Hydrobiologia (2024) 851:4213–4229
https://doi.org/10.1007/s10750-024-05576-5

PRIMARY RESEARCH PAPER

The effect of shoreline habitats on native and non-native fish species in a set of Neotropical reservoirs

Ana Clara Sampaio Franco · **Ana Cristina Petry** · **Emili García-Berthou** · **Luciano Neves dos Santos**

Received: 2 July 2023 / Revised: 6 May 2024 / Accepted: 15 May 2024 / Published online: 30 May 2024

Abstract Biodiversity is declining worldwide due to anthropogenic impacts, especially noxious for freshwater ecosystems, considering their close relationship with human activities. Damming is one of the most harmful human impacts that leads to the loss of several riverine fish through habitat loss or change. Herein, we aimed to assess the relationship between the composition of fish assemblages in reservoirs and the availability of littoral habitats, and whether these patterns differ between native and non-native species. Fish assemblages of fifteen reservoirs from up to downstream the Paraíba do Sul river basin were evaluated. Habitat availability was more important for native than for non-native species, after controlling for the influence of reservoir features. Local drivers were crucial for the occurrence of non-native species which thrived in the absence of complex habitats. Macrophytes seemed to play two key but quite antagonistic roles for fish species. They were positively related to native small characids, probably acting as shelter against predation, but they were also related to hypoxic conditions in eutrophic reservoirs. These findings stress the importance of preserving or restoring physically complex habitats as beneficial for native fish species through providing grounds for feeding (catfishes on leaves) and recruitment (juveniles of characids in macrophytes banks).

Keywords Fish assemblage · Forage fish · Habitat structure · Invasion · Limnology

Handling editor: Fernando Mayer Pelicice

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-024-05576-5.

A. C. S. Franco (✉) · A. C. Petry
Graduate Course in Ecology (PPGE), Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil
e-mail: anaclara306@gmail.com

A. C. S. Franco · L. N. dos Santos
Graduate Course in Neotropical Biodiversity (PPGBIO), Universidade Federal do Estado do Rio de Janeiro, Av. Pasteur, 458, Rio de Janeiro, RJ 22290-240, Brazil

A. C. S. Franco · E. García-Berthou
GRECO, Institute of Aquatic Ecology, University of Girona, 17003 Girona, Catalonia, Spain

A. C. Petry
Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro, Avenida São José do Barreto, 764, Macaé, RJ 27965-045, Brazil

Introduction

Habitat is an essential resource for species, strongly related to local biodiversity as it is used for nesting, spawning, feeding, and as a refuge from predators (Werner et al., 1983; Persson, 1993). The availability of complex habitats supports the existence of distinct niches, mediates species interactions and allows the coexistence of a greater variety of species

(Levin, 1981; Pianka, 1988). Historically, species evolve to adapt to local abiotic and biotic conditions and need to find a suitable habitat that allows coexistence with other species. The importance of habitats is even more evident when human activities interfere with the structure, coverage, and quality of this resource (Sala et al., 2000; Lewis et al., 2021; Guedes & Araújo, 2022; Araújo et al., 2023). In aquatic ecosystems, riparian vegetation removal, damming, pollution, and water withdrawal are examples of human activities that can lead to the destruction of key habitats for aquatic species (Teresa et al., 2015; Araújo et al., 2023). It often leads to extinction or species declines, also altering the networks of species interaction, which ultimately may interfere with ecosystem functioning since it is supported by those interactions, especially when non-native species are involved, considering potential feedback loops among different stressors (Gorman & Karr, 1978; Simberloff, 1988; Willis et al., 2005; Villéger et al., 2010; Winemiller, 2018; Pyšek et al., 2020). Thus, assessing species–habitat association may help to elucidate community patterns in response to novel conditions like dammed rivers.

Currently, more than one million dams fragment rivers around the world, but many others continue to be planned and built, especially within the largest hydrographic basins of the world, namely the Congo, Mekong and Amazon (Poff et al., 2007; Winemiller et al., 2016; Grill et al., 2019). Dam construction directly affects fish populations through habitat fragmentation and flow regulation (Nilsson et al., 2005; Grill et al., 2015; Reid et al., 2019), disrupting fish migration routes and connectivity between ecosystems (Vannote et al., 1980; Fukushima et al., 2007; Ziv et al., 2012). These disruptions can lead to shifts in fish assemblage composition, with the proliferation of lentic-adapted and non-native species and the decline of rheophilic species, contributing to biotic homogenization (Agostinho et al., 2008; Winemiller, 2018). Furthermore, the fragmentation of river systems can lead to cumulative effects, resulting in spatial variations in native species diversity, known as the cascading effect (Santos et al., 2018; Loures & Pompeu, 2019; Ganassin et al., 2021). The ongoing alteration of flow regimes within reservoirs exacerbates habitat degradation, destabilizing marginal banks and leading to habitat loss and decreased microhabitat availability (Santos et al., 2011a; Guedes & Araújo, 2022; Araújo et al., 2023). This simplification of aquatic landscapes creates harsher species interactions due to reduced habitat availability for fish reproduction, nesting, recruitment, and feeding (Bunn & Arthington, 2002; Poff et al., 2007). Consequently, there is a decline in functional diversity and loss of endemic species, potentially increasing the establishment of non-native species through temporary resource availability windows (Johnstone, 1986). The introduction of non-native predators further exacerbates these impacts by intensifying predation pressure on native prey species, leading to population declines or extirpations (Kovalenko et al., 2010a; Alexander et al., 2014; Pelicice et al., 2015).

Fish species are closely associated with various types of aquatic vegetation and inorganic materials on the reservoir bottom, playing a crucial role in habitat structuring (Quist et al., 2005; Alexander et al., 2014; Bittencourt et al., 2020). Despite the importance of habitat, research on its significance for both native and non-native species in reservoirs is limited. Existing studies have identified associations between fish species and submerged habitats, both natural and artificial, while also highlighting the negative impacts of reservoir operations on habitat degradation (Santos et al., 2011b; 2013; Pelicice & Agostinho, 2009; Pelicice et al., 2015; Miranda et al., 2010). However, most studies focus on specific habitat types or single ecosystems, limiting the generalizability of their findings. Therefore, our study aims to analyse species–habitat relationships in 15 reservoirs along an upstream–downstream gradient in southeastern Brazil, considering various submerged and marginal habitats. Understanding these relationships in different reservoir contexts, including age, size, altitude, and water residence time, not only enhances our knowledge of species–habitat dynamics in natural ecosystems but also provides valuable insights for the hydropower industry and conservation managers (see Pelicice et al., 2022 for further insights). We specifically aimed to: (i) evaluate habitat composition among systems and the influence of reservoir features in the maintenance of habitat diversity; (ii) characterize the availability or absence of shoreline habitats and their associated fish assemblage in reservoirs; (iii) assess the importance of habitat availability and limnological features in determining fish assemblage composition by controlling for damming cumulative effects; and (iv) test whether these patterns are similar for native and non-native species.

Materials and methods

Study area

The Paraíba do Sul river basin drains a surface area of 62,074 km^2 and flows through the three most populated and industrialized Brazilian states (Rio de Janeiro, São Paulo and Minas Gerais), providing water and electricity for approximately 14 million inhabitants (Ovalle et al., 2013; Kahn et al., 2017). The climate is tropical savanna with dry-winter and an average annual maximum temperature of 27 °C (Kottek et al., 2006; Pacheco et al., 2017). The ecological integrity of the Paraíba do Sul river has been declining for a long time due to increasing pollution by industrial and agricultural wastes, damming and water derivation, groundwater withdrawal, and degradation of riparian forest (Kahn et al., 2017; Pacheco et al., 2017). During the last decades, its native fish diversity has been further threatened by the introduction of 62 non-native fish species along the basin (Bizerril, 1999; Honji et al., 2017; Moraes et al., 2017), such as in the case of the peacock bass *Cichla* sp. which has been introduced to the Paraíba do Sul river basin in the 1950s, accounting for one of the oldest introduction of the genus outside Amazon (Franco et al., 2021).

Fifteen reservoirs distributed from the headwaters (i.e. Paraibuna reservoir) to the middle–lower reach (i.e. Ilha dos Pombos reservoir) of the Paraíba do Sul river basin were sampled (Fig. 1; Online Resource 1; Franco et al., 2022a). By studying reservoirs in a single watershed, we aimed to limit the effects of large-scale filters (i.e. biogeographic) on biotic composition. These reservoirs are located along a gradient of altitude, and even though they are mainly characterized by high water temperature, low conductivity, and oligo-mesotrophic conditions, they vary in age, water regime operation, habitat structure, and limnological conditions. Further information on reservoir and limnological features of the studied system is also available in related studies (Franco et al., 2018; 2022a, b and Online Resource 1).

Fish sampling

Fish sampling was carried out once in each reservoir, between April and June of the years 2014 (Funil, Tocos, Lajes, Santana, Vigário, Pereira Passos and Paracambi) and 2016 (Paraibuna, Igaratá, Santa Branca, Queluz, Areal, Anta, Santa Fé and Ilha dos Pombos). Sampling was conducted immediately following the conclusion of the wet season to capture a

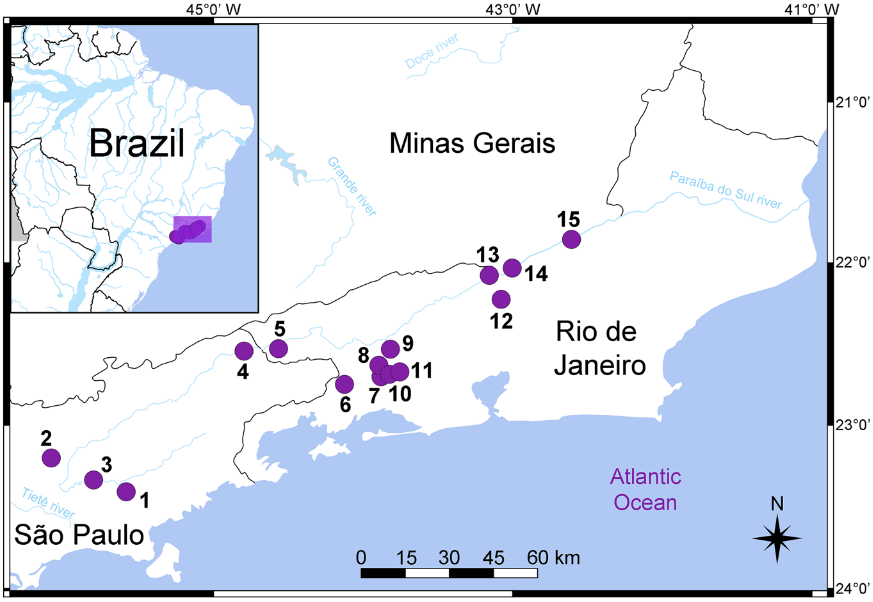

Fig. 1 Geographical location of the fifteen studied reservoirs in the Paraíba do Sul river basin, Brazil (1—Paraibuna; 2—Igaratá; 3—Santa Branca; 4—Queluz; 5—Funil; 6—Tocos; 7—Lajes; 8—Vigário; 9—Santana; 10—Pereira Passos; 11—Paracambi; 12—Areal; 13—Santa Fé; 14—Anta; and 15—Ilha dos Pombos). Further information on each system can be found in Online Resource 1

diverse range of size classes, as many species exhibit reproductive activity during this period (Winemiller, 1989; Mello, 2001; Mazzoni et al., 2018). Gillnet sets (60 m × 1.5 m; sections of 15, 30, and 45 mm mesh joined consecutively) were installed in the early afternoon and retrieved the next morning in three sites (i.e. one gillnet set per site totalling three gillnet sets per reservoir) located within the lentic portion of each reservoir to depict the composition and structure of fish assemblages. Fish abundance was standardized as catch per unit of effort (CPUE; using fish per m^2 per 24 h). All specimens were kept on ice until their transportation to the laboratory, where they were identified, measured (total length, mm) and weighed (to the nearest g).

Limnological features (temperature, pH, conductivity, turbidity, total dissolved solids, dissolved oxygen, and chlorophyll *a*) were recorded at each gillnet sampling site using a multiparameter probe, whereas water transparency was measured with a Secchi disc. On these sites, the structural complexity of wet littoral habitats one metre below the water surface was also estimated as the per cent cover of the categories of grass, shrubs, logs, litter, macrophytes, gravel, sand, mud, and structure-less margins (Online Resource 2). This evaluation was performed visually by the same boarded observer, which covered a 100 m stretch of shoreline and approximately 400 m^2 of area evaluated per sampling site (as in Franco et al., 2018).

Statistical analysis

All statistical analyses were performed in the R statistical language and environment version 4.3.1 (R Core Team, 2023). We used site as sampling unit in order to be able to evaluate within system variation in habitat composition and its potential relation with species composition. We used a principal component analysis (PCA) to ordinate the reservoirs based on their habitat availability (grass, shrub, log, leaf, macrophyte, gravel, sand, mud, and structure-less margins; per cent cover by each habitat arcsine square root transformed) using function *rda* in the *vegan* package (Wang et al., 2022; Oksanen et al., 2016). This transformation was chosen to reduce the variance and to linearize the proportional habitat data in order to be fitted to multivariate analyses. PCA is an ordination method suitable for quantitative variables, which preserves the Euclidean distance among sites based on eigenvectors (Borcard et al., 2011). We used the function *PCAsignificance* to estimate the number of significant axes based on the broken-stick criterion, as available in package *BiodiversityR* (Kindt, 2017). The broken-stick criterion provides an accurate estimation of the dimensionality of the data, retaining only components of the PCA with eigenvalues greater than those given by a null model (Jackson, 1993).

A redundancy analysis (RDA) was used to assess the relationship of habitat availability with limnological features (temperature, pH, and $\log_{10}$ transformations of conductivity, total dissolved solids, turbidity, oxygen, transparency, and chlorophyll *a*) in each site and reservoir features (age, and $\log_{10}$ transformations of area, altitude, and residence time), using function *rda* of the *vegan* package (Oksanen et al., 2016). Another RDA was performed to test for the relationship of fish assemblages (CPUE; using fish per m^2 per 24 h for gillnet sets) with habitat availability. RDA is a constrained linear ordination method combining regression and principal component analysis, which allows the modelling of multivariate response data (Borcard et al., 2011; Legendre & Legendre, 2012). A forward model selection routine was used for all RDAs and performed with function *ordiR2step* in *vegan* (9,999 permutations; Blanchet et al., 2008), in order to select a parsimonious model with the highest adjusted R^2. In the second RDA analysis, the Hellinger transformation (Legendre & Gallagher, 2001) was used for the abundance matrix of fish assemblages. The Hellinger transformation was used to standardize species abundance data. It involves taking the square root of the relative abundance values, which helps to reduce the influence of extremely large values and standardizes the data to account for differences in sample total abundances (Legendre & Gallagher, 2001). The significance of RDA axes and terms was assessed with function *anova.cca* and 999 permutations as available in the *vegan* package.

In order to assess patterns that may be related to species origin, we classified all the species according to their biogeographical and historical distribution into native and non-native species (see Soto et al., 2023 for nomenclature definitions and discussion and Bizerril, 1999; Honji et al., 2017; Moraes et al., 2017 for the classification of the Paraíba do Sul fish assemblage). To further assess the predictors of species composition, we performed three variation partitioning (VP): one for the community composition (native + non-native species), only for native species, and the last one using only abundance of non-native species (a total of eight species, excluding the peacock bass *Cichla* sp.; Online Resource 3) using the function *varpart* in the *vegan* package. The VPs were used to quantify the relative importance of different sets of predictors in explaining the fish abundance (CPUE) through evaluating abiotic and biotic filters that may interact to determine the occurrence and abundance of the community. We used as abiotic predictors the: limnological features (temperature, pH, and $\log_{10}$ transformations of conductivity, total dissolved solids, turbidity, oxygen, transparency and chlorophyll *a*), habitat composition (grass, shrub, log, leaf, macrophyte, gravel, sand, mud, and structure-less margins; per cent cover by each habitat arcsine square root transformed) and reservoir traits (age, and $\log_{10}$ transformations of area, altitude, and residence time). We used the abundance of peacock bass *Cichla* spp. (fish per hour captured through angling) as a biotic filter that may also influence species occurrence through predation of small-sized species and competition with native predators (see Franco et al., 2022a). Considering the invasional meltdown (Simberloff & von Hole, 1999) and disturbance hypothesis (Elton, 1958; Hobbs & Huenneke, 1992), the occurrence of the peacock bass may also be positively associated with other non-native species. We highlighted the peacock bass *Cichla* spp. since this invader accounts for the oldest introductions in the analysed reservoirs and also for the greatest abundance among invaders (see Franco et al. 2018; 2022a, b for more information). Analyses at the community level incorporated abundance data of the peacock bass obtained through gillnets (CPUE; using fish per m^2 per 24 h for gillnet sets) to ensure comparability with the other species.

The systems differ in terms of ageing of the reservoirs, which is often considered the major driver of abiotic and biotic changes in aquatic ecosystems (Winemiller et al., 2016; Agostinho et al., 2018). These changes may alter both the species composition, limnological conditions and habitat composition due to numerous factors, such as artificial hydrological variation and siltation. Therefore, to assess the association of species with the habitat composition free from the influence of reservoir history, we applied a forward selection procedure with the *forward.sel* function of the package *packfor* (Dray et al., 2016) to assess the variable that accounted for most of the explained variation within the subset of reservoir traits for the three groups of species (community composition, only native, and only non-native). The variable selected (if any) was incorporated as a random factor in a distance-based permutational analysis of variance (PERMANOVA) using the *adonis2* function of the *vegan* package. We tested for the relationship of habitat composition and limnological features with the abundance of each of the three groups of species based on Euclidean distance as a linkage function and 9,999 permutations of raw data (Anderson, 2008).

Results

Habitat availability

The shoreline of the studied reservoirs was largely devoid of complex habitats or colonized by a varied proportion of floating macrophytes and shrubs (Table 1), with a considerable variation in habitat composition within systems. A principal component analysis (64%; eigenvalues PC1 = 0.246 and PC2 = 0.085) discriminated systems in which macrophytes and grasses were dominant from those where structure-less littoral zones and rocks were more prevalent (Online Resource 2). The most commonly found genera of floating macrophytes were: *Eichhornia*, *Pistia*, *Salvinia*, *Egeria*, and *Myriophyllum*. Contribution of each genera was not quantified individually. Reservoirs dominated by shrubs and logs were discriminated from those where other habitats prevailed along the second axis. Overall structure-less littoral zones were related to headwater and larger reservoirs (e.g. Funil, Santa Branca and Igaratá; Table 1 and Online Resources 2), whilst macrophyte and grass cover were more common in smaller reservoirs (e.g. Areal and Santa Fé). Shrubs and logs were more dominant in Ilha dos Pombos and a few other sites from other reservoirs. Gravel and leaves were common in all reservoirs.

A forward model selection applied to a redundancy analysis (RDA) identified water transparency, conductivity, altitude, water residence time and reservoir age as the variables most related to habitat availability (Fig. 2). Macrophytes were related to reservoirs with higher water conductivity (e.g. Queluz, Santana, and Santa Fé) and were separated, along the first RDA

Table 1 Mean values of the per cent cover of the categories of submerged and littoral habitats in the fifteen reservoirs of the Paraíba do Sul river basin

Category	Reservoir														
	Paraibuna	Igaratá	Santa Branca	Queluz	Funil	Tocos	Lajes	Vigário	Santana	Pereira Passos	Paracambi	Areal	Anta	Ilha dos Pombos	Santa Fé
Rocks (%)	7.3	11.7	11.3	1.7	8	43.3	3.3	0	0	28.3	6.7	0	12.3	7.0	2.0
Leaves (%)	0	0	0	0	0	0	12.0	0	0	0	0	0	0	0	3.3
Macrophytes (%)	16.7	12.0	0	61.3	0	0	0	40.0	60.0	0	18.3	41.7	26.7	5.7	20.0
Gravel (%)	0	1.7	0	0	0	1.7	0	0	0	0	0	0	0	0	0
Shrub (%)	27.3	15.0	25.0	7.7	5.7	26.7	21.3	50.0	19.7	13.3	10.0	14.0	6.0	21.3	31.7
Log (%)	2.3	3.0	0	1.3	13.3	6.7	13.3	5.0	10.3	10.0	31.7	10.3	17.0	31.3	13.7
Grass (%)	24.7	14.3	1.7	22.0	0	0	0	0	0	0	0	22.7	12.0	31.7	24.3
Non-structured (%)	21.7	42.3	62.0	6.0	73.0	21.7	50.0	5.0	10.0	48.3	33.3	11.3	26.0	3.0	5.0

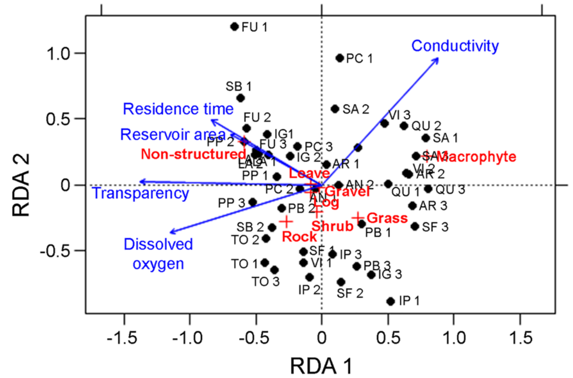

Fig. 2 Ordination of the three sampling sites of the fifteen reservoirs from Paraíba do Sul river basin according to a redundancy analysis (RDA) of the limnological and reservoir features and shoreline habitats cover

constrained axis (67.0%; eigenvalue = 0.12) from systems with higher water residence time, high transparency and low conductivity, which were dominated by structure-less shorelines (e.g. Santa Branca). Structure-less margins were also found in systems with smaller contributions of grass and rocks (e.g. Funil and Paracambi) along the second RDA axis (19.8%; eigenvalue = 0.04).

Predictors of species composition

A total of 1,635 individuals belonging to 31 species were captured in the lentic zones of 15 reservoirs of the Paraíba do Sul river basin (Online Resource 3). Characids accounted for the greatest abundances, while Cichlidae was the family with the highest number of species detected (six species). Nine non-native species (*Coptodon rendalli* (Boulenger, 1897), *Cichla* spp., *Hoplosternum littorale* (Hancock, 1828), *Metynnis lippincottianus* (Cope, 1870), *Oreochromis niloticus* (Linnaeus, 1758), *Pimelodus fur* (Lütken, 1874), *Pimelodus maculatus* Lacepède 1803, *Plagioscion squamosissimus* (Heckel, 1840), and *Steindachnerina* sp. were detected and together accounted for 16.1% of total richness and 14.1% of total abundance (Online Resource 3).

The highest species richness was detected in Areal (16 species), followed by Paracambi (13 species) reservoirs, while the lowest was found in Igaratá (4 species; Online Resource 3). Characidae was the family with more species in Santa Fé, Funil, and Paracambi reservoirs (Online Resource 3). In reservoirs where non-native species were detected, at least two co-occurring species were found, e.g. the peacock basses *Cichla* spp. and the South American silver croaker *P. squamosissimus* in Vigário and Igaratá systems. Headwater reservoirs, especially Santa Branca and Igaratá, had more non-native species ($N=3$) than the other ones (Online Resource 3).

A forward selection applied to a redundancy analysis (RDA) of species composition (response variable) and habitat availability (explanatory variables) (Fig. 3) identified macrophytes, structure-less shorelines, leaves, and logs as the best predictors of the fish fauna. The first RDA axis (24.1%; eigenvalue = 0.12) separated the characids *Astyanax* cf. *bimaculatus* (Linnaeus, 1758), *Psalidodon fasciatus* (Cuvier, 1819) and *Oligosarcus hepsetus* (Cuvier, 1829), which were related to greater macrophyte cover (e.g. Areal) from the non-native *Cichla* spp. and *P. maculatus*, both related to structure-less littoral zones (e.g. Santa Branca). A smaller proportion of logs and leaves were related to an increased abundance of *H. littorale, P. maculatus, P. fasciatus,* and *P. squamosissimus* along the second RDA axis (7.1%; eigenvalue = 0.04, while the papaterra *Cyphocharax gilbert* (Lütken, 1875) and *A.* cf. *bimaculatus* were associated with high cover of logs and leaves.

Heat maps highlighted the shifts in species composition in response to the habitat availability categories: structure-less (Fig. 4A), macrophytes (Fig. 4B), leaves (Fig. 4C) and logs (Fig. 4D). The characids *A.* cf. *bimaculatus*, *P. fasciatus* and *O. hepsetus* were

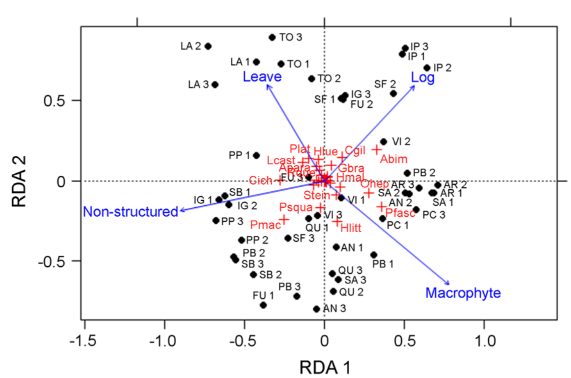

Fig. 3 Ordination of the three sampling sites of the fifteen reservoirs from Paraíba do Sul river basin according to a redundancy analysis (RDA) of the shoreline habitat composition influence on species composition

associated with greater macrophyte, leaf, and log coverage, whereas the non-native peacock basses *Cichla* spp. and *P. maculatus* were more related to structure-less shorelines.

Native and non-native species–habitat association

The variation partitioning of the whole fish assemblage showed that reservoir traits, limnological features and habitat availability had significant unique effects and also explained the greatest amounts of variation (13, 10 and 7%, respectively). Joint effects were generally minor with much of the variation jointly explained by reservoir traits and habitat composition, among these two and peacock bass abundance, and between the peacock bass abundance and limnological features (Fig. 5A). The forward selection of reservoir features selected altitude as the variable that accounts for most of the variation explained. The distance-based PERMANOVA of the influence of habitat on species composition, assuming reservoir altitude as a random factor, indicated that the community composition (native + non-native species) is predicted by the presence of rocks ($F_{1,\ 45}=2.62$; $P=0.003$), leaves ($F_{1,\ 45}=2.14$; $P=0.012$), logs ($F_{1,\ 45}=2.41$; $P=0.002$) and structure-less margins ($F_{1,\ 45}=1.93$; $P=0.024$). The fish assemblage was also related to temperature ($F_{1,\ 45}=4.17$; $P=0.001$), pH ($F_{1,\ 45}=3.73$; $P=0.001$), conductivity ($F_{1,\ 45}=3.81$; $P=0.001$), turbidity ($F_{1,\ 45}=2.48$; $P=0.003$), oxygen ($F_{1,\ 45}=1.97$; $P=0.016$), and transparency ($F_{1,\ 45}=1.94$; $P=0.030$) when controlled by reservoir altitude in a PERMANOVA.

The VP of the native community showed that reservoir and limnological features (12 and 8%, respectively; Fig. 5B) were the most important followed by habitat composition (4%). The contribution of the abundance of peacock basses was negligible, both individually and jointly. Approximately 6% of the variation in native species abundance was jointly explained by reservoir features and habitat composition. The forward selection did not select any reservoir feature, but the altitude was indicated by a distance-based PERMANOVA as the only predictor of native fish within this predictor set. Therefore, the PERMONOVA of habitat composition controlled by the influence of altitude selected the cover of logs ($F_{1,\ 45}=3.83$; $P=0.025$) as a habitat predictor of the native fish assemblage. Among limnological features,

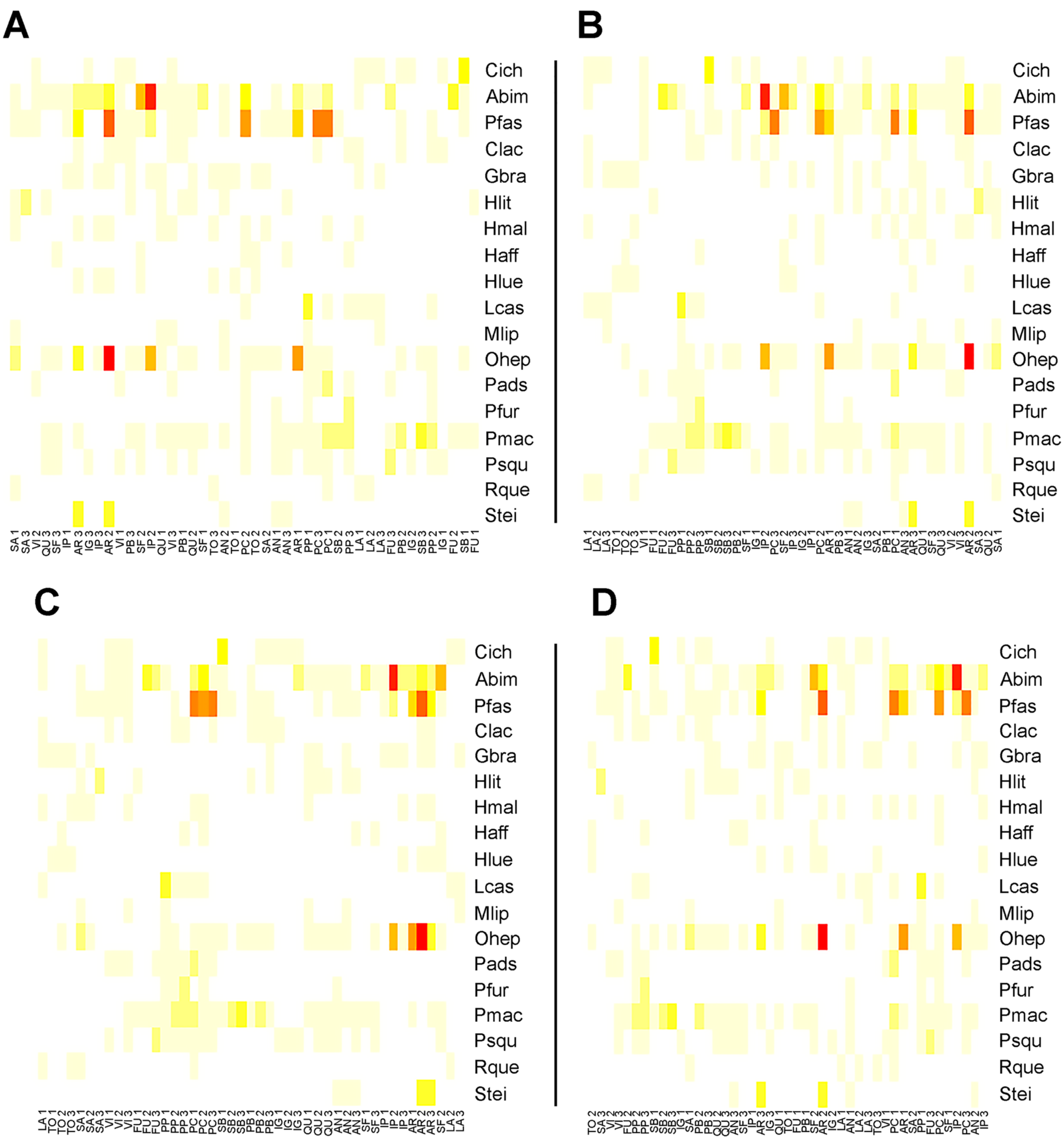

Fig. 4 Heat maps of species composition (CPUE) as a function of increasing per cent cover of structureless shorelines (**A**), macrophyte (**B**), leaf (**C**), and log (**D**) habitats. More reddish colours indicate higher CPUE; white indicates species not recorded in that reservoir. Species occurring in up to four reservoirs were removed

temperature ($F_{1,\ 45}=6.76$; $P=0.001$) and transparency ($F_{1,\ 45}=4.97$; $P=0.013$) were selected as the main predictors of native fish, after controlling by the effect of altitude. The variation in the abundance of non-native fish species captured at the reservoirs of the Paraíba do Sul river basin was mostly explained by limnological features (19%), followed by habitat composition (10%) and reservoir traits (10%). The association with the abundance of the peacock basses was small (2%) with the majority of the effects jointly

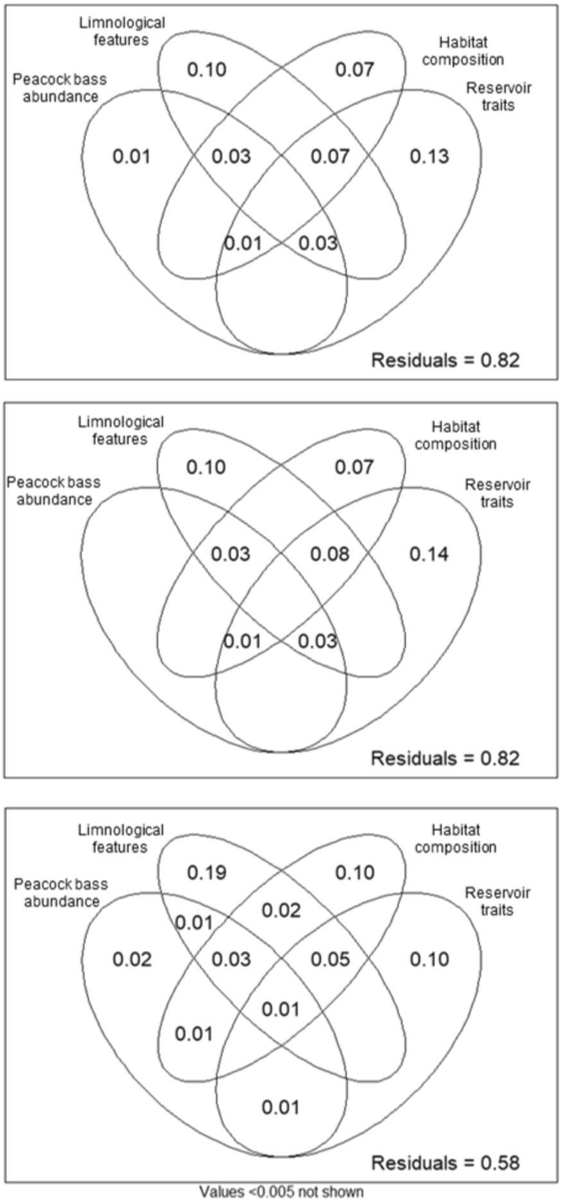

Fig. 5 Variation partitioning of the (**A**) abundance of the whole fish assemblage (fish per m^2 CPUE), (**B**) only native species abundance, and (**C**) non-native species abundance using the abundance of the peacock bass, limnological features, habitat composition, and reservoir features as explanatory sets. Values ≤ 0.005 are not shown

explained with limnology and habitat composition (3%) (Fig. 5C). No reservoir variable was selected by the forward selection nor by the distance-based PERMANOVA; therefore, no random factor was added to the PERMANOVA. Only rocks ($F_{1,\ 45}=2.96$; $P=0.034$) were selected as important predictors of non-native fish among habitats. Regarding limnological features, temperature ($F_{1,\ 45}=2.95$; $P=0.035$), pH ($F_{1,\ 45}=7.34$; $P=0.002$), turbidity ($F_{1,\ 45}=3.55$; $P=0.006$), and transparency ($F_{1,\ 45}=5.25$; $P=0.001$) were relevant predictors of the abundance of non-native fish.

Discussion

The presence of specific habitats was more relevant for native species (e.g. macrophytes for small-sized characids) than for non-native species (more related to structure-less margins). The absence of submerged and shoreline structures probably enhances the success in prey capture for visually oriented predators such as the peacock bass (Novaes et al., 2004; Alexander et al., 2014). Those structure-less areas were prevalent in large, older and more lentic reservoirs with transparent and oxygenated waters, probably related to the constant water level fluctuations that can lead habitats to be degraded by siltation or desiccation and, consequently, the littoral zones become structurally simple and homogeneous (Santos et al., 2011b). Our findings also indicate that the abiotic filter imposed by river damming is an important selector of native species, as other studies have already shown (Agostinho et al., 2008; Tickner et al. 2020; Liu et al., 2022), while non-native species, which are often lentic-adapted, were more related to water conditions (e.g. transparency and temperature). This environmental filtering process could be related to a cascading effect among some of the reservoirs evaluated (e.g., from Tocos to Pereira Passos) which could influence the composition of native species (Santos et al., 2018; Loures & Pompeu, 2019; Ganassin et al., 2021). Cascading effects are also key aspects that may produce a spatial effect of increasing species richness from up to downstream systems (Pelicice et al., 2018; Loures & Pompeu, 2019; Ganassin et al., 2021). Our findings show that the lowest fish diversity were, in fact, detected in the most upstream reservoirs, indicating that local factors as long as the ageing of the reservoir may be more relevant to determine species composition in the Paraíba do Sul reservoirs.

The close association of non-native species with human activities is a well-described and vastly proven relation in the literature (Leprieur et al., 2008; Liu et al., 2020a; Franco et al., 2022b). However, it is also important to identify fine-scale correlates of non-native species occurrence in order to understand niche-related processes that may be related to establishment success (Strubbe et al., 2014; Liu et al., 2020b). Depicting drivers that operate at different scales (local and regional) is crucial for the development of early-detection measures and actions of impact mitigation at lower costs and increased success rates (Cuthbert et al., 2022). Our findings showed that non-native species were more related to local predictors (i.e. water conditions) than regional processes (i.e. damming). The non-native species identified in our study are all lentic-adapted; therefore, they are all predisposed to be successful in dammed systems. Furthermore, the disturbance hypothesis highlights that anthropogenic pressures increase the vulnerability of ecosystems to the establishment of non-native species (Hobbs & Huenneke, 1992; Davis et al., 2000). Thus, in order to examine this relation in detail, it would require comparing the abundance of non-native fish between rivers and reservoirs or before and after damming. Even in reservoirs, which we already established as beneficial for the nine non-native species (see Online Resource 5) found in our study, they need to overcome the abiotic filter imposed by water conditions that may limit their ability to survive and establish a viable population in a given system in order to exploit reproductive and feeding grounds within the reservoir (Blackburn et al., 2011).

Local water conditions were more related to non-native species within different regions of a given reservoir and among reservoirs than other local (habitat composition) and regional (damming) processes. Success in the invasion process has been related to several context-dependencies, even though invasibility and invasiveness components are key to the overall process, pre-adaptation to local conditions may be essential to successfully establish a sustainable population (Blanchet et al., 2009; González-Moreno et al., 2014; Hui et al., 2023). Our findings indicated that temperature, pH and transparency were essential for non-native species occurrence, which may be reflecting a niche-related feature during the invasion process in the Paraíba do Sul river basin, since not all reservoirs hold the same abiotic conditions. Most non-native species have been shown to conserve their native niche during the invasion process, but a degree of flexibility in resource use may also be a key feature to separate the winners from the losers, allowing for their occurrence in varied environmental conditions and providing a competitive advantage over native counterparts (Duncan et al., 2003; Clavel et al., 2010; Seebens et al., 2016; Liu et al., 2020b). It is important to highlight that some species identified in our study were observed across multiple systems. For instance, the peacock bass, while captured in only five systems through gillnets, was actually recorded in 12 systems based on angling census data by Franco et al. (2018). Similarly, *P. maculatus* was found in 10 systems, and *P. squamosissimus* in 8 systems. Some of them are co-occurring species in their native range, which stresses the importance of matching conditions among the native and non-native range for invasion success. Understanding these relations between non-native species and water conditions provides insightful information for ecosystem prioritization for monitoring. Hence, environmental agencies overseeing the aquatic ecosystems of the Paraíba do Sul river basin can anticipate encountering a comparable array of non-native species in reservoirs characterized by warmer and more transparent water conditions.

Structure-less sites were related to the non-native *Cichla* spp. and to adults of *P. maculatus*, both in large and more lentic reservoirs with warmer and transparent water conditions. These two carnivores may colonize these sites due to the greater predatory opportunities they offer since barren littoral areas expose prey individuals, especially the small characids. Peacock basses *Cichla* spp. are piscivores which rely on vision to capture their prey actively (Jepsen et al., 1997) and feed on small-sized individuals (approximately a third of its own size) (Mendonça et al., 2018; Franco et al., 2022a) (Online Resource 6). These invaders are often observed patrolling the margins of reservoirs both individually and as shoals of young adults. Once they visualize a prey, they vigorously attack, often generating waves at the margins due to their voraciousness and swimming speed (ACS Franco, personal observations). Aggregations of small-sized species such as small cichlids or characids are frequent targets in reservoirs (Andrade & Pelicice, 2022). It can be expected that structure-less zones will increase through time in reservoirs due to continuous daily or seasonal water level fluctuations which prevent shoreline colonization through habitat siltation or desiccation (Geraldes & Boavida, 2005;

Zohary & Ostrovsky, 2011). Therefore, biotic interactions among non-native predators and native small-sized prey will tend to become more tightened with reservoir ageing processes until the native characids are displaced or even extirpated through predation (Pelicice et al., 2015). The non-native catfish *P. maculatus* also use these areas for chasing small fish and invertebrates (Lima-Junior & Goitein, 2003), and are favoured by defensive structures (e.g., spines) that prevent them from being preyed on by other carnivorous while they are still young.

Despite aquatic macrophytes have been considered to provide limited protection against peacock basses predation through microcosm experiments (Kovalenko et al., 2010b), our findings indicate that macrophyte beds in Paraíba do Sul reservoirs support characids diversity, especially throughout the structure-less littoral area. These findings suggest that at least in structure-less zones of reservoirs, macrophytes played an important role in providing refuge for the small-sized characids *A.* cf. *bimaculatus*, *P. fasciatus* and *O. hepsetus*, probably alleviating the predation pressure from predators like the non-native *Cichla* spp., which were negatively related to those habitats. It is common to find juveniles (e.g. the characins in our study) associated with macrophyte beds, which not only provide shelter against predation but also offer better conditions of dissolved oxygen and food availability (Delariva et al., 1994; Casatti et al., 2003; Bittencourt et al., 2020). However, the alleviation effect might be negated in the long-term if these native species still get displaced in their adult stage by non-native ones when using different habitats aside from vegetated areas (Acreman et al., 2019; Williamshen et al., 2021; Huntsman et al., 2022). Therefore, the mediating role played by habitat in interspecific interactions is crucial due to the numerous anthropogenic interferences in aquatic systems. Thus, by altering these habitats, human activities also interfere with species assembly, abundance, and competitive and non-competitive fish relationships in lentic ecosystems (Christensen et al., 1996; Jennings et al., 1999; Dudgeon et al., 2006). Even though the exact nature of those interactions, whether they are competitive or not, or the exact role played by each habitat type (through its presence or absence), is beyond the scope of this study, these findings indicate a key role played by habitat availability in supporting native fish species diversity. Further analyses are required, especially those involving experimental designs, to unravel those patterns, potentially highlighting that actions towards habitat restoration may be promising to alleviate the effects of habitat loss promoted by river damming.

Although playing a key role for fish assemblages in reservoirs, macrophytes, when in excessive densities and coverage levels, can also be associated with poor water conditions in reservoirs due to great input of nutrients from sewage inflow and high plant biomass and decomposition, which results in low dissolved oxygen and high turbidity (Akhurst et al., 2017). Our findings showed a clear association between higher levels of macrophyte cover with higher water conductivity and lower dissolved oxygen and transparency in small reservoirs, which may indicate poor water conditions. Moreover, the greatest abundance of the *H. littorale*, a facultative air-breathing catfish was detected at one site within the Santana reservoir (SA 3), which was also the site with the lowest dissolved oxygen concentrations (1.7 mg L^{-1} on average) and highest macrophyte cover (=60%; Table 1). These findings provide further evidence of the presence of poor water conditions associated with macrophytes at reservoirs of the Paraíba do Sul river basin, especially since this catfish is highly tolerant to hypoxic conditions (Brauner et al., 1995). In this sense, macrophytes seem to have at least a dual role in reservoirs, either by providing shelter for small-sized species against predators when at low to moderate coverage levels, and also by potentially worsening the water conditions when in excess, due to the high production of plant biomass that increases the biochemical oxygen demand (BOD). Therefore, any management decision regarding the removal of macrophytes in reservoirs, which often disregards the ecological importance of this habitat, should consider the findings of this study, even though we are aware that these decisions are contingent on each reservoir specific management procedures and thresholds (e.g., reservoir size and depth). Experimental studies are encouraged to establish a threshold of macrophyte cover (or biomass) that is necessary to maintain its ecological role as recruitment, growing and refuge grounds without jeopardizing water conditions.

The importance of shoreline habitats for fish colonization was apparently species-specific. Macrophytes were highly used by characids, leaves were related to catfishes, and logs seemed to be of great importance for the curimatid *C. gilbert*, the cichlid *Geophagus brasiliensis* (Quoy & Gaimard 1824), and the native predator trahira *Hoplias malabaricus* (Bloch 1794). Catfishes feed mainly on organic material, especially vegetal material, which could explain their relationship with leaves. These species are adapted to grasp substrates which contains organic matter, dwelling on benthonic microhabitats (Garavello & Garavello, 2004; Villares-Junior et al., 2016). On the other hand, logs had different roles for the species more associated with this substrate. The curimatid *C. gilbert* colonized regions with a greater cover of logs, probably due to the presence of macroinvertebrates, which usually prefer woody substrates (Connor, 1991; Tupinambás et al., 2007). The Erythrinidae *H. malabaricus* was also associated with woody substrates, where small forage fish usually seek shelter from predation, so favouring the ambush behaviour of this native predator (Petry et al., 2010; Corrêa et al., 2012). These findings indicate that the degree of habitat use is variable among fish species in reservoirs of the Paraíba do Sul river basin, highlighting the importance of maintaining and restoring, when necessary, those shoreline structures. The evaluation of different habitats in studies focusing on fish assemblage description emerges as another relevant conclusion of this study since the patterns and variations found can be related to auto-ecological traits and interspecific interactions.

Conclusion

Our findings stress that the maintenance and potential restoration of shoreline habitats of reservoirs are critical for sustaining fish diversity of the Paraíba do Sul river basin. We showed that biological interactions within these habitats are species-specific and stressed the importance of maximizing habitat variety for sustaining native fish diversity. Macrophytes play an important role in providing shelter against predation for small characids and by alleviating the adverse effects of non-native peacock basses, when in low to intermediate levels. However, dense beds of floating macrophytes are often associated with poor water conditions, selecting only hypoxic-adapted species, such as *H. littorale*. Structure-less littoral zones were prevalent in old, large, and more lentic reservoirs, confirming that continuous water level fluctuations are deleterious for the preservation of shoreline habitats and, consequently, to the native fish fauna. Therefore, preserving or restoring vegetated littoral zones seems likely to benefit native fish species, balance natural predator–prey relationships, and alleviate the adverse effects of non-native predators on small-sized native fish. Further studies focusing on comparing river and reservoirs or before–after designs are important to advance our findings regarding non-native species requirements at different scales. Local factors were more important and highlighted the context-dependencies of the invasion process, even within similar systems, but understanding regional drivers (e.g., nestedness in species diversity due to cascading effect; Loures & Pompeu, 2019) is also key for environmental agencies to track novel introductions and manage native diversity.

Authors' contributions All authors contributed to the study conception and design. Material preparation was performed by all authors. Data sampling was performed by ACSF and LNS. Data analysis was performed by ACSF and EGB. The first draft of the manuscript was written by ACSF, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding This work was funded by Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (post-doctoral scholarship to ACSF, E-26/202.243/2019, and research grant to LNS, E-26/202.755/2018), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (Research Grant to LNS, ref. 312194/2015-3; 314379/2018-5), and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) (sandwich doctorate scholarship to ACSF, ref. 88887.127440/2016-00 and visiting professorship to EGB, ref. 88881.068352/2014-01). EGB was also supported by the Spanish Ministry of Science (Projects PID2019-103936 GB-C21 and RED2018-102571-T) and the Government of Catalonia (Ref. 2017 SGR 548).

Availability of data and material The datasets analysed during the current study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interests The authors declare that they have no conflict of interest.

Ethical approval (include appropriate approvals or waivers) Approval was obtained from the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) under the sampling license number #49357.

Consent to participate Not applicable.

Consent to publication Not applicable.

References

Acreman, M., K. Hughes, A. Arthington, D. Tickner & M. Dueñas, 2019. Protected areas and freshwater biodiversity: a novel systematic review distils eight lessons for effective conservation. Conservation Letters 13: e12684. https://doi.org/10.1111/conl.12684.

Agostinho, A. A., F. M. Pelicice & L. C. Gomes, 2008. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. Brazilian Journal of Biology 68: 1119–1132. https://doi.org/10.1590/S1519-69842008000500019.

Akhurst, D. J., G. B. Jones, M. Clark & A. Reichelt-Brushett, 2017. Effects of fish and macrophytes on phytoplankton and zooplankton community structure in a subtropical freshwater reservoir. Limnologica 62: 5–18. https://doi.org/10.1016/j.limno.2016.09.009.

Alexander, M. E., H. Kaiser, O. L. F. Weyl & J. T. A. Dick, 2014. Habitat simplification increases the impact of a freshwater invasive fish. Environmental Biology of Fishes. https://doi.org/10.1007/s10641-014-0278-z.

Anderson, M. J., 2008. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26: 32–46.

Andrade, G.S., & F.M. Pelicice, 2022. Coexistence of endemic peacock basses (Cichla) in a Neotropical reservoir (Cichlidae: Cichliformes). Neotropical Ichthyology 20: https://doi.org/10.1590/1982-0224-2022-0039

Araújo, F. G., M. C. C. de Azevedo, G. H. S. Guedes & B. C. T. Pinto, 2023. Trait–environment relationship of riverine fish assemblages across a human footprint mosaic. Hydrobiologia. https://doi.org/10.1007/s10750-023-05370-9.

Bittencourt, S. C. S., D. M. Zacardi, T. Monteiro, L. Nakayama & H. L. Queiroz, 2020. Juvenis de peixes associados a macrófitas aquáticas em ambientes de várzea na Amazônia Central, Brasil. Biota Amazônia 10: 38–45.

Bizerril, C. R. S. F., 1999. A ictiofauna da bacia do rio Paraíba do Sul. biodiversidade e padrões biogeográficos. Brazilian Archives of Biology and Technology 42: 233–250. https://doi.org/10.1590/S1516-89131999000200014.

Blackburn, T. M., P. Pyšek, S. Bacher, J.T. Carlton, R.P. Duncan, V. Jarošík, J. R. U. Wilson, & D.M. Richardson, 2011. A proposed unified framework for biological invasions. Trends in Ecology and Evolution 26, 333–339.

Blanchet, G., P. Legendre & D. Borcard, 2008. Forward selection of spatial explanatory variables. Ecology 89: 2623–2632.

Blanchet, S., F. Leprieur, O. Beauchard, J. Staes, T. Oberdorff & S. Brosse, 2009. Broad-scale determinants of non-native fish species richness are context-dependent. Proceedings of the Royal Society b: Biological Sciences 276: 2385–2394. https://doi.org/10.1098/rspb.2009.0156.

Borcard, D., F. Gillet & P. Legendre, 2011. Numerical Ecology with R, Springer Science, New York:, 319.

Brauner, C. J., C. L. Ballantyne, D. J. Randall & A. L. Val, 1995. Air breathing in the armoured catfish (*Hoplosternum littorale*) as an adaptation to hypoxic, acidic, and hydrogen sulphide rich waters. Canadian Journal of Zoology 73: 739–744. https://doi.org/10.1139/z95-086.

Bunn, S. E. & A. H. Arthington, 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30: 492–507.

Casatti, L., H. F. Mendes & K. M. Ferreira, 2003. Aquatic macrophytes as feeding site for small fishes in the Rosana Reservoir, Paranapanema River, Southeastern Brazil. Brazilian Journal of Biology 63: 213–222. https://doi.org/10.1590/S1519-69842003000200006.

Christensen, D. L., B. J. Herwig, D. E. Schindler & S. R. Carpenter, 1996. Impacts of lakeshore residential development on course woody debris in north temperate lakes. Ecological Applications 6: 1143–1149.

Clavel, J., R. Julliard & V. Devictor, 2010. Worldwide decline of specialist species: toward a global functional homogenization? Frontiers in Ecology and the Environment 9: 222–228. https://doi.org/10.1890/080216.

Connor, N. A., 1991. The effects of habitat complexity on the macroinvertebrates colonising wood substrates in a lowland stream. Oecologia 85: 504–512.

Corrêa, F., M. C. Claudino, R. F. Bastos, et al., 2012. Feeding ecology and prey preferences of a piscivorous fish in the Lagoa do Peixe National Park, a Biosphere Reserve in Southern Brazil. Environmental Biology of Fishes 93: 1–12. https://doi.org/10.1007/s10641-011-9881-4.

Cuthbert, R. N., C. Diagne, E. J. Hudgins, A. Turbelin, D. A. Ahmed, C. Albert, T. W. Bodey, E. Briski, F. Essl & P. J. Haubrock, 2022. Biological invasion costs reveal insufficient proactive management worldwide. Science of the Total Environment 819: 153404. https://doi.org/10.1016/j.scitotenv.2022.153404.

Davis, M. A., J. P. Grime & K. Thompson, 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88: 528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x.

Delariva, R. L., A. A. Agostinho, K. Nakatani & G. Baumgartner, 1994. Ichthyofauna associated to aquatic macrophytes in the Upper Paraná river floodplain. Revista UNIMAR 16: 41–60.

Dray, S., P. Legendre, & G. Blanchet, 2016. Packfor: Forward Selection with permutation (Canoco p.46). R packageversion 0.0-8/r136. https://R-Forge.R-project.org/projects/sedar/

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A. H. Prieur-Richard, D. Soto, M. L. J. Stiassny & C. A. Sullivan,

2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81: 163–182. https://doi.org/10.1017/S1464793105006950.

Duncan, R. P., T. M. Blackburn & D. Sol, 2003. The ecology of bird introductions. Annual Review of Ecology, Evolution, and Systematics 34: 71–98. https://doi.org/10.1146/annurev.ecolsys.34.011802.132353.

Elton, C. S., 1958. The ecology of invasions by animals and plants, Methuen:

Franco, A. C. S., L. N. Santos, A. C. Petry & E. García-Berthou, 2018. Abundance of invasive peacock bass increases with water residence time of reservoirs in southeastern Brazil. Hydrobiologia 817: 155–166.

Franco, A. C. S., E. García-Berthou & L. N. Santos, 2021. Ecological impacts of an invasive top predator fish across South America. Science of the Total Environment 71: 143296. https://doi.org/10.1016/j.scitotenv.2020.143296.

Franco, A. C. S., A. C. Petry, M. R. Tavares, T. R. G. de Fátima & L. N. Santos, 2022b. Global distribution of the South American peacock basses *Cichla* spp. follows human interference. Fish and Fisheries 23: 407–421.

Franco, A.C.S., A.C. Petry, E. García-Berthou, & L.N. Santos, 2022a. Invasive peacock basses (*Cichla* spp.) and decreased abundance of small native fish in Brazilian reservoirs. Aquatic Conservation: Marine and Freshwater Ecosystems. https://doi.org/10.1002/aqc.3874

Fukushima, M., S. Kameyama, M. Kaneko, K. Nakao & E. A. Steel, 2007. Modelling the effects of dams on freshwater fish distributions in Hokkaido, Japan. Freshwater Biology 52: 1511–1524.

Ganassin, M. J. M., R. Muñoz-Mas, F. J. M. Oliveira, C. M. Muniz, N. C. L. Santos, E. García-Berthou & L. C. Gomes, 2021. Effects of reservoir cascades on diversity, distribution, and abundance of fish assemblages in three Neotropical basins. Science of the Total Environment 778: 146246. https://doi.org/10.1016/j.scitotenv.2021.146246.

Garavello, J. C. & J. P. Garavello, 2004. Spatial distribution and interaction of four species of the catfish genus *Hypostomus* Lacépède with bottom of Rio São Francisco, Canindé do São Francisco, Sergipe, Brazil (Pisces, Loricariidae, Hypostominae). Brazilian Journal of Biology 64: 103–141. https://doi.org/10.1590/S1519-69842004000400006.

Geraldes, A. M. & M. J. Boavida, 2005. Seasonal water level fluctuations: implications for reservoir limnology and management. Lakes & Reservoirs 10: 59–69. https://doi.org/10.1111/j.1440-1770.2005.00257.x.

González-Moreno, P., J. M. Diez, I. Ibáñez, X. Font & M. Vilà, 2014. Plant invasions are context-dependent: multiscale effects of climate, human activity and habitat. Diversity and Distributions 20: 720–731. https://doi.org/10.1111/ddi.12206.

Gorman, O. T. & J. R. Karr, 1978. Habitat structure and stream fish communities. Ecology 59: 507–515.

Grill, G., B. Lehner, A. E. Lumsdom, G. K. MacDonald, C. Zarfl & C.R. Liermann, 2015. An index-based framework for assessing patterns and trends in river fragmentation and flow regulation by global dams at multiple scales. Environmental Research Letter 10: 015001.

Grill, G., B. Lehner, M. Thieme, B. Geenen, D. Tickner, F. Antonelli, S. Babu, P. Borrelli, L. Cheng & H. Crochetiere, 2019. Mapping the world's free-flowing rivers. Nature 569: 215–221.

Guedes, G. H. S. & F. G. Araújo, 2022. Underwater drones reveal different fish community structures on the steep slopes of a tropical reservoir. Hydrobiologia 849: 1301–1312. https://doi.org/10.1007/s10750-021-04790-9.

Hobbs, R. J. & L. F. Huenneke, 1992. Disturbance, diversity, and invasion – implications for conservations. Conservation Biology 6: 324–337. https://doi.org/10.1046/j.1523-1739.1992.06030324.x.

Honji, R. M., C. E. Tolussi, D. Caneppele, et al., 2017. Biodiversidade e conservação da ictiofauna ameaçada de extinção da bacia do rio Paraíba do Sul. Revista Da Biologia 17: 18–30. https://doi.org/10.7594/revbio.17.02.05.

Hui, C., P. Pyšek & D. M. Richardson, 2023. Disentangling the relationships among abundance, invasiveness and invasibility in trait space. NPJ Biodivers 2: 13. https://doi.org/10.1038/s44185-023-00019-1.

Huntsman, B. M. E.R. Merriam, C.T. Roja, & J.T. Petty, 2022. Non-native species limit stream restoration benefits for brook trout. Restoration Ecology 31: e13678. https://doi.org/10.1111/rec.13678.

Jackson, D. A., 1993. Stopping rules in principal component analysis: a comparison of heuristical and statistical approaches. Ecology 74: 2204–2214.

Jennings, M. J., M. A. Bozek, G. R. Hatzenbeler, E. E. Emmons & M. D. Staggs, 1999. Cumulative effects of incremental shoreline habitat modification on fish assemblages in north temperate lakes. North American Journal of Fisheries Management 19: 18–27.

Jepsen, D. B., K. O. Winemiller & D. C. Taphorn, 1997. Temporal patterns of resource partitioning among Cichla species in a Venezuelan blackwater river. Journal of Fish Biology 51: 1085–1108. https://doi.org/10.1111/j.1095-8649.1997.tb01129.x.

Johnstone, I. M., 1986. Plant invasion windows – a time-based classification of invasion potential. Biological Reviews of the Cambridge Philosophical Society 61: 369–394.

Kahn, J. R., W. F. Vásquez & C. E. de Rezende, 2017. Choice modeling of system-wide or large scale environmental change in a developing country context: Lessons from the Paraíba do Sul River. Science of the Total Environment. https://doi.org/10.1016/j.scitotenv.2017.04.059.

Kindt, R., 2017. Package "BiodiversityR" for Community Ecology and Suitability Analysis. R package version 2.8–0. https://cran.r-project.org/web/packages/BiodiversityR/BiodiversityR.pdf

Kottek, M., J. Grieser, C. Beck, et al., 2006. World Map of the Köppen-Geiger climate classification updated. Meteorol Zeitschrift 15: 259–263. https://doi.org/10.1127/0941-2948/2006/0130.

Kovalenko, K.E., E.D. Dibble, A.A. Agostinho, & F.M. Pelicice, 2010a. Direct and indirect effects of an introduced piscivore, *Cichla kelberi* and their modification by aquatic plants. Hydrobiologia: 245–253.

Kovalenko, K.E., E.D. Dibble, A.A. Agostinho, & F.M. Pelicice, 2010b. Recognition of non-native peacock bass, *Cichla kelberi* by native prey: Testing the naiveté hypothesis. Biological Invasions. https://doi.org/10.1007/s10530-010-9698-7

Legendre, P. & E. D. Gallagher, 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129: 271–280.

Legendre, P. & L. Legendre, 2012. Numerical ecology, 3rd ed. Elsevier, Amsterdam:

Leprieur, F., O. Beauchard, S. Blanchet, T. Oberdorff & S. Brosse, 2008. Fish Invasions in the World's River Systems: when natural processes are blurred by human activities. Plos Biology 6: e28. https://doi.org/10.1371/journal.pbio.0060028.

Levin, S.A., 1981. Mechanisms for the generation and maintenance of diversity. In: The mathematical theory of the dynamics of biological populations, Academic Press, London, England.

Lewis, J. S., S. Spaulding, H. Swanson, W. Keeley, A. R. Gramza, S. VandeWoude & K. R. Crooks, 2021. Human activity influences wildlife populations and activity patterns: implications for spatial and temporal refuges. Ecosphere 12: e03487. https://doi.org/10.1002/ecs2.3487.

Lima-Junior, S. E. & R. Goitein, 2003. Ontogenetic diet shifts of a Neotropical catfish, *Pimelodus maculatus* (Siluriformes, Pimelodidae): an ecomorphological approach. Environmental Biology of Fishes 68: 73–79. https://doi.org/10.1023/A:1026079011647.

Liu, X., T. M. Blackburn, T. Song, X. Wang, C. Huang & Y. Li, 2020a. Animal invaders threaten protected areas worldwide. Nature Communications 11: 1–3. https://doi.org/10.1038/s41467-020-16719-2.

Liu, C., C. Wolter, W. Xian & J. M. Jeschke, 2020b. Most invasive species largely conserve their climatic niche. Proceedings of the National Academy of Sciences 117: 23643–23651. https://doi.org/10.1073/pnas.2004289117.

Liu, X., J. D. Olden, R. Wu, S. Ouyang & X. Wu, 2022. Dam construction impacts fish biodiversity in a subtropical river network, China. Diversity 14: 476. https://doi.org/10.3390/d14060476.

Loures, R. C. & P. S. Pompeu, 2019. Temporal changes in fish diversity in lotic and lentic environments along a reservoir cascade. Freshwater Biology 64: 1806–1820. https://doi.org/10.1111/fwb.13372.

Mazzoni, R., M. P. Pinto, R. Iglesias-Rios & R. Costa, 2018. Fish movement in an Atlantic forest stream. Neotropical Ichthyology 16: e170065. https://doi.org/10.1590/1982-0224-20170065.

Mello, W. Z., 2001. Precipitation chemistry in the coast of the Metropolitan Region of Rio de Janeiro, Brazil. Environmental Pollution 114: 235–242. https://doi.org/10.1016/S0269-7491(00)00209-8.

Mendonça, H. S., A. C. A. Santos, M. M. Martins & F. G. Araújo, 2018. Size-related and seasonal changes in the diet of the non-native *Cichla kelberi* Kullander & Ferreira, 2006 in a lowland reservoir in the southeastern Brazil. Biota Neotropica 18: e20170493.

Miranda, L. E., M. Spickard, T. Dunn, K. M. Webb, J. N. Aycock & K. Hunt, 2010. Fish habitat degradation in US reservoirs. Fisheries 35: 175–184.

Moraes, M. B., C. Natacha, M. Polaz & E. P. Caramaschi, 2017. Espécies exóticas e alóctones da Bacia do Rio Paraíba do Sul: implicações para a conservação. Biodiversidade Brasileira 7: 34–54.

Nilsson, C., C. A. Reidy, M. Dynesius & C. Revenga, 2005. Fragmentation and flow regulation of the world's large river systems. Science 308: 405–408.

Novaes, J. L. C., E. P. Caramaschi & K. O. Winemiller, 2004. Feeding of *Cichla monoculus* Spix, 1829 (Teleostei: Cichlidae) during and after reservoir formation in the Tocantins River, Central Brazil. Acta Limnologica Brasiliensia 16: 41–49.

Oksanen, J., F.G. Blanchet, M. Friendly, R. Kindt, P Legendre, D McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, E. Szoecs, & H. Wagner, 2016. vegan: Community ecology package. R package version 2.4-1. https://CRAN.R-project.org/package=vegan

Ovalle, A. R. C., C. F. Silva, C. E. Rezende, et al., 2013. Long-term trends in hydrochemistry in the Paraíba do Sul River, southeastern Brazil. Journal of Hydrology 481: 191–203. https://doi.org/10.1016/j.jhydrol.2012.12.036.

Pacheco, F. S., M. Miranda, L. P. Pezzi, et al., 2017. Water quality longitudinal profile of the Paraíba do Sul River, Brazil during an extreme drought event. Limnology and Oceanography 62: S131–S146. https://doi.org/10.1002/lno.10586.

Pelicice, F. M. & A. A. Agostinho, 2009. Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir. Biological Invasions 11: 1789–1801. https://doi.org/10.1007/s10530-008-9358-3.

Pelicice, F. M., J. D. Latini & A. A. Agostinho, 2015. Fish fauna disassembly after the introduction of a voracious predator: main drivers and the role of the invader's demography. Hydrobiologia 746: 271–283. https://doi.org/10.1007/s10750-014-1911-8.

Pelicice, F. M., V. M. Azevedo-Santos, A. L. H. Esguícero, A. A. Agostinho & M. S. Arcifa, 2018. Fish diversity in the cascade of reservoirs along the Paranapanema River, southeast Brazil. Neotropical Ichthyology 16: e170150. https://doi.org/10.1590/1982-0224-20170150.

Pelicice, F. M., L. S. Damasceno, E. A. Ferreira, C. S. Agostinho & R. Fernandes, 2022. Contrasting continental patterns and drivers of taxonomic and functional turnover among fish assemblages across Brazilian reservoirs. Hydrobiologia 849: 373–384. https://doi.org/10.1007/s10750-020-04388-7.

Persson, L., 1993. Predator-mediated competition in prey refuges: the importance of habitat dependent prey resources. Oikos 68: 12–22.

Petry, A. C., L. C. Gomes, P. A. Piana & A. A. Agostinho, 2010. The role of the predatory trahira (Pisces: Erythrinidae) in structuring fish assemblages in lakes of a Neotropical floodplain. Hydrobiologia 651: 115–126. https://doi.org/10.1007/s10750-010-0281-0.

Pianka, E. R., 1988. Evolutionary Ecology, Harper and Row, New York:

Poff, N. L., J. D. Olden, D. M. Merritt & D. M. Pepin, 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proceeding of the National Academy of Sciences 104: 5732–5737. https://doi.org/10.1073/pnas.0609812104.

Pyšek, P., P. E. Hulme, D. Simberloff, S. Bacher, T. M. Blackburn, J. T. Carlton, W. Dawson, F. Essl, L. C. Foxcroft, P. Genovesi, J. M. Jeschke, I. Kühn, A. W. Liebhold, N. E. Mandrak, L. A. Meyerson, A. Pauchard, J. Pergl, H. E. Roy, H. Seebens, M. van Kleunen, M. Vilà, M. J. Wingfield & D. M. Richardson, 2020. Scientists' warning on invasive alien species. Biological Reviews 95: 1511–1534. https://doi.org/10.1111/brv.12627.

Quist, M. C., F. J. Rahel & W. A. Hubert, 2005. Hierarchical faunal filters: an approach to assessing effects of habitat and nonnative species on native fishes. Ecology of Freshwater Fish 14: 24–39. https://doi.org/10.1111/j.1600-0633.2004.00073.x.

R Core Team, 2023. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org/

Reid, A. J., A. K. Carlson, I. F. Creed, E. J. Eliason, P. A. Gell, P. T. J. Johnson, K. A. Kidd, T. J. MacCormack, J. D. Olden, S. J. Ormerod, J. P. Smol, W. W. Taylor, K. Tockner, J. C. Vermaire, D. Dudgeon & S. J. Cooke, 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological Reviews 94: 849–873.

Sala, O. E., F. S. Chapin III., J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker & D. H. Wall, 2000. Global Biodiversity Scenarios for the Year 2100. Science 287: 1770–1774. https://doi.org/10.1126/science.287.5459.1770.

Santos, L. N., A. A. Agostinho, C. Alcaraz, et al., 2011a. Artificial macrophytes as fish habitat in a Mediterranean reservoir subjected to seasonal water level disturbances. Aquatic Sciences 73: 43–52. https://doi.org/10.1007/s00027-010-0158-3.

Santos, L. N., E. García-Berthou, A. A. Agostinho & J. D. Latini, 2011b. Fish colonization of artificial reefs in a large Neotropical reservoir: material type and successional changes. Ecological Applications 21: 251–262. https://doi.org/10.1890/09-1283.1.

Santos, A. F. G. N., E. García-Berthou, C. Hayashi & L. N. Santos, 2013. When habitat complexity increases predation risk: experiments with invasive and neotropical native fishes. Marine and Freshwater Research 64: 752–760. https://doi.org/10.1071/MF12264.

Santos, N. C. L., E. García-Berthou, J. D. Dias, T. M. Lopes, I. P. Affonso, W. Severi, L. C. Gomes & A. A. Agostinho, 2018. Cumulative ecological effects of a Neotropical reservoir cascade across multiple assemblages. Hydrobiologia 819: 77–91. https://doi.org/10.1007/s10750-018-3630-z.

Seebens, H., N. Schwartz, P. J. Schupp & B. Blasius, 2016. Predicting the spreadof marine species introduced by global shipping. Proceedings of the National Academy of Sciences 113: 5646–5651. https://doi.org/10.1073/pnas.1524427113.

Simberloff, D., 1988. The contribution of population and community biology to conservation science. Annual Review of Ecology and Systematics 19: 473–511.

Simberloff, D. & B. Von Holle, 1999. Positive interactions on nonindigenous species: invasional meltdown? Biological Invasions 1: 21–32.

Soto, I.A., Balzani, P., Carneiro, L., et al., 2023. Taming the terminological tempest in invasion science. EcoEvoRxiv, https://doi.org/10.32942/X24C79

Strubbe, D., O. Beauchard & E. Matthysen, 2014. Niche conservatism among non-native vertebrates in Europe and North America. Ecography 38: 321–329. https://doi.org/10.1111/ecog.00632.

Teresa, F. B., L. Casatti & M. V. Cianciaruso, 2015. Functional differentiation between fish assemblages from forested and deforested streams. Neotropical Ichthyology 13(2): 361–370. https://doi.org/10.1590/1982-0224-20130229.

Tickner, D., J. J. Opperman, R. Abell, M. Acreman, A. H. Arthington, S. E. Bunn, S. J. Cooke, J. Dalton, W. Darwall, G. Edwards, I. Harrison, K. Hughes, T. Jones, D. Leclère, A. J. Lynch, P. Leonard, M. E. McClain, D. Muruven, J. D. Olden, S. J. Ormerod, J. Robinson, R. J. Tharme, M. Thieme, K. Tockner, M. Wright & L. Young, 2020. Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. BioScience 70: 330–342.

Tupinambás, T. H., M. Callisto & G. B. Santos, 2007. Benthic macroinvertebrate assemblages structure in two headwater streams, south-eastern Brazil. Revista Brasileira De Zoologia 24: 887–897. https://doi.org/10.1590/S0101-81752007000400005.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.

Villares-Junior, G. A., I. B. Cardone & R. Goitein, 2016. Comparative feeding ecology of four syntopic *Hypostomus* species in a Brazilian southeastern river. Brazilian Journal of Biology 76: 692–699. https://doi.org/10.1590/1519-6984.00915.

Villéger, S., J. R. Miranda, D. F. Hernández & D. Mouillot, 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecological Applications 20: 1512–1522.

Wang, Q., K. Feng, X. Du, J. Yuan, J. Liu & Z. Li, 2022. Effects of land use and environmental gradients on the taxonomic and functional diversity of rotifer assemblages in lakes along the Yangtze River, China. Ecological Indicators 142: 109199. https://doi.org/10.1016/j.ecolind.2022.109199.

Werner, E. E., J. F. Gilliam & G. G. Mittelbach, 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540–1548.

Williamshen, B. O., T. A. O'Rear, M. K. Riley, P. B. Moyle & J. R. Durand, 2021. Tidal restoration of a managed wetland in California favors non-native fishes. Restoration Ecology 29: e13392. https://doi.org/10.1111/rec.13392.

Willis, S. C., K. O. Winemiller & H. Lopez-Fernandez, 2005. Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. Oecologia 142: 284–295.

Winemiller, K. O., 1989. Patterns of variation in life history among South American fishes in seasonal environments. Oecologia 81: 225–241.

Winemiller, K. O., 2018. Trends in biodiversity: freshwater. In DellaSala, D. A. & M. I. Goldstein (eds), The encyclopedia of the Anthropocene Elsevier, Oxford, UK: 151–161.

Winemiller, K. O., P. B. McIntyre, L. Castello, et al., 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. Science 351: 128–129. https://doi.org/10.1126/science.aac7082.

Ziv, G., E. Baran, S. Nam, I. Rodríguez-Iturbe & S. A. Levin, 2012. Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin. Proceedings of the National Academy of Sciences of the United States of America 109: 5609–5611.

Zohary, T. & I. Ostrovsky, 2011. Ecological impacts of excessive water level fluctuations in stratified freshwater lakes. Inland Waters 1: 47–59.