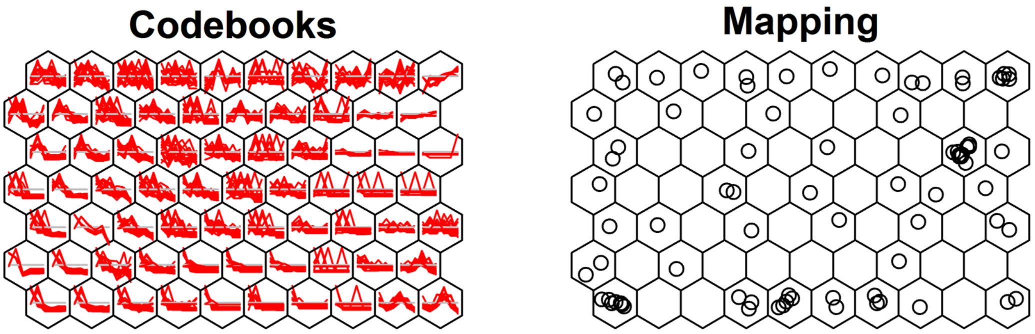

Figure S8f. Overlay of the codebooks of the optimal Super-SOM summarising the ecological trends in the São Francisco River Basin (Left). Mapping of the species and environmental, morphological, and spatial factors within the optimal Super-SOM (Right).

S9. Clusters of Super-SOM analysis

Table S9a. Percentages of the variables that were included in each group of factors of the three clusters formed for each basin (Iguaçu, Paranapanema and São Francisco).

Iguaçu

	Species	Environmental	Morphological	Spatial
Cluster 1	46.7%	25.0%	42.8%	66.7%
Cluster 2	43.3%	50.0%	57.1%	33.3%
Cluster 3	10.0%	25.0%	0.0%	0.0%

Paranapanema

	Species	Environmental	Morphological	Spatial
Cluster 1	44.44%	37.5%	14.3%	66.7%
Cluster 2	29.17%	62.5%	14.3%	0.0%
Cluster 3	26.39%	0.0%	71.4%	33.3%

São Francisco

	Species	Environmental	Morphological	Spatial
Cluster 1	41.7%	25.0%	57.1%	33.3%
Cluster 2	41.7%	75.0%	42.9%	66.7%
Cluster 3	16.7%	0.0%	0.0%	0.0%

Table S9b. Complete list of variables assigned to each cluster of each basin. Number 1 indicates selection of the variable in the respective cluster.

Iguaçu River basin			
Features	**Cluster 1**	**Cluster 2**	**Cluster 3**
Astyanax lacustris	1	0	0
Psalidodon bifasciatus	1	0	0
Astyanax dissimilis	1	0	0
Psalidodon gymnodontus	1	0	0
Astyanax minor	1	0	0
Apareiodon vittatus	1	0	0
Bryconamericus ikaa	0	1	0
Bryconamericus sp.	0	1	0
Cyprinus carpio	0	1	0
Australoheros cf. *facetus*	0	1	0
Ctenopharyngodon idella	0	1	0
Crenicichla iguassuensis	1	0	0
Corydoras paleatus	0	0	1
Crenicichla sp2	1	0	0
Cyphocharax santacatarinae	1	0	0
Geophagus iporangensis	0	1	0
Glanidium ribeiroi	0	1	0
Hypostomus commersoni	1	0	0
Hypostomus derbyi	0	1	0
Hoplias gr. *malabaricus*	0	1	0
Hypostomus myersi	0	1	0
Megaleporinus macrocephalus	1	0	0
Odontesthes bonariensis	1	0	0
Oligosarcus longirostris	1	0	0
Pimelodus britskii	0	0	1
Pimelodus ortmanni	1	0	0
Rhamdia branneri	0	1	0
Rhamdia voulezi	0	1	0
Tatia jaracatia	0	1	0
Coptodon rendalli	0	0	1
Chlorophyll	0	1	0
Conductivity	0	1	0
Dissolved.oxygen	0	0	1
pH	0	0	1
Secchi	1	0	0
Temperature	1	0	0
Total.phosphorus	0	1	0
Turbity	0	1	0

Accumulated.volume	1	0	0
Age	0	1	0
Area	1	0	0
Depth	0	1	0
Length	1	0	0
Residence.time	0	1	0
Volume	0	1	0
Altitude	0	1	0
Cascade.position	1	0	0
Distance.source	1	0	0

Paranapanema River basin

Features	**Cluster 1**	**Cluster 2**	**Cluster 3**
Apareiodon affinis	1	0	0
Astyanax lacustris	1	0	0
Apteronotus brasiliensis	0	0	1
Psalidodon bockmanni	1	0	0
Psalidodon fasciatus	1	0	0
Acestrorhynchus lacustris	1	0	0
Astronotus ocellatus	1	0	0
Apareiodon piracicabae	1	0	0
Ageneiosus militaris	0	0	1
Crenicichla britskii	1	0	0
Crenicichla haroldoi	1	0	0
Cichla kelberi	1	0	0
Crenichicla sp.	1	0	0
Crenicichla sp2	1	0	0
Geophagus iporangensis	1	0	0
Gymnotus carapo	0	0	1
Galeocharax gulo	0	0	1
Hypostomus ancistroides	0	1	0
Hypostomus cf. *auroguttatus*	1	0	0
Hypophthalmus oreomaculatus	0	1	0
Hypostomus hermanii	0	0	1
Hoplosternum littorale	1	0	0
Hoplias gr. *malabaricus*	0	0	1
Moenkhausia bonita	0	0	1
Hypostomus nigromaculatus	0	0	1
Hypostomus regani	0	0	1
Hypostomus strigaticeps	0	0	1
Hypostomus sp1	0	0	1

Hypostomus spp	0	0	1
Iheringichthys labrosus	1	0	0
Leporinus amblyrhynchus	1	0	0
Leporinus sp1	0	0	1
Leporinus sp2	0	0	1
Leporinus friderici	0	0	1
Leporinus lacustris	0	1	0
Megaleporinus obtusidens	0	1	0
Leporinus octofasciatus	0	0	1
Loricariichthys platymetopon	0	1	0
Leporellus vittatus	1	0	0
Moenkhausia intermedia	1	0	0
Metynnis cf. *maculatus*	0	1	0
Megalancistrus parananus	0	1	0
Pimelodus absconditus	0	1	0
Trachelyopterus galeatus	0	1	0
Pterodoras granulosus	0	1	0
Pimelodella gracilis	0	1	0
Prochilodus lineatus	0	1	0
Pimelodus maculatus	1	0	0
Pimelodus ortanus	0	1	0
Pinirampus pirinampu	0	1	0
Proloricaria prolixa	0	0	1
Proloricaria sp.	0	1	0
Plagioscion squamosissimus	0	0	1
Rhinelepis aspera	0	0	1
Roeboides descalvadensis	0	1	0
Rhinodoras dorbignyi	1	0	0
Rhamphichthys hahni	0	1	0
Rhamdia quelen	1	0	0
Rhaphiodon vulpinus	0	1	0
Schizodon borellii	0	1	0
Salminus brasiliensis	1	0	0
Sternopygus macrurus	1	0	0
Serrasalmus maculatus	1	0	0
Serrasalmus marginatus	0	1	0
Schizodon nasutus	1	0	0
Satanoperca sp.	0	1	0
Steindachnerina brevipinna	1	0	0
Steindachnerina insculpta	1	0	0
Triportheus angulatus	1	0	0
Tatia neivai	1	0	0
Chlorophyll	0	1	0

Conductivity	1	0	0
Dissolved.oxygen	0	1	0
pH	0	1	0
Secchi	0	1	0
Temperature	1	0	0
Total.phosphorus	0	1	0
Turbity	1	0	0
Accumulated.volume	1	0	0
Age	0	1	0
Area	0	0	1
Depth	0	0	1
Length	0	0	1
Residence.time	0	0	1
Volume	0	0	1
Altitude	0	0	1
Cascade.position	1	0	0
Distance.source	1	0	0

São Francisco River basin

Features	**Cluster 1**	**Cluster 2**	**Cluster 3**
Acestrorhynchus britskii	0	0	1
Acestrorhynchus lacustris	1	0	0
Astronotus ocelatus	0	1	0
Astyanax lacustris	1	0	0
Anchoviella vaillanti	0	0	1
Bryconops affinis	0	0	1
Brycon orthotaenia	1	0	0
Bergiaria westermanni	0	1	0
Conorhynchos conirostris	0	1	0
Cichla spp	0	1	0
Crenicichla lepidota	0	1	0
Curimatella lepidura	1	0	0
Colossoma macropomum	1	0	0
Cichlasoma sanctifranciscense	0	1	0
Duopalatinus emarginatus	0	1	0
Leporinus sp.	1	0	0
Eigenmanni virescens	1	0	0
Franciscodoras marmoratus	0	1	0
Gymnotus carapo.1	0	1	0
Hoplias intermedius	0	1	0
Hoplosternum littorale	1	0	0

Hoplias gr. *malabaricus*	1	0	0
Hypostomus spp.1	0	1	0
Lophiosilurus alexandri	0	1	0
Leporinus melanopleura	0	1	0
Leporinus piau	0	0	1
Leporinus taeniatus	1	0	0
Leporellus vittatus	1	0	0
Megalancistrus barrae	0	1	0
Megaleporinus reinhardti	1	0	0
Moenkhausia costae	0	0	1
Metynnis spp	1	0	0
Myleus micans	0	1	0
Orthospinus franciscensis	1	0	0
Oreochromis niloticus	1	0	0
Prochilodus argenteus	1	0	0
Prochilodus brevis	0	1	0
Pseudoplatystoma corruscans	1	0	0
Prochilodus costatus	0	0	1
Pterygoplichthys etentaculatus	0	1	0
Pachyurus francisci	0	0	1
Phenacogaster franciscoensis	0	1	0
Trachelyopterus galeatus	1	0	0
Pimelodus spp	1	0	0
Pimelodus maculatus	0	1	0
Pygocentrus piraya	1	0	0
Pachyurus squamipinnis	0	1	0
Plagioscion squamosissimus	0	0	1
Rhinelepis aspera.1	0	1	0
Rineloricaria sp.	0	1	0
Roeboides xenodon	0	0	1
Serrasalmus brandtii	0	0	1
Steindachnerina elegans	0	1	0
Salminus franciscanus	1	0	0
Schizodon knerii	1	0	0
Sternopygus macrurus.1	0	1	0
Synbranchus marmoratus	0	1	0
Tetragonopterus franciscoensis	1	0	0
Triportheus guentheri	1	0	0
Chlorophyll	0	1	0
Conductivity	0	1	0
Dissolved.oxygen	0	1	0
pH	0	1	0
Secchi	0	1	0

Temperature	0	1	0
Total.phosphorus	1	0	0
Turbity	1	0	0
Accumulated.volume	0	1	0
Age	0	1	0
Area	1	0	0
Depth	0	1	0
Length	1	0	0
Residence.time	1	0	0
Volume	1	0	0
Altitude	1	0	0
Cascade.position	0	1	0
Distance.source	0	1	0

3 FISH TROPHIC GUILDS ORGANIZATION IN RESERVOIRS WITH DIFFERENT ENVIRONMENTAL, SPATIAL, AND MORPHOLOGICAL FEATURES

ABSTRACT

Several studies have shown that reservoirs and their morphological characteristics alters the continuity in matter, energy, and nutrient transfer in rivers, which can alter resource availability, food supply and, ultimately fish trophic structure. We sampled 29 reservoirs to verify the main factors related to the structure of their fish trophic guilds. We determined the relative importance of spatial, morphological and environmental characteristics of the reservoirs (predictors) on the distribution patterns of fish trophic guilds. To assess the influence of these sets of predictors on the composition and abundance of fish trophic guilds, we used variation partitioning analyses. Distance-based redundancy analysis was used to examine the influence of predictors on the spatial distribution of samples for the three components of variation partitioning. The structure of fish trophic guilds revealed that the spatial features were the most important predictors, followed by the environmental and the morphological ones. The trophic guilds that showed spatial segregation were herbivores and omnivores. Reservoirs with higher concentration of total nitrogen had a greater abundance of herbivores and detritivores, whereas higher concentrations of total suspended material were related to greater abundance of piscivores. Older reservoirs had lower abundances of herbivores and piscivores and greater abundances of omnivores. Larger reservoirs had a greater abundance of piscivores and omnivores. Longer water retention time was related to a greater abundance of piscivores. Our findings have important implications for the management of reservoirs since changes in the abundance of trophic guilds can severely modify the networks of ecosystem interactions.

Keywords: Ecoregions · Iguaçu River · Neotropical fish · Upper Paraná · Water resource management

3.1 Introduction

Ecological communities and the study of their structuring factors have a long and rich history. Especially for freshwater fish, several factors were listed for acting simultaneously influencing the structuring of these communities, such as historical events, biotic interactions, environmental variables, and dispersal (Poff 1997; Jackson et al. 2001; Cetra et al. 2017). However, the modification of aquatic environments as a result of anthropogenic actions (e.g., dam constructions) can lead to additional and important changes in the distribution and structure of aquatic biota, being one of the major threats to freshwater fish (Poff 1997; Tejerina-Garro et al. 2005; Agostinho et al. 2016; Pelicice et al. 2018).

Most of the world's large rivers are already fragmented by dams, with many fluvial systems converted into series of impoundments. A wide range of studies has shown that the construction of dams in rivers constitutes one of the main sources of fish assemblage alterations due to changes in natural flow regimes (Poff and Zimmerman 2010; Pelicice et al. 2015; Winemiller et al. 2016; Dias et al. 2020). The formation of huge lentic areas (e.g., reservoirs) changes several environmental filters that regulate local assemblages, related mainly to hydrological, morphological, and limnological conditions (Poff 1997; Agostinho et al. 2016). Specifically, impoundments alter the continuity in the matter, energy, and nutrient transfer (Vannote et al. 1980; Ward and Stanford, 1983), which can alter resource availability (Luz-Agostinho et al. 2008; Abujanra et al. 2009), reproductive success, and recruitment (Agostinho et al. 2004; Oliveira et al. 2015; Angulo-Valencia et al. 2016), and ultimately fish species composition (Ganassin et al. 2021).

One of the main factors that limit the establishment and initial accommodation of the fish fauna in these new environments is the water dynamic (Mérona and Vigouroux

2012). This occurs because the rapid changes from the flooding and new flow conditions change the diet and the trophic structure of the fish fauna, favoring the proliferation of some species and the disappearance of others (Delariva et al. 2013; Dias et al. 2020). In the initial phases of reservoir formation, it is observed an intense heterotrophic activity, due to the incorporation of the terrestrial organic material into the aquatic environment (Loureiro-Crippa and Hahn 2006; Agostinho et al. 2007; Gubiani et al. 2011). After few years, it is possible to detect a process of trophic accommodation and depression, with a decrease in nutrient availability due to sedimentation and exportation processes (i.e., marginal areas do not have much influence on the trophic structure of fish assemblages) (Agostinho et al. 2007; Cunha-Santino et al. 2013). Therefore, these changes in food availability cause a large restructuration of the food web, which results in a new trophic ecosystem structure (Baxter 1977). Additionally, the morphological characteristics in local and regional factors of the dams (i.e., design of construction and its operational procedures), such as morphometry of the catchment, discharge, patterns of water circulation, depth, habitat structure, species pool, and surface area are important determinants of the degree of alteration in the structure and dynamics of the local biota (Agostinho et al. 2016), which also influence the trophic structure.

Regarding the organization of trophic guilds in reservoirs, it is expected that environmental variables act as proxies of productivity, and morphological variables operate together in determining higher or lower values of the abundance of certain guilds (Ximenes et al. 2011; Lima et al. 2018; Muniz et al. 2020). For instance, reservoirs that have higher water residence values (i.e., reduced flow) show an increase in sedimentation rates, which over time causes changes in productivity and limnology in these environments, reducing the abundance of herbivores and detritivores (Muniz et al. 2020; Santos et al. 2020). However, under these conditions, omnivorous species (i.e., species considered trophic opportunists) can be favored due to pre-adaptations favorable to the consumption of a wide variety of food resources (Agostinho et al. 2016). The age of the reservoirs is also determinant in the abundance of guilds (Muniz et al. 2020). For example, older reservoirs have lower primary production values, which causes a reduction in the abundance of the majority of the trophic guilds and an increase in small opportunistic fish. Consequently, piscivores are favored in these environments, because they prey small opportunistic fish that became abundant (Gubiani et al. 2011; Agostinho et al. 2016).

Understanding the variations caused in the trophic composition of the ichthyofauna in dammed environments is essential to assess the real impacts of reservoirs and to support in management and operation plans of these artificial systems. Thus, this study aimed to verify the main factors that explain the structure of fish trophic guilds in 29 Neotropical reservoirs. We determine the relative importance of spatial, morphological and environmental characteristics of reservoirs on the distribution patterns of fish trophic guilds. We expect to find that environmental, and morphological variables of reservoirs will be more correlated with the distribution of fish trophic guilds than spatial variables. More specifically, we expect higher abundance of herbivores, detritivores, invertivores, and insectivores guilds in reservoirs with higher concentrations of organic matter and nutrients (i.e., more strongly correlated with environmental variables), and higher abundance of piscivores and omnivores guilds are expected in larger/deeper, older, and with longer water residence time reservoirs (i.e., more strongly correlated with morphological variables).

3.2 Methods

3.2.1 Study area

We studied 29 reservoirs located in rivers of the Paraná State and neighboring states in Brazil (Fig. 1 and Table S1 in Supplementary File 1). Twelve reservoirs are located in the Iguaçu River basin; seven in the Paranapanema River basin; four in the Coastal (or Litorânea) drainage basin; two in the Tibagi River basin; two in the Ivaí River basin; and two in the Piquiri River basin (Fig. 1 and Table S1 in Supplementary File 1). Therefore, out of the 29 studied reservoirs, 25 belong to the Paraná River basin (Paranapanema, Tibagi, Ivaí, Piquiri, and Iguaçu rivers), all running westward (i.e., Inland Slope), and another four reservoirs belong to the Coastal basin in drainages emptying directly into the Atlantic Ocean (i.e., Atlantic Slope). However, the Iguaçu River basin is isolated from the Paraná River by an insurmountable barrier for fish (the Iguaçu Falls), while the other river basins running in the Inland Slope belong to the upper Paraná River basin. Thereby, for better visualization, the reservoirs were classified as belonging to three distinct ichthyofauna provinces: i) Iguaçu - reservoirs located within the limits of the Iguassu ecoregion (sensu Abell et al. 2008); ii) Paraná - reservoirs within the limits of the upper Parana ecoregion (sensu Abell et al. 2008) encompassing the Tibagi, Piquiri, Ivaí and Paranapanema rivers; iii) Coastal - reservoirs within the limits of the Ribeira de Iguape and Southeastern Mata Atlântica ecoregions (sensu Abell et al. 2008) situated in the Atlantic Slope.

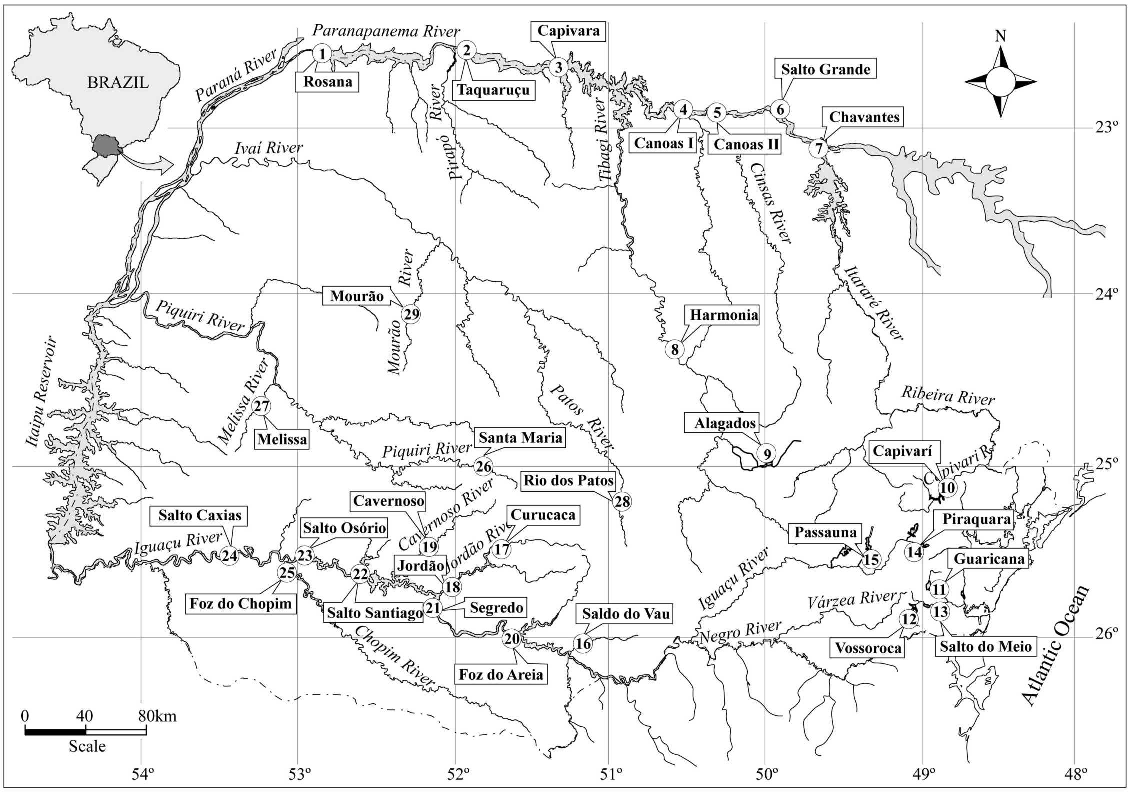

Fig. 1 Map showing the location of the 29 studied reservoirs in river basins from Paraná State and neighboring states

3.2.2 Data collection

3.2.2.1 *Fish samplings*

Fish assemblages were sampled in the lacustrine region of the reservoirs, in different habitat (littoral, surface—pelagic, and near the bottom—bathypelagic) using gillnets of different mesh sizes (2.4 – 14 cm between opposing knots) exposed for 24 h. Fish were collected in the morning, afternoon, and night. The collections were carried out in 2001 in the dry (july) and rain (november) periods. Taxonomic identification of the fishes collected in the Iguaçu River basin follows Baumgartner et al. (2012) and Mezzaroba et al. (2021), Frota et al. (2016) and Reis et al. (2020) to the Ivaí River basin, Cavalli et al. (2018) and Reis et al. (2020) to the Piquiri River basin, Jarduli et al. (2020) and Reis et al. (2020) to the Paranapanema and Tibagi River basins, and Oyakawa et al. (2006), Frota et al. (2019), and Reis et al. (2020) to the Coastal basin. The list of species captured in each river basin is presented in Table S2 in Supplementary File 2.

3.2.2.2 *Characterization of trophic guilds*

The use of trophic guilds has been widely used to detect changes caused by disturbances in fish communities (Delariva et al. 2013; Félix et al. 2013; Ferrareze et al. 2015; Garcia et al. 2018; Lima et al. 2018; Dias et al. 2020). Given the fact that guild is defined as "a group of species that exploits the same class of environmental resources in a similar way" (Root 1967), the guild-based approach is promising since it can aggregate species from different taxonomic positions, because it simplifies community analysis and allows comparisons between different locations and environments (Gerking 1994; Growns 2004; Welcomme et al. 2006; Vasconcelos et al. 2014; Dias et al. 2020). Thus, comparing trophic structures of fish assemblages from different reservoirs through the guild approach can facilitate to understand the processes and impacts that occur after reservoir is formed, and, maybe, reveal commons patterns. Also, the guild-based approach accounts for intrinsic differences in the identity of species, providing an overview of how fish populations are distributed and what influences this distribution as a result of the changes generated by the construction of dams and associated reservoirs (Arantes et al. 2019).

Fish species were classified into six trophic guilds (Table S3 in Supplementary File 3) based on published papers (see references in Supplementary File 4), as follow: i) Herbivores – species that feed primarily on algae and superior plants such as leaves, seeds, and fruits; ii) Invertivores – species that explore the river floor mainly in the bottom strata, feeding on benthic organisms such as testate amoebae, microcrustaceans, and small mollusks; iii) Insectivores – species that predominantly ingest aquatic and terrestrial insects at different stages of development; iv) Omnivores – species that consume plants ranging from algae to higher plants and animals from invertebrates to fish (these species feed on at least three trophic levels, without an obvious predominance of any particular resource); v) Piscivores – species that consume mainly fish including foraging species and juveniles of large-sized fish species, and that can complement their diet with insects, plants or invertebrates but in low proportions; vi) Detritivores – species that consume large amounts of debris or sediment along with associated organisms, such as algae, larvae of aquatic insects (especially chironomids), fragments of plants, adult insects, and benthic invertebrates.

3.2.2.3 *Environmental data*

Limnological conditions have a strong influence on the structure of fish assemblages at local scales, as they are related to productivity, ecological tolerance, and fitness (Huston 1979, 2004; Miranda and Krogman, 2015). Limnological variables (i.e., environmental features) were measured from surface water samples obtained on the same day of fish sampling. Conductivity (µS cm^{-1}), pH, turbidity (NTU), and dissolved oxygen (mg L^{-1}) were measured in the field with a multiparameter probe. Water collected with a Van Dorn sampler (2.5 L) was stored in polyethylene bottles, placed on ice, and preserved in low temperatures until analysis. Following standard protocols (Mackereth et al. 1978; APHA 2005), we obtained the following variables: total suspended material (mg L^{-1}), alkalinity (mEq L^{-1}), total phosphorus (µg L^{-1}; APHA 2005), orthophosphate (µg L^{-1}; APHA 2005), phosphate (µg L^{-1}; APHA 2005), total dissolved phosphorus (µg L^{-1}; APHA 2005), chlorophyll-*a* (µg L^{-1}; Nusch 1980), total nitrogen (µg L^{-1}; Mackereth et al. 1978), nitrate (µg L^{-1}; Mackereth et al. 1978), ammonia (µg L^{-1}; Mackereth et al. 1978), dissolved organic carbon (µg L^{-1}; Shimadzu–TOC5000A) and biovolume of phytoplankton (mm^3 L^{-1}).

3.2.2.4 *Spatial data*

To summarize the spatial structure of reservoirs, we used Principal Coordinates of Neighbour Matrices (PCNM). For the construction of the spatial data matrix, we used the hydrological distance between the reservoirs. The hydrologic distance is calculated on a shapefile representing the hydrographic network, using as starting and finishing points the geographical coordinates of each reservoir (i.e., latitude and longitude). The calculation of the distances is performed with the Dijkstra algorithm, which measures the smallest distances between two points (Dijkstra 1959; Loro et al. 2015). We performed the calculation with the QNEAT3 complement (Qgis Network Analysis Tool- box), implemented in Qgis 3.0 (QGIS Development Team 2018).

The PCNM method is used to model spatial structure at multiple spatial scales and to incorporate this representation in statistical analysis (Borcard et al. 2011). The spatial structure, derived from the hydrological distances among reservoirs, was summarized in a resemblance matrix (Euclidean distance) and this matrix was truncate to retain only the distances among close neighbors. Then, a Principal Coordinates Analysis (PCoA) of the truncated distance matrix was conducted to summarize the spatial structure in PCNMs (axes generated in the PCoA). The eigenvectors were then used as spatial explanatory variables in a model. The scores of the first PCNM represent the greatest scale in the sample sites, while the last represents the smaller scale (i.e., the PCNM produces a spectral decomposition of space and can model spatial structure at all the spatial scale that can be perceived by the data set; Borcard et al. 2004). This procedure was performed in *R*, using the “pcnm” function implemented in the *vegan* package.

3.2.2.5 *Morphological data*

Following Gubiani et al. (2011) and Pelicice et al. (2015), we also recorded some variables that are more related to the morphology and operation of the studied reservoirs: reservoir age, area, depth, volume, water residence time, and if a reservoir belongs, or not, to a reservoir cascade (Table S1 in Supplementary File 1). These variables are directly related to the structuring of fish communities in reservoirs. As reservoirs age, changes in diversity and functioning of fish communities are expected, such as a reduction in species richness and selection of species that have more generalist strategies (Miranda and Krogman 2015; Muniz et al. 2020). The variables area, depth, and volume refer to the size of the reservoir and are directly related to the species-area hypothesis and habitat heterogeneity, one of the main structuring elements of fish communities (Bailly et al. 2016). The residence time of the water is related to the flow and fluctuations in water level of the environment; frequent and unpredictable fluctuations directly affect the species that inhabit the littoral region, whether for shelter or foraging (Santos et al. 2017). Since reservoir cascades have predictable environmental variations (e.g., increased water transparency in the downstream direction), fish communities belonging to this system respond to these variations (Santos et al. 2017; Ganassin et al. 2021). All of these influences in the structure of the fish communities mentioned above have direct effects on food webs, also leading to direct effects on composition of trophic guilds in reservoirs.

3.2.3 Data analysis

We used variation partitioning analyses to assess the influence of three predictor sets on the composition and abundance of fish trophic guilds. These predictor sets of variation partition were: environmental (which included total nitrogen (TOTN), total suspended material (TSM), chlorophyll-*a*, and conductivity); morphological (age, area, water residence time, and a categorical variable that indicates whether the reservoir belong to a cascade); and spatial (which included PCNM15, PCNM5, PCNM1, PCNM6, PCNM13, PCNM4, PCNM11, and PCNM2). Distance-based redundancy analysis (dbRDA), using the Euclidean distance in the Hellinger-transformed matrix of composition and abundance of trophic guilds, was used to examine the influence of three components of variation partitioning on the spatial distribution of species, as described by the composition of trophic guilds in multivariate space. For the visualization of the results detected by the dbRDA we used a canonical analysis of principal coordinates (CAP), which generates graphic clusters through permutation (Anderson and Willis 2003).

For all statistical analyses some data transformations and variables selection were performed, as described below. The environmental variables (except pH) were $\log_{10}(x)$ transformed to homogenize the scale of the different units of measurement included in this matrix. To reduce the effects of very abundant guilds, we transformed the abundance of trophic guilds into square roots (Clarke and Gorley 2006). For each set of variables that represent the evaluated components, the correlation value between them was evaluated, and for the pairs of variables that presented Pearson correlation ($|r|$) > 0.7, one of them was removed, as recommended by Dormann et al. (2013). This procedure is important to avoid multicollinearity problems in models. Then, with the environmental variables selected, we carried out a forward selection procedure to select only the environmental variables that had significant influences on the composition and abundance of fish trophic guilds. This procedure was also performed for the spatial component since it had 24 PCNMs and it is the most recommended selection of variables in these cases (Borcard et al. 2011). Forward selection is recommended when there is a large set of variables and the objective is to reduce dimensionality, to increase the predictive power of models (i.e., reduce the loss of degrees of freedom).

3.3 Results

Variation partitioning analyses (Fig. 2 and Table 1) regarding the structure of fish trophic guilds revealed that: i) the spatial characteristics (18%) were the most important predictors, followed by environmental features (5%); ii) rather surprisingly, morphological features of the reservoirs explained minimal variation (only 1%); iii) the joint variation explained by environmental and spatial features was also very important (13%). All these predictors explained 43% of the data set variability. Spatial variables, especially PCNM2 and PCNM5, showed significant correlations with environmental and morphological variables (Fig. 3). This correlation shows spatial patterns of large scales in the assessed environmental and morphological variables. Furthermore, all morphological variables were correlated in some way with environmental variables, especially with conductivity, chlorophyll-*a*, and total suspended material, showing that the morphology of the reservoir affects the environmental conditions and local productivity (which explains the significance of its overall effect rather than the unique; Table 1).

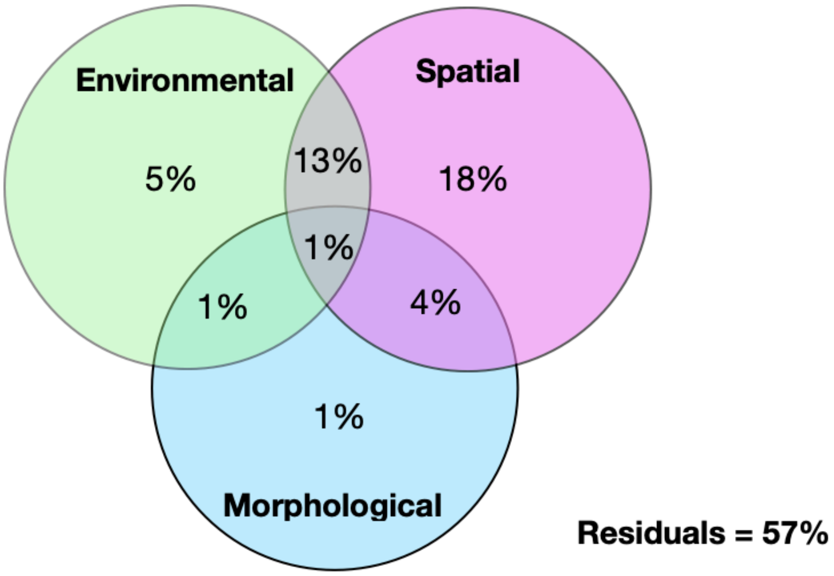

Fig 2 Results of the variation partitioning analyses of the key structural components of fish trophic guilds. The figures correspond to percentages. The analysis used three sets of predictors: environmental features; spatial components; and morphological features. See Methods for further details

Table 1 Variation partitioning analyses of three predictor sets on the metrics of all fish trophic guilds. The explained variation (R^2_{adj}) and corresponding P value are shown

Response variable	**Factors**	$\boldsymbol{R^2_{\text{adj}}}$ **overall**	$\boldsymbol{P}$	$\boldsymbol{R^2_{adj}}$ **unique**	$\boldsymbol{P}$
Abundance of all trophic guilds	Environmental	0.202	**0.001**	0.054	**0.021**
	Spatial	0.360	**0.001**	0.181	**0.001**
	Morphological	0.068	**0.011**	0.013	0.233

Note: Bolding indicates significant *P* values. *P* significance based on 9999 randomizations.

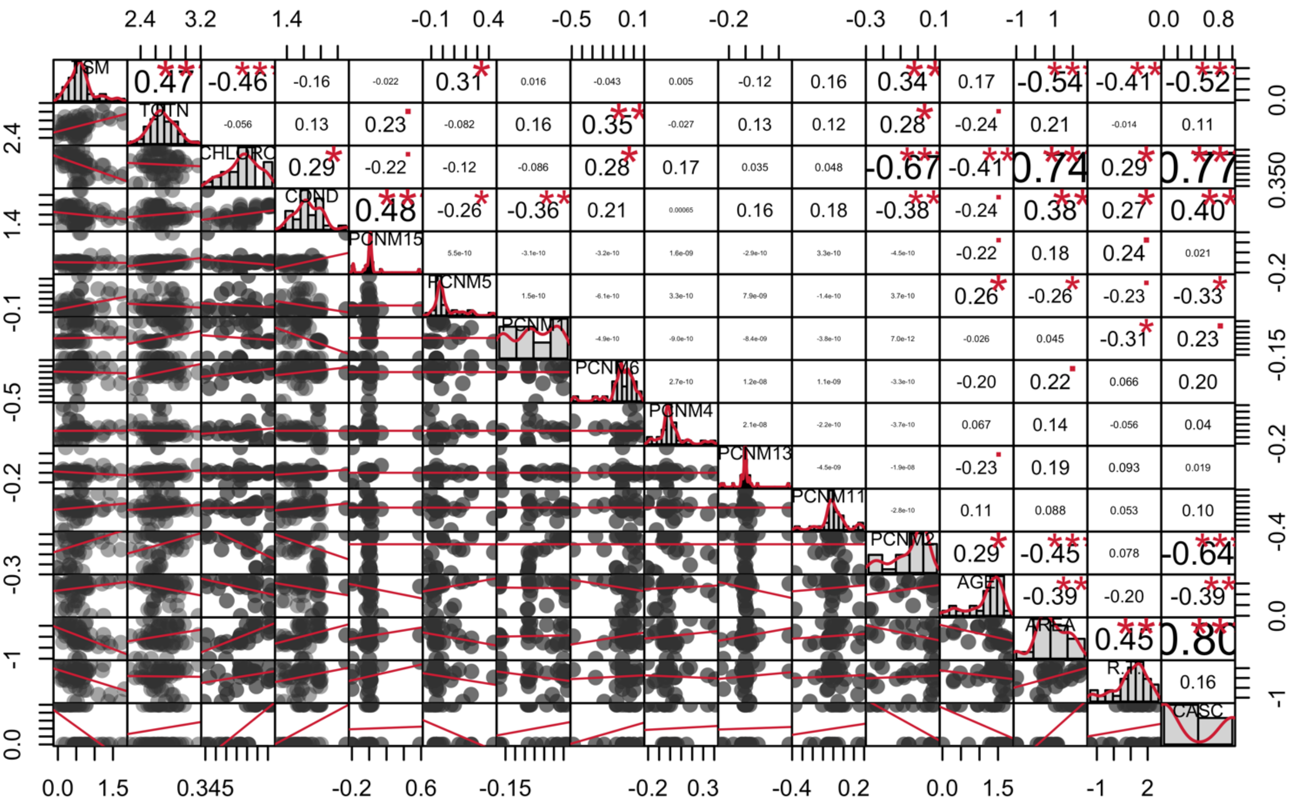

Fig 3 Pairwise relationships between all selected predictors for evaluation of shared effects. Below the diagonal, the bivariate scatterplots with the linear regression function are shown; the diagonal shows the histogram with an estimated Kernel density function; above the diagonal, the Pearson correlation coefficients with significance levels (▪, *P* < 0.10; *, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001)

Through the results of the dbRDA, we were able to indicate more specific relationships among the predictors selected in the three evaluated components (environmental, spatial and morphological) and the fish trophic guilds. Regarding the environmental component, it was possible to observe that herbivores had high positive correlation with total nitrogen concentrations, i.e., they were in greater abundances in reservoirs with higher values of this variable, especially in reservoirs of the Iguaçu province (Fig. 4a). On the other hand, omnivores and invertivores were found in greater abundances in reservoirs with higher values of total suspended material and conductivity, respectively. The guilds piscivores, insectivores, and detritivores did not seem to be related to any of the environmental variables, although detritivores showed a tendency to increase abundances in reservoirs with higher concentration of nitrogen and suspended total material (see Fig. S1 in Supplementary File 5).

The spatial variables PCNM 1, PCNM15, and PCNM6 tended to separate reservoirs of the Iguaçu province from the others (Fig. 4b). Most of the reservoirs in this province showed high abundances of herbivores. Furthermore, PCNM5 seems to contain most reservoirs of the Paraná province, with high abundance of omnivores. The other trophic guilds did not show such clear differences between the provinces (see Fig. S2 in Supplementary File 5).

Finally, for the morphological component, it is possible to notice that the different characteristics of the reservoirs had fewer effects in the differentiation of guilds (Fig. 4c; all guilds are near in this figure). However, some significant relationships have been verified (see Fig. S3 in Supplementary File 5). Age of reservoirs showed positive relationships with the abundance of omnivores and negative relationships with the abundance of piscivores, detritivores, and herbivores. From the visual inspection of the dbRDA graph, it is possible to verify that the oldest reservoirs are inserted in the Paraná province. On the other hand, reservoirs with larger areas, common in the Iguaçu province, presented a greater abundance of piscivores and herbivores. In addition, the guild of piscivores also appears to be correlated with the residence time of the water, and herbivores related to the insertion of the reservoir in a cascade system. The other trophic guilds showed no differences considering the morphological component.

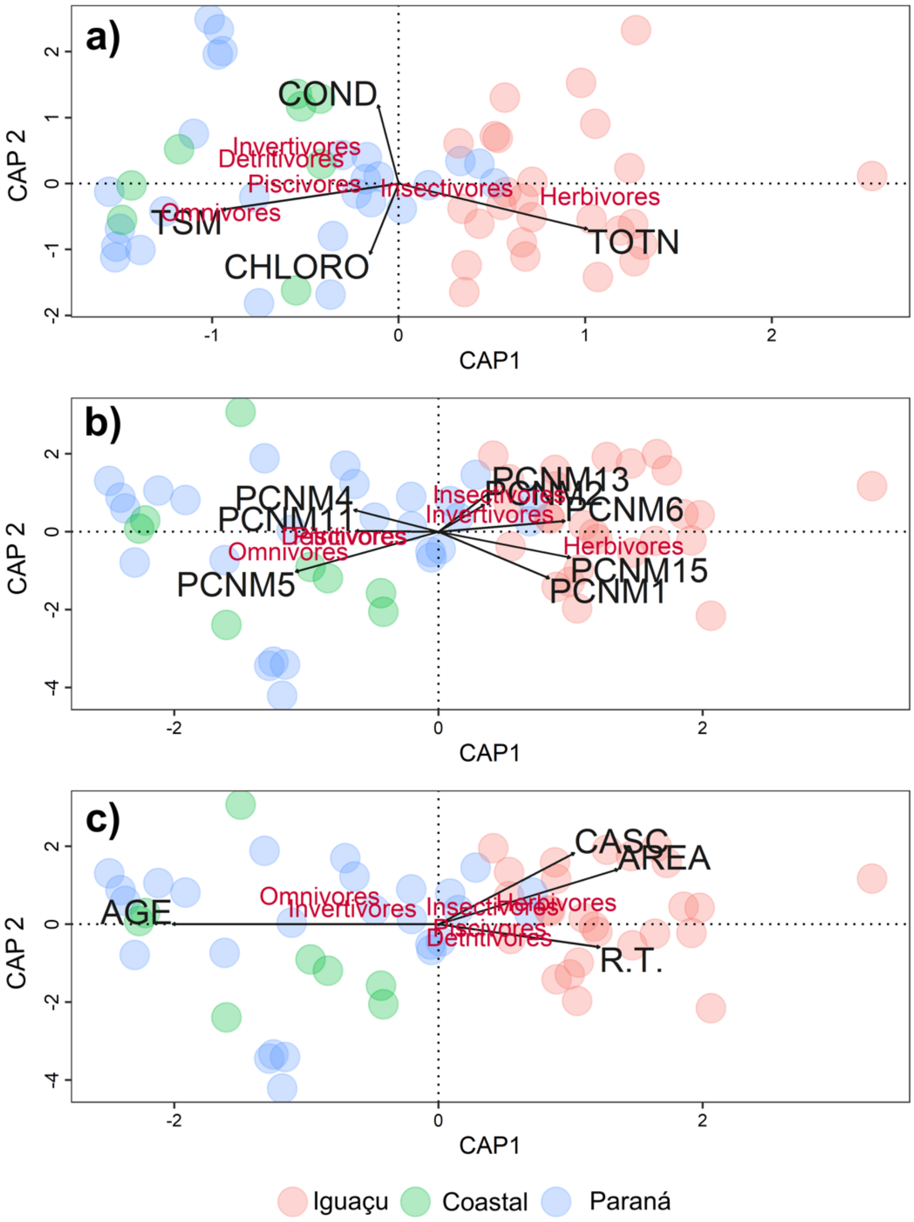

Fig 4 Ordination plots of the canonical analysis of principal coordinates (CAP) used in dbRDA for (a) environmental, (b) spatial, and (c) morphological components. The different colors represent the three ichthyofaunistic provinces in which the reservoirs are inserted

3.4 Discussion

Overall, spatial, environmental, and morphological components showed significant effects on the composition of trophic guilds in the studied reservoirs. However, only the spatial and environmental components had significant unique effects. Among them, the one that presented the greatest variability explained for the composition of the guilds was the spatial, followed by the environmental and morphological. In addition, the shared effect between the environmental and spatial, and between spatial and morphological components showed a considerable percentage of the explained variability. When we evaluated the components separately, we observed that some variables influenced certain trophic guilds. In relation to the spatial component, the trophic guilds that showed spatial segregation were herbivores and omnivores. The environmental component showed that reservoirs with a higher concentration of total nitrogen had a greater abundance of herbivores and detritivores species, and higher concentrations of total suspended material were related to a greater abundance of piscivores. On the other hand, reservoirs with higher conductivity showed greater abundance of invertivores species. Regarding the morphological component, it was found that older reservoirs had lower abundances of herbivores and piscivores and greater abundances of omnivores. Larger reservoirs have a greater abundance of piscivores and omnivores, and the longer the water retention time, the greater the abundance of piscivores.

The greatest explanation for the spatial component was due to the fact that the studied reservoirs are distributed in different ichthyofaunistic provinces belonging to different ecoregions (Abell et al. 2008). Large-scale spatial patterns are expected to be important in the distribution of fishes and, consequently, in the trophic guilds. Indeed, fish composition of the reservoirs may differ between basins because they have different biogeographic origins, and consequently, different species pool (Muniz et al. 2021). Each province studied here (i.e., Iguaçu, Paraná, and Coastal) harbor distinct ichthyofaunas as a result of evolution and isolation over a long period (Ribeiro 2006; Abell et al. 2008; Albert et al. 2020), presenting its own limnological and geomorphological characteristics (Luiz et al. 2003; Pool et al. 2010). Muniz et al. (2021) evaluated the taxonomic and functional structures of the ichthyofauna of these same reservoirs and also found that the basin is important in determining species composition concerning these two parameters (i.e., reservoirs inserted in the same province/ecoregion were closer in the multidimensional space). For instance, we observed a clear spatial separation in herbivores among the different ichthyofaunistic provinces, with greater abundances in the Iguaçu province. In fact, a greater abundance of herbivores is expected for this province due to the high richness and abundance of species of the genera *Astyanax* and *Psalidodon* (Reis et al. 2020). Species of these genera are generally classified as omnivores, but many studies show a clear tendency to herbivory (Pini et al. 2019). The variation in the feeding spectrum may be linked to the seasonal feeding plasticity present in such species, which can facilitate coexistence among them in the Iguaçu province (Neves et al. 2021).

Environmental conditions, the second component that most explained the variability in the composition and distribution of guilds, are known to directly affect fish communities and food dynamics, especially in dammed environments (Agostinho et al. 2008; Vidotto-Magnoni and Carvalho 2009; Zeng et al. 2017; Schmutz and Moog 2018). The interruption of natural flow, alteration in water level, in the flow of matter and energy caused by dams are changes that change limnology and productivity of reservoirs, reflecting in the structuring of the fish trophic guilds (Agostinho et al. 2008; Miranda and Krogman 2015). Although the morphology does not have a unique significant effect, its global effect can be explained by the correlation of environmental variables with the characteristics of the reservoirs (Fig. 3). This high correlation occurs because many of these environmental changes are directly related to age, the shape of the reservoir (e.g., area, depth), its location (i.e., inserted in cascade), and scheme of operation (i.e., water residence time). Thus, these reservoir characteristics can lead to real variation in the limnological features of these environments and, therefore in the trophic guild composition (Agostinho et al. 2007; Vidotto-Magnoni and Carvalho 2009; Schmutz and Moog 2018).

As expected, the herbivore guild showed different patterns of abundance and distribution across the reservoirs. Its greater abundances were verified in younger, with larger areas and more productive reservoirs (i.e., with higher concentrations of total nitrogen). Muniz et al. (2020) evaluating the association between age of the reservoir and different functional traits found that recent reservoirs presented higher abundances of herbivores species compared to the older ones. Reducing the abundance of herbivores species along the reservoir aging may be associated with decreased food resources (i.e., reduction of macrophytes, phytoplankton, and periphyton) or increased abundance of species with a wider food spectrum (i.e., strong competitors). In fact, the early years of reservoirs are characterized by the large contribution of allochthonous resources and flooded vegetation. Over time, due to the reduced interface between riparian vegetation and reservoirs, these resources become scarce in these environments, which may explain the decrease in the abundance of herbivores in older reservoirs (Dias et al. 2020; Muniz et al. 2020).

Similarly, the greater abundance of detritivores found in younger reservoirs and with higher concentrations of total nitrogen and total suspended material was also expected and may be related to the quality of detritus and its access. Detritivores are considered trophic specialists with morphological adaptations of the mouth and digestive tract that do not allow them to use other types of resources (Fugi et al. 2001; Delariva et al. 2013). Although this resource is apparently unlimited, detritivores are highly selective and tend to feed on protein-rich material with a higher level of organic matter (Bowen 1987). Thus, the changes that occur over time in reservoirs, mainly due to diminished nutrients (total phosphorus and nitrogen), productivity (chlorophyll-*a*), and more intense sedimentation process, may alter the nutritional quality of detritus (Santos et al. 2020), which justifies the lower abundance of individuals belonging to this guild in older and less productive reservoirs. Still, previous studies carried out in reservoirs arranged in cascade show that the abundance of detritivores is even smaller in reservoirs further downstream, due to the intense oligotrophization and intensity of these processes in the last reservoirs of a cascade (Santos et al. 2020).

The omnivore guild, as we expected, had its greatest abundance in older reservoirs. Previous studies carried out in the studied reservoirs have also found that the age of the reservoir has a strong association with functional traits related to fish feeding, with older reservoirs showing high abundances of omnivorous species (Muniz et al. 2020). The main resources consumed in reservoirs are autochthonous (e.g., zooplankton, insects, other aquatic invertebrates, debris, fish), thus, species that consume these types of food prevail and are favored (Agostinho et al. 2007). However, these items are rarely consumed in a restricted way by specialist taxa, and the ingestion of different items, usually the most available, is the most common diet pattern, belonging to omnivores. Besides, few species have pre-adaptations to thrive in lacustrine conditions in the Neotropical region. Thus, species that have functional traits (e.g., omnivory) that allow greater plasticity will benefit (Gomes and Miranda 2001; Agostinho et al. 2016). Therefore, dammed environments, which are frequently disturbed, favor the establishment of these species because they have adaptive advantages compared to others with a more specialized and restricted diet (Jepsen and Winemiller 2002).

Our results suggested that the greatest abundance of piscivores was recorded for reservoirs with larger areas and longer water residence time. Among the studied reservoirs, those with the lowest chronological age were also those with the largest areas and longest water residence times. These variables reflect the morphological and operational characteristics of the reservoir and have direct relationships with the degree of impact of these projects on fish populations (Ganassin et al. 2021). This is because reservoirs with larger areas generally have longer water residence times, which provides heterogeneity of physical structure, habitat diversity, trophic resources, shelter and, greater richness and abundance of fish species (Leira and Cantonati 2008; Logez et al. 2016; Ganassin et al. 2021). For instance, larger reservoirs are expected to have higher invertebrate species richness than smaller reservoirs (Santos et al. 2016), resulting in greater availability of food for the prey of piscivores. Moreover, in reservoirs with longer water residence time, greater transparency is expected, and this increase in water transparency may favor visually-oriented piscivores (Rodríguez and Lewis 1997; Tejerina-Garro et al. 1998).

Contrary to what we expected, piscivores showed lower abundance in older reservoirs. This may be related to the fact that in the first years of the reservoir formation, the large incorporation of organic matter produces a marked increase in food availability, especially for small fish (Trophic upsurge period; Kimmel and Groeger 1986). Thus, this increase in small species can lead to the proliferation of piscivores in subsequent moments (Agostinho et al. 2007; Pereira et al. 2016). However, over time there is a reduction and homogenization of the ichthyofauna including the prey for piscivores, which may explain the lower abundances of individuals belonging to bottom-up control in older reservoirs.

No clear relationship was found for the distribution of invertivores and insectivores guilds regarding the different characteristics of the reservoirs. Perhaps reservoirs are not very suitable environments for individuals belonging to these guilds. In fact, the construction of reservoirs reduces the water-margin interface (i.e., after some time), which decreases the contribution of allochthones items in the fish diet (Agostinho et al. 2007), especially important for insectivores. Still, the retention of water and the decrease of flow that occur in all reservoirs due to the dams enhance sedimentation rates (Straskraba and Tundisi 1999), which over time, causes sediment accumulation, anoxia patterns, decrease of depth and, as a consequence, homogenizes the bottom habitats, which is the most important sources of resources for invertivores (Santos et al. 2016).

3.5 Conclusions

Our findings suggest that alterations caused by damming are reflected in the structure of the food chain according to the trophic guild considered. Specifically, the region where the reservoir is inserted, variables related to its form and operation scheme, as well as the environmental characteristics (e.g., productivity levels) are determinant in the distribution and abundance of the different guilds. Due to the major changes expected for aquatic bodies in the coming years with the construction of several dams (Zarlf et al. 2015), understand structuring factors of the trophic network is fundamental. This is true by the fact that in freshwater ecosystems fishes are mediators of ecosystem functions (Closs et al. 2016). Therefore, changes in the trophic structure of the fish assemblage leads to changes in the structure of the aquatic community as a whole (Holmund and Hammer 1999). Thus, our results have important implications for management and conservation actions, since changes in the abundance of trophic guilds can result in severe modifications to networks of ecosystem interactions (Acevedo and Cassinello 2009). Still, further assessments of fish trophic changes are necessary to systematically evaluate the ecosystem functioning and its vulnerability to river fragmentation by dams, especially in reservoirs constructed in sequences (i.e., reservoirs cascade), given changes in natural taxonomic and phylogenetic patterns (Zhang et al. 2019) and the inevitable amplification of negative effects on fish diversity.

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SUPPLEMENTARY INFORMATION

APPENDIX S1 – Characteristics of the studied reservoirs

Table S1. Characteristics of the 29 study reservoirs located in the Paraná State, Brazil. Age: difference between 2001 (fish samplings) and the year of reservoir formation; Depth = maximum depth; R.T. = water residence time; Cascade insertion = 1 – inserted in a reservoir cascade, 0 – not inserted in a reservoir cascade; MAWT = mean annual water temperature

Reservoir	River basin	Province	Age (years)	Area (km²)	Depth (m)	R.T. (days)	Volume (km³)	Cascade insertion	MAWT (°C)
Alagados	Tibagi	Paraná	56	7.2	9.3	46.00	0.03	0	19.85
Canoas I	Paranapanema	Paraná	2	30.8	26.0	6.00	207.00	1	23.95
Canoas II	Paranapanema	Paraná	2	22.5	16.5	4.40	140.00	1	23.55
Capivara	Paranapanema	Paraná	26	419.3	52.5	126.80	10540.00	1	23.70
Capivari	Litorânea	Coastal	31	12.0	43.0	48.00	156.00	0	19.95
Cavernoso	Iguaçu	Iguaçu	36	2.9	8.3	0.60	4.02	0	19.50
Chavantes	Paranapanema	Paraná	31	400	78.0	352.70	8795.00	1	21.90
Curucaca	Iguaçu	Iguaçu	19	2.0	10.5	47.00	26.10	0	17.55
Foz do Areia	Iguaçu	Iguaçu	21	139	135	102.00	5779.00	1	20.70
Foz do Chopim	Iguaçu	Iguaçu	31	2.9	6.0	59.10	26.10	0	20.05
Guaricana	Litorânea	Coastal	44	7.0	17.0	13.00	4.02	0	19.95
Harmonia	Tibagi	Paraná	51	3.0	12.0	11.50	8.00	0	20.90
Jordão	Iguaçu	Iguaçu	5	3.4	60.0	5.60	110.00	0	18.45
Melissa	Piquiri	Paraná	39	2.9	5.3	0.04	8.00	0	17.90
Mourão	Ivaí	Paraná	37	11.3	12.7	70.00	0.06	0	20.95
Passauna	Iguaçu	Iguaçu	23	14.0	15.0	420.00	0.50	0	16.50
Patos	Ivaí	Paraná	52	1.3	5.8	0.20	26.10	0	18.50
Piraquara	Iguaçu	Iguaçu	22	3.3	18.0	438.00	0.50	0	19.90
Rosana	Paranapanema	Paraná	15	220	26.0	18.60	1920.00	1	24.15
Santa Maria	Piquiri	Paraná	51	0.1	4.3	11.10	44.22	0	16.70
Salto Caxias	Iguaçu	Iguaçu	3	124	53.0	31.00	3573.00	1	21.80
Salto Grande	Paranapanema	Paraná	43	12	9.2	1.40	44.20	1	21.95
Salto do Meio	Litorânea	Coastal	70	0.1	6.2	0.70	0.04	0	18.35
Salto Osório	Iguaçu	Iguaçu	26	51	43.0	16.00	1270.00	1	21.20
Salto Santiago	Iguaçu	Iguaçu	22	208	78.0	51.00	6753.00	1	21.60
Salto Segredo	Iguaçu	Iguaçu	9	82.5	100.0	47.00	3573.00	1	21.80
Salto do Vau	Iguaçu	Iguaçu	42	2	3.5	0.04	0.04	0	16.20
Taquaruçu	Paranapanema	Paraná	9	80.1	26.5	7.90	672.50	1	23.60
Vossoroca	Litorânea	Coastal	52	5.1	12.5	106.30	0.04	0	19.95

APPENDIX S2 – List of species collected in the studied reservoirs

Table S2. List of the species collected in the sampled reservoirs. The 'X' indicates presence of the species collected in each river basin

ORDER **Family** Species	**River basins**					
	Coastal	**Iguaçu**	**Ivaí**	**Paranapanema**	**Piquiri**	**Tibagi**
CYPRINIFORMES						
Cyprinidae						
Ctenopharyngodon idella (Valenciennes, 1844)		X				
Cyprinus carpio Linnaeus, 1758	X	X	X		X	
Hypophthalmichthys molitrix (Valenciennes, 1844)		X				
Hypophthalmichthys nobilis (Richardson, 1845)		X				
CHARACIFORMES						
Crenuchidae						
Characidium travassosi Melo, Buckup & Oyakawa, 2016		X				
Erythrinidae						
Hoplias lacerdae Miranda Ribeiro, 1908			X			
Hoplias aff. *malabaricus* (Bloch, 1794)	X	X	X	X	X	X
Parodontidae						
Apareiodon affinis (Steindachner, 1879)				X		
Apareiodon ibitiensis Amaral Campos, 1944				X		
Apareiodon piracicabae (Eigenmann, 1907)				X		
Apareiodon vittatus Garavello, 1977		X				
Cynodontidae						
Rhaphiodon vulpinus Spix & Agassiz, 1829				X		
Serrasalmidade						
Colossoma macropomum (Cuvier,1816)						X
Metynnis lippincottianus Cope, 1870	X			X		

Piaractus mesopotamicus (Holmberg, 1887)						X
Serrasalmus maculatus Kner, 1858				X		
Serrasalmus marginatus Valenciennes, 1837				X		
Anostomidae						
Leporellus vittatus (Valenciennes, 1850)				X		
Leporinus amblyrhynchus Garavello & Britski, 1987				X		
Leporinus friderici (Bloch, 1794)				X		
Leporinus lacustris Amaral Campos, 1945				X		
Leporinus octofasciatus Steindachner, 1915				X		
Leporinus sp. 1				X		
Leporinus sp. 2				X		
Megaleporinus macrocephalus (Garavello & Britski, 1988)		X				
Megaleporinus piavussu (Britski, Birindelli & Garavello, 2012)				X		
Schizodon borellii (Boulenger, 1900)				X		
Schizodon nasutus Kner, 1858				X		
Curimatidae						
Cyphocharax modestus (Fernández-Yépez, 1948)		X				
Steindachnerina brevipinna (Eigenmann & Eigenmann, 1889)				X		
Prochilodontidae						
Prochilodus lineatus (Valenciennes, 1837)	X		X	X	X	X
Triportheidae						
Triportheus nematurus (Kner, 1858)				X		
Bryconidae						
Salminus brasiliensis (Cuvier, 1816)				X		
Acestrorhynchidae						
Acestrorhynchus lacustris (Lütken, 1875)				X		
Characidae						
Aphyocharax anisitsi Eigenmann & Kennedy, 1903				X		
Aphyocharax dentatus Eigenmann & Kennedy, 1903				X		
Astyanax dissimilis Garavello & Sampaio, 2010		X				

Astyanax lacustris (Lütken, 1875)	X	X	X	X	X	X
Astyanax laticeps (Cope 1894)	X					
Astyanax minor Garavello & Sampaio, 2010		X				
Astyanax serratus Garavello & Sampaio, 2010		X				
Astyanax sp. 1		X				
Astyanax sp. 2	X					
Astyanax sp. 3	X					
Astyanax sp. h		X				
Astyanax sp. i			X			
Astyanax sp. l			X		X	
Astyanax sp. m	X					
Astyanax sp. n	X					
Bryconamericus aff. *iheringii* (Boulenger, 1887)					X	X
Bryconamericus ikaa Casciotta, Almirón & Azpelicueta, 2004		X				
Bryconamericus pyahu Azpelicueta, Casciotta & Almirón, 2003		X				
Bryconamericus sp.c		X				
Bryconamericus sp.d		X				
Deuterodon iguape Eigenmann, 1907	X					
Deuterodon sp.	X					
Galeocharax gulo (Cope, 1870)				X		
Hyphessobrycon eques (Steindachner, 1882)				X		
Mimagoniates microlepis (Steindachner, 1877)	X	X				
Moenkhausia cf. *gracilima* Eigenmann, 1908				X		
Moenkhausia aff. *intermedia* Eigenmann, 1908				X		
Oligosarcus longirostris Menezes & Géry, 1983		X				
Oligosarcus paranensis Menezes & Géry, 1983			X		X	
Piabarchus stramineus (Eigenmann, 1908)				X		
Psalidodon bifasciatus (Garavello & Sampaio, 2010)	X	X				
Psalidodon bockmanni (Vari & Castro, 2007)				X		
Psalidodon aff. *fasciatus* (Cuvier, 1819)				X		

Psalidodon gymnodontus Eigenmann, 1911		X				
Psalidodon gymnogenys (Eigenmann,1911)		X				
Psalidodon aff. *paranae* (Eigenmann, 1914)					X	X
Roeboides descalvadensis Fowler, 1932				X		
Serrapinnus heterodon (Eigenmann, 1915)				X		
GYMNOTIFORMES						
Gymnotidae						
Gymnotus cf. *carapo* Linnaeus, 1758		X	X	X		
Gymnotus sylvius Albert & Fernandes-Matioli, 1999					X	
Rhamphichthyidae						
Rhamphichthys hahni (Meinken, 1937)				X		
Sternopygidae						
Eigenmannia sp.				X		
Sternopygus macrurus (Bloch & Schneider, 1801)				X		
Apteronotidae						
Apteronotus ellisi (Alonso de Arámburu, 1957)				X		
SILURIFORMES						
Auchenipteridae						
Ageneiosus militaris Valenciennes, 1836				X		
Auchenipterus osteomystax (Miranda Ribeiro, 1918)				X		
Glanidium ribeiroi Haseman, 1911		X				
Tatia jaracatia Pavanelli & Bifi, 2009		X				
Tatia neivai (Ihering, 1930)				X		
Trachelyopterus galeatus (Linnaeus, 1766)				X		
Doradidae						
Pterodoras granulosus (Valenciennes, 1821)				X		
Rhinodoras dorbignyi (Kner, 1855)				X		
Heptapteridae						
Pimelodella gracilis (Valenciennes, 1835)				X		
Rhamdia branneri Haseman, 1911		X				
Rhamdia aff. *quelen* (Quoy & Gaimard, 1824)	X		X	X	X	X

Rhamdia voulezi Haseman, 1911		X				
Pimelodidae						
Hypophthalmus oremaculatus Nani & Fuster, 1947				X		
Iheringichthys labrosus (Lütken, 1874)				X		
Pimelodus britskii Garavello & Shibatta, 2007		X				
Pimelodus maculatus Lacepède, 1803				X		
Pimelodus microstoma Steindachner, 1877				X		
Pimelodus ornatus Kner, 1858				X		
Pimelodus ortmanni Haseman, 1911		X				
Pinirampus pirinampu (Spix & Agassiz, 1829)				X		
Clariidae						
Clarias gariepinus (Burchell, 1822)		X				
Callichthyidae						
Callichthys callichthys (Linnaeus, 1758)	X					
Corydoras ehrhardti Steindachner , 1910	X		X			X
Corydoras aff. *paleatus* (Jenyns, 1842)	X	X				
Corydoras sp.		X				
Hoplosternum littorale (Hancock, 1828)				X		
Loricariidae						
Hypostomus ancistroides (Ihering, 1911)				X	X	
Hypostomus cf. *aspilogaster* (Cope 1894)			X			
Hypostomus cf. *auroguttatus* Kner, 1854				X		
Hypostomus commersoni Valenciennes, 1836	X	X	X			
Hypostomus derbyi (Haseman, 1911)		X				
Hypostomus hermanni (Ihering, 1905)				X		
Hypostomus margaritifer (Regan, 1908)				X		
Hypostomus myersi (Gosline, 1947)		X				
Hypostomus nigromaculatus (Schubart, 1964)				X		
Hypostomus regani (Ihering, 1905)				X		
Hypostomus strigaticeps (Regan, 1908)				X		
Hypostomus sp. 1				X		

Hypostomus sp. 2				X		
Loricariichthys platymetopon Isbrücker & Nijssen, 1979				X		
Megalancistrus parananus (Peters, 1881)				X		
Proloricaria prolixa (Isbrücker & Nijssen, 1978)				X		
Proloricaria sp.				X		
Rhinelepis aspera Spix & Agassiz, 1829				X		
Rineloricaria kronei (Miranda Ribeiro, 1911)	X					
Rineloricaria latirostris (Boulenger, 1900)			X		X	
Rineloricaria maacki Ingenito, Ghazzi, Duboc & Abilhoa, 2008		X				
Ictaluridae						
Ictalurus punctatus (Rafinesque, 1818)		X				
ATHERINIFORMES						
Atherinopsidae						
Odontesthes bonariensis (Valenciennes, 1835)		X				
CICHLIFORMES						
Cichlidae						
Astronotus crassipinnis Heckel, 1840				X		
Australoheros cf. *facetus* (Jenyns, 1842)	X					
Australoheros kaaygua Casciotta, Almirón & Gómez, 2006		X				
Cichla kelberi Kullander & Ferreira, 2006				X		
Coptodon rendalli (Boulenger, 1897)	X	X	X	X	X	X
Crenicichla britskii Kullander, 1982			X	X		
Crenicichla jaguarensis Haseman, 1911				X		
Crenicichla iguassuensis Haseman, 1911		X				
Crenicichla sp. (Holmberg, 1891)				X		
Crenicichla tesay Casciotta & Almirón, 2009		X				
Geophagus aff. *brasiliensis* (Quoy & Gaimard, 1824)		X	X	X	X	X
Geophagus iporangensis Haseman, 1911	X					
Oreochromis niloticus (Linnaeus, 1758)	X	X			X	
Satanoperca sp.				X		

CYPRINODONTIFORMES					
Poeciliidae					
Phalloceros harpagos Lucinda, 2008	X	X			X
PERCIFORMES					
Sciaenidae					
Plagioscion squamosissimus (Heckel, 1840)				X	
Centrarchidae					
Micropterus salmoides (Lacepède, 1802)	X		X		

APPENDIX S3 – Species belonging to each trophic guild

Table S3. Species belonging to each trophic guild. Pisc = piscivore; Det = detritivore; Ins = insectivore; Omn = omnivore; Inv = invertivore; Her = herbivore. See references in supporting information S3

Species	**Trophic guilds**					
	Pisc	**Det**	**Ins**	**Omn**	**Inv**	**Her**
Acestrorhynchus lacustris	X					
Ageneiosus militaris					X	
Apareiodon affinis		X				
Apareiodon ibitiensis		X				
Apareiodon piracicabae		X				
Apareiodon vittatus		X				
Aphyocharax anisitsi					X	
Aphyocharax dentatus			X			
Apteronotus ellisi			X			
Astronotus crassipinis	X					
Astyanax lacustris				X		
Astyanax dissimilis						X
Astyanax laticeps			X			
Astyanax minor						X
Astyanax serratus				X		
Astyanax sp. 1				X		
Astyanax sp. 2				X		
Astyanax sp. 3				X		
Astyanax sp. h				X		
Astyanax sp. i				X		
Astyanax sp. l				X		
Astyanax sp. m				X		
Astyanax sp. n				X		
Auchenipterus osteomystax			X			
Bryconamericus iheringii		X				
Bryconamericus ikaa		X				
Bryconamericus pyahu		X				
Bryconamericus sp. c			X			
Bryconamericus sp. d			X			
Callichthys callichthys			X			
Characidium travassosi					X	
Cichla kelberi	X					
Australoheros cf. *facetus*				X		
Clarias gariepinus	X					
Colossoma macropomum				X		
Coptodon rendalli			X			
Corydoras aff. *paleatus*					X	
Corydoras ehrhardti			X			
Corydoras sp.			X			
Crenicichla britskii			X			
Crenicichla iguassuensis	X					
Crenicichla jaguarensis				X		
Crenicichla sp.			X			
Crenicichla tesay	X					
Ctenopharyngodon idella						X
Cyphocharax modestus		X				
Cyprinus carpio				X		

Deuterodon iguape				X		
Deuterodon sp.			X			
Eigenmannia sp.			X			
Galeocharax gulo	X					
Geophagus brasiliensis					X	
Glanidium ribeiroi				X		
Gymnotus carapo					X	
Gymnotus sylvius					X	
Hoplias aff. *malabaricus*	X					
Hoplias lacerdae	X					
Hoplosternum littorale					X	
Hyphessobrycon eques			X			
Hypophthalmichthys molitrix			X			
Hypophthalmichthys nobilis			X			
Hypophthalmus oreomaculatus					X	
Hypostomus ancistroides		X				
Hypostomus cf. *aspilogaster*		X				
Hypostomus cf. *auroguttatus*		X				
Hypostomus commersoni		X				
Hypostomus derbyi		X				
Hypostomus hermanni		X				
Hypostomus margaritifer		X				
Hypostomus myersi		X				
Hypostomus nigromaculatus		X				
Hypostomus regani		X				
Hypostomus sp. 1		X				
Hypostomus sp. 2		X				
Hypostomus strigaticeps		X				
Ictalurus punctatus	X					
Iheringichthys labrosus					X	
Leporellus vittatus			X			
Leporinus amblyrhynchus					X	
Leporinus friderici				X		
Leporinus lacustris				X		
Leporinus octofasciatus				X		
Leporinus sp. 1				X		
Leporinus sp. 2				X		
Loricariichthys platymetopon		X				
Megalancistrus parananus		X				
Megaleporinus macrocephalus				X		
Megaleporinus piavussu				X		
Metynnis lippincottianus						X
Micropterus salmoides	X					
Mimagoniates microlepis			X			
Moenkhausia cf. *gracilima*			X			
Moenkhausia intermedia					X	
Odontesthes bonariensis					X	
Oligosarcus longirostris	X					
Oligosarcus paranensis	X					
Oreochromis niloticus					X	
Phalloceros harpagos				X		
Piabarchus stramineus			X			
Piaractus mesopotamicus						
Pimelodella gracilis			X			
Pimelodus britskii				X		
Pimelodus maculatus				X		
Pimelodus microstoma				X		
Pimelodus ornatus				X		
Pimelodus ortmanni				X		
Pinirampus pirinampu	X					

Plagioscion squamosissimus	X					
Prochilodus lineatus		X				
Proloricaria prolixa						X
Proloricaria sp.		X				
Psalidodon bifasciatus						X
Psalidodon bockmanni						X
Psalidodon aff. *fasciatus*				X		
Psalidodon gymnodontus			X			
Psalidodon gymnogenys					X	
Psalidodon aff. *paranae*						X
Pterodoras granulosus				X		
Rhamdia branneri	X					
Rhamdia aff. *quelen*	X					
Rhamdia voulezi	X					
Rhamphichthys hahni			X			
Rhaphiodon vulpinus	X					
Rhinelepis aspera		X				
Rhinodoras dorbignyi					X	
Rineloricaria latirostris		X				
Rineloricaria maacki						
Rineloricaria kronei		X				
Roeboides descalvadensis			X			
Salminus brasiliensis	X					
Satanoperca sp.		X				
Schizodon borellii						X
Schizodon nasutus						X
Serrapinnus heterodon						
Serrasalmus maculatus	X					
Serrasalmus marginatus	X					
Steindachnerina brevipinna		X				
Sternopygus macrurus			X			
Tatia jaracatia					X	
Tatia neivai			X			
Trachelyopterus galeatus				X		
Triportheus nematurus			X			

APPENDIX S4 – References used to determine the species trophic guilds

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APPENDIX S5 – Additional results

Pairwise relationships between each predictor and fish trophic guilds composition for evaluation of shared effects.

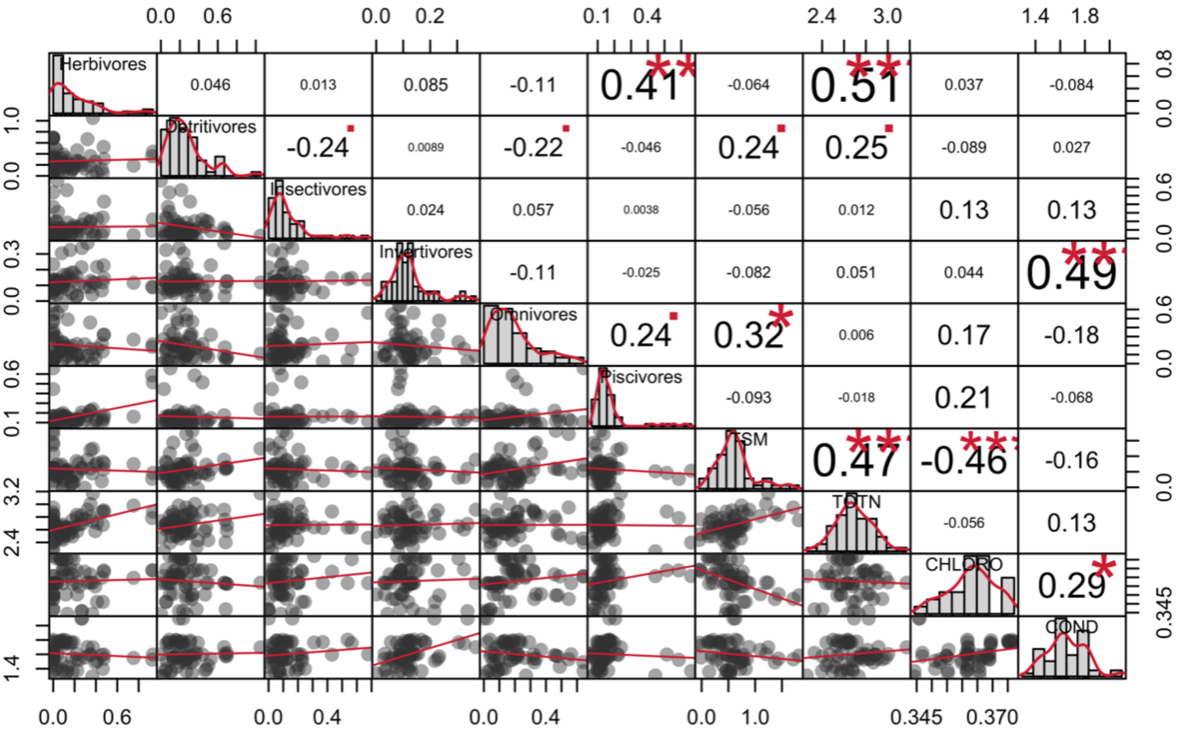

Figure S1. Pairwise relationships between environmental predictors and the fish trophic guilds composition for evaluation of shared effects. Below the diagonal, the bivariate scatterplots with the linear regression function are shown; the diagonal shows the histogram with an estimated kernel density function; above the diagonal, the Pearson correlation coefficients with significance levels (▪, $P < 0.10$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$)

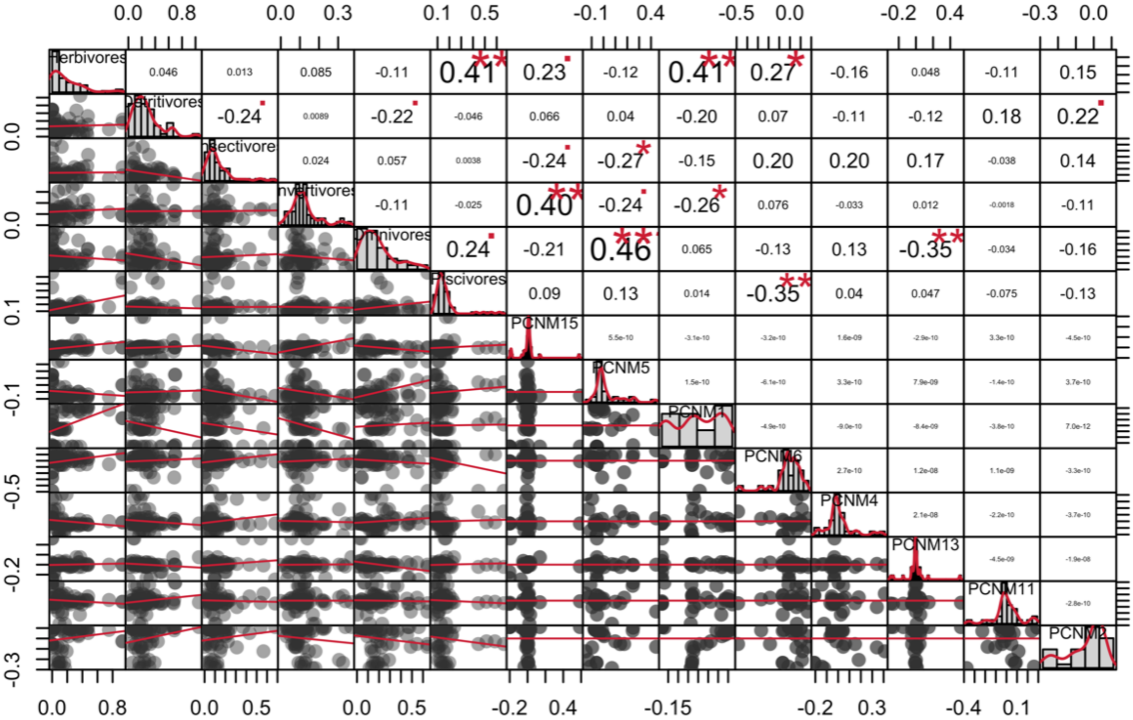

Figure S2. Pairwise relationships between spatial predictors and the fish trophic guilds composition for evaluation of shared effects. Below the diagonal, the bivariate scatterplots with the linear regression function are shown; the diagonal shows the histogram with an estimated kernel density function; above the diagonal, the Pearson correlation coefficients with significance levels (▪, $P < 0.10$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$)

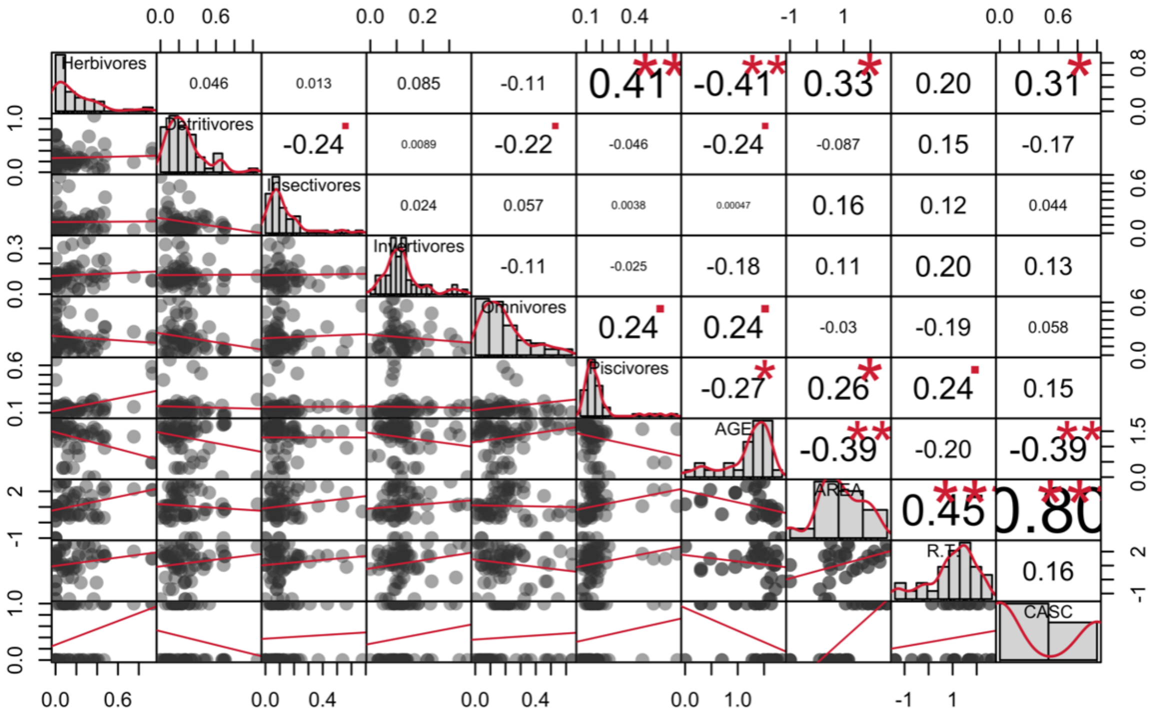

Figure S3. Pairwise relationships between morphological predictors and the fish trophic guilds composition for evaluation of shared effects. Below the diagonal, the bivariate scatterplots with the linear regression function are shown; the diagonal shows the histogram with an estimated kernel density function; above the diagonal, the Pearson correlation coefficients with significance levels (▪, $P < 0.10$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$)

4 CONCLUDING REMARKS

Based on the results obtained, it was possible to identify different patterns related to the distribution of fish communities due to the presence of dams. In dammed environments, the environmental changes caused by the reservoirs, as well as their characteristics and modes of operation, evidenced changes in the composition, abundance, richness and distribution of fish species, as well as their trophic guilds. Reservoirs arranged in cascade in different hydrographic basins showed reductions in diversity in the upstream-downstream direction and, above all, in the abundance of many fish species. Approximately 50% of the species showed decreases in their abundances along the reservoir succession, showing that only a small portion of the species manages to maintain their populations or even benefit from environments altered by reservoirs, especially when they are in a cascade system, where the changes are more intense and synergistic. Still, evaluating the composition of different trophic guilds of fish belonging to different reservoirs, it is noted that the changes caused in these environments due to the construction of the dam can act as filters, selecting greater or lesser abundances of certain guilds. Specifically, newer and more productive reservoirs have the highest abundances of herbivores and detritivores, while older reservoirs have the highest abundances of omnivores. Reservoirs with larger areas and water residence time were the ones that had greater abundances of piscivores. However, it should be noted that the evidence presented in both approaches of this work is configured in hypotheses in search of convergent patterns, requiring future and extensive investigations in other reservoirs and at other spatial scales.