



Effects of reservoir cascades on diversity, distribution, and abundance of fish assemblages in three Neotropical basins



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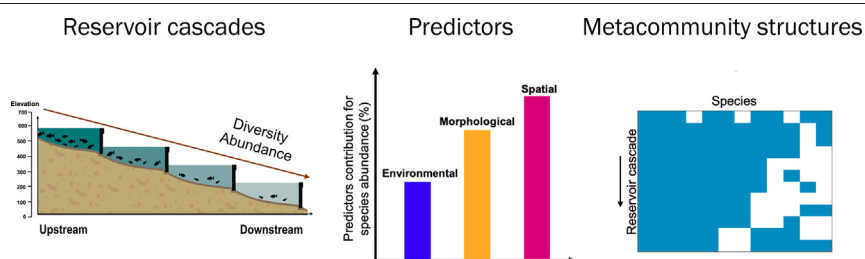
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HIGHLIGHTS

- We investigated longitudinal patterns of fish assemblages along reservoir cascades
- Lowest diversity generally occurred in the downstream reservoirs of the cascades
- Patterns of species distribution along the reservoir cascades varied for each basin
- Approximately 50% of the species in two of the three basins experienced a reduction in their abundance along the cascades
- Understand the effects of cascades on fish assemblage is important since hundreds of reservoirs are planned for construction

GRAPHICAL ABSTRACT



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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 (β_{sor}) and species turnover (β_{sim}) between pairs of reservoirs increased along reservoir cascades, especially at the downstream end, whereas nestedness (β_{sne})

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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.

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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 Mikkelsen, 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., 2013).

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; Zarlf 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; Zarlf et al., 2015). Only in Brazil, 1027 dams, including large and small

hydroelectric, are under construction or inventoried (Zarlf 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 (Tóffoli, 2015). Modifications in environmental conditions, following reservoir construction, can result in varied effects on the original fish assemblages (Bailey 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. Methods

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 ($2.8 \cdot 10^6 \text{ km}^2$) after the Amazon basin (Galves et al., 2009; Stevaux et al., 1997) and is the

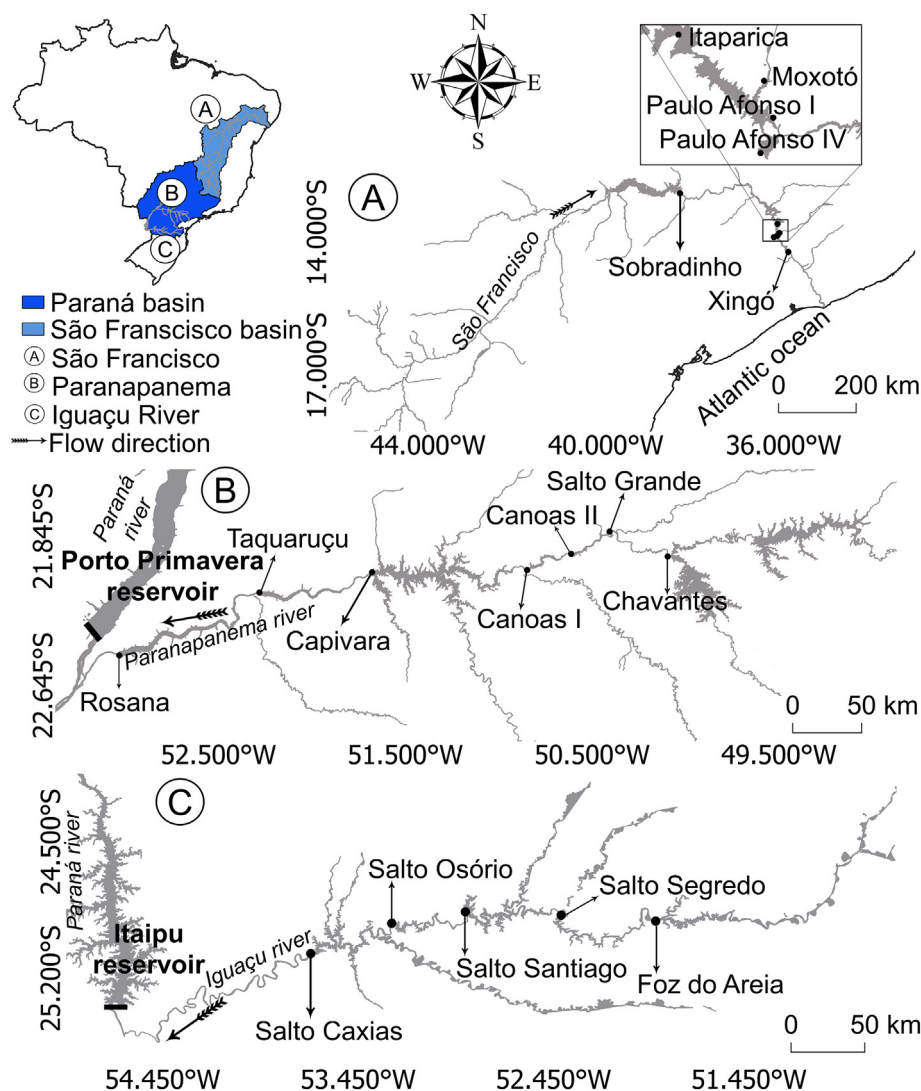


Fig. 1. Location of the hydrographic basins and their respective reservoir cascades in Brazil: A) Iguaçu River basin, B) Paranapanema River basin, and C) São Francisco River basin.

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).

The Iguaçu River basin has an area of approximately $7.2 \cdot 10^3$ km² and runs 1060 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 1800 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. Data collection

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 ($\mu\text{S cm}^{-1}$), 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* ($\mu\text{g L}^{-1}$; Nusch, 1980) and, nitrate and total phosphorus

concentrations ($\mu\text{g L}^{-1}$; 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. 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).

2.2.3. 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, 2018), implemented in QGIS 3.0 (QGIS Development Team, 2018).

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 m² 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).

2.3. 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).

2.3.1. Diversity patterns 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, 0D) and the exponential of Shannon's index (Hill number of order 1, 1D). 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, 2020). 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).

2.3.2. 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 Mikkelsen (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, 2020). 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 9999 permutations.

Complementarily, we evaluated the correlation (Spearman) between the cascade position (mid-point between reservoirs) and the beta diversity (β_{sor}) and its turnover (β_{sim}) and nestedness (β_{sne}) 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 (β_{sor} , β_{sim} and β_{sne}) 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 "ordisep" functions (9999 permutations) were used to perform DistLM and dbRDA, both from the *vegan* package (R Core Team, 2020).

2.3.3. Super-organizing maps

Super-organizing maps (Kohonen, 1982; Wehrens and Buydens, 2007; Wehrens and Krusselbrink, 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 Iguazu 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.

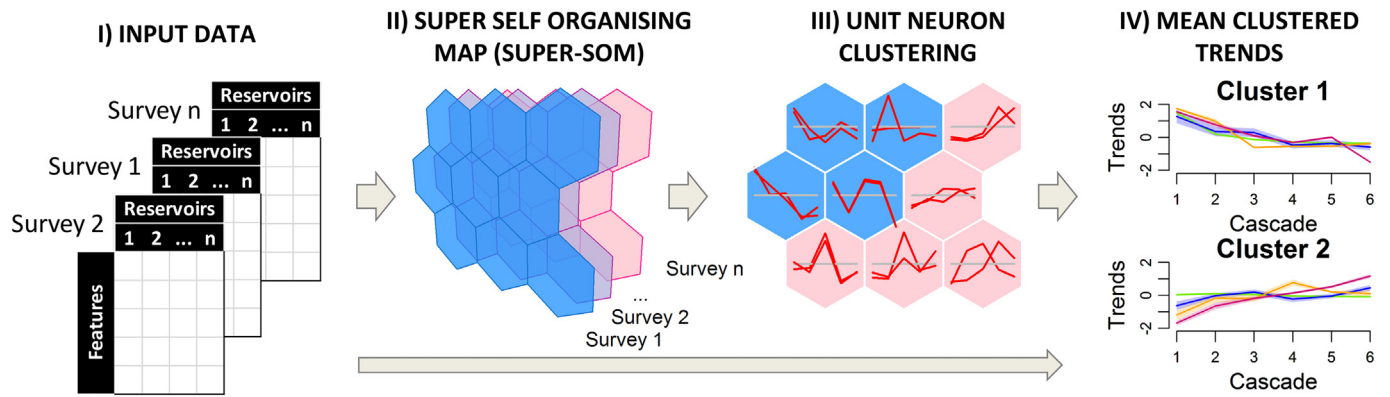


Fig. 2. Flowchart depicting the process followed to find common trends among species abundances (CPUEs) and environmental, morphological, and spatial variables along the reservoir cascades with super-organizing maps.

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 where codebooks are arrayed into a single matrix, super-organizing maps 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).

3. Results

3.1. Diversity patterns along cascades

The fish diversity of reservoirs showed differences among cascades (see Fig. S4 in Supplementary Information): i) in Iguazu, the species richness did not vary along the cascade but the exponential of Shannon index (1D) 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 1D ; 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 1D) 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).

3.2. Fish metacommunities structure and beta diversity

In the three river basins (Iguazu, 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 Iguazu 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 1). 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).

In Iguazu 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

Table 1

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

Diversity metrics ($R^2_{adjusted}$)	Source of variation	SS	d.f.	F-value	P
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



Fig. 3. Species presence (in blue) in the reservoirs of the Iguaçú (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.

beta-diversity (β_{sor}) and turnover (β_{sim}) 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 β_{sor} and β_{sim} did not vary much along the cascade to markedly decrease in the last downstream pair of reservoirs (Fig. 4). By contrast, nestedness (β_{sne}) depicted distinct trends in each river basin. It was mainly increasing in São Francisco, whereas in Iguaçú 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 ($r_s = 1.0, P = 0.017$).

The DistLM for all basins included morphological and environmental variables for total beta-diversity (β_{sor}) and turnover (β_{sim}): area,

depth, residence time and nitrate, respectively. For nestedness (β_{sne}), only the morphological variable area was included (see Table S7 in Supplementary Information) (Fig. 5).

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 Fig. S8 in Supplementary Information for additional results). The clusters indicated different trends along cascades in each river basin and the uncertainty was higher for Iguaçú and Paranapanema due to the smaller number of surveys, although the largest uncertainty among surveys

Table 2

Elements of metacommunity structure (EMS) analysis of the Iguaçú, 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	<i>z</i>	<i>P</i>	Mean	SD	Rep	<i>z</i>	<i>P</i>	Mean		SD	Morisita's index	<i>P</i>
Iguaçú	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

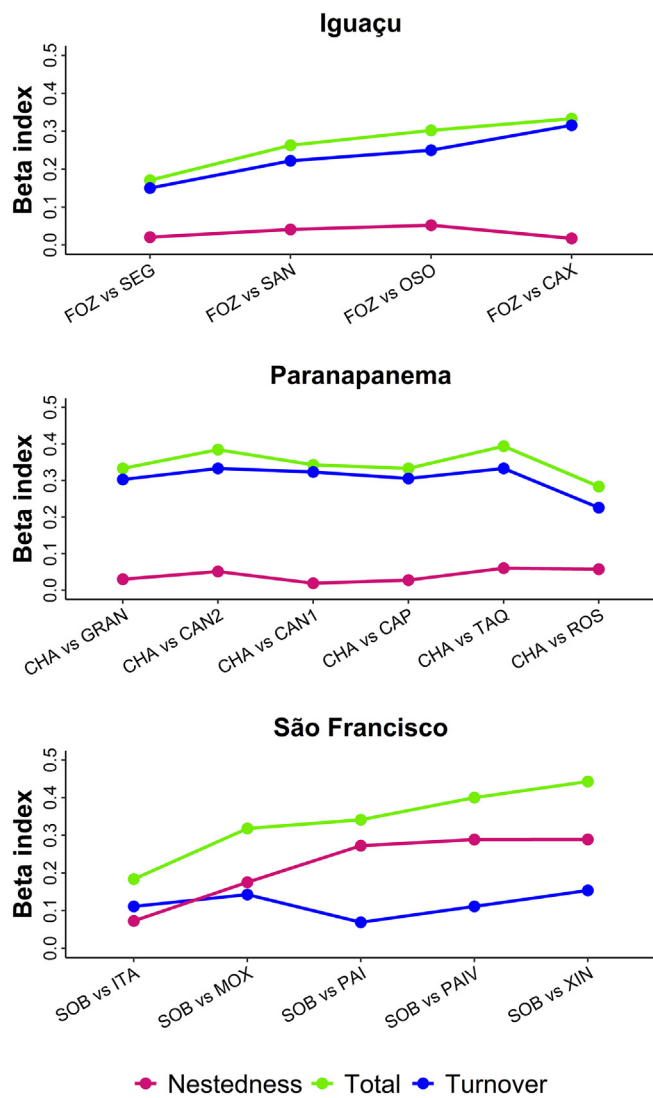


Fig. 4. Total beta diversity and its components (nestedness and turnover) of fish in reservoir along the three cascades (river basins). Each of the reservoirs was compared with the first, most upstream reservoir.

corresponded to the environmental variables collected in the Iguaçú River basin regardless of the cluster (Fig. 7).

The first cluster of the Iguaçú 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 *Triporthus 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 Table S9 (Supplementary Information).

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 Iguaçú) 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 Iguaçú and Paranapanema. This is reflected in the analyzed cascades of the Iguaçú 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 pattern 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.

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 Iguaçú and Paranapanema basins did not present as clear patterns, partly due to the smaller

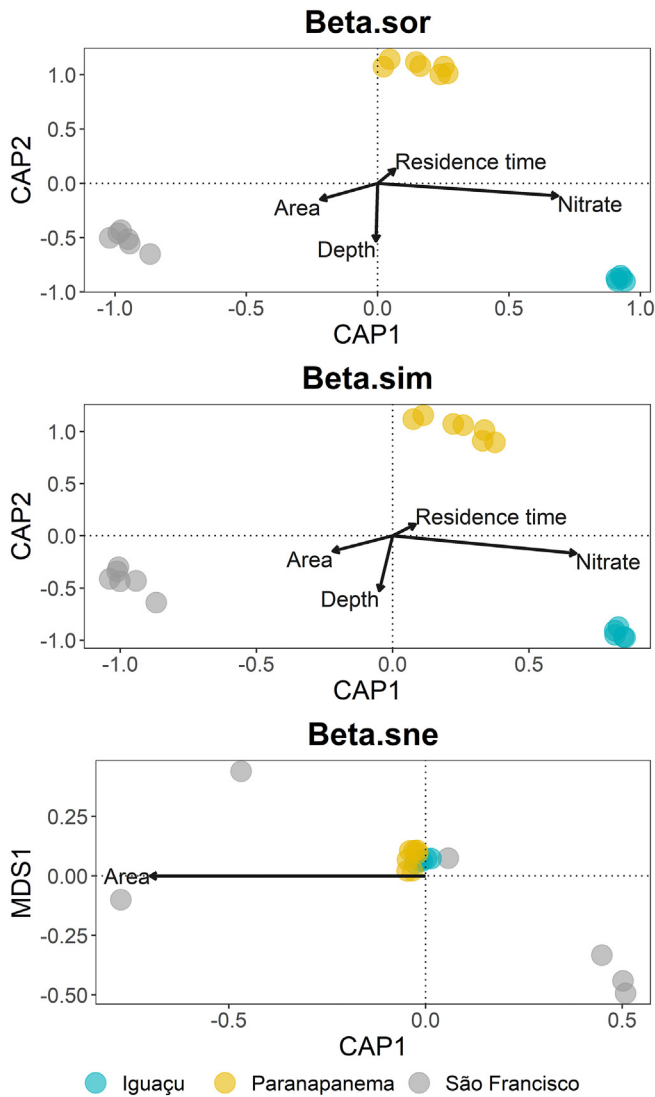


Fig. 5. Distance-based redundancy analysis (dbRDA) with the predictor variables (area, residence time, depth and nitrate) showing the greatest importance for the linear model DistLM.

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.

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 Iguaçú 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 Iguaçú River is known for having large waterfalls along its entire route (Baumgartnet et al., 2012), which favored the appearance

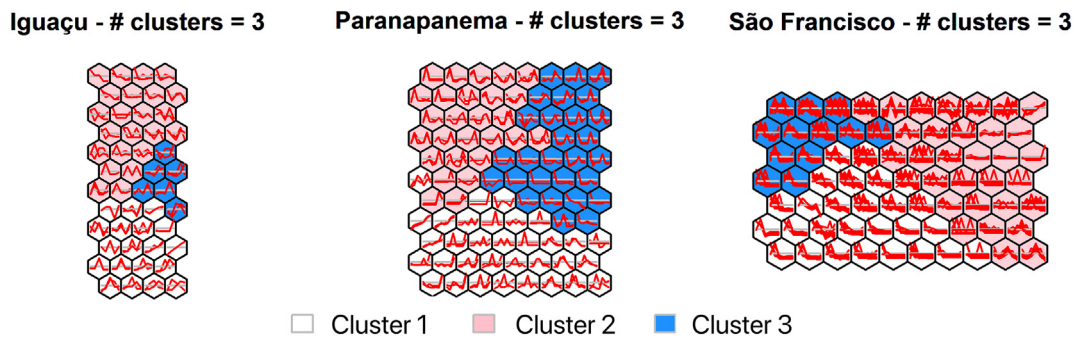


Fig. 6. Depiction of the optimal super-organizing maps obtained for every river basin. Overlaid red lines are the prototype codebooks obtained in every layer of the optimal super-organizing map. The different color patterns highlight the different clusters.

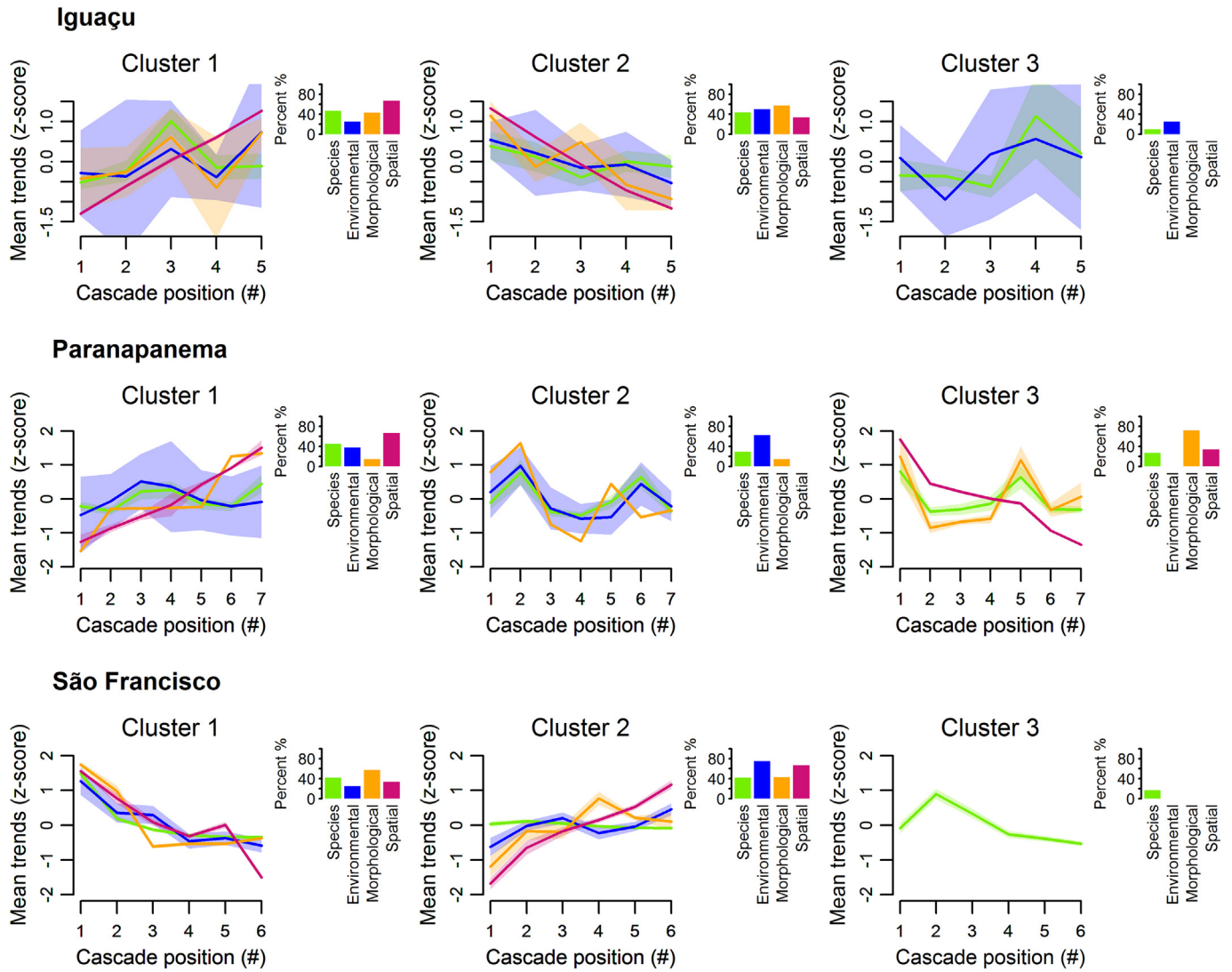


Fig. 7. Line charts depicting the mean values of the original trends assigned to each unit neuron cluster obtained after clustering the prototype codebooks of the super-organizing maps. The shaded areas correspond to 95% confidence intervals. The small bar plots next to the line charts depict the proportion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

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 specific 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, 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.

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 Iguaçú River basin.

4.4. Limitations 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., Iguaçú 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.

5. Conclusions

We analyzed the effects of the reservoir cascades on fish diversity, distribution, and abundance using large-scale spatial analyses (i.e., across river basins). 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 (Zarlf 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.

CRedit authorship contribution statement

Maria Julia: Conducting a research and investigation process, specifically performing the experiments, or data/evidence collection;

Rafael Muñoz-Mas: Application of statistical, or other formal techniques to analyze or synthesize study data;

Maria Julia Mileo Ganassin: Writing - Original Draft Preparation, creation and/or presentation of the published work, specifically writing the initial draft.

Maria Julia Mileo Ganassin, Rafael Muñoz-Mas, Fagner Junior Machado de Oliveira, Carolina Mendes Muniz, Natalia Carneiro Lacerda dos Santos, Emili García-Berthou, Luiz Carlos Gomes: Writing - Review & Editing Preparation, creation and/or presentation of the published work by those from the original research group, specifically critical review, commentary or revision.

Emili García-Berthou, Luiz Carlos Gomes: Supervision Oversight and leadership responsibility for the research activity planning and execution,

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.146246>.

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SUPPLEMENTARY INFORMATION

Effects of reservoir cascades on diversity, distribution, and abundance of fish assemblages in three Neotropical basins

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Table S1. Mean (\pm standard deviation) of environmental variables used in this study. IG = Iguaçú river; 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 \pm 5.7	7.00 \pm 0.1	10.77 \pm 7.8	7.72 \pm 9.1	7.66 \pm 1.2	43.13 \pm 5.5	461.50 \pm 84.1	13.10 \pm 1.7	1.95 \pm 0.0
Salto Segredo	IG	2	22.8 \pm 7.3	6.76 \pm 0.2	10.57 \pm 5.8	3.28 \pm 1.7	6.95 \pm 0.2	39.59 \pm 10.4	558.50 \pm 37.5	9.70 \pm 4.7	1.33 \pm 0.6
Salto Santiago	IG	2	23.0 \pm 6.0	7.04 \pm 0.1	4.79 \pm 3.6	11.22 \pm 14.8	7.70 \pm 1.3	38.49 \pm 1.9	422.50 \pm 68.6	11.65 \pm 2.1	2.03 \pm 1.2
Salto Osório	IG	2	22.6 \pm 5.6	7.23 \pm 0.2	8.98 \pm 0.0	12.01 \pm 14.7	7.75 \pm 1.4	37.68 \pm 1.3	503.00 \pm 8.5	6.20 \pm 4.0	1.50 \pm 0.4
Salto Caxias	IG	2	23.1 \pm 4.0	7.04 \pm 0.2	2.70 \pm 0.3	3.65 \pm 3.5	7.11 \pm 0.4	37.64 \pm 1.6	508.00 \pm 50.9	10.45 \pm 2.3	2.53 \pm 0.2
Chavantes	PP	2	22.4 \pm 3.1	7.49 \pm 0.4	3.71 \pm 4.1	2.82 \pm 3.0	6.98 \pm 0.4	55.39 \pm 1.0	172.50 \pm 46.0	7.20 \pm 0.8	5.15 \pm 1.1
Salto Grande	PP	2	20.3 \pm 0.6	7.85 \pm 0.0	4.73 \pm 0.7	2.74 \pm 1.7	7.34 \pm 0.1	59.76 \pm 1.8	227.00 \pm 49.5	14.40 \pm 5.8	5.80 \pm 0.0
Canoas II	PP	2	26.0 \pm 0.7	6.87 \pm 0.6	7.42 \pm 5.4	4.72 \pm 3.7	6.80 \pm 0.1	58.99 \pm 2.6	200.50 \pm 65.8	10.70 \pm 2.4	1.18 \pm 0.6
Canoas I	PP	2	26.2 \pm 0.9	6.60 \pm 0.4	9.73 \pm 12.0	0.94 \pm 0.8	6.89 \pm 0.2	57.95 \pm 1.7	191.50 \pm 55.9	10.25 \pm 0.5	1.95 \pm 0.6
Capivara	PP	2	25.8 \pm 0.3	6.45 \pm 0.4	3.41 \pm 0.6	3.55 \pm 0.2	6.82 \pm 0.2	57.64 \pm 1.8	293.00 \pm 28.3	8.35 \pm 4.0	2.20 \pm 0.6
Taquaruçu	PP	2	20.0 \pm 0.1	7.34 \pm 0.6	5.22 \pm 2.0	4.16 \pm 1.1	7.54 \pm 0.4	59.49 \pm 3.1	330.50 \pm 91.2	8.60 \pm 5.8	4.10 \pm 0.0
Rosana	PP	2	19.2 \pm 0.9	7.33 \pm 0.2	4.85 \pm 2.3	1.96 \pm 2.3	6.96 \pm 0.1	59.54 \pm 1.0	361.00 \pm 76.4	9.90 \pm 0.0	2.10 \pm 0.2
Sobradinho	SF	18	27.4 \pm 1.6	7.66 \pm 0.6	14.99 \pm 9.1	2.52 \pm 1.4	7.84 \pm 0.3	63.80 \pm 24.9	46.00 \pm 39.1	66.50 \pm 19.6	1.20 \pm 0.6
Itaparica	SF	18	26.5 \pm 2.0	7.75 \pm 0.4	4.96 \pm 2.5	2.83 \pm 1.1	7.92 \pm 0.3	70.92 \pm 17.9	37.50 \pm 22.5	59.50 \pm 17.0	2.70 \pm 1.1
Moxotó	SF	18	26.7 \pm 1.9	7.65 \pm 0.4	4.40 \pm 1.8	2.58 \pm 1.0	8.01 \pm 0.4	109.4 \pm 40.1	45.00 \pm 38.2	66.00 \pm 17.8	3.00 \pm 1.2
Paulo Afonso I	SF	18	26.6 \pm 1.6	7.63 \pm 0.7	2.60 \pm 2.1	1.71 \pm 0.8	7.82 \pm 0.5	69.00 \pm 15.0	65.00 \pm 35.7	50.50 \pm 19.6	3.25 \pm 0.9
Paulo Afonso IV	SF	18	26.3 \pm 2.0	7.60 \pm 0.4	3.68 \pm 1.2	1.93 \pm 0.6	7.99 \pm 0.4	72.80 \pm 17.1	23.50 \pm 27.8	50.50 \pm 16.4	3.23 \pm 1.4
Xingó	SF	18	27.7 \pm 1.5	7.55 \pm 0.3	3.24 \pm 1.3	3.29 \pm 1.4	8.08 \pm 0.2	73.09 \pm 20.2	37.00 \pm 29.2	49.00 \pm 9.5	3.65 \pm 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 (hm ³)	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 $\Delta AIC_c < 2$) to perform the linear model analysis of fish richness and the exponential of Shannon's index (Hill number of order 1, 1D).

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
1D	-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

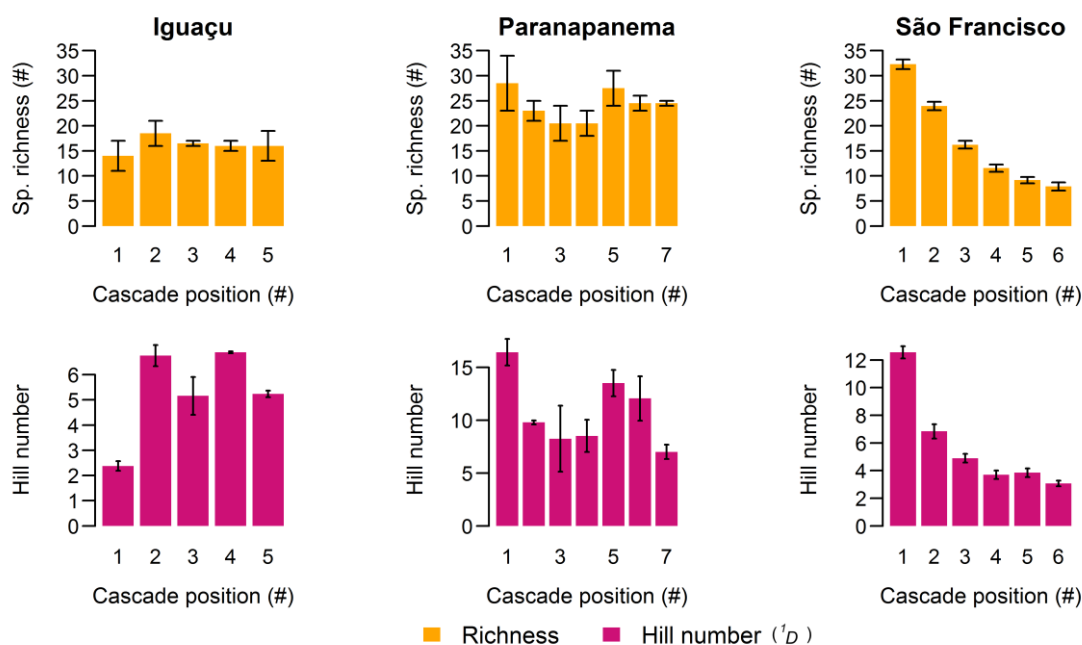


Figure S4. Box plots of diversity metrics (richness and the exponential of Shannon's index (Hill number of order 1, 1D) along the reservoirs cascades in the three river basins.

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	<i>P</i> -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); β_{sor} = beta diversity; β_{sim} = turnover component; β_{sne} = Nestedness component. *P* values < 0.05 are bolded.

Basin	Variable	r_s	<i>P</i> -value
Iguaçu	β_{sor}	1.0	0.083
	β_{sim}	1.0	0.083
	β_{sne}	-0.2	0.916
Parapanema	β_{sor}	-0.2	0.741
	β_{sim}	-0.2	0.741
	β_{sne}	0.5	0.356
São Francisco	β_{sor}	1.0	0.017
	β_{sim}	0.3	0.553
	β_{sne}	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	<i>P</i> -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

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

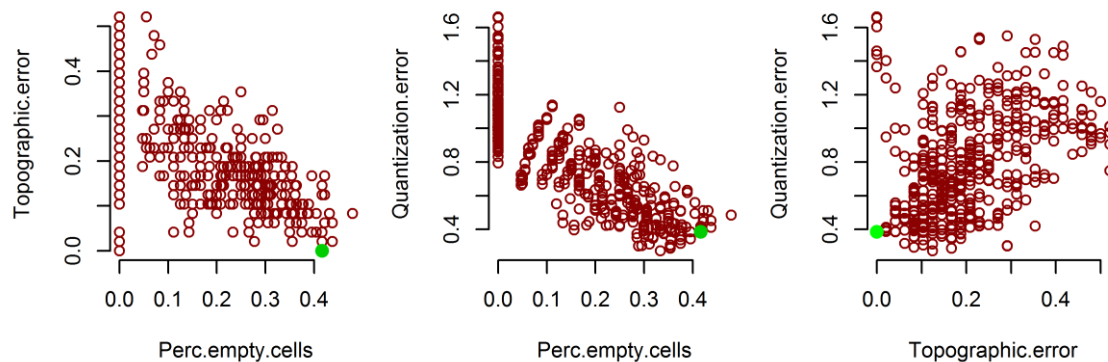
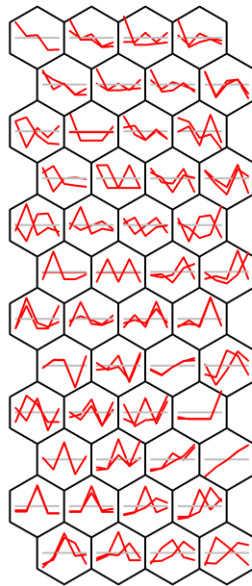


Figure S8a. Relationships of topographic and quantization errors with percentage of empty cells (i.e. unit neuron nodes) obtained during the optimisation of the dimensions (X , Y) of the super-organising map (Super-SOM) used to scrutinise the ecological trends in the Iguazu River Basin. The selected 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.

Codebooks



Mapping

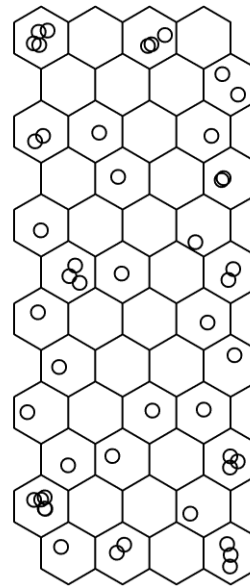


Figure S8b. Overlay of the codebooks of the optimal super-organising map (Super-SOM) summarising the ecological trends in the Iguaçú River Basin (left). Mapping of the species and environmental, morphological and spatial factors within the optimal Super-SOM (right).

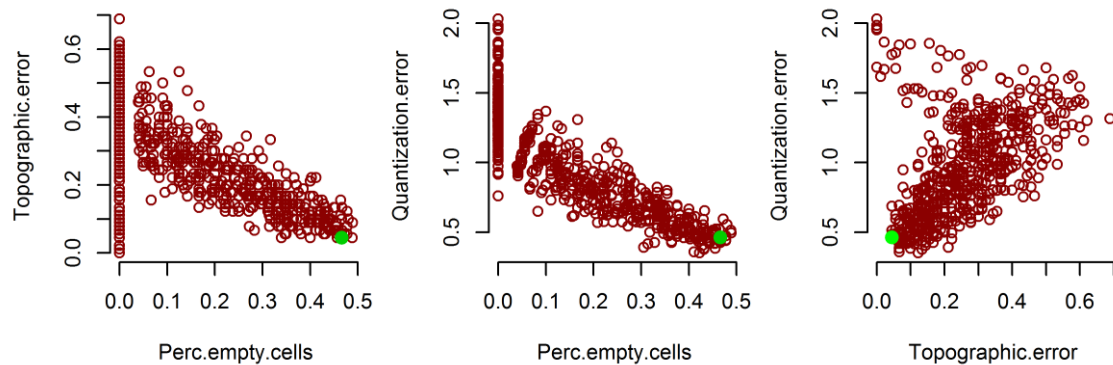


Figure S8c. Relationships of topographic and quantization errors with percentage of empty cells (i.e. unit neuron nodes) obtained during the optimisation of the dimensions (X, Y) of the Super-SOM used to scrutinise the ecological trends in the Paranapanema River Basin. The selected Super-SOM rendered 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.

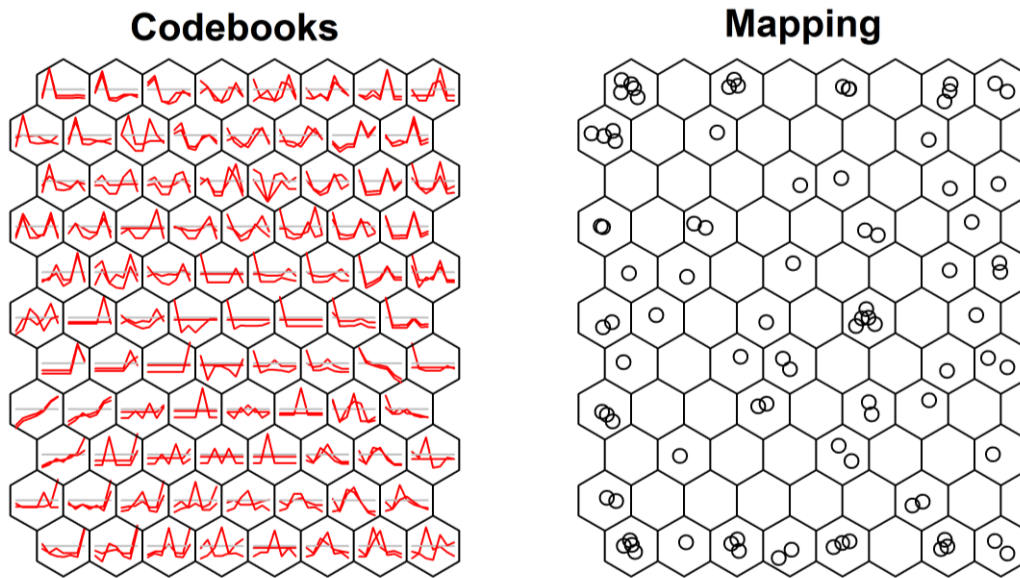


Figure S8d. Overlay of the codebooks of the optimal Super-SOM summarising the ecological trends in the Paranapanema River Basin (Left). Mapping of the species and environmental, morphological and spatial factors within the optimal Super-SOM (Right).

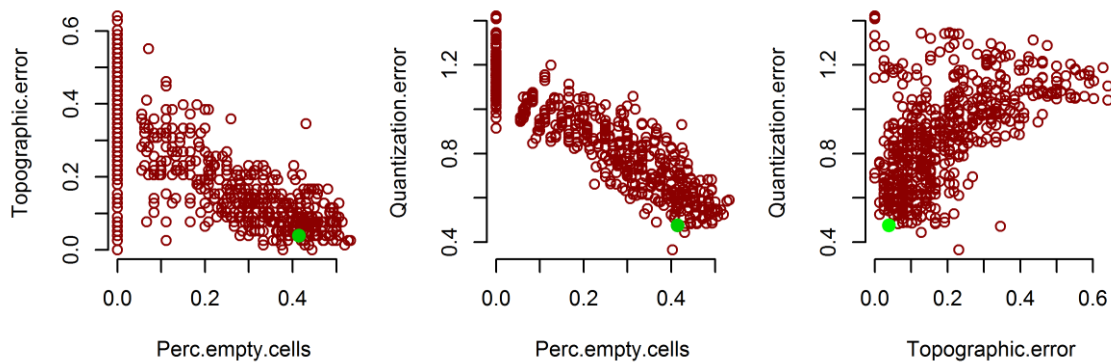


Figure S8e. Relationships of topographic and quantization errors with percentage of empty cells (i.e. unit neuron nodes) obtained during the optimisation of the dimensions (X , Y) of the Super-SOM used to scrutinise the ecological trends in the São Francisco River Basin. The selected Super-SOM rendered 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.

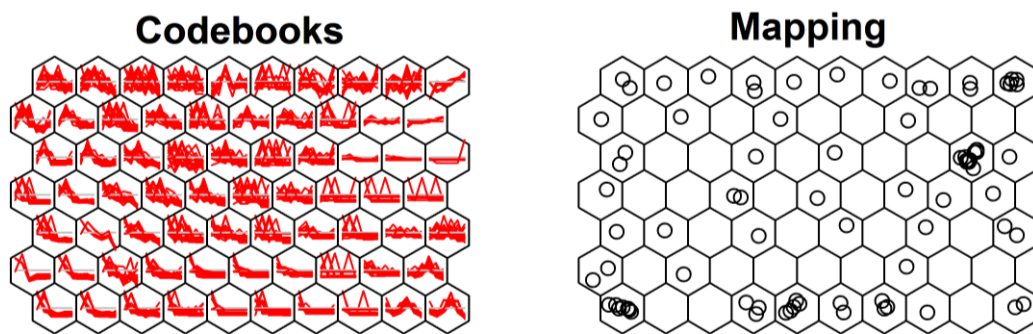


Figure S8f. Overlay of the codebooks of the optimal Super-SOM summarising the ecological trends in the São Francisco River Basin (Left). Mapping of the species and environmental, morphological and spatial factors within the optimal Super-SOM (Right).

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
<i>Astyanax lacustris</i>	1	0	0
<i>Psalidodon bifasciatus</i>	1	0	0
<i>Astyanax dissimilis</i>	1	0	0
<i>Psalidodon gymnodontus</i>	1	0	0
<i>Astyanax minor</i>	1	0	0
<i>Apareiodon vittatus</i>	1	0	0
<i>Bryconamericus ikaa</i>	0	1	0
<i>Bryconamericus</i> sp.	0	1	0
<i>Cyprinus carpio</i>	0	1	0
<i>Australoheros</i> cf. <i>facetus</i>	0	1	0
<i>Ctenopharyngodon idella</i>	0	1	0
<i>Crenicichla iguassuensis</i>	1	0	0
<i>Corydoras paleatus</i>	0	0	1
<i>Crenicichla</i> sp2	1	0	0
<i>Cyphocharax santacatarinae</i>	1	0	0
<i>Geophagus iporangensis</i>	0	1	0
<i>Glanidium ribeiroi</i>	0	1	0
<i>Hypostomus commersoni</i>	1	0	0
<i>Hypostomus derbyi</i>	0	1	0
<i>Hoplias</i> gr. <i>malabaricus</i>	0	1	0
<i>Hypostomus myersi</i>	0	1	0
<i>Megaleporinus macrocephalus</i>	1	0	0
<i>Odontesthes bonariensis</i>	1	0	0
<i>Oligosarcus longirostris</i>	1	0	0
<i>Pimelodus britskii</i>	0	0	1
<i>Pimelodus ortmanni</i>	1	0	0
<i>Rhamdia branneri</i>	0	1	0
<i>Rhamdia voulezi</i>	0	1	0
<i>Tatia jaracatia</i>	0	1	0
<i>Coptodon rendalli</i>	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
Turbidity	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	Cluster	Cluster
	1	2	3
<i>Apareiodon affinis</i>	1	0	0
<i>Astyanax lacustris</i>	1	0	0
<i>Apteronotus brasiliensis</i>	0	0	1
<i>Psalidodon bockmanni</i>	1	0	0
<i>Psalidodon fasciatus</i>	1	0	0
<i>Acestrorhynchus lacustris</i>	1	0	0
<i>Astronotus ocellatus</i>	1	0	0
<i>Apareiodon piracicabae</i>	1	0	0
<i>Ageneiosus militaris</i>	0	0	1
<i>Crenicichla britskii</i>	1	0	0
<i>Crenicichla haroldoi</i>	1	0	0
<i>Cichla kelberi</i>	1	0	0
<i>Crenichicla sp.</i>	1	0	0
<i>Crenicichla sp2</i>	1	0	0
<i>Geophagus iporangensis</i>	1	0	0
<i>Gymnotus carapo</i>	0	0	1
<i>Galeocharax gulo</i>	0	0	1
<i>Hypostomus ancistroides</i>	0	1	0
<i>Hypostomus cf. auroguttatus</i>	1	0	0
<i>Hypophthalmus oreomaculatus</i>	0	1	0
<i>Hypostomus hermanii</i>	0	0	1
<i>Hoplosternum littorale</i>	1	0	0
<i>Hoplias gr. malabaricus</i>	0	0	1
<i>Moenkhausia bonita</i>	0	0	1
<i>Hypostomus nigromaculatus</i>	0	0	1
<i>Hypostomus regani</i>	0	0	1

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

<i>Tatia neivai</i>	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
<i>Acestrorhynchus britskii</i>	0	0	1
<i>Acestrorhynchus lacustris</i>	1	0	0
<i>Astronotus ocelatus</i>	0	1	0
<i>Astyanax lacustris</i>	1	0	0
<i>Anchoviella vaillanti</i>	0	0	1
<i>Bryconops affinis</i>	0	0	1
<i>Brycon orthotaenia</i>	1	0	0
<i>Bergiaria westermanni</i>	0	1	0
<i>Conorhynchus conirostris</i>	0	1	0
<i>Cichla spp</i>	0	1	0
<i>Crenicichla lepidota</i>	0	1	0
<i>Curimatella lepidura</i>	1	0	0
<i>Colossoma macropomum</i>	1	0	0
<i>Cichlasoma sanctifranciscense</i>	0	1	0
<i>Duopalatinus emarginatus</i>	0	1	0
<i>Leporinus sp.</i>	1	0	0
<i>Eigenmanni virescens</i>	1	0	0
<i>Franciscodoras marmoratus</i>	0	1	0
<i>Gymnotus carapo.1</i>	0	1	0

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