

# Alien fish in Neotropical reservoirs: Assessing multiple hypotheses in invasion biology

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## ARTICLE INFO

### Keywords:

Biological invasions  
Biotic acceptance  
Damming  
Freshwater ecosystems  
Resource availability  
Land-use change  
Propagule pressure

## ABSTRACT

Invasive alien species are one of the main components of global ecological change, the second known cause of animal extinctions, and very costly in terms of ecosystem services. Invasive alien species and damming are two of the most impacting alterations in freshwater ecosystems, and understanding the processes that govern biological invasions in these habitats is of enormous conceptual and practical importance. About 39 competing and overlapping hypotheses have been proposed in invasion biology that have been recently grouped in four (or five) concept clusters, namely the: propagule, resource availability, biotic interaction and Darwin's clusters. We analyzed the relative importance of three of these concept clusters in Neotropical fish assemblages, using data from 29 reservoirs and variation partitioning analyses. We show that alien fish assemblages respond to variation in limnological characteristics in a way similar than native species, usually with positive effects of increased temperature, conductivity and chlorophyll-*a* concentration and decreasing turbidity. Overall, we found support for some hypotheses included in resource availability and Darwin's clusters, such as increased resource availability and biotic acceptance, and no evidence of strong biotic resistance, marked effects of human disturbance, as measured by land-use changes, or propagule/colonization pressures. We discuss the potential reasons and management implications of these findings. Our study illustrates that analyzing the importance of classical hypotheses of invasion biology in tropical freshwaters and other ecosystems enhances ecological understanding and provides practical implications to prioritize management interventions and mitigate ecological impacts.

## 1. Introduction

Invasive alien species (IAS) are one of the main components of global ecological change (Vitousek et al., 1997), the second known cause of animal extinctions (Clavero and GarciaBerthou, 2005; Bellard et al., 2016) and very costly in terms of ecosystem services (Pejchar and Mooney, 2009). Biological invasions are also a unique opportunity to advance ecological and evolutionary understanding by providing natural experiments at larger spatial and temporal scales than manipulative experiments and traditional observational studies (Sax et al., 2005; Cadotte et al., 2006). A recent synthesis (Enders et al., 2020) has shown that there are about 39 competing and overlapping hypotheses in invasion biology that can be grouped in four (or five) concept clusters,

namely the: propagule, resource availability, biotic interaction and Darwin's clusters. The hypotheses included in the propagule cluster relate the numbers of non-native individuals or species introduced to the probability that they will become established and invasive (Enders et al., 2020). Propagule pressure measuring considers the number of introduction events (propagule numbers) and the number of individuals introduced per event (propagule size) and is related to establishment likelihood (Lockwood et al., 2005, 2009). On the other hand, colonization pressure is the number of species introduced or released in a certain location, which influences the number of species that will become established (Lockwood et al., 2009). Propagule pressure is non-linearly related to colonization pressure, the former being more a population and the latter a community-level process (Lockwood et al.,

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<https://doi.org/10.1016/j.ecolind.2020.107034>

Received 3 August 2020; Received in revised form 28 September 2020; Accepted 1 October 2020

Available online 25 October 2020

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2009). Since propagule and colonization pressures are often unknown, proxies such as shipping frequency, aquarium trade imports or the human influence index are often used for aquatic alien species (Gallardo et al., 2015).

The hypotheses of the resource availability cluster link invasion success with invader access to resources and include the increased resource availability hypothesis, which postulates that invasion success of non-native species increases with the availability of resources (e.g. due to eutrophication or abiotic disturbance), or the disturbance hypothesis that similarly relates invasion success to increased disturbance (e.g. eutrophication, damming or clearing) (Catford et al., 2009; Enders et al., 2020). On the other hand, the hypotheses in Darwin cluster highlight the importance of evolutionary legacies emphasizing the importance of exotic–native phylogenetic similarity (Diez et al., 2008; Enders et al., 2020) and include: i) the biotic resistance or diversity-invasibility hypothesis, which postulates that ecosystems with high biodiversity are more resistant to invasions (e.g. because of competition with native species); ii) the similar and also well-known enemy release hypothesis, which suggests that the absence of enemies such as predators or parasites in the exotic range explains invasion success; or iii) the biotic acceptance hypothesis, which suggests that natural ecosystems tend to accommodate the coexistence of introduced species despite the presence of native species and thus explains the often observed positive correlations between native and IAS at larger spatial scales (Stohlgren et al., 2006; Catford et al., 2009; Enders et al., 2020). The biotic interaction cluster highlights the role of interspecific (mostly negative) interactions in species invasion success and include for instance, the enemy release and specialist-generalist hypotheses (Keane and Crawley, 2002; Callaway et al., 2004). The trait cluster is in fact nested in the Darwin's cluster and includes hypotheses relating the role of traits to invasive success (Enders et al., 2020).

Understanding the relative importance of the abovementioned hypotheses is crucial for preventing and managing IAS, particularly in freshwater ecosystems which are crucial for biodiversity and ecosystems services but also very prone to biological invasions (Havel et al., 2005; Muniz et al., 2020). Although IAS are still less dominant and impacting in tropical than in temperate freshwater ecosystems (Leprieur et al., 2008), increasing damming worldwide promotes biological invasions due altered physiochemical and hydrological features and other factors (Havel et al., 2005; Johnson et al., 2008; Caiola et al., 2014). The Paraná River basin is one of the regions most affected by damming throughout South America (Agostinho et al., 2008; Ortega et al., 2015), where some of these hypotheses of biological invasions have already been suggested. For instance, in reservoirs of the Paraná, higher alien fish species richness is correlated with greater native richness (Ortega et al., 2018). The same pattern is observed in dam-free river stretch in this basin, where biodiversity and environmental heterogeneity is high, and patterns suggesting biotic acceptance have been found at various study scales, from smaller lakes to floodplain systems (Santos et al., 2018). In agreement with hypotheses in the resource availability cluster, fish richness in Paraná reservoirs follows a latitudinal gradient, with warmer environments having higher primary productivity and greater richness for both native and alien species (Bailly et al., 2016; Ortega et al., 2018). Moreover, studies of temporal dynamics have shown constant increases in the abundance of IAS species and declines in native species phylogenetically close to them (Gois et al., 2015; Rodrigues et al., 2018), which is worrying in a region with high endemism and other recorded negative impacts of IAS like biotic homogenization (Júlio Júnior et al., 2009; Daga et al., 2016). Since the study area is strongly impacted by reservoirs and by the introduction of alien species, understanding the processes that lead to the increase in IAS richness and abundance is imperative for conservation and management projects and also informative for other tropical freshwaters.

Therefore, the main objective of this study is to assess the importance of three of the concept clusters of invasion biology hypotheses in Neotropical reservoirs. We tested the role of human population density

and proximity to urban centers (propagule pressure cluster), land-use change (resource availability cluster), limnological features and native species diversity (Darwin's cluster) in structuring native and alien fish assemblages, using richness, abundance and biomass as response variables. By comparing native and alien metrics, the role of the predictors can be further understood. For instance, after accounting for limnological features and land-use change, we might expect a unique positive effect of human population density on alien fish (propagule pressure cluster) but not on native species. Moreover, if the relationship between native and alien species is positive, this would give support to the biotic acceptance hypothesis, whereas if it is negative it would suggest biotic resistance. We predicted that the richness, abundance and biomass of alien fish would increase with propagule pressure, increased resource availability, and environmental disturbance, whereas native fish should only benefit from increased resource availability (Bailly et al., 2016; Ortega et al., 2018). Therefore, we expected patterns in agreement with the biotic acceptance hypotheses, as suggested in previous studies of this region (Bailly et al., 2016; Santos et al., 2018; Ortega et al., 2018). We also hypothesized that propagule pressure might play a less critical role because it is relatively high in many of these reservoirs and because when alien species are introduced in an upstream reservoir, they can colonize those downstream.

## 2. Material and methods

### 2.1. Study area

We studied 29 reservoirs, 25 in river belonging to the Paraná River basin (Parapanema, Ivaí, Piquiri and Iguçu basin) and other four reservoir belonging to coastal basins (Atlantic basin) of the Paraná state (Fig. 1). The reservoirs have distinct morphometric and productivity characteristics (see Appendix S1 for details).

The studied reservoirs show different degrees of disturbance in their catchment basins (MapBiomias project, 2020). The Parapanema river is located in one of the most impacted regions by damming in Brazil (Ortega et al., 2015). In the Iguçu river, known by high fish endemism, the introduction of IAS has been remarkable and has caused a high impact, especially by direct competition with native fish species (Daga et al., 2016). The littoral rivers have lower degrees of human influence but also suffer from the introduction of non-native species, mainly from aquaculture farms (Frota et al., 2019).

### 2.2. Characterization of reservoirs

To estimate the propagule pressure/human population and land-use components used in the analyses, some variables were obtained to characterize the basin upstream of each reservoir. For the component propagule pressure/human influence, we used population density (number of inhabitants in the basin per km<sup>2</sup>) and distance from urban centers (km) as potential indicators of propagule/colonization pressures and environmental degradation (Colangelo et al., 2017; Leprieur et al., 2008). Population density explains much of the variation of global non-native fish richness (Leprieur et al., 2008) and can be related to propagule pressure but also disturbance, whereas distance to urban centers has also been shown to be important to explain fish introductions as a proxy of propagule and colonization pressures (Miró and Ventura, 2013). To calculate the population density of the basin upstream of each reservoir, we used a GIS database with cities and population densities (Linke et al., 2019). To calculate the distance from urban centers, we measured the distance between the reservoir and the centroid of the nearest city (either upstream or downstream) with more than 10<sup>5</sup> inhabitants. To measure land-use in the basin of influence, we used the MapBiomias database (MapBiomias project, 2020). We selected the agriculture and urban unvegetated areas for reservoir characterization since these variables are related to environmental degradation (e.g. water pollution and siltation; Atique and An, 2020) and changes in

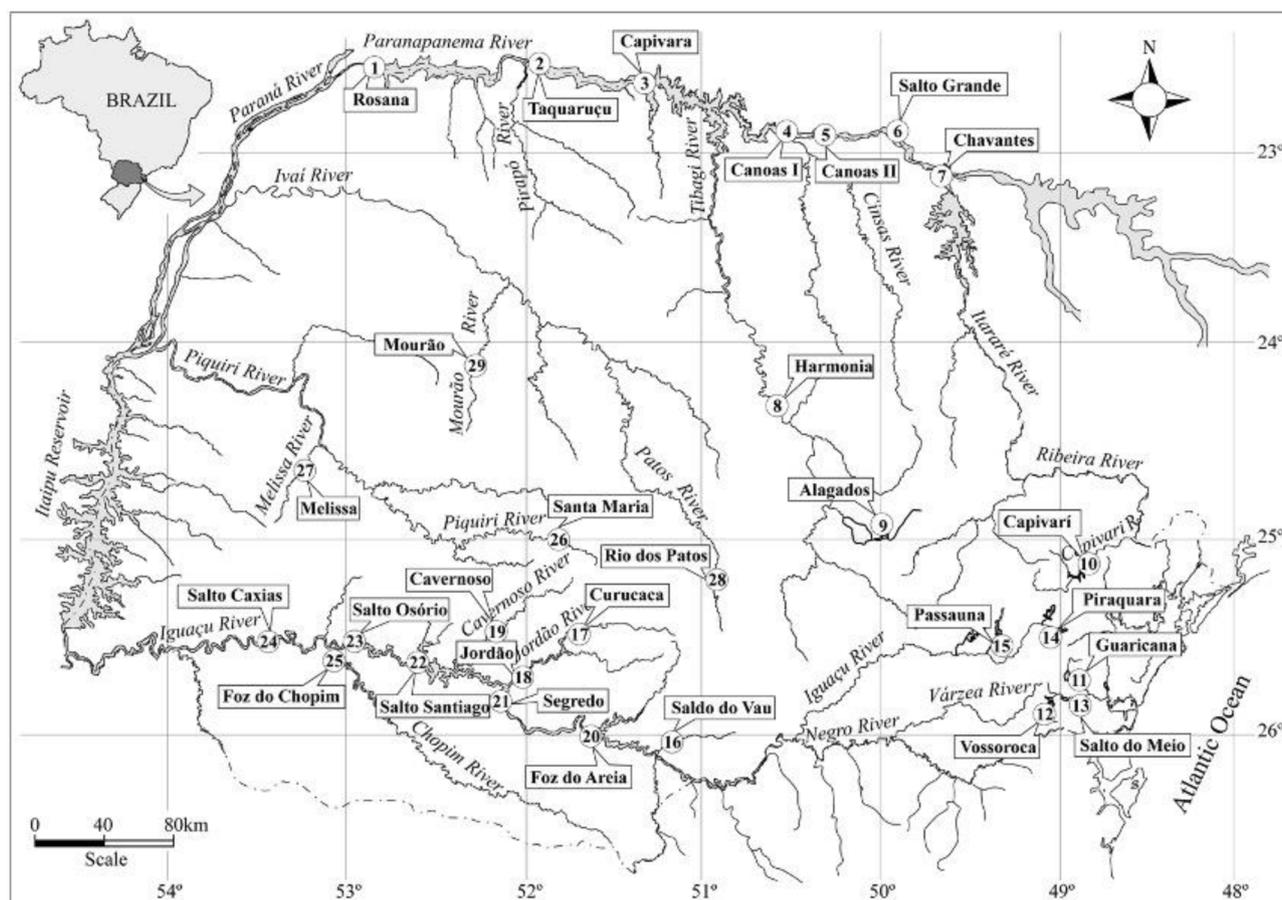


Fig. 1. Map of the Paraná State (Brazil) showing the locations of the 29 studied reservoirs. See Appendix S1 for selected features of the reservoirs.

hydrological conditions (e.g. water abstraction and modification of the flow regime), factors that influence native and alien fish species (Leprieur et al., 2008; Pelicice et al., 2017). The mapping unit adopted in the MapBiomias project was defined based on the subdivision of the International Chart of the World at the 1:250,000 scale. Each rectangle of this subdivision covers an area of  $1^{\circ}30'$  of longitude by  $1^{\circ}$  of latitude, totalizing 558 charts (or sheets) for the Brazilian territory.

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

### 2.3. Fish species sampling

Fish assemblages were sampled in the lacustrine region of the reservoirs at different depths (at the surface of the limnetic zone and at deep bottoms, with reservoirs ranging from 3.5 to 100 m maximum

depth), using gillnets of different mesh sizes (2.4 to 14.0 cm between opposing knots) set for 24 h; fish were collected in the morning, afternoon and night. The sampling was carried out in July and November 2001, corresponding to the dry and rainy seasons, respectively. Numerical abundance of each species captured was expressed as catch per unit effort (CPUE; number of individuals in 1000  $\text{m}^2$  of gillnet during 24 h). Taxonomic identification was based on Reis et al. (2003), except for the following families: Clariidae and Ictaluridae, for which we used Burges (1989); Centrarchidae (Singler and Singler, 1987); and Cyprinidae (Cavender and Coburn, 1992).

### 2.4. Fish metrics

The biotic acceptance hypothesis predicts a positive relationship between native and alien richness whereas, the biotic resistance hypothesis predicts a negative relationship. A negative relationship is also expected if the alien is impacting the native assemblage. Therefore, we used separate fish metrics for native and alien species to test these hypotheses. We used four structural metrics of fish assemblages: i) species richness; ii) total abundance (CPUE of all species); iii) total biomass of all species; and iv) Shannon diversity index. We used these four metrics because they were weakly correlated (see Appendix S2 for details) and they should respond differently to the different pressures and environmental conditions and thus allow to test different hypotheses. For instance, in contrast to CPUE, biomass integrates abundance and size structure, and thus better reflects energy availability and trophic relationships; similarly, Shannon index integrates richness and evenness.

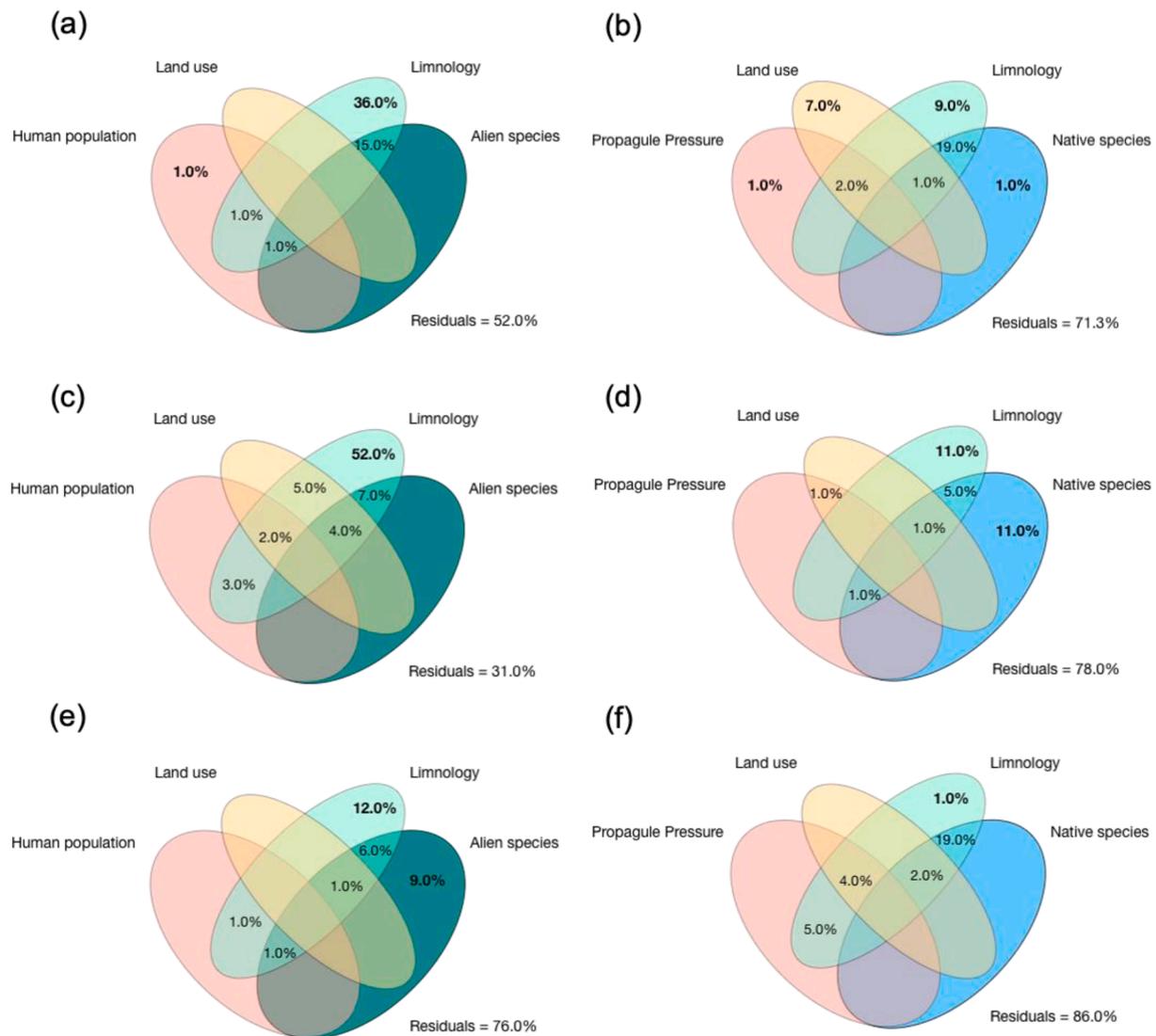
## 2.5. Data analysis

In order to reduce the number of limnological variables and collinearity, which affects many statistical procedures, we removed predictors with Pearson's  $|r| > 0.7$ , as recommended by Dormann et al. (2013), often using hierarchical cluster analysis to select the most relevant predictor among collinear predictors (see Supplementary material for more details). This procedure identified four clusters among limnological variables (Fig. S4) and we thus selected conductivity, turbidity, chlorophyll *a* and annual water temperature as essential predictors. The other predictors used in the analyses had  $|r| < 0.7$ . We used variation partitioning (VP) analyses to assess the influence of four sets of predictors on three structural metrics (richness, abundance and biomass) of the native and alien fish assemblages. The four predictor sets of VPs were: propagule pressure (which included human population density and distance to urban centers) (we termed this set as human population when testing native metrics); land-use (% of agriculture use and % of urban use); limnology (conductivity, turbidity, chlorophyll *a* and annual water temperature); and the opposite native and alien assemblage (e.g. richness, abundance, biomass, and diversity of native species when analyzing alien metrics). For all statistical analyses, richness,

abundance, all limnological variables and all population density variables were log-transformed ( $\log_{10}(x + 1)$  for chlorophyll *a* concentration), whereas land-use variables were arcsin transformed. We also log-transformed the fish response variables ( $\log_{10}(x + 1)$  for alien richness) because these transformations were indicated as preferable by a modified Box-Cox procedure (Hawkins and Weisberg, 2017), as available in the function "powerTransform" (family = "bcnPower") of the "car" package (Fox and Weisberg, 2019) and because residual plots showed that the statistical assumptions were thus satisfied.

## 3. Results

Variation partitioning analyses (Fig. 2, Table S2) revealed that the four sets of predictors had some similarities but considerable differences in explaining the metrics of native and alien assemblages. Some similarities were that: i) limnological features were the most important predictors, followed by the opposite native and alien assemblages; ii) rather surprisingly, human population and land-use changes explained very little variation; iii) the variation explained jointly by limnological features and the fish assemblage (but not shared with the two other predictor sets) was often very important. Notable differences between



**Fig. 2.** Variation partitioning analyses of key structural components of the native (left) and alien (right) fish assemblages: (a) = native richness; (c) = native abundance (CPUE); (e) = native biomass; (b) = richness of alien species; (d) = abundance (CPUE) of alien species; (f) = biomass of alien species. The figures correspond to percentages (zero or negative values are omitted). All analyses used four sets of predictors: propagule pressure/population density; land-use change; limnological features; and the opposite native or alien assemblages. See Methods and Table S2 for further details.

the native and alien metrics were that: i) overall explained variation was in general higher for native species; ii) although limnological features and the opposite alien and native assemblages were the most important predictor sets, the former was more important for native species; iii) the unique effects were mostly significant for limnological features, but much more important for native species (12–52% of variation vs. 1–11% for alien species); and iv) some unique effects of the fish assemblage were important, in particular the effects of alien on native abundance and the effects of native species on alien richness.

In general, the structure of both native and alien assemblages had as main predictors the limnological features of reservoirs. Richness, abundance and biomass of alien increased with average annual water temperature, and some of them with chlorophyll *a* concentration and conductivity (Fig. 3). These and other limnological features were positively but moderately correlated (Fig. 3, see Appendix S2 for details). Still, the structure of the native assemblage was also an important predictor of the structure of the alien assemblage and the opposite was also true. Richness, abundance and biomass of native species were less correlated among them and often positively correlated with alien metrics (Fig. 3). The metrics of native species were also positively correlated with water temperature, conductivity, and chlorophyll *a* concentration. Alien fish richness was not clearly related to native richness but positively correlated with native abundance and biomass (Fig. 3, see Fig. S5 for details). Alien abundance and biomass were positively correlated with native biomass and the former also with native richness. No alien metric was clearly related to the diversity of native species, but alien richness was related with native abundance that were negatively related with the Shannon index (see Fig. S5 for details).

#### 4. Discussion

We found that the shared and unique effects of limnological variables

and the opposite assemblage were the main predictors of both native and alien assemblages, respectively. Fish assemblages tended to respond positively to increased temperature, conductivity and chlorophyll *a* concentration and negatively to increased turbidity. However, the different metrics (e.g. richness, abundance and biomass), within the same assemblage responded differently. On the other hand, when these metrics were evaluated between assemblages, they were rather positively correlated. Overall, this gives support to some hypotheses included in the resource availability and Darwin's clusters, such as increased resource availability and biotic acceptance (Enders et al., 2020), whereas the hypotheses of biotic resistance and effects of human disturbance are refuted. We did not find either support for the hypotheses included in the propagule pressure cluster such as marked effects of propagule/colonization pressures and human disturbance.

##### 4.1. Resource availability and Darwin's cluster

Previous studies had already found positive relationships between richness of native species and IAS in Neotropical reservoirs (Baillly et al., 2016; Ortega et al., 2018), but this study is the first to also use abundance and biomass metrics as response variable in these relationships. These variables can offer different information about invasion dynamics: while species richness is related to environmental heterogeneity and the number of niche opportunities, abundance and biomass provides insights into the carrying capacity of the environment (Millar and Meyer, 2000; Silvertown, 2004). The unique effect of the native assemblage on the richness of alien species shows a positive correlation. However, native abundance was negatively correlated to the Shannon index of native assemblages, indicating dominance of a few species in the most productive reservoirs. Thus, assemblages with higher abundance (i.e., greater support capacity) and greater species dominance have greater niche opportunities for IAS (i.e., support a greater number of alien

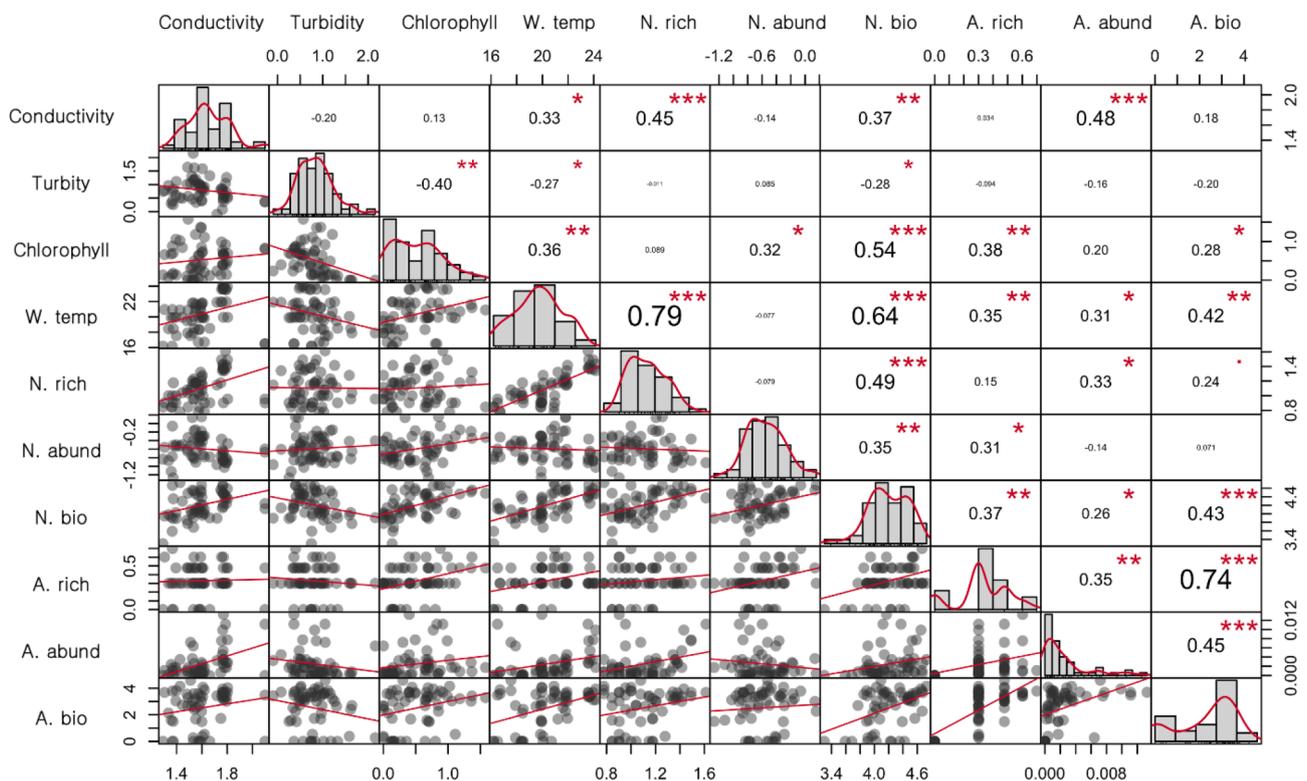


Fig. 3. Pairwise relationships between selected limnological predictors and the metrics of native and alien fish species. Below the diagonal, the bivariate scatterplots with the linear regression function are shown; the diagonal shows the histogram with an estimated kernel density function; above the diagonal, the Pearson correlation coefficients with significance levels (■,  $P < 0.10$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ). W. temp = water temperature; N. rich = native richness; N. abund = native abundance; N. bio = Native biomass; A. rich = alien richness; A. abund = alien abundance; A. bio = alien biomass.

species). These results support the biotic acceptance hypothesis in the studied reservoirs and show that reservoirs that have greater abundance of some native species also have more invasive species.

The analysis of the effects of limnological variables on both native and alien assemblages provides further understanding of the process of biotic acceptance. In general, conductivity, chlorophyll *a* and water temperature had positive effects in the structural components of both assemblages, but the effect was greater for the native one. However, the assemblages had some differences as to the type of structural component affected by limnological variables: conductivity positively affected the richness and biomass of native species and the abundance of alien species; chlorophyll *a* affected the abundance and biomass of native species and the richness and biomass of alien species while, temperature affected the richness and biomass of native species and all structural components of alien species.

The greater importance of limnological variables for the native assemblage is expected since physical and chemical factors are key in structuring local fish communities (Jackson et al., 2001). The same direction of the effects indicates that more favorable environmental conditions are so both for native and alien species. This suggests that limnological variation affects the structure of the native and alien assemblages and, therefore, can influence their biogeographic patterns, since some of these patterns followed a latitudinal gradient that is mostly related to temperature (Leprieur et al., 2008).

Our results show that the warmest reservoirs were those with the highest concentration of nutrients and primary productivity (i.e., the highest conductivity and chlorophyll *a* concentration, respectively) and also supported greater richness, abundance and biomass of native species and consequently greater biomass, richness, and abundance of alien species. The influence of productivity-related variables on alien species corroborates the hypothesis of increased resource availability. More specifically, our results showed a positive relationship between alien richness and biomass and chlorophyll-*a* concentration (Fig. 3). Environments with a higher concentration of chlorophyll *a* indicate a greater supply of energy for primary producers that increases the energy flow between trophic levels, and consequently a greater number of fish species and biomass (Brown et al., 2004). This shows that the likelihood of invasion success can be modulated by productivity processes. If chlorophyll *a* is thus one of the drivers of the invasion process, we can deduce that a bottom-up mechanism of regulation of IAS populations is occurring. In fact, some studies had already identified latitudinal gradients in the fish richness of the region's reservoirs, with temperature as a key factor (Bailly et al., 2016; Ortega et al., 2018). Those studies showed that the reservoirs in warmest regions of the Paraná basin were more resistant to local extinction of native species but at the same time more susceptible to biological invasions since they are more productive environments (Ortega et al., 2018). However, these studies did not assess multiple biological invasion hypotheses.

Our results also show that while the pure effects of limnological variables were the main predictor of the structure of the native assemblage, the joint effect of limnological and native species proved to be the most important for alien assemblage. Biological invasion is a complex process and its beginning can be shaped by several factors like limnological conditions, resource availability and native assemblage structure (see opportunity windows hypothesis in Catford et al., 2009). This may also explain the low percentage of explained variation observed in our study when we performed spatial analyses, due to the idiosyncratic features of each reservoir. Unfortunately, the precise history of introductions is unknown, and there is no reliable data on propagule pressure for the studied reservoirs. The need for monitoring of native and alien assemblages has been repeatedly emphasized by scientists, mainly to provide a more mechanistic understanding of the drivers of native decline and biological invasions and to subsidize proper management techniques (Radinger et al., 2019).

Finally, we did not find much support for the disturbance hypothesis. The land-use changes explained a negligible part of the variation of all

fish metrics and were not needed to explain the effects of limnology. Although disturbance, in general, promotes invasions (disturbance hypothesis), and land-use changes were correlated with some limnological variables in our dataset (turbidity and nitrogen concentration), limnological variables unrelated to anthropogenic perturbation seem much more important to explain both native and alien fish assemblages. The lack of effects of land-use changes on fish metrics might be related to wide agricultural land-use of the regions and the "ghost of land-use past", i.e. past land-uses might be more relevant to explain fish biodiversity, especially because minor alterations in land-use might have large consequences for fish populations in long-term scale (Harding et al., 1998). Moreover, reservoirs are artificial ecosystems strongly impacting rivers, and land-use changes might be less relevant in structuring fish assemblages than the limnological features due to the position, size and operation of the dam. Land-use has been shown to be more relevant in explaining Brazilian stream fish assemblages, through effects on macrophyte cover and instream habitat (Dala-Corte et al., 2016).

#### 4.2. Propagule pressure cluster

We did not find much support for the propagule and colonization pressure hypotheses. Human population density in the upstream basin catchment and the distance of reservoir to urban centers were negatively but weakly correlated and explained very little variation of the fish metrics, either uniquely or shared with other predictors. Population density was correlated to urban land-use but not significantly to agricultural use and the unique or shared effects of the propagule pressure set were always negligible. If propagule pressure was important independently of land-use and limnology changes, we would expect an important unique effect of population density.

This lack of evidence for the propagule and colonization pressures hypothesis has various potential explanations: it might be related to the spatial scale used, with stronger importance at larger scales, such as countries and whole river basins (Leprieur et al., 2008); it could also be related to the fact that reservoirs often do not act as barriers to alien species in the upstream-downstream direction (Muniz et al., 2020); widespread municipal initiatives for introducing fingerlings of IAS into aquatic bodies in some cities (Agostinho and Gomes, 2002); widespread escape of individuals produced by aquaculture in cage nets (Ortega et al., 2015); alternatively, population density and distance to urban centers might be poor proxies of propagule and colonization pressures in this system (Drake et al., 2015).

#### 4.3. Final considerations

Our results show that native and alien fish species of these Neotropical reservoirs respond in a similar way to limnological characteristics, providing support for the increased resource availability and biotic acceptance hypotheses. The abundance and richness of both native and alien species tend to increase with the productivity of reservoirs, which is mostly related to nutrient concentration and water temperature. By contrast, biotic resistance and propagule and colonization pressures seem to play a minor role on fish invasions in these systems, perhaps in part because of their connectivity in the downstream direction. Therefore, many other IAS might be predicted to establish and preventing this might be the focus of management. Considering the ongoing biotic homogenization due to fish invasions, and the considerable ecological impacts in the region (Daga et al., 2015), identifying invasion drivers and processes is essential for management programs. Therefore, analyzing the importance of these hypotheses in tropical reservoirs might provide further conceptual and practical understanding to assist decision makers in environmental policies and better ecosystem management.

## Declaration of Competing Interest

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

## Acknowledgements

We express our appreciation to the PRONEX-MCT/CNPq for financial support and to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, Brazil, process number 88882.344464/2019-01) and to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Brazil, process number 165319/2017-8) for the fellowships to graduate students. AAA received scientific productivity fellowships from CNPq. We are also grateful for the funding provided by CAPES through “Programa de Doutorado-sanduíche no Exterior” (PDSE, processes number 88881.361907/2019-01 and 88881.361938/2019-01) that allowed a research stay of CMM and MMG at the University of Girona. Additional financial support was provided by the Spanish Ministry of Science and Innovation (projects RED2018-102571-T and PID2019-103936GB-C21) and the Government of Catalonia (ref. 2017 SGR 548).

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.107034>.

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## SUPPLEMENTARY INFORMATION

### **Alien fish in Neotropical reservoirs: assessing multiple hypotheses in invasion biology**

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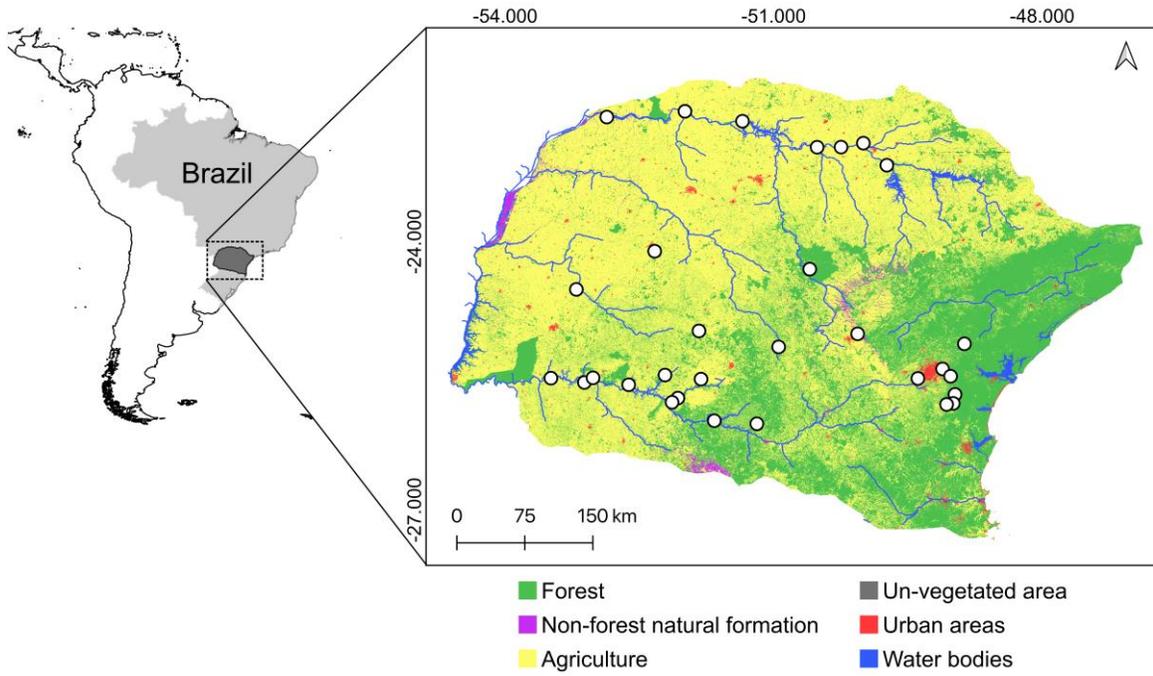
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## **Appendix S1: Study reservoirs and environmental variables**

### Location, study reservoirs and land-use

Land-use information was taken from the Map Biomes website, which use a 30 m accuracy scale (pixels) (MapBiomas project, 2020). The project classifies land-use into 33 categories. For the current study, we reclassified them as follows into six categories (Fig. S1), of which: natural forest, savanna formation, mangrove and planted forest were classified as forest; natural non-forest humid area, countryside formation, apicum and other non-forest natural formations were classified as non-forest natural formation; pasture, agriculture, annual perennial culture, semi-perennial culture and mosaic of agriculture and pasture were classified as agriculture; non-vegetated area, beach and dune, rocky outcrop and other non-vegetated areas were classified as non-vegetated area; river, lake, ocean and aquaculture were classified as water bodies; and finally areas of urban infrastructure. The variables exposed here are intended to be used as a proxy for propagule pressure and human disturbance in the reservoirs.



**Figure S1** Location of the studied area, reservoirs (circles) and land-use in the region (extracted from Mapbiomas, 2020).

**Table S1** Characteristics of the 29 study reservoirs located in the State of Paraná, Brazil.; MAWT = mean annual water temperature; Agri = percent of agricultural land-use in the upstream basin.

Reservoir	Basin	Area (km <sup>2</sup> )	MAWT (°C)	Agri (%)	Alien Richness	Chlorophyll <i>a</i> (µg L <sup>-1</sup> )	
						July	Nov.
Alagados	Tibagi	7.2	19.8	54.5	1	3.4	11.9
Canoas1	Paranapanema	30.8	23.9	69.4	1	3.5	2.1
Canoas2	Paranapanema	22.5	23.5	68.5	1	1.6	7.3
Capivara	Paranapanema	419.3	23.7	71.7	2	3.9	3.7
Capivari	Litorânea	12.0	19.9	19.2	3	1.5	3.9
Cavernoso	Iguaçu	2.9	19.5	66.4	2	0.3	0.0
Chavantes	Paranapanema	400.0	21.9	62.9	1	0.7	1.5
Curucaca	Iguaçu	2.0	17.5	55.0	2	0.4	1.0
Foz do Areia	Iguaçu	139.0	20.7	39.9	2	1.3	14.2
Foz do Chopim	Iguaçu	2.9	20.0	71.5	1	0.4	0.0
Guaricana	Litorânea	7.0	19.9	1.1	2	10.4	6.0
Harmonia	Tibagi	3.0	20.9	58.2	2	9.6	36.9
Jordão	Iguaçu	3.4	18.4	63.4	1	0.2	0.5
Melissa	Piquiri	2.9	17.9	84.0	2	0.0	0.0
Mourão	Ivaí	11.3	20.9	81.9	4	3.6	6.6
Passauna	Iguaçu	14.0	16.5	45.5	2	5.3	5.7
Patos	Ivaí	1.3	18.5	53.3	1	0.0	0.3
Piraquara	Iguaçu	3.3	19.9	33.6	1	4.0	3.7
Rosana	Paranapanema	220.0	24.1	74.4	1	3.4	4.9
Santa Maria	Piquiri	0.1	16.7	68.9	1	0.1	0.6
Salto Caxias	Iguaçu	124.0	21.8	50.8	2	1.2	6.1
Salto Grande	Paranapanema	12.0	21.9	68.0	2	0.4	0.4
Salto do Meio	Litorânea	0.1	18.3	8.5	0	0.8	3.4
Salto Osório	Iguaçu	51.0	21.2	45.9	3	1.6	22.4
Salto Santiago	Iguaçu	208.0	21.6	45.3	2	0.7	21.7
Salto Segredo	Iguaçu	82.5	21.8	39.3	3	4.5	2.1
Salto do Vau	Iguaçu	2.0	16.2	19.6	0	0.4	0.4
Taquaruçu	Paranapanema	80.1	23.6	72.4	3	1.5	8.7
Vossoroca	Litorânea	5.1	19.9	8.5	4	1.8	4.1

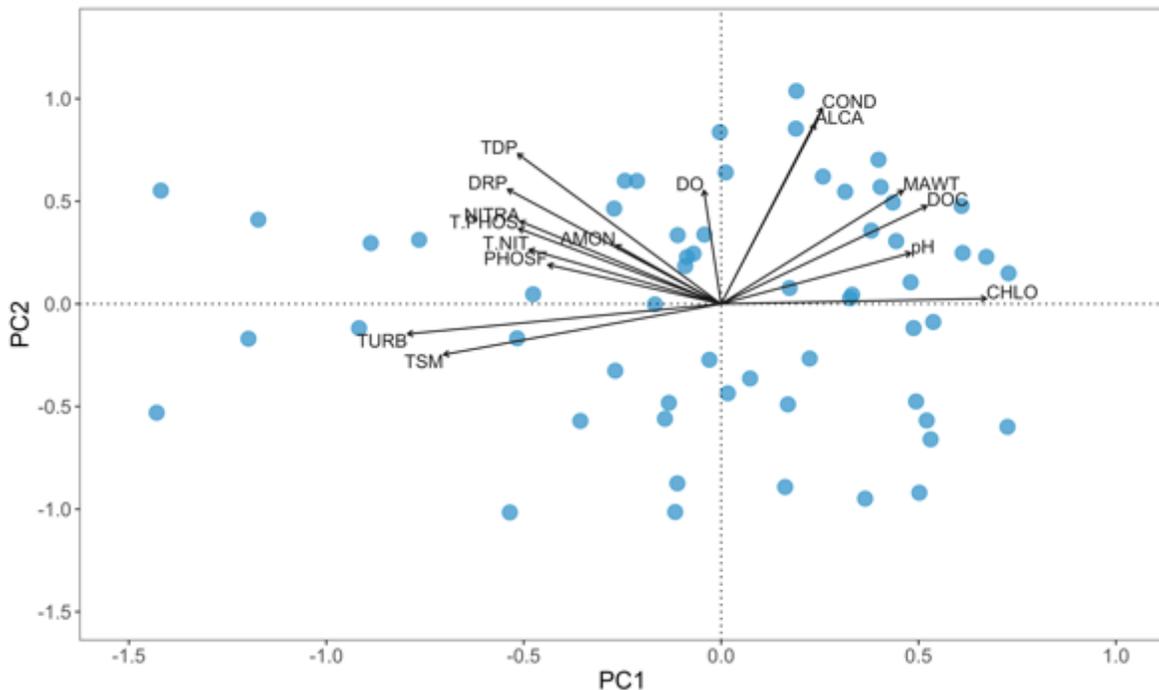
Source: Gubiani *et al.* (2007)

## Reference

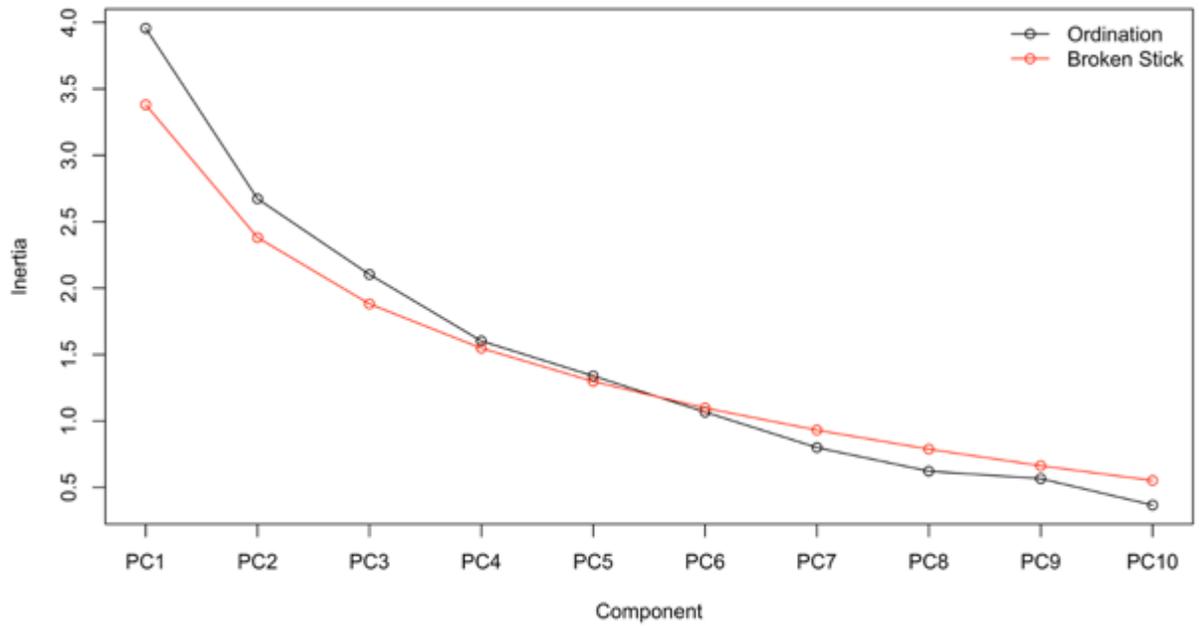
MapBiomass project. 2020 – Coleção 2 da Série Anual de Mapas de Cobertura e Uso de Solo do Brasil. ATDB do Estado do Paraná, São Paulo e Santa Catarina. Acessado em 20 de novembro de 2019 através do link: <http://map-biomass.org>.

## Appendix S2: Selection of limnological variables

Exploratory analyses of limnological variables showed relatively low correlation among them. A broken stick model (Jackson 1993; Legendre and Legendre, 1998) revealed that the first five axes of the principal component analysis (PCA) were necessary to properly summarize the entire data set (Figure S3).



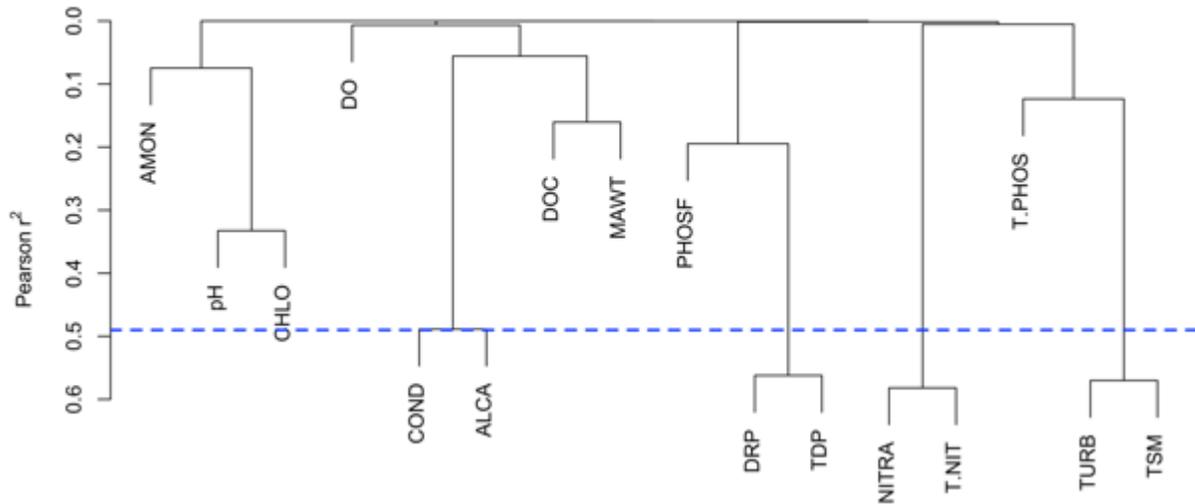
**Figure S2** Principal component analysis of the limnological variables across the 29 study reservoirs. AMON = ammonia ( $\mu\text{g L}^{-1}$ ); CHLO = chlorophyll  $\alpha$  ( $\mu\text{g L}^{-1}$ ); DO = dissolved oxygen ( $\text{mg L}^{-1}$ ); COND = conductivity ( $\mu\text{S cm}^{-1}$ ); ALCA = alkalinity ( $\text{mEq L}^{-1}$ ); DOC = dissolved organic carbon ( $\mu\text{g L}^{-1}$ ); MAWT = annual median of water temperature ( $^{\circ}\text{C}$ ); PHOSF = phosphate ( $\mu\text{g L}^{-1}$ ); DRP = orthophosphate ( $\mu\text{g L}^{-1}$ ); TDP = total dissolved phosphorus ( $\mu\text{g L}^{-1}$ ); NITRA = nitrate ( $\mu\text{g L}^{-1}$ ); T. NIT = total nitrogen ( $\mu\text{g L}^{-1}$ ); T. PHOS = total phosphorus ( $\mu\text{g L}^{-1}$ ); TURB = turbidity (NTU); MST = measured total suspended material ( $\text{mg L}^{-1}$ ).



**Figure S3** Inertia values for the ordering axes and broken-stick model.

Hierarchical variable clustering based on correlation matrix also indicated relatively low collinearity (Figure S4). For the variation partitioning analysis, we selected four limnological variables (conductivity, turbidity, chlorophyll and annual water temperature) that may be related to human disturbances in the basin (*i.e.*, input of nutrients from sewage and land-use), reservoir productivity (*i.e.*, primary productivity) and other natural and anthropogenic gradients and which were only weakly correlated.

( $|r| < 0.7$ ; Dormann et al., 2013) among them (Figure S4).



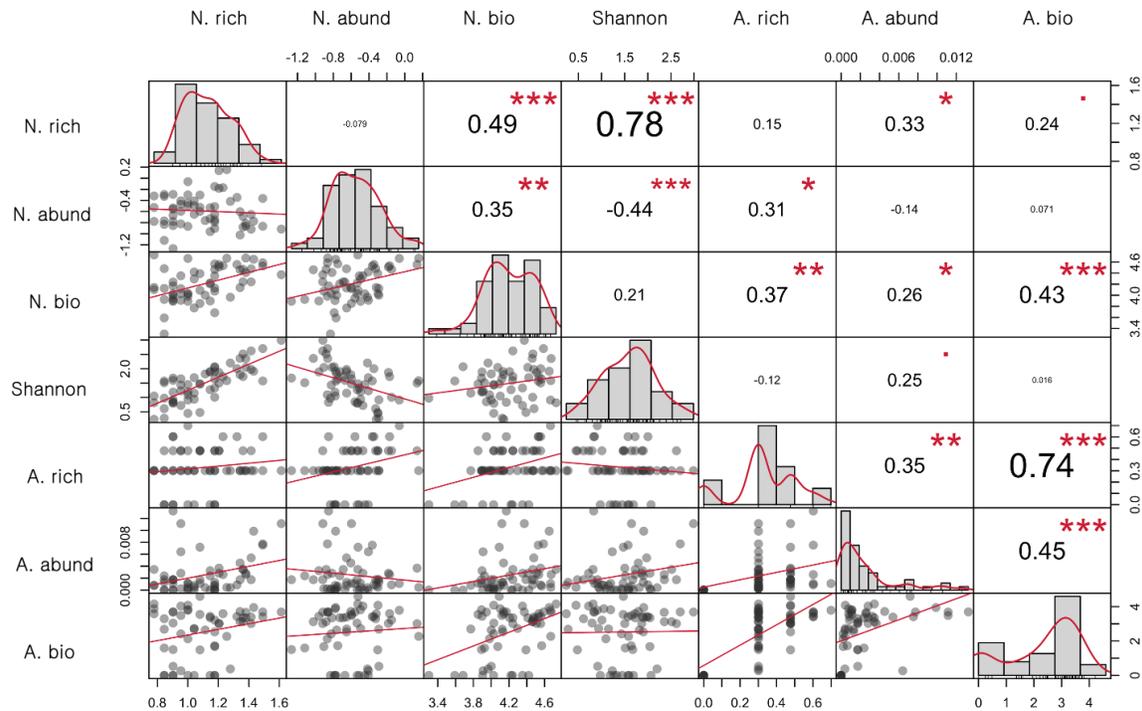
**Figure S4** Dendrogram built through a hierarchical cluster analysis using Pearson's correlation index. The blue line indicates the cut-off criterion for highly correlated variables. AMON = ammonia ( $\mu\text{g L}^{-1}$ ); CHLO = chlorophyll  $\alpha$  ( $\mu\text{g L}^{-1}$ ); DO = dissolved oxygen ( $\text{mg L}^{-1}$ ); COND = conductivity ( $\mu\text{S cm}^{-1}$ ); ALCA = alkalinity ( $\text{mEq L}^{-1}$ ); DOC = dissolved organic carbon ( $\mu\text{g L}^{-1}$ ); MAWT = annual median of water temperature ( $^{\circ}\text{C}$ ); PHOSF = phosphate ( $\mu\text{g L}^{-1}$ ); DRP = orthophosphate ( $\mu\text{g L}^{-1}$ ); TDP = total dissolved phosphorus ( $\mu\text{g L}^{-1}$ ); NITRA = nitrate ( $\mu\text{g L}^{-1}$ ); T. NIT = total nitrogen ( $\mu\text{g L}^{-1}$ ); T. PHOS = total phosphorus ( $\mu\text{g L}^{-1}$ ); TURB = turbidity (NTU); MST = measured total suspended material ( $\text{mg L}^{-1}$ ).

**Table S2** Variation partitioning analyses of four predictor sets on the metrics of alien and native fish species. The explained variation ( $R^2_{adj}$ ) and corresponding  $P$  value are shown.

Response variable	Factors	$R^2_{adj}$	$P$	$R^2_{adj}$	$P$
		overall		unique	
Biomass of alien species	Propagule pressure	-0.016	0.591	0.013	0.241
	Land-use	0.018	0.241	-0.074	<b>0.038</b>
	Limnology	0.241	<b>0.004</b>	0.094	0.072
	Native species	0.201	<b>0.007</b>	0.003	0.375
Richness of alien species	Propagule pressure	-0.024	0.729	-0.027	0.826
	Land-use	-0.021	0.664	-0.001	0.393
	Limnology	0.123	<b>0.014</b>	0.125	<b>0.045</b>
	Native species	0.160	<b>0.010</b>	0.115	<b>0.041</b>
Abundance of alien species	Propagule pressure	0.003	0.319	-0.024	0.718
	Land-use	0.008	0.288	-0.011	0.456
	Limnology	0.229	<b>0.007</b>	0.009	0.360
	Native species	0.103	<b>0.038</b>	-0.056	0.917
Biomass of native species	Human population	0.004	0.334	0.014	0.223
	Land-use	-0.009	0.512	-0.015	0.717
	Limnology	0.500	<b>0.001</b>	0.362	<b>0.001</b>
	Alien species	0.150	<b>0.009</b>	-0.018	0.727
Richness of native species	Human population	0.017	<b>0.252</b>	-0.007	0.614
	Land-use	0.101	<b>0.025</b>	-0.008	0.690
	Limnology	0.700	<b>0.001</b>	0.508	<b>0.001</b>
	Alien species	0.077	0.062	-0.007	0.571
Abundance of native species	Human population	-0.021	0.638	-0.024	0.738
	Land-use	-0.018	0.624	-0.021	0.683
	Limnology	0.198	<b>0.005</b>	0.120	0.058
	Alien species	0.148	<b>0.015</b>	0.095	<b>0.051</b>

Bolding indicates significant  $P$  values;

$P$  significance based on 9999 randomizations



**Figure S5** Pairwise relationships between the metrics (richness, abundance and biomass) of native (including Shannon index) and alien fish species. Below the diagonal, the bivariate scatterplots with the linear regression function are shown; the diagonal shows the histogram with an estimated kernel density function; above the diagonal, the Pearson correlation coefficients with significance levels (▪,  $P < 0.10$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ )

## References

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