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# Environmental filters predict the trait composition of fish communities in reservoir cascades

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**Abstract** Dam construction alters flow regimes and can change the composition of aquatic communities. Using data from three Brazilian hydrographic basins, we tested the hypothesis that reservoir cascades act as environmental filters for fish traits. This dataset included information on different environmental variables and fish traits (diet, migration, fecundation, parental care, position in the water column, and body size), and we used multivariate analysis (partial RLQ) to quantify the relationships between environmental

variables, species abundance and traits. We found that the abundance of migratory species declined towards downstream reservoirs, which tend to be smaller and less turbid with a shorter water residence time than upstream reservoirs. We also found evidence of an association between reservoir age and the domination of fish communities by small-sized species with parental care, external fecundation, and benthic habits. Our findings suggest that particular fish traits are selected for across reservoir cascades.

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## Introduction

Studies of environment–trait relationships are increasingly recognized as central to a better understanding of the processes underlying fish community structure (McGill et al., 2006; Webb et al., 2010; Dala-Corte et al., 2016; Ribeiro et al., 2016). A trait-based approach improves the ability to predict changes in community structure in response to environmental variation (Pease et al., 2012). This is expected to be so because the response of a group of species that share a given trait to environmental variation is less idiosyncratic than the response of individual species (Brind’Amour et al., 2011). Additionally, this approach can foster generality as a given environment–trait relationship, if proven to be strong and recurrent, can be applied to different biogeographic regions, independent of taxonomic classifications (Jung et al., 2010; Laughlin, 2014; Pease et al., 2015 and references therein). Thus, a more direct understanding of the mechanisms underlying community structure can be achieved (Webb et al., 2010).

The impacts of dams on fish community structure are pervasive (Agostinho et al., 2016). The decline of migratory fish populations in regulated rivers is emblematic of these impacts, but the identification of the causal mechanisms should consider the environmental changes caused by impoundments in addition to the effect of a dam as physical barrier to fish movement. These environmental changes (e.g., changes in turbidity, water temperature, and hydrology) represent efficient ecological barriers “to free movements along the river” (Pelicice et al., 2015). Thus, different sets of traits related to locomotion, habitat use, behavior, and physiology should influence the distribution and abundance of fish in rivers. Previous studies have also shown that reservoir-dwelling fish assemblages are dominated by species with feeding plasticity, low dispersal ability (sedentary lifestyle), parental care, small body size, and low market value (Hoeinghaus et al., 2009; Agostinho et al., 2016).

Dams cause discontinuities in the physical and biological characteristics of rivers, especially in the dynamics of materials, energy, and nutrients as described by the Serial Discontinuity Concept (Ward & Stanford, 1983, 1995). When reservoirs are arranged in cascades, one can expect more pronounced biotic and abiotic modifications that will affect fish

assemblages and trait compositions, both within the reservoirs and along the basin (Miranda et al., 2008). For example, Miranda & Dembkowski (2015) found an increase in species richness and abundance of rheophilic species “upstream within each reservoir and downstream across the chain of reservoirs” in the Tennessee River (USA). According to these authors, this sawtooth pattern is probably because riverine conditions in the reservoir cascade mainly occur upstream, within reservoirs, and downstream.

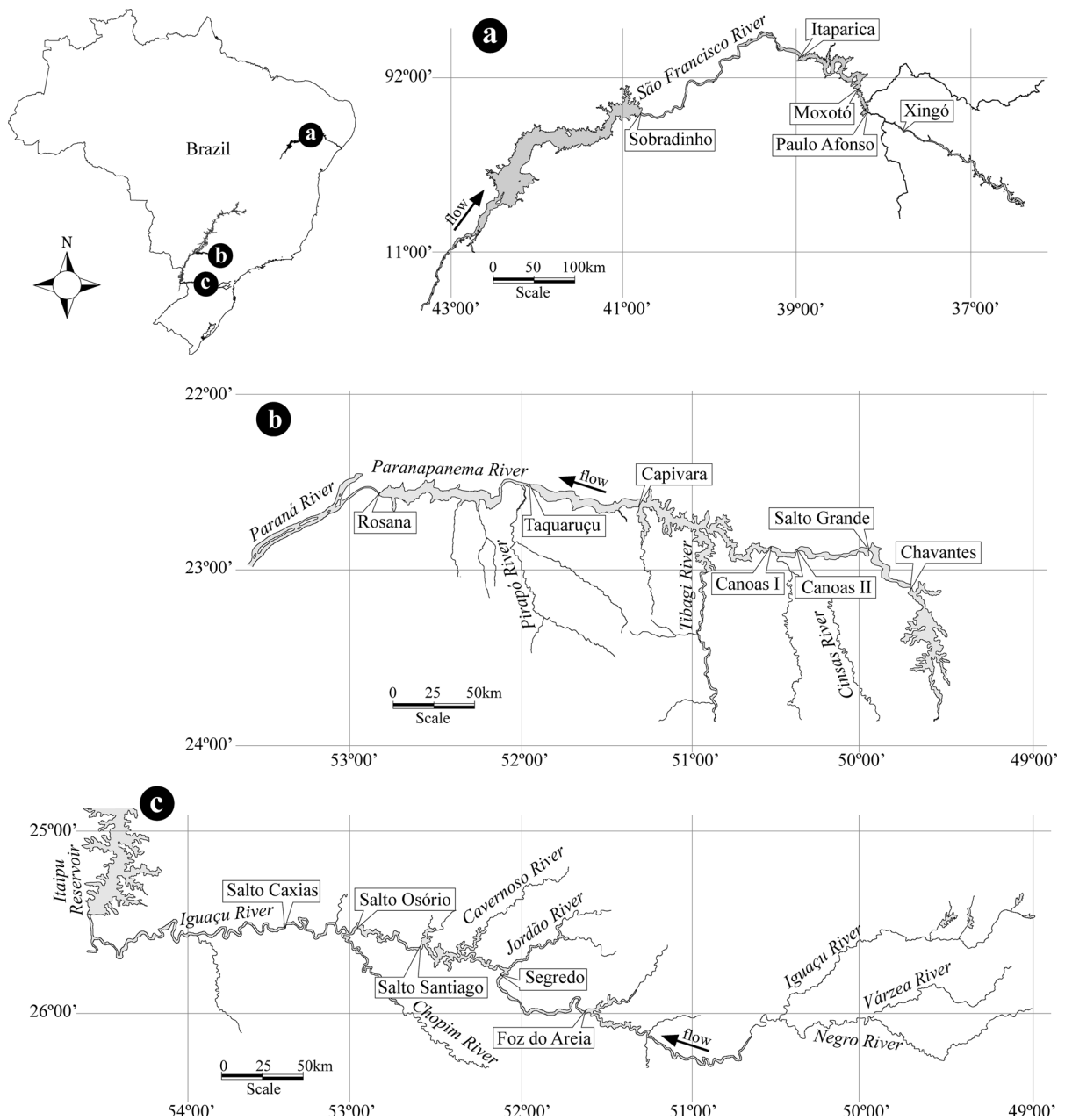
Most studies in impounded rivers have focused in single reservoirs, whereas the cumulative effects of multiple dams in a hydrographic basin are less understood (Castello & Macedo, 2015; Cheng et al., 2015). Thus, our objective was to analyze the changes in trait compositions across three reservoir cascades in Brazil. Despite the exploratory nature of our study, we expected a higher abundance of sedentary, small-sized, trophically plastic, and reproductively flexible species (i.e., opportunist sensu Winemiller, 1989) in the reservoirs that are older, smaller, and downstream in the cascade. Due to an expected decrease in turbidity across reservoir cascades (Barbosa et al., 1999) and assuming that more transparent waters favor piscivorous species, we predicted a greater abundance of piscivorous species in the reservoirs located downstream of the cascades. Finally, we expected a greater proportion of long-distance migratory species in large reservoirs located upstream in the cascade.

## Methods

### Study area

The data used in this study were collected from three large Brazilian basins: the São Francisco River Basin, the Paranapanema River Basin, and the Iguaçu River Basin (Fig. 1; Table S1). The two last basins are located in the Paraná River Basin, the main river of the La Plata Basin, and the river with the second-largest extent in South America with a drainage area of  $2.8 \times 10^6 \text{ km}^2$  (Agostinho et al., 2007b).

The São Francisco Basin (SFB) has a drainage area of approximately  $636,420 \text{ km}^2$ , and it is highly impacted by reservoirs with a total inundated area of  $5856.2 \text{ km}^2$ . The reservoir cascade of the São Francisco Basin (the Sobradinho, Itaparica, Moxotó, Paulo Afonso I, II, III,



**Fig. 1** Localization of the hydrographic basins in Brazil: **a** São Francisco River Basin, **b** Paranapanema River Basin, and **c** Iguaçu River Basin. Arrows indicate the direction of flow

and IV, and Xingó reservoirs) is the only one in Latin America located in a semiarid region (Fig. 1a) with marked seasonal variations in water flow.

The Paranapanema Basin (PB) begins in Serra do Paranapiacaba, approximately 500 km from its mouth in the Paraná River (Castro et al., 2003), and it has a drainage basin of approximately 920 km<sup>2</sup> (Sampaio,

1944). The reservoir cascade in the PB (the Chavantes, Salto Grande, Canoas II, Canoas I, Capivara, Taquaruçu, and Rosana reservoirs, Fig. 1b) floods approximately 1,800 km<sup>2</sup> of its drainage basin (Agostinho et al., 2007a).

The Iguaçu Basin (IB) has an area of approximately 70,800 km<sup>2</sup> and extends more than 1,000 km from its

source to its mouth in the Paraná River (Maack, 2002). The main river in this basin (the Iguçu River) is impacted by a reservoir cascade consisting of five dams (the Foz do Areia, Segredo, Salto Osorio, Salto Santiago, and Caxias reservoirs; Fig. 1c).

#### Environmental variables

The limnological data used in this study were obtained by the Departamento de Pesca-Universidade Federal Rural de Pernambuco (for the SFB) and Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura-Universidade Estadual de Maringá (for the PB and the IB). The data were gathered between October 2006 and July 2009 in the Sobradinho Reservoir and between December 2007 and September 2010 in the other reservoirs of the SFB during quarterly campaigns, and data from the PB and the IB were obtained between July and November 2001. The following limnological variables were available for this study: temperature (°C), dissolved oxygen (mg/l), turbidity (NTU), and chlorophyll *a* (µg/l).

Following Pelicice et al. (2015), we also recorded the following variables: position of the reservoir in the cascade, area (km<sup>2</sup>), reservoir length (km), reservoir age (years), type of operation [a dummy variable to differentiate between accumulation (0) or run-of-the-river reservoirs (1)] and water residence time (days). For position in the cascade, we assigned a value of 1 for the most-upstream reservoir, 2 for the reservoir located immediately downstream of the first, and so on. Accumulation reservoirs are usually located in the superior regions of the rivers, and run-of-the-river reservoirs operate with smaller flooded areas (ANEEL, 2002). We obtained data on reservoir age and type of operation from the websites of the power-generating companies (Companhia HidroElétrica do São Francisco, Duke Energy Brasil, and Tractebel Energia).

#### Biotic data

Our dataset was based on 96 sampling campaigns (see Supplementary Material, Table S1 for the number of samples per reservoir). For the São Francisco River Basin, fish samples were taken using gill nets with varying mesh sizes (1.2–9 cm between knots) every two months between November 2006 and September

2009 in the Sobradinho Reservoir and between February 2008 and December 2010 in the other reservoirs. There was no overlap between the biotic and limnological sampling periods as limnological data were always obtained after the biotic data; so, the limnological data for the months nearest to the fish sampling campaigns were used in our analysis. For the Paranapanema and Iguçu River basins, reservoirs were sampled in July and November 2001.

Fish were caught in the lacustrine region of the reservoirs with gill nets of different mesh sizes (2.4–14 cm between knots), which were exposed for 24 h in each reservoir and revisited at 8:00, 16:00, and 22:00 h. For all basins, we expressed abundance as the capture per unit of effort (CPUE) for each sample unit; we divided the number of individuals by the sampling effort (meters of net) and multiplied the result by 1,000. The number of sampling campaigns per reservoir ranged from 2 to 18, and our final data table consisted of 96 rows.

#### Traits

We evaluated six traits (see the Supplementary Material, Table S2). Trait data were obtained from the literature. In cases where there were no data for the sampled species, we used traits from congener species (8.5% of species). We selected traits related to feeding strategy, habitat use (pelagic, benthic–pelagic, and benthic), and reproductive strategy (migratory behavior, type of fecundation, and parental care).

For the São Francisco Basin, we obtained diet information from stomach analyses in the laboratory, and the importance of food items was assigned according to the volume percentage of each resource, which estimated separately for species and sampling periods. The relative ratio (%) was calculated from the weight of each food item through the gravimetric method (Hyslop, 1980). At least 30 individuals of each species were analyzed, and food items were identified to the lowest possible taxonomic level (e.g., Britski et al., 1984; Merritt & Cummins, 1996). For the other basins, we classified species into trophic groups following the literature (see Supplementary Material, Table S3), but this classification was based on data gathered from the IB and the PB (Supplementary Material, Table S3).

Data on body length were obtained from Fishbase (Froese & Pauly, 2014). Then, we classified the species as small ( $\leq 200$  mm), medium (200–400 mm), and large ( $> 400$  mm).

### Data analysis

To evaluate the response of the traits to the environmental variables, we used partial RLQ analysis (Dolédéc et al., 1996). The traditional RLQ is a multivariate technique that associates environmental variables to traits while weighting by species abundance, and it ordinales three independent matrices (**R**, **L**, and **Q**), resulting in scores for samples, species, traits, and environmental variables along orthogonal axes. In this study, the matrices were the following: **R** ( $n \times m$ ), containing data of  $m$  environmental variables for each of  $n$  samples; **L** ( $n \times p$ ), with CPUE data from  $p$  species for  $n$  samples; and **Q** ( $p \times q$ ), containing  $q$  traits for  $p$  species. Matrix **L** was square-root transformed (Legendre & Legendre, 2012) and submitted to correspondence analysis (CA), and matrix **R** was submitted to Hill–Smith analysis (Hill & Smith, 1976). Finally, matrix **Q** was analyzed by multiple correspondence analysis (MCA).

We used a partial RLQ (Wesuls et al., 2012) to control for the temporal dependence of the data and biogeographical differences between the basins. For the partial RLQ, we used a matrix, **W**, containing hydrographic basin and sampling year (concatenated into a single dummy variable to represent each combination of reservoir and sampling month) as a covariate and performed the partial RLQ in two steps. First, we calculated two multivariate regressions using matrix **W** as the explanatory matrix and matrices **R** and **L** as response matrices to generating the matrices **R<sub>r</sub>** and **L<sub>r</sub>**, which contained the residuals of the respective models (Wesuls et al., 2012). The residual matrices represent the variation in environmental variables and the abundances of the species independent of biogeographical or temporal effects (Wesuls et al., 2012). Second, we performed a modified RLQ using the original matrix **Q** and matrices **R<sub>r</sub>** and **L<sub>r</sub>** (Wesuls et al., 2012). We conducted all the analyses in the software R (R Core Team, 2015) with the ‘ade4’ package (Dray & Dufour, 2007). We used the ‘dudi.coa’ to perform a CA with **L** matrix, the ‘dudi.hillsmith’ to perform Hill–Smith analysis with **R** matrix and MCA with **Q** matrix, and ‘wca’ function to compute the partial RLQ.

### Results

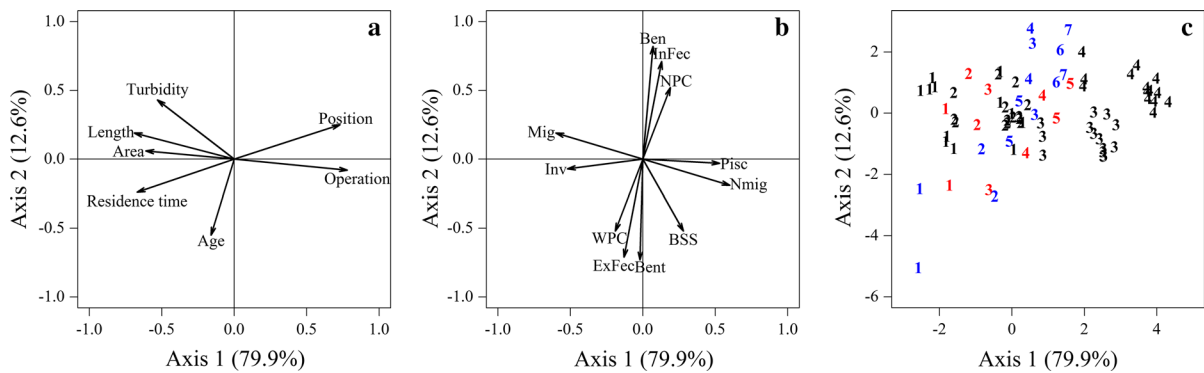
The first two axes of the partial RLQ (RLQ hereafter) accounted for 92.5% of the co-inertia among the tables. The first RLQ axis was negatively correlated with reservoir length, water residence time, area, and turbidity, and it was also positively correlated with the type of operation and the position of the reservoir in the cascade. The second RLQ axis was negatively correlated with age (Fig. 2a). The correlations between species traits and RLQ axis 1 indicated that the abundances of invertivore and migratory fishes tended to increase in larger reservoirs with longer water residence times and more turbid waters. On the other hand, piscivorous and sedentary fishes tended to be more associated with run-of-the-river reservoirs, which are generally positioned downstream in the cascade. The second RLQ axis also indicated positive associations between reservoir age and small-bodied fishes with a benthopelagic habit, external fecundation and parental care (Fig. 2b; Table S4).

Upstream reservoirs were positioned on the negative side of the first RLQ axis (Fig. 2c). In general, these are accumulation reservoirs with large areas and long water residence times (e.g., Sobradinho, Itaiparica, Foz do Areia, Segredo, Chavantes, and Salto Grande). More downstream, run-of-the-river reservoirs (e.g., Xingó, Caxias, Capivara, Taquaruçu, Rosana, Moxotó, Salto Osório, Canoas II, and Canoas I) tended to be smaller than upstream reservoirs (Fig. 2c).

### Discussion

Considering data from three independent reservoir cascades, we found interesting associations between fish traits and environmental variables. Remarkably, we found that simple variables were the main correlates of the trait compositions of fish communities. For example, the type (accumulation or run-of-the-river) and position of the reservoirs in the cascades showed the highest correlations with the first RLQ axis, which differentiated “migratory/invertivorous” from “piscivorous/sedentary” communities. The occurrence of the first type of community in larger/upstream reservoirs with longer water residence times (or the opposite in the case of the second type of community) is likely explained by two reasons. First, these





**Fig. 2** Relationship between environmental variables and the first two axes of the partial RLQ analysis (a). Trait coefficients (b) and the reservoir scores (c) are also shown. Numbers indicate the position of the reservoirs in the cascades on the São Francisco River (black 1 Sobradinho, 2: Itaparica, 3: Moxotó, 4: Xingó), the Iguaçu River (red 1 Foz do Areia, 2: Segredo, 3: Salto Santiago, 4: Salto Osório, 5: Caxias) and the Paranapanema

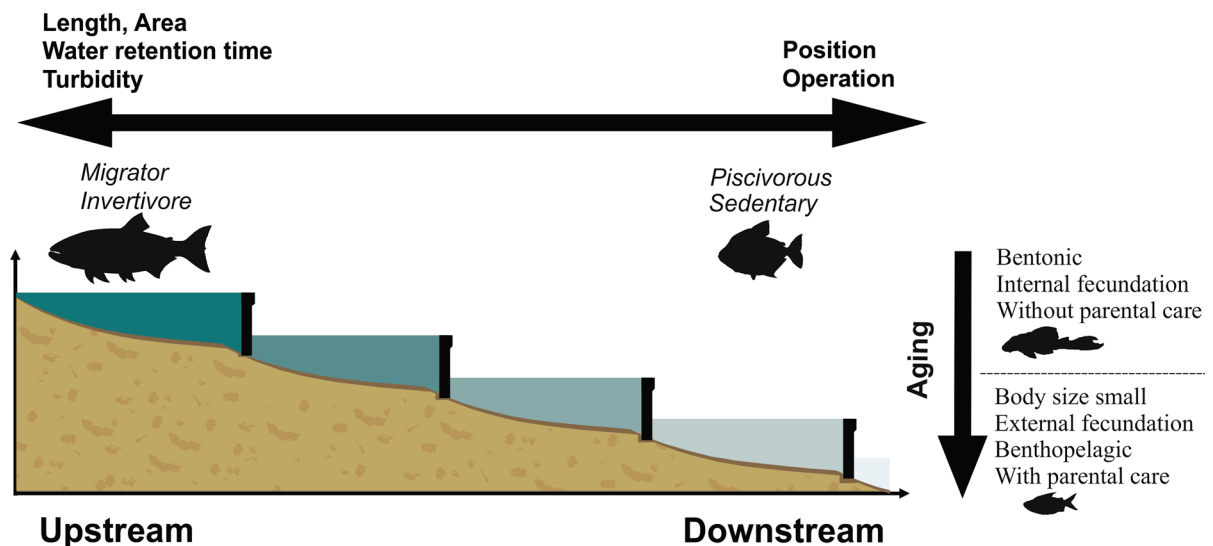
River (blue 1 Chavantes, 2: Salto Grande, 3: Canoas II, 4: Canoas I, 5: Capivara, 6: Taquaruçu, 7: Rosana). Codes *Inv* invertivore; *Pisc* piscivore; *Mig* migratory; *Nmig* non-migratory; *ExFec* external fecundation; *InFec* internal fecundation; *WPC* with parental care; *NPC* no parental care; *Bent* benthopelagic; *Ben* benthonic; *BSS* small body size. Note that only environmental variables and traits with values 0.5 are shown

reservoirs are at the beginning of the cascade, and so they do not present physical barriers to the upstream movement of rheophilic species (Petts, 1980; Liermann et al., 2012; Pelicice et al., 2015). Second, owing to their large dimensions, these reservoirs would favor short-distance migrators (Agostinho et al. 2007a) (Fig. 3).

The positive association between invertivorous fish and reservoir size is also worth speculation. Either due to passive sampling (Coleman et al., 1982) or an

increase in environmental heterogeneity (Stein et al., 2014), larger reservoirs are expected to have higher invertebrate species richness than smaller reservoirs (Santos et al., 2016). This increase in the amount of food resources may account for the increased occurrence of invertivorous fish in large, upstream reservoirs.

We envisage at least one explanation for the increased abundance of sedentary and piscivorous in reservoirs located downstream in the cascades, which are generally run-of-the-river reservoirs. Turbidity is



**Fig. 3** Schematic representation summarizing the results of the partial RLQ analysis. Decreasing turbidity (from upstream to downstream reservoirs) is represented by different levels of shading

expected to decrease along a reservoir cascade due to sedimentation (Ney, 1996; Barbosa et al., 1999), and this increase in water transparency may favor visually oriented piscivores (Rodríguez & Lewis 1997; Tejerina-Garro et al., 1998). Independent of the underlying mechanism, this pattern is consistent with earlier studies showing that piscivores in lentic waters are ubiquitous in small environments (Agostinho & Júlio 1999).

We found that age was a second important factor differentiating fish communities. Indeed, different ichthyological changes have been hypothesized to emerge as reservoirs age (Lenhardt et al., 2009; Agostinho et al., 2016), which according to Agostinho et al. (1999), include “a reduction in the number of top predators, mean size of species, and species richness. Pelagic species are expected to become dominant as benthic organisms decline and littoral habitat deteriorates. Short-lived species with fast growth or reproductive compensation are expected to have survival advantages.” Our results support some of these predictions. For example, we found that small-bodied, benthopelagic species with external fecundation and parental care were associated with the prevailing environmental conditions in older reservoirs. Conversely, negative associations were also found between reservoir age and the traits of benthic habit, internal fecundation, and parental care.

Our results have important conservation and management implications. First and foremost, they indicate the importance of dam-free stretches of river for the conservation of fish communities (Agostinho et al., 2004, 2016; Lees et al., 2016). Previous research emphasized the need to account for the spatially cumulative impacts of multiple dams on the different biotic and abiotic characteristics of rivers (Winemiller et al., 2016). Second, our findings also suggest the need to consider the impacts of reservoirs that accumulated over time as reservoirs age. For example, Hoeinghaus et al. (2009) reported a strong decline in total fisheries yield in the Itaipu Reservoir (Brazil) despite an increase in total fishing effort, and so assuming the generality of this aging effect, we suggest that environmental compensation programs for fishery losses should be long-lasting. Finally, we encourage further research aimed at testing the effects of reservoir cascades on fish communities as the cumulative effects of multiple dams in a hydrographic basin are much less understood.

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