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CAROLINA MENDES MUNIZ

Biological fish invasion process in Neotropical reservoirs: looking for general patterns that determine the success of invasive alien species in these systems

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

Processo de invasão biológica de peixes em reservatórios Neotropicais: em busca de padrões gerais que determinem o sucesso de espécies invasoras exóticas nesses sistemas

RESUMO

O conhecimento dos mecanismos controladores do processo de invasão é um desafio atual na ecologia. Esse conhecimento torna-se de extrema importância, uma vez que a introdução de espécies exóticas tem se tornado muito difundida em todo o mundo e possui importantes implicações para a conservação da vida selvagem. Atualmente, estudos tem mostrado que espécies exóticas podem causar diversos impactos ambientais como homogeneização biótica e desestabilização da comunidade nativa, sendo considerada uma das principais ameaças à biodiversidade e perda de serviços ecossistêmicos. A fim de investigar o processo de invasão de peixes em reservatórios da região neotropical, foram avaliados 29 reservatórios que possuem diferentes cenários ambientais e de invasão biológica. Na primeira abordagem, avaliou-se a importância de três agrupamentos conceituais de hipóteses de invasão biológica nos reservatórios estudados. Dentre as hipóteses testadas para invasão biológica, os resultados corroboraram a de aumento da disponibilidade de recurso e aceitação biótica. Na segunda abordagem, avaliou-se os índices funcionais que representam sobreposição/complementaridade de nicho entre as espécies nativas são preditores da dominância de espécies exóticas no ambiente. Os resultados indicaram que a dominância de espécies exóticas é maior quando a uniformidade dos recursos disponíveis é maior e a probabilidade de competição entre as espécies nativas é menor. Também foi possível observar que quanto menor a complementaridade de nicho das espécies nativas mais abundantes, menor é a dominância das espécies exóticas. Os resultados gerados pelas duas abordagens fornecem importantes informações sobre os mecanismos que levam ao aumento de espécies exóticas nos reservatórios estudados. Essas informações são de extrema importância para programas de gestão de espécies invasoras.

Palavras-chave: Aceitação biótica. Barragem. Diversidade funcional. Invasão biológica. Reservatório.

Process of biological invasion of fishes in Neotropical reservoirs: in search of general patterns that determine the success of invasive alien species in these systems

ABSTRACT

Knowledge of the controlling mechanisms of the invasion process is a current challenge in ecology. This knowledge becomes extremely important since the introduction of alien species has become widespread and has important implications for the wildlife conservation. Currently, studies have shown that alien species can cause several environmental impacts, such as biotic homogenization and destabilization of the native community, being considered one of the main threats to biodiversity and loss of ecosystem services. To investigate the process of fish invasion in reservoirs in the neotropical region, 29 reservoirs that have different environmental and biological invasion scenarios were used. In the first approach, we evaluated the importance of three hypotheses' concept clusters of biological invasions in the studied reservoirs. Among all the hypotheses tested for biological invasion, the results corroborated the increased resource availability and biotic acceptance hypothesis. In the second approach, we assess whether the functional indices that represent niche overlap/complementarity between native species are predictors of the dominance of alien species in the environment. The results indicate that the dominance of alien species is greater when the uniformity of available resources is greater and the probability of competition between native species is less. It was also possible to observe that the smaller the niche complementarity of the more abundant native species, the lower the dominance of alien species. The results generated by the two approaches provide important information about the mechanisms that lead to the increase of alien species in the studied reservoirs. This information is extremely important for programs for the management of invasive species.

***Keywords*:** Biological invasion. Biotic acceptance. Damming. Functional diversity. Reservoir.

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SUMMÁRY

1 INTRODUCTION

Understanding the mechanisms that control the invasion process is a current challenge in ecology. This knowledge becomes extremely important since the introduction of species has become widespread and has important implications for wildlife conservation (Simberloff et al., 2013). Currently, studies have shown that invasive alien species (IAS) can cause several environmental impacts such as biotic homogenization and native community destabilization (Olden et al., 2006; Castaño-Sánchez et al., 2018; Erős et al., 2020), being considered one of the main threats to biodiversity and loss of ecosystem services. As it is a complex process, where many factors can act together, many hypotheses have been formulated to explain the success of invasions in invaded environments (Enders et al., 2020). These hypotheses are related to the process of transport, introduction, colonization, naturalization, dispersion, and possible environmental impacts of these species (Catford et al., 2009).

There are about 39 existing hypotheses in invasion biology that can be grouped in 5 concept clusters, namely propagule, resource availability, biotic interaction, trait, and Darwin's clusters (Enders et al., 2019). These hypotheses cover all biological invasion processes from the transport and introduction to successful establishment and dispersion of alien species (Catford et al., 2009). The hypothesis contained in the propagule pressure cluster assume that one of the primary mechanisms leading to successful invasion of alien species are propagule and colonization pressure, related to population and community concepts, respectively (Colautti et al., 2006; Lockwood et al., 2005). Propagule pressure is the number of individuals introduced into the environment that is related to the success of population establishment (e.g., minimum viable population size). On the other hand, colonization pressure is the number of species introduced or released in environment, some of which will establish and maintain viable populations and others not, and it is closely related to the quantity and types of resources in the site. Thus, it is expected that the probability of establishing success of the non-native species and number of invasive species is directly related to proximity and frequency of introductions performed by the potential source in the environment (Lockwood et al., 2005).

A determining factor for the intensity of propagule and colonization pressure is human occupation, which is associated with the human commensalism and disturbance hypothesis (contained in propagule pressure, resource availability and trait cluster; sensu Enders et al., 2019). This hypothesis predicts that, species that are related to humans (e.g., species of economic importance and pets) are more likely to succeed in invasion than other species. In addition to having direct participation, we must consider the indirect participation of human beings in the invasion process, through environmental degradation. The hypothesis of environmental disturbance, included in the resource availability cluster, predicted that by degrading the environment and increasing the propagule pressure, human activities facilitate the establishment of non-native species (Hobbs and Huenneke, 1992; Meyerson and Mooney, 2007). Thus, beyond your participation the process of transporting and introducing, the land-cover change of the natural landscape by humans may have direct consequences on environmental natural conditions and structure of native community (Arantes et al., 2019). It is important to note that these factors can also alter water quality and the structure of the native aquatic community, which plays an important role in the process of establishing alien species.

After the IAS introduction, the hypothesis contained in the resource availability cluster assume that the abiotic and biotic conditions of the environment can determine its success in colonization. Abiotic factors are related to the species' ability to remain in those conditions and the amount of available resource. In this sense, the dynamic balance theory predicts that degraded environments with high productivity are those where alien species are more likely to establish themselves and become dominant (Huston 1979). The way in which the invasive species will use the resource will determine its relationship with the native species in the environment and the hypothesis that include these relationships are contained in the Darwin's clusters: i) when alien species take advantage of resource underutilization by native species, the biotic acceptance process takes place, that is, there is no competition between them; ii) on the other hand, in the case of competition for resources between the alien species and the native species, the process of biotic resistance takes place (Fridley et al., 2007). However, some studies show that the process of acceptance and biotic resistance is linked to the scale of the study (invasion paradox; Sax & Brown, 2000). Broad-scale studies usually show the process of biotic acceptance, while small-scale studies (e.g., experimental studies) find the process of biotic resistance (Shea & Chesson, 2002; Levine et al., 2004; Davies et al., 2005; Fridley et al., 2007; Alofs & Fowler, 2013). All these processes, from the propagule pressure to the interaction with the related native species and are determinant for the process of naturalization and dispersion of the invasive species.

Determining these relationships is crucial for the prevention and management of alien species, especially in continental aquatic environments where there is great biodiversity and are very important environments by ecosystem services and are also very susceptible to biological invasion (Havel et al., 2005; Muniz et al., 2020). And one of the reasons that increase the susceptibility to invasion is the presence of reservoirs in rivers, whose physical-chemical and hydrological changes provide ideal environments for the establishment of invasive species (Havel et al., 2005; Johnson et al., 2008; Caiola et al., 2014). This is because the construction of the dam reduces the heterogeneity of habitats, making the environment less suitable for native species, allowing better resource use by invasive species (i.e., more generalists) (Elton 1958; Davis et al. 2000). Some hypotheses within invasion biology predict greater success in colonization and establishment of alien species in environments with greater resource availability, i.e., more productive and with quantity of available habitats (Catford et al., 2009). The dynamic equilibrium hypothesis predicts that an alien species may even establish itself in an undisturbed and productive environment, but it only becomes dominant and has the environmental impacts potential in environments with high productivity and a high degree of disturbance (Huston, 2004). Therefore, more attention should be paid at the invasion process in reservoirs, as in addition to being favorable environments for the development of IAS, they have high connectivity with the environments in their surroundings, becoming a source of potential propagule (Havel et al. 2005, Muniz et al., 2020).

In Brazil, the state of Paraná is one of the regions most impacted by dams (Agostinho et al., 2008; Ortega et al., 2015) and some patterns of biological invasion of fish have already been described. In dammed environments a greater richness of IAS was found in reservoirs with a greater richness of native species (Ortega et al., 2018). Also, the richness of native and alien fish in these environments follow a longitudinal pattern, where warmer reservoirs with higher primary productivity have greater richness of both (Bailly et al., 2016; Ortega et al., 2018). The same pattern is repeated in undammed natural environments, where biotic acceptance patterns are found at various scales, from small lagoons to the floodplain system (Santos et al., 2018). Some temporal studies carried out in the Upper Paraná River floodplain have shown that there are records of constant increase in the abundance of IAS and decline of phylogenetically related species (Gois et al., 2015; Rodrigues et al., 2018). This fact becomes even more worrying since in regions with high endemism negative impacts of invasive species have already been recorded (Júlio-Junior et al., 2009; Daga et al., 2016).

One way to better understand biotic acceptance patterns is through analysis of resource use, i.e., niche overlap/complementarity between species. The greater the niche overlap between species, the greater the strength of competition between them, whether for space or for food (Pastore et al., 2021). The opposite is also true, the greater the niche complementarity between species, the less competitive interaction between them (Ashton et al., 2010). Thus, since native and alien fish species tend to respond in the same way to environmental pressures (Bailly et al., 2016; Ortega et al., 2018), an environment with a more competitive native community will result in a more competitive environment for alien species, increasing the biotic resistance of the community. On the other hand, more complementary native communities may be more susceptible to invasion, since the community's competitive strength is less, thus increasing biotic acceptance. One way to assess these components is through the analysis of functional indices, which help to understand how species use the resource available in the environment (Manson et al., 2005). Therefore, we can make the relationship of the way the resource is used with the context of biotic acceptance and resistance.

In all chapters we used fish assemblage data from 29 reservoirs sampled throughout the state of Paraná. The samplings were standardized and carried out during two periods throughout 2001 (July and November, corresponding to the dry and rainy period). Therefore, to answer the questions we used spatial analysis to look for general patterns within reservoirs inserted in the Neotropical region.

In the first chapter, we assess the importance of three conceptual clusters related to the invasion hypotheses proposed by Anders et al., 2020. Thus, we test the influence of limnological conditions on land use changes (cluster “available resources”), population density human and proximity of reservoirs to urban centers (cluster “propagule pressure”) and species diversity (cluster “Darwin”) in the structuring of assemblages of native and alien species. The results showed that both assemblages respond similarly to limnological environmental variations, providing support for the hypotheses related to increased resource availability and biotic acceptance.

Once evidence of biotic acceptance was found, in the second chapter we evaluated whether the relationship between the dominance of IAS and the structure of the native community can predict the ecological mechanisms that drive the process of biological invasion into reservoirs, using a functional approach. It was tested the hypothesis that reservoirs that have more complementary native communities and therefore less competitive interactions between species lead to a greater dominance of IAS. The results indicated that the size and niche distribution in the functional space of native species proved to be a strong determinant for the dominance of IAS.

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2 ALIEN FISH IN NEOTROPICAL RESERVOIRS: ASSESSING MULTIPLE HYPOTHESES IN INVASION BIOLOGY

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. The 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.

Keywords: biological invasions, biotic acceptance, damming, freshwater ecosystems, resource availability, land-use change, propagule pressure.

2.1 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 García-Berthou, 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. 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., 2010) 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, 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-Junior 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.

2.2 Material and methods

2.2.1 Study area

We studied 29 reservoirs, 25 in river belonging to the Paraná River basin (Paranapanema, Ivaí, Piquiri and Iguaçu 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).

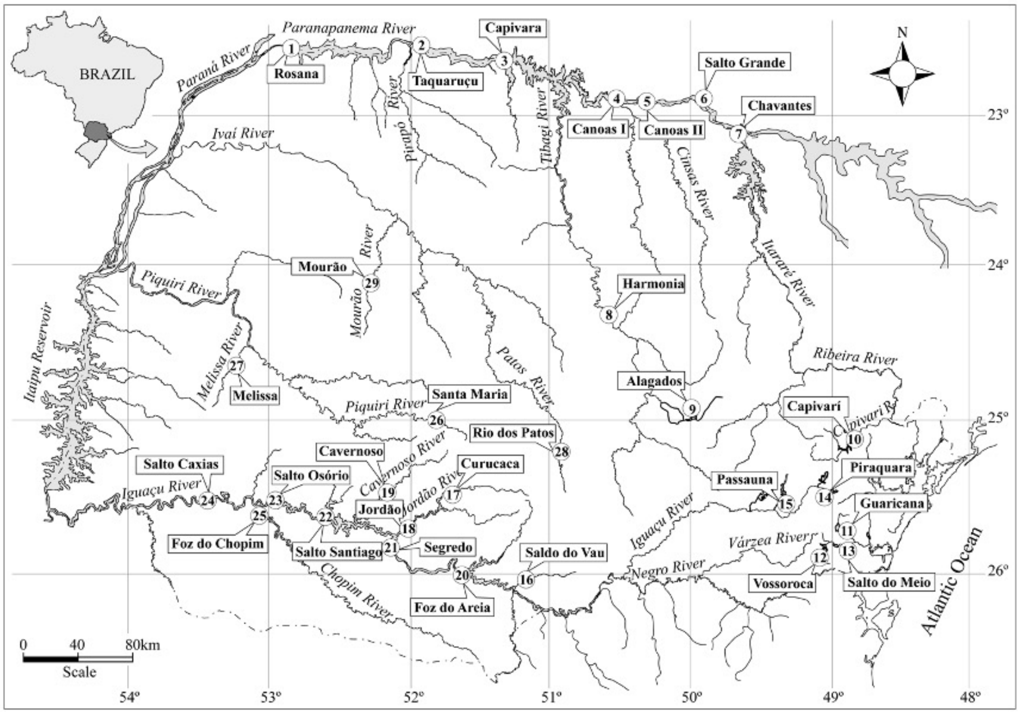

Figure 1. Map of the Paraná State (Brazil) showing the locations of the 29 studied reservoirs. See Appendix S1 for selected features of the reservoirs.

The studied reservoirs show different degrees of disturbance in their catchment basins (MapBiomas project, 2020). The Paranapanema River is located in one of the most impacted regions by damming in Brazil (Ortega et al., 2015). In the Iguaçu 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).

2.2.2 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^2) 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 10^5 inhabitants. To measure land-use in the basin of influence, we used the MapBiomas database (MapBiomas 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 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 MapBiomas 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°30' of longitude by 1° 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 (µS cm^{-1}), pH, turbidity (NTU), and dissolved oxygen (mg L^{-1}) were measured in the field with a multiparameter probe. Water collected with a Van Dorn sampler (2.5 L) was stored in polyethylene bottles, placed on ice and preserved in low temperatures until analysis. Following standard protocols (Mackereth et al., 1978, APHA 2005), we obtained the following limnological variables: total suspended material (mg L^{-1}), alkalinity (mEq L^{-1}), total phosphorus (µg L^{-1}; APHA 2005), orthophosphate (µg L^{-1}; APHA 2005), phosphate (µg L^{-1}; APHA, 2005), total dissolved phosphorus (µg L^{-1}; APHA, 2005), chlorophyll *a* (µg L^{-1}; Nusch, 1980), total nitrogen (µg L^{-1}; Mackereth et al., 1978), nitrate (µg L^{-1}; Mackereth et al., 1978), ammonia (µg L^{-1}; Mackereth et al., 1978), and dissolved organic carbon (µg 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).

2.2.3 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 hours; 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 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).

2.2.4 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.

2.2.5 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.

2.3 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 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.

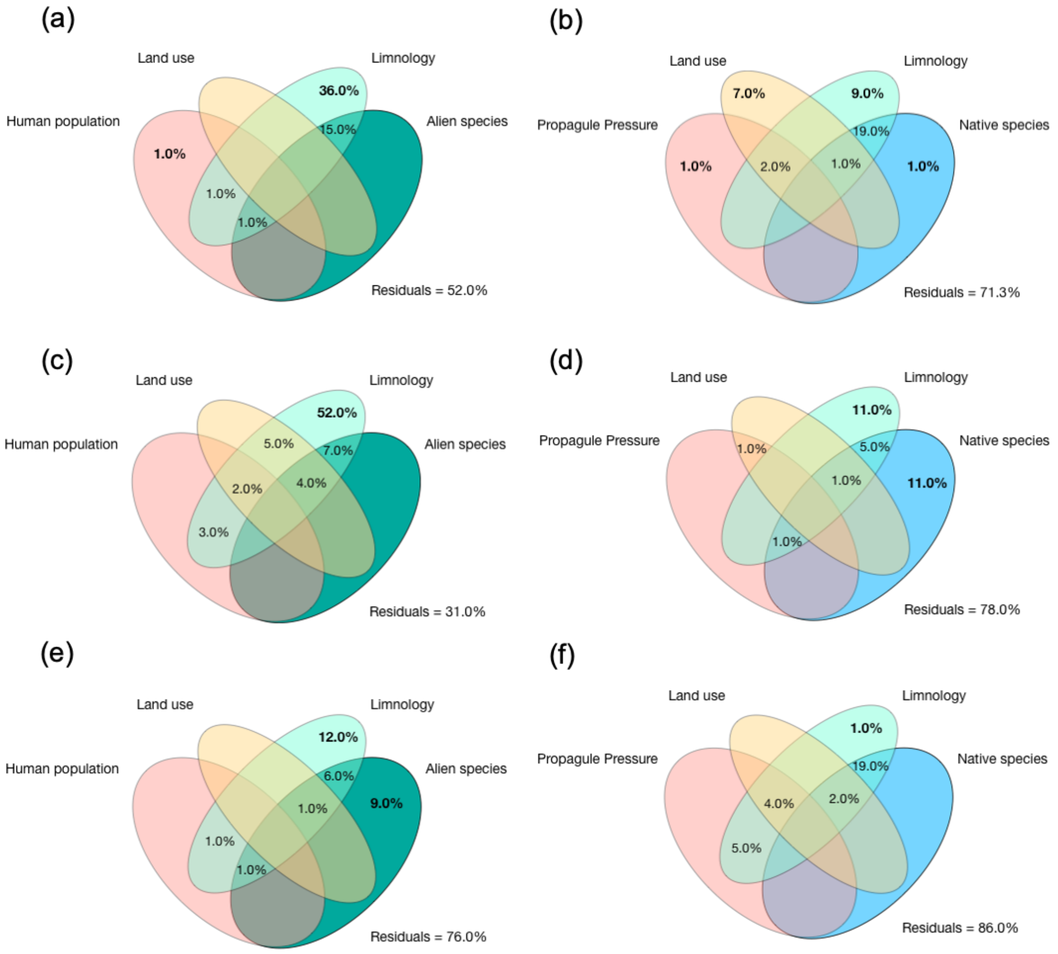

Figure 2 Variation partitioning analyses of key structural components of the native (left) and alien (right) fish assemblages: **(a)** = native richness; **(c)** = native abundance (CPUE); **(e)** = native biomass; **(b)** = richness of alien species; **(d)** = abundance (CPUE) of alien species; **(e)** = 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.

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).

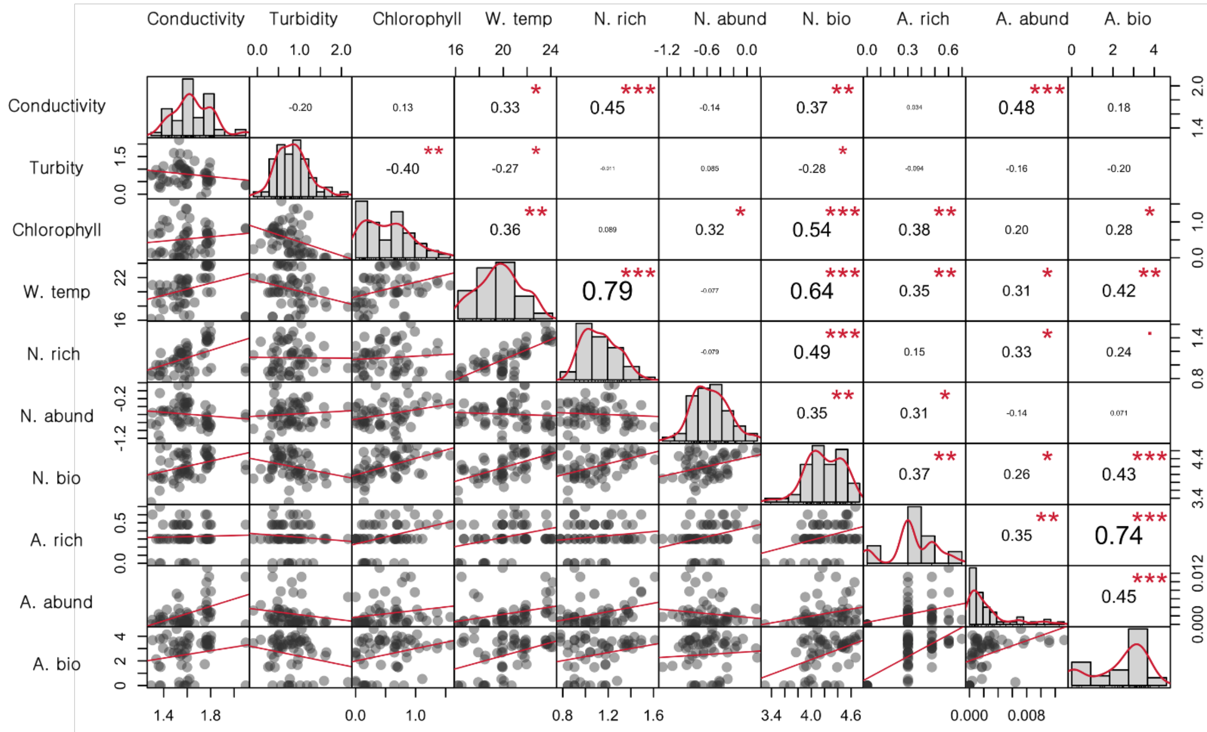

Figure 3 Pairwise relationships between selected limnological predictors and the metrics of native and alien fish species. Below the diagonal, the bivariate scatterplots with the linear regression function are shown; the diagonal shows the histogram with an estimated kernel density function; above the 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;

2.4 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 turbity. 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.

2.4.1 Resource availability and Darwin's cluster

Previous studies had already found positive relationships between richness of native species and IAS in Neotropical reservoirs (Bailly 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 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).

The 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, the 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.

The 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 the 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 subside 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 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).

2.4.2 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 urbans centers might be poor proxies of propagule and colonization pressures in this system (Drake et al., 2015)

2.4.3 Final considerations

The 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.

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SUPPLEMENTARY INFORMATION

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 study, we reclassified them into six (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.

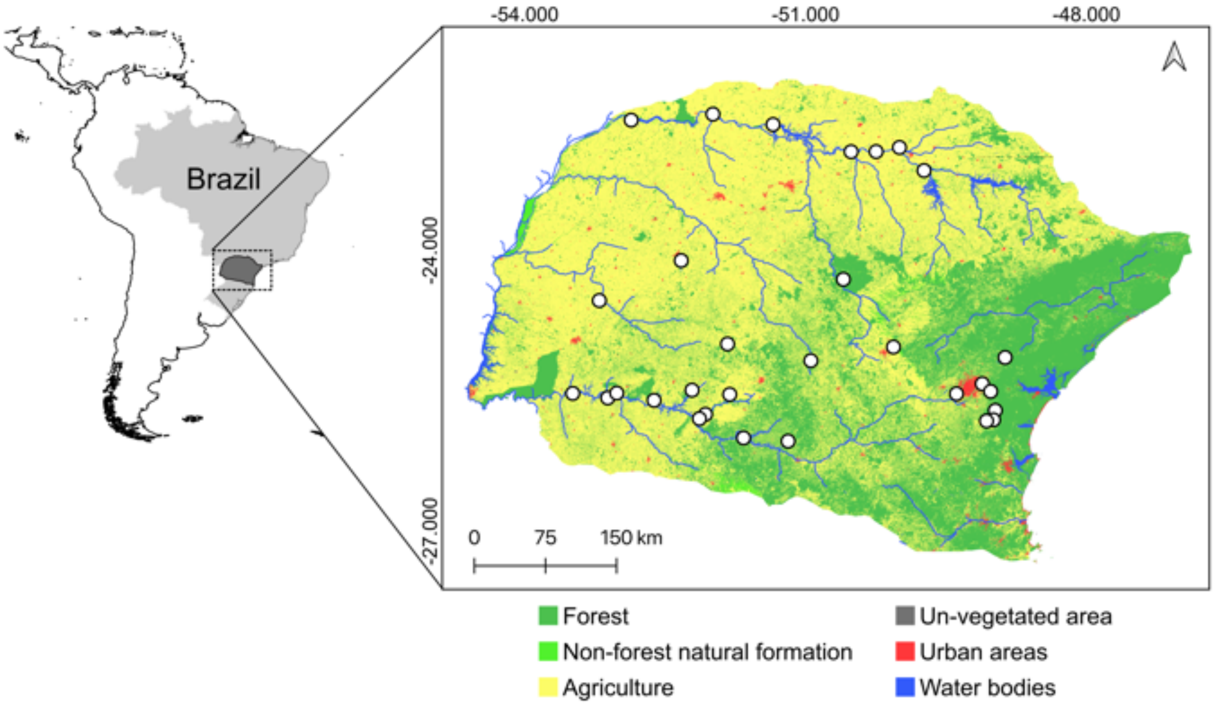

Figure S1 Location of the study area, study reservoirs (circles) and land use in the region (extracted from Mapbiomas, 2020).

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

Reservoir	Basin	Area (km²)	MAWT (°C)	Agri (%)	Alien Richness	July	Nov.
						Chlorophyll *a* (µg L^{-1})	
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

MapBiomas 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- biomas.org.

APPENDIX S2 - Selection of limnological variables

Exploratory analyses of limnological variables showed relatively low correlation among them. A broken stick model (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).

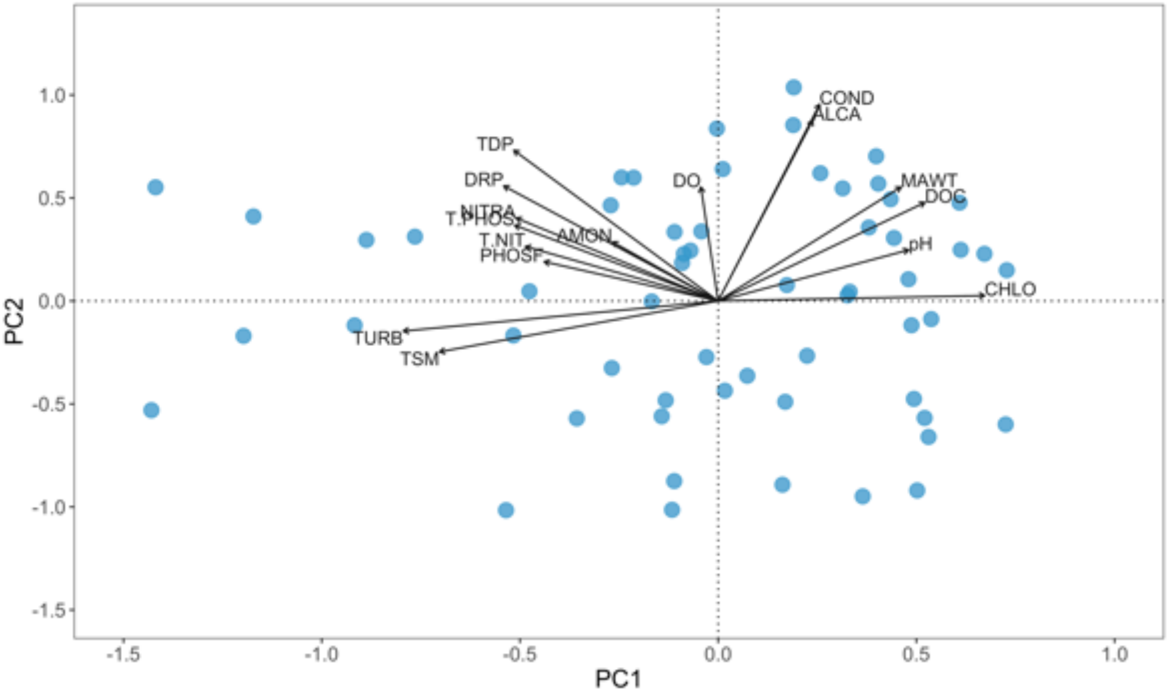

Figure S2- Principal component analysis of the limnological variables across the 29 study reservoirs. AMON = ammonia (µg L^{-1}); CHLO = chlorophyll α (µg L^{-1}); DO = dissolved oxygen (mg L^{-1}); COND = conductivity (µS cm^{-1}); ALCA = alkalinity (mEq L^{-1}); DOC = dissolved organic carbon (µg L^{-1});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

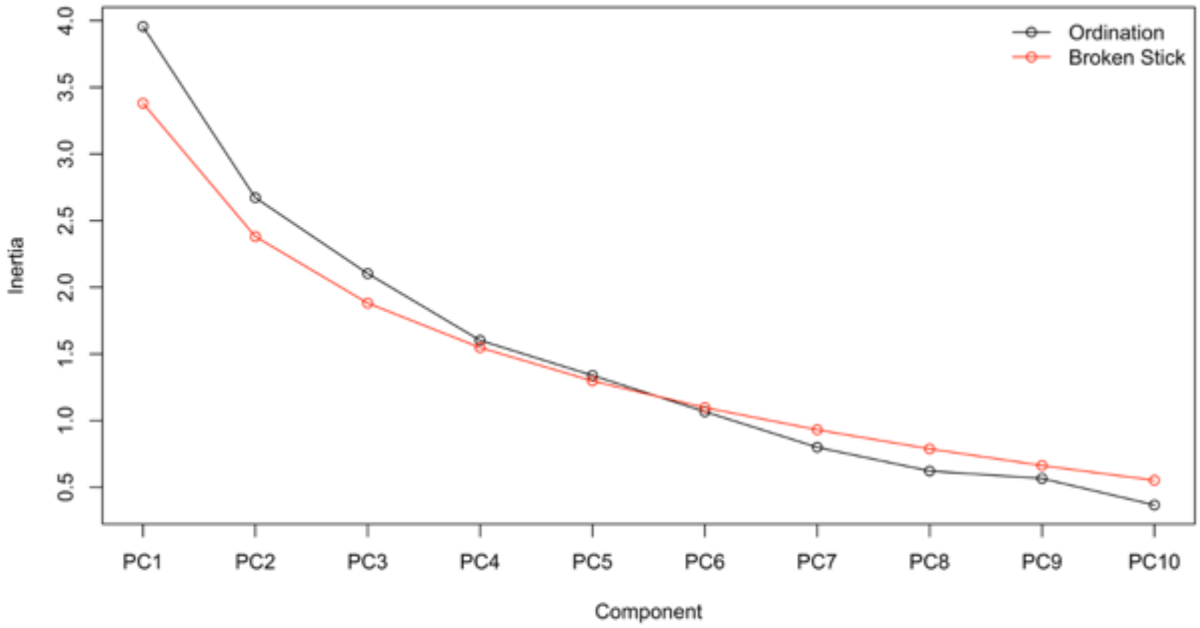

Figure S3 - Inertia values for the ordering axes and broken-stick model.

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 had low correlation (|*r*| < 0.7; Dormann et al., 2013) among them (Figure S4). .

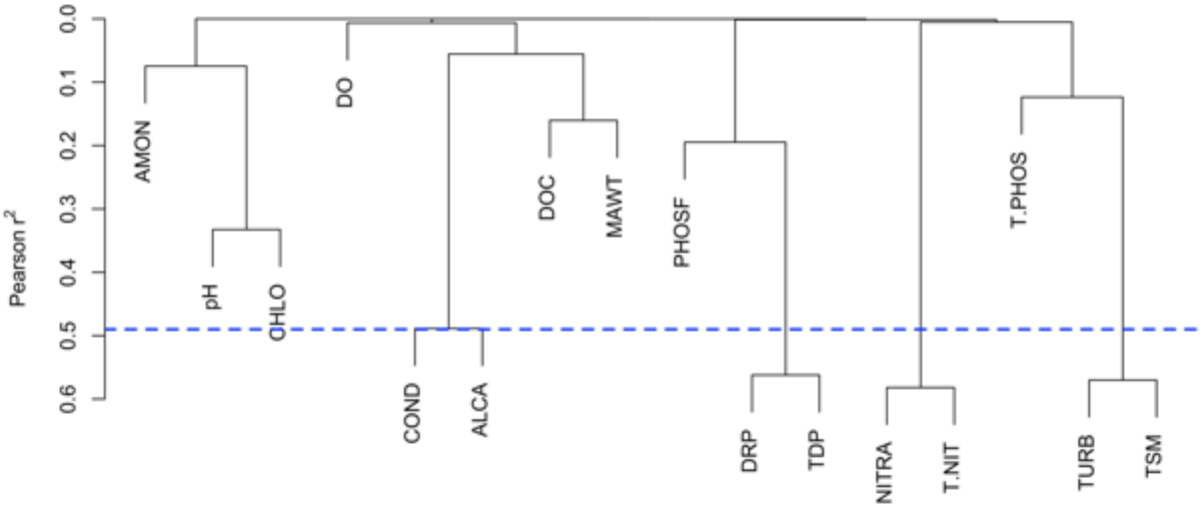

Figure S4 - Dendrogram built through a hierarchical cluster analysis using Pearson's correlation index. The blue line indicates the cut-off criterion for highly correlated variables. AMON = ammonia (µg L^{-1}); CHLO = chlorophyll α (µg L^{-1}); DO = dissolved oxygen (mg L^{-1}); COND = conductivity (µS cm^{-1}); ALCA = alkalinity (mEq L^{-1}); DOC = dissolved organic carbon (µg L^{-1}); MAWT = annual median of water temperature (ºC); PHOSF = phosphate (µg L^{-1}); DRP = orthophosphate (µg L^{-1}); TDP = total dissolved phosphorus (µg L^{-1}); NITRA = nitrate (µg L^{-1}); T. NIT = total nitrogen (µg L^{-1}); T. PHOS = total phosphorus (µg L^{-1}); TURB = turbidity (NTU); MST = measured total suspended material (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} overall**	***P***	**R^2_{adj} unique**	***P***
Biomass of alien species	Propagule pressure	-0.016	0.591	0.013	0.241
	Land-use	0.018	0.241	-0.074	**0.038**
	Limnology	0.241	**0.004**	0.094	0.072
	Native species	0.201	**0.007**	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	**0.014**	0.125	**0.045**
	Native species	0.160	**0.010**	0.115	**0.041**
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	**0.007**	0.009	0.360
	Native species	0.103	**0.038**	-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	**0.001**	0.362	**0.001**
	Alien species	0.150	**0.009**	-0.018	0.727
Richness of native species	Human population	0.017	**0.252**	-0.007	0.614
	Land-use	0.101	**0.025**	-0.008	0.690
	Limnology	0.700	**0.001**	0.508	**0.001**
	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	**0.005**	0.120	0.058
	Alien species	0.148	**0.015**	0.095	**0.051**

Bolding indicates significant *P* values;
P significance based on 9999 randomizations

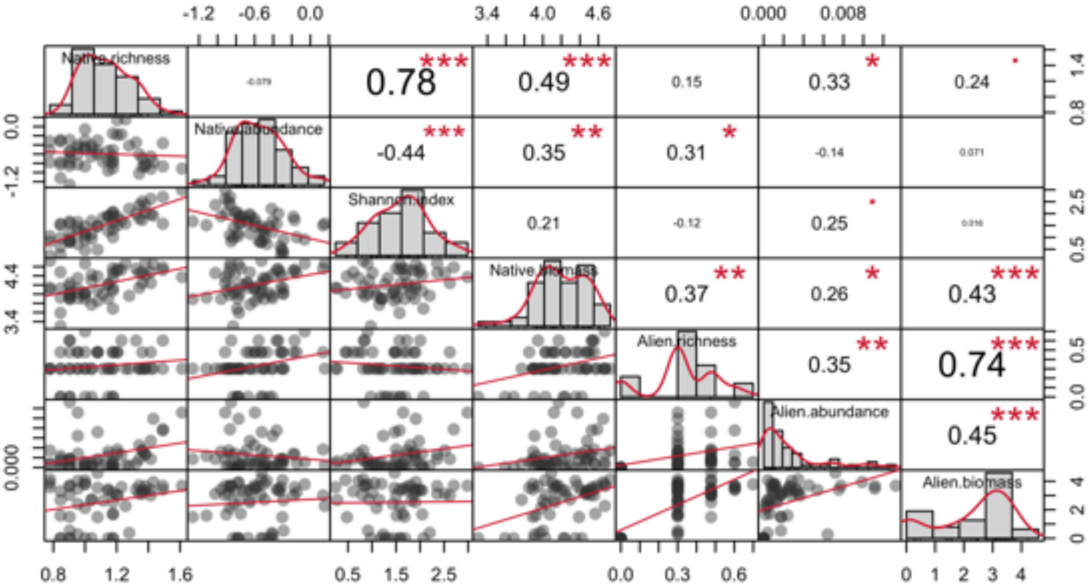

Figure S5- Pairwise relationships between the metrics (richness, abundance and biomass) of native (including Shannon index) and alien fish species. Below the diagonal, the bivariate scatterplots with the linear regression function are shown; the diagonal shows the histogram with an estimated kernel density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

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3 FUNCTIONAL INDICES AS PREDICTORS OF THE DOMINANCE OF INVASIVE ALIEN SPECIES IN NEOTROPICAL RESERVOIRS

ABSTRACT

Positive relationships between native and alien communities indicate the process of biotic acceptance into the environment. Therefore, environmental conditions, whether biotic or abiotic, which favor the increase in richness, abundance and biomass of native species, will also favor the alien community. The amount and diversity of resources in the environment shape biotic relationships according to the way the species uses the resource. Communities where species have more complementary niches, competition between them is less and the possibility of increasing populations is greater. Thus, it is expected that native communities that are less competitive, are less resistant to invasion, and enable an increase in the dominance of alien species. One way to assess the native community's niche complementarity/overlapping is through the assessment of functional indices, which measure the size and disposition of species abundance in a multivariate niche space. We hypothesized that higher level of niche complementarity of native community and lower competitive interactions increase the dominance of IAS in reservoirs. We studied 29 reservoirs in three sub-basins of the Paraná River basin and small neighboring littoral rivers of the Paraná state. We used beta regression to assess the influence of the functional diversity indices of the native community and functional similarity between the native community and IAS on the relative abundance and biomass of IAS. The results showed that reservoirs with higher FEve and FDis showed a higher relative abundance of IAS, but surprisingly FDiv presented an opposite relationship. Still, the degree of interaction between the native community and IAS, measured by the niche overlap between them, was not related to the dominance of IAS. On the other hand, when using the relative biomass of IAS, no predictor was found. Finally, we discuss how high levels of higher level of niche complementarity of native community benefit the increase in IAS dominance. In conclusion, the distribution of the niche in the functional space of native species proved to be a determinant factor for the dominance of IAS.

Keywords: biological invasion, functional diversity, functional indices, alien dominance, damming, freshwater.

3.1 Introduction

Currently, many hypotheses have been proposed to explain the biological invasion and the invasive alien species (IAS) success in the invaded environments (Enders et al., 2020). Some of them take into account the relationship between the invader and native community structure because they can be a strong indicator of processes driving biological invasion (Sax and Brow, 2000). In the case of negative relationships between invader and native communities, a process of biotic resistance is suggested, regulated by competition or predation of the native species (Seabloom et al., 2003). However, this pattern is usually found in experimental or small-scale studies (Byers and Noonburg, 2003). In these cases, the resistance is exerted by one or few native species, and when evaluated at the community level this effect is diluted (Byers and Noonburg, 2003). On the other hand, positive relationships suggest a biotic acceptance, in which the presence of greater richness of native species is usually an indication of good habitats for alien species (Poessel et al., 2013). This pattern is normally found in studies carried out on larger scales and it is closely related to the amount and variety of resources available in the environment (Sax and Brow, 2000; Stohlgren et al. 2006).

Thus, determining the relationship between native and invasive communities, taking into account environmental resources and niche overlap/complementarity is crucial for preventing and managing invasive species. This must be reinforced for freshwater ecosystems which has a high biodiversity and provides several ecosystem services but is very susceptible to biological fish invasions (Havel et al., 2005; Muniz et al., 2020a). One of the factors that make these environments prone to invasion is the construction of dams and associated reservoirs (Havel et al., 2005). Because these environments have their physico-chemical and hydrological properties altered, opening niche opportunities can appear for IAS (Johnson et al., 2008; Caiola et al., 2014). This is because native fishes can leave the region in search for more suitable sites or because some species do not present pre-adaptations to explore new resources provided by these modified environments (Agostinho et al., 2016; Gomes and Miranda, 2001). Therefore, in situations which available resource is diverse, abundant or underutilized by native species, introduced species are expected to have more success in the invasion process (MacArthur, 1970; Davis et al., 2000).

One way of evaluating the species' ability to use the resources of the environment is through the evaluation of the functional structure of the native community (Díaz and Cabido, 2001). Using functional structure information also helps to understand patterns in how this native community uses the available resources in an environment and associate it to contexts of biotic resistance or biotic acceptance. For instance, native communities with high functional richness (FRic) can represent few niches opportunities for IAS (i.e., high biotic resistance). At the same time, high FRic values may indicate high resource diversity in recipient reservoirs that can be also explored by IAS (i.e., biotic acceptance) (Manson et al., 2013). On its turn, other abundance-weighted indices like functional evenness (FEve), functional dispersion (FDis) and functional divergence (FDiv) may reflect niche overlap/complementarity between species. High FEve, for example, can represent great uniformity in how native species are using the resources, indicating low niche underutilization and stronger biotic resistance (Manson et al., 2005). Contrarily, in a biotic acceptance context, high FEve in native community may represent high quantity of distinct resources in reservoir.

For instance, high FDis values can represent low empty or underused niches by native community (Mouchet et al., 2010). However, in a biotic acceptance context, high FDis may represent great resource diversity that are being exploited by native species and that have the potential to be exploited by invasive species as well. Finally, high FDiv values represent high niche complementarity in native community that can be associated to stronger biotic resistance (Manson et al., 2013). In addition to these functional indices, the evaluation of niche overlap (i.e., functional similarity) between native and invasive communities can provide essential information on how biotic interactions drive invasion success (Zengeya et al., 2015; Jackson et al., 2016). This is because high functional similarity with native species may increase competition, preventing invader community success in environments (i.e., biotic resistance). Therefore, understanding the use of resources by native species and how they are functionally similar with invasive community, despite little explored, can provide important insights into the mechanisms that lead to the fish invasion success in reservoirs (Latombe et al., 2021).

In South America, the Paraná River basin is considered one of the regions most affected by damming (Agostinho et al., 2008; Ortega et al., 2015), and some patterns of biological invasion of fish have already been recorded (Bailly et al., 2016). In a recent work, structural taxonomic metrics (i.e., richness, abundance and biomass) of the native and invasive fish communities in reservoirs from Parana River Basin were evaluated (Muniz et al., 2021). These authors found a positive influence of these taxonomic metrics of native community on invasive community which was related to a biotic acceptance context in these reservoirs (see Muniz et al., 2021). Through the evaluation of the relationships of structural taxonomic metrics of the native and invasive community it is possible to observe the direction of the responses between them. However, it is not possible to draw, from these results, inferences on the degree of dominance of the invader species (i.e., the proportion of abundance and biomass). That is, how representative is the structure of the invader community, for the entire fish community. Changes in the dominance of invaders in recipient system is an essential metric to be evaluated in invasion ecology once it seems to be highly related to changes in resource availability. According to the theory of dynamic equilibrium model, disturbed environments with high productivity are more likely for an invasive species to become dominant (Huston, 1979, 2004). In addition, it may represent the success of invasion and degree of potential impacts in the invaded environment (Hejda et al., 2009).

As a reservoir ages, there is a change in the structure of the native fish community, due to changes in the availability of environmental resources (Miranda and Krogman, 2015). The reservoirs of the present study have different ages, and, therefore, different degrees of resource availability, and a biotic acceptance context has already been found in these highly connected reservoirs (on a large scale) (Muniz et al., 2021). Considering that the functional structure (i.e., functional diversity) of the native community can be a sourgate to the way in which the resource is used by native species, and thus to be related to contexts of resistance and biotic acceptance. Also considering that low functional similarity between native and invader communities represents weaker competitive interactions against the invasion process. We aimed, in the present study, to assess if the relationship with native species may predict the ecological mechanism driving invasion process in reservoirs, using a functional approach. We hypothesized that higher level of niche complementarity of native community and lower competitive interactions lead to increased dominance of

IAS in reservoirs. We expect that, under a biotic acceptance context, the dominance of IAS is related to higher functional diversity (i.e., FRic, FEve, FDis and FDiv) of native community and lower functional similarity among native and invader communities.

3.2 Material and methods

3.2.1 Study area

We studied 29 reservoirs in three sub-basins of the Paraná River basin and small neighboring littoral rivers of the Paraná state (Atlantic basin) (Fig. 1). Among the 29 study reservoirs, 25 belong to the Paraná River basin (Paranapanema, Ivaí, Piquiri and Iguaçu Rivers) and four to the Atlantic basin (coastal rivers).

The studied reservoirs also show different degrees of disturbance in their upstream basins (MapBiomas project, 2020). The Paranapanema River is located in one of the most impacted regions by damming in Brazil (Ortega et al., 2015). In the Iguaçu River, known to be a region of high endemism, the introduction of the invasive alien species has been marked and has caused great impacts, by direct competition with native species (Daga et al., 2016). Coastal rivers have lower degrees of human influence but also suffer from the introduction of IAS, mainly from aquaculture (Frota et al., 2019).

3.2.2 Fish species sampling

Fish communities were sampled in the lacustrine zone of the reservoirs (Sensu Thornton et al., 1990) at different depths (in the surface of the limnetic zone and near the bottom, 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 hours; fish were collected in the morning, afternoon and night. Samplings were 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 m^2 of gillnet during 24 h). Taxonomic identification followed Reis et al. (2003), except for the following families: Clariidae and Ictaluridae (Burges, 1989); Centrarchidae (Singler and Singler 1987); and Cyprinidae (Cavender and Coburn 1992).

3.2.3 Functional traits of fish community

There are a large number of biological traits that have been used to describe a species ecological niche. For freshwater fishes, traits related to life-history, habitat, morphology, trophic category and behavior are very useful for describing species distribution to environmental gradients (e.g., Santos et al., 2017; Muniz et al., 2020b). Data on traits were obtained from extensive literature review, and, in cases when there were no data for a given species, we used data from the nearest related species (e.g., the same genus). We selected the followed traits: i) trophic category (e.g., detritivores, herbivores, insectivores, invertivores, omnivores and piscivores); ii) occupied position in the water column (e.g., pelagic, benthic and demersal); iii) type of fertilization (e.g., internal and external); iv) parental care (e.g., absent and present); v) type of spawning (e.g., continuous, in several batches and total); vi) migratory behavior (e.g., absent and present); vii) standard length. Traits such as trophic category, position in the water column, type of fertilization and spawning were treated as categorical variables. While the traits presence of parental care and migratory behavior were treated as dichotomous. Standard length was considered a quantitative variable.

The choice of functional traits was based on the need required by each of them in the use of environmental resources (Winemiller et al., 2015). For example: trophic categories are related to the type of food resource present in the environment; position in the water column is related to the available of the resource space (i.e., habitat); the type of fertilization, spawning and parental care may be related to the presence of suitable substrate for species to complete their reproductive cycle (i.e., life history); migratory behavior is related to the size of the habitat and adequate environmental dynamics to complete life cycle (i.e., life-history and behavior); and size is related to the limitation of adequate space and the carrying capacity of the environment (i.e., morphology).

3.2.4 Functional indices

We consider functional diversity as the diversity in distribution and range of functional traits, in which the traits are species characteristics that influence ecosystem processes (Díaz and Cabido, 2001; Petchey and Gaston 2006). To characterize the native community in relation to its niche functional structure, we calculated functional indices (Functional richness (FRic), Functional evenness (FEve), Functional divergence (FDiv) and Functional dispersion (FDis) (Villéger et al., 2008) for each reservoir and sampling month. Fos this, we first calculated a trait distance matrix for all sampled native species using a modified version of the Gower distance that accommodates multiple types of traits (e.g., categorical, dichotomous, and quantitative; Pavoine et al., 2009). Using this distance matrix, we then computed the functional indices using functions availabe at http://villeger.sebastien.free.fr/Rscripts.html.As explained in introduction section, we chose these indices because they provide different information about distribution of available resources and interaction between species based on the assessment of niche complementarity: i) FRic represents the amount of functional space filled by the community; ii) FEve describes the evenness of abundance distribution in a functional trait space; iii) FDiv represents how abundance is spread along a functional trait axis, within the range occupied by the community; iv) The FDis represent the dispersion of species in the functional space and represents the mean distances of species to the community centroid, weighted by their abundance. In ecological term, functional richness tends to increase when niche complementarity between species that co-occur increases (Manson et al., 2012). Functional evenness describes the uniformity of species abundance in relation to the niche occupied by them (Manson et al., 2005). Functional divergence increases when niche complementarity increases the relative abundance of species (Manson et al., 2012). Functional dispersion, on the other hand, is associated with the degree of niche differentiation between species, and therefore the probability of competition between them (Mouchet et al., 2010). We used these four metrics because they were weakly correlated (Fig. S1), and they can offer different insights into the mechanisms that may explain the success of IAS in occupying a given environment.

3.2.5 Ecological distances among species

To establish the degree of niche overlap and the interaction between native and invasive species, we used metrics of functional similarity. For this, we applied the Gower distance in the data matrix of traits composition for all species pool (i.e., native and IAS).

Since we are working with all IAS sampled in each reservoir, it was necessary to adapt the metrics of i) distance to the nearest native species (DNNS; Thruiller et al., 2010) and ii) mean distance to the native species (MDNS; Thuiller et al., 2010). Therefore, we calculated the averages among all IAS. Thus, we obtained a mean value of DNNS and MDNS for each sampling unit (Fig. S2 and S3). The use of DNNS implies that we are assuming that native species with the trait combination closest to IAS is the one that offers the greatest biotic resistance. On the other hand, the use of MDNS implies that all native species have equivalent contributions to biotic resistance (Thuiller et al., 2010). Thus, using these adapted metrics, we expect that lower averages of DNNS and MDNS, represent stronger biotic resistance.

3.2.6 Data analysis

3.2.6.1 Model building

To test the relationship between the response variables (i.e., the relative abundance and biomass of IAS) and the predictors variables (i.e., FRic, FEve, FDiv, FDis, MDNS and DNNS), beta regression were used. Sampling month was also used as a covariate, to control the influence of seasonality in the data set. The model with the beta distribution is considered the most appropriate when values of the response variable vary from 0 to 1 (Simas et al., 2010). Initially, two models were built for each response variable (i.e., four models in total), as we were interested in evaluating the effect of two correlated variables that represent the interaction between IAS and native species (i.e., MDNS e DNNS). This division of models was necessary because these variables were highly correlated ($\rho = 0.65$,

$p < 0.05$; Fig. S1). The interaction between functional structure (i.e., functional indices) and the level of interaction between IAS and native species (i.e., MDNS and DNNS) was tested, but there were no significant values. Thus interactions were not included in the final models. Therefore, we selected the most parsimonious model (for each response variable) with the lowest value of the Akaike information criterion corrected for small sample size (AICc) and two associated measures: $\Delta AICc < 2$ and Akaike weight closest to 1 (Burnham and Anderson, 2002). Considering that DNNS and MDNS both represent the level of native-IAS functional similarity and are highly correlated, only results of the most parsimonious model (with lower AICc), for each response variable, were presented in results section. To assess the variance explained by the models, we observe the values of Pseudo-R2 (Lüdecke et al., 2020).

To reduce the collinearity of predictors variables in the beta regression (using betareg function from "betareg" package), which affects several statistical procedures, we removed predictors with Pearson correlations $|r| > 0.6$, as recommended by Dormann et al. (2013). Then, we calculated the variance inflation factors (VIF) for each model (Fox and Monette, 1992); all variables had $VIF < 2$ indicating no problem with collinearity in predictors variables in the model (Zur et al., 2009).

Since the sampling sites have spatial divisions, related to the hydrographic basins, and that closer points in space are more likely to have a more similar fish assemblage structure, it is necessary to evaluate the spatial autocorrelation. Thus, spatial autocorrelation of residuals for each model were examined using the Moran's Index estimated with the Moran I function from the package "ape" (Paradis et al., 2004)

The predictors effects were centered and standardized, which allowed to compare the magnitude of the regression coefficients and to make their effects biologically interpretable (Schielzeth, 2010). Standardized residuals were plotted against fitted values and the resulting plots were inspected for homoscedasticity.

3.3 Results

Study reservoirs present different scenarios of functional structuring of the native community and dominance of IAS (Table S1). In all samples, we registered 143 fish species and, among them, 17 species were identified as IAS (Table S2). The relative abundance of IAS ranged from 0.001 to 0.38 (Mean = 0.07 ± 0.08 SD), whereas the percentage of the biomass of the community composed of IAS ranged from 0.0001 to 0.8476 (Mean = 0.15 ± 0.16 SD). Reservoirs showed great variability in the values of the functional indices: FRic ranged from 0.0001 to 0.6931 (Mean = 0.20 ± 0.19 SD); FEve ranged from 0.1774 to 0.7089 (Mean = 0.46 ± 0.11 SD); FDiv ranged from 0.3044 to 0.9888 (Mean = 0.83 ± 0.13 SD); and FDis ranged from 0.0145 to 0.8562 (Mean = 0.48 ± 0.21 SD).

The best two models for each response variable (i.e., with the smallest AICc) were generated to explain the variation in IAS relative abundance and biomass (Table S3). The most parsimonious model explaining the variation in the IAS relative abundance was the one with the variable DNNS. But, for the variable IAS relative biomass, the most parsimonious model was the one with the variable MDNS. We did not find significant spatial autocorrelation in the residuals of the models with IAS relative abundance (Moran's I = 0.08; *P* = 0.25) and IAS relative biomass (Moran's I = -0.01; *P* = 0.95). The predictor variables that explained the variation in IAS relative abundance were FEve, FDiv, FDis and month of sampling (Table I). Among these predictors, FEve and FDis had positive parameters and FDiv had a negative parameter (Fig. 3). On the other hand, no variable examined had a significant influence on the relative biomass of IAS (see Table I).

Table I - Result of the two best GLMM for the response variables: the relative abundance and biomass of IAS. FRic = Functional richness; FEve = Functional evenness; FDiv = Functional Divergence; FDis = Funcional Dispersion; DNNS = mean distance of the nearest native species; MDNS = mean of mean distance to the native species; SE, standard error of the estimate represents the average distance that the observed values fall from the regression line; t-value, t-distributed for generalizes linear mixed models; P-value, probability of a random influence of factor; Conditional R^2, values associated with fixed effects plus random effects; Marginal R^2, values associated only with fixed effects.

Predictor variables	**Response variables**	**Estimate**	**SE**	**t-value**	**P-value**
(Intercept)	**Relative abundance of IAS**	-2.94	0.17	-17.15	**0.00**
FRic		-0.14	0.14	-1.00	0.32
FEve		0.28	0.10	2.70	**0.01**
FDiv		-0.33	0.13	-2.49	**0.01**
FDis		0.49	0.15	3.32	**0.00**
DNNS		0.21	0.11	1.90	0.06
Month		0.47	0.21	2.20	**0.03**
Pseudo-R^2 = 0.27					
(Intercept)	**Relative biomass of IAS**	-1.80	0.20	-9.04	**0.00**
FRic		-0.11	0.16	-0.68	0.49
FEve		0.03	0.13	0.21	0.83
FDiv		0.01	0.15	0.09	0.93
FDis		-0.13	0.18	-0.72	0.47
MDNS		-0.20	0.12	-1.60	0.11
Month		0.22	0.26	0.83	0.41
Pseudo-R^2 = 0.07					

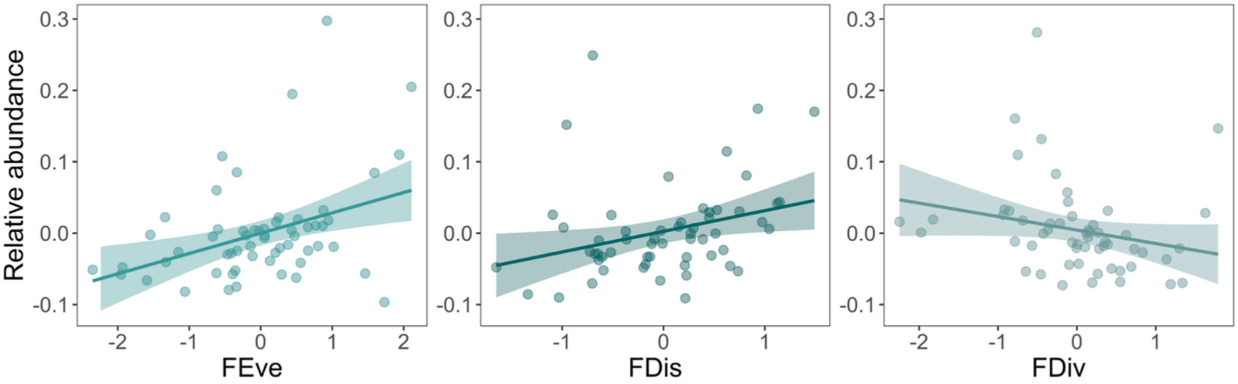

Figure 3 - Partial residual plots of the beta regression showing the influence of significant variables on the relative abundance of IAS. FEve = Functional evenness; FDiv = Functional divergence; FDis = Funcional dispersion;

3.4 Discussion

The hypothesis that higher level of niche complementarity of native community and lower competitive interactions favor the success of alien communities in reservoirs was partially corroborated. In fact, reservoirs with higher FEve and FDis showed higher relative abundance of IAS, but, surprisingly, FDiv presented an opposite tendency. Still, the degree of interaction between the native community and IAS, measured by the niche overlap between them (DNNS e MDNS), was not related to the dominance of IAS. On the other hand, these patterns were only evident when we assessed dominance using the relative abundance of IAS and when analyzing the relative biomass of IAS, no predictor was significant. The positive relationship between FEve and FDis and the relative abundance of IAS shows that when the niche uniformity of native species is greater and the probability of competition between them is smaller, the dominance by invasive fishes is greater. Conversely, the negative relationship between FDiv and the relative abundance of IAS shows that the lower niche complementarity of the most abundant native species, the greater dominance of IAS.

The results indicate that when resource use strategies by native species are more homogeneously distributed within the community and have greater variability (i.e., high values of FEve and FDis), there is a greater dominance by IAS in reservoir. High values of FEve and FDis indicate a more productive native community with a greater number of species in different environmental functions (Chanteloup and Bonis, 2013). Therefore, these findings corroborate with the invasion hypothesis of biotic acceptance in reservoirs. This means that reservoirs with more favorable environmental configuration for native fish species will also be preferable environments for IAS. This result goes in the opposite direction to that expected in natural environments, in which communities that present greater uniformity in the use of the resource by species are more resistant to invasion (Mulder et al., 2004). A possible explanation for this is that communities with a lower FEve have one or few dominant native species, and these greater abundances may be the result of a more efficient use of limited resources by them (Tilman, 1982), leading to a reduction in invasiveness. Thus, the results suggest that native fish community with higher FEve is less efficient in using available resources in reservoirs. This is probably explained by the lack of ecological pre-adaptations to these lentic environments (Olden et al., 2006; Agostinho et al., 2008). The lack of species with pre-adaptations to these environments reduces the functional space that could be occupied by native community. On the other hand, several IAS identified in the present study (e.g., *C. carpio*, *M. salmoides*, *O. niloticus* and *C. rendalli*) have greater niche amplitude and successfully invaded several environments worldwide (Lowe et al., 2000). Especially in reservoirs, most invasive species are generalist and have great advantages to complete their life cycle (Olden et al., 2006).

The positive influence of FDis and the lack of importance of FRic to changes in IAS dominance showed that the species abundance in the environment is more important than only their variety. These results also evidence that native communities which presented greater niche complementarity between species, showed greater IAS dominance. Native communities with high FDis have greater niche amplitudes and the competitive interactions among species are lower (Mouchet et al., 2010). Previous studies show that IAS have similar responses to native species in relation to environmental changes (Muniz et al., 2020). Thus, if the environmental configuration leads to low interactions among native fish species, it will also lead to a low interaction with IAS (e.g., less competitive interaction).

However, a greater niche amplitude of the native communities increases the probability that IAS will share resources with at least one resident species.

Both explanations seem contradictory, but we need to deeply understand them as they may not be mutually exclusive. The niche amplitude of the native community reflects the variety of resources available in the environment (Feizabadi et al., 2021; Mokany et al., 2008). Therefore, environments that have native communities with a greater niche range will also provide possibilities for a greater niche range for the alien community. Still, even in the presence of native species that are potential competitors, IAS are favored in human-changing environments taking advantage of the underutilization of resources by native species (David et al., 2017). In fact, previous studies have already shown that in situations of niche overlap (i.e., competition) between native species and IAS, native species lose out and have their populations reduced (Olden et al., 2006). Thus, the environmental configuration in which provides greater niche opportunities for fish species, along with the underutilization of resources by native species, creates an optimal scenario for IAS to become dominant (Olden et al., 2006).

The negative relationship between the relative abundance of IAS and FDiv shows that the dominance of invasive species tends to be greater when niche complementarity of native species is smaller. By assessing niche complementarity, we can make some relationships between diversity and ecosystem processes (Tilman et al., 2001; Petchey 2003), to better understand undergoing invasion processes. When the most abundant native species in the community are not complementary, there is a greater niche overlap among them, leading to a smaller amplitude of occupied niches. The opportunistic invasive species that exhibit generalist characteristics can take advantage of this situation: they can avoid competitive interactions by using other resources less required by the abundant native species. Thus, niche complementarity can be related to the resistance of a community to invasion: communities that present greater niche complementarity between species have a greater resistance to invasion once resources in the environment are being used more efficiently (Dukes, 2001; Petchey, 2003).

The lack of relationship between DNNS and MDNS and the relative abundance shows that functional similarity between communities is not a good predictor for IAS dominance. Regardless of the functional similarity, the native community does not exercise enough biotic resistance to reduce the dominance of IAS. Still, the lack of relationship between FRic and the relative abundance of IAS, reveals that the way in which species use the resource (i.e., distribution of niches among native species) is more important than the size of the niche. In addition, the lack of patterns found for biomass may be related to the variety of fish size (Standard length – SL) for the species of the invasive communities (lower IAS = 27.4 mm SL and higher IAS = 470 mm SL; Fig. S4). Since the invading communities had different compositions, we did not find any relationship with the relative biomass.

In this study, we tested the influence of native functional diversity on the process of biological invasion of fish in reservoirs, even though most studies test opposite relationships (i.e., biological invasion by modifying the functional structure of the native community; Shuai et al., 2018). However, several of these studies have been conducted with plants (i.e., sessile organisms, Maron and Marler, 2007; Wang et al., 2019), and these relationships may differ in more dynamic environments, where species have greater possibility of dispersion. In these dynamic environments, the invader plasticity can be as determinant as his competitive power in the invasion process, therefore these, relationships are not so clear. We opted for this approach because previous studies have evidenced the process of biotic acceptance in such environments, where the invading community showed positive relationships with the native community and similar responses to environmental variation (Muniz et al., 2021). However, we believe that more studies are needed to test these relationships. One suggestion to answer these questions is to test the conductive, passing and opportunistic conceptual models of the environmental variations proposed by MacDougall and Turkington (2005).

In conclusion, the distribution of the niche in the functional space of native species proved to be a determinant factor for the dominance of IAS: i) reservoirs that presented low dominance of native species in the occupation of niches, i.e., greater equitability in the use of resources, presented greater IAS dominance; ii) the greater the niche complementarity among the more abundant native species, the lesser is the dominance of native species over the use of the more available resources, and the greater the IAS dominance; and iii) the greater the interdependence between native species, the greater is the probability of IAS becoming dominant. The findings obtained offer evidence that patterns of IAS dominance in reservoirs are related to the unsaturated niche space of the native community, which is a result of the formation of the reservoir. Finally, the results provide insights into drivers that lead to an increase in the population of alien species in reservoirs. Therefore, this is valuable information for the development of better strategies for managing environments that have already been invaded.

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SUPPLEMENTARY INFORMATION

APPENDIX S1 – Study reservoir and functional structure of native community

Table S1 Characteristics of the 29 study reservoirs located in the State of Paraná, Brazil. IAS = Invasive alien species; Nat = Native species; FRic = Functional Richness; FDiv = Functional Divergence; FEve = Functional Evennes; FSpe = Functional Specialization.

Reservoirs	Sampling Month	IAS Rel. Abundance	DNNS Nat vs IAS	Nat FRic	Nat FDiv	Nat FEve	Nat FSpe
Alagados	July	0.037	0.385	0.002	0.362	0.258	0.376
	November	0.038	0.385	0.012	0.738	0.243	0.535
Canoas I	July	0.064	0.409	0.427	0.863	0.506	0.618
	November	0.120	0.409	0.603	0.751	0.572	0.563
Canoas II	July	0.044	0.409	0.394	0.879	0.628	0.627
	November	0.176	0.410	0.704	0.886	0.545	0.672
Capivara	July	0.042	0.439	0.435	0.865	0.487	0.587
	November	0.053	0.410	0.638	0.740	0.465	0.558
Capivari	July	0.198	0.442	0.028	0.973	0.453	0.582
	November	0.075	0.543	0.098	0.967	0.306	0.594
Cavernoso	July	0.062	0.422	0.196	0.878	0.442	0.638
	November	0.071	0.430	0.208	0.903	0.519	0.622
Chavantes	July	0.077	0.420	0.170	0.793	0.603	0.598
	November	0.060	0.417	0.380	0.885	0.555	0.613
Curucaca	July	0.014	0.435	0.056	0.664	0.525	0.631
	November	0.163	0.484	0.059	0.830	0.436	0.628
Foz do Areia	July	0.010	0.410	0.183	0.924	0.475	0.647
	November	0.022	0.523	0.174	0.964	0.510	0.647
Foz do Chopim	July	0.005	0.412	0.115	0.855	0.493	0.640
	November	0.037	0.430	0.313	0.943	0.447	0.633
Guaricana	July	0.019	0.568	0.013	0.932	0.498	0.589
	November	0.053	0.493	0.065	0.950	0.398	0.589
Harmonia	July	0.044	0.567	0.008	0.940	0.459	0.533
	November	0.023	0.626	0.031	0.733	0.616	0.526
Jordão	July	0.004	0.448	0.077	0.985	0.467	0.585
	November	0.003	0.410	0.111	0.965	0.414	0.597
Melissa	July	0.023	0.495	0.083	0.681	0.478	0.609
	November	0.043	0.496	0.377	0.892	0.432	0.615
Mourão	July	0.032	0.511	0.073	0.762	0.412	0.460
	November	0.011	0.399	0.055	0.850	0.339	0.589
Passauna	July	0.072	0.578	0.008	0.719	0.229	0.485
	November	0.256	0.415	0.070	0.908	0.565	0.487
Patos	July	0.063	0.501	0.024	0.985	0.431	0.631
	November	0.048	0.416	0.034	0.860	0.429	0.635
Piraquara	July	0.319	0.561	0.046	0.918	0.382	0.723
	November	0.276	0.643	0.037	0.919	0.653	0.764
Rosana	July	0.040	0.425	0.047	0.770	0.654	0.630
	November	0.120	0.425	0.032	0.915	0.800	0.614
Santmaria	July	0.020	0.580	0.583	0.908	0.584	0.647
	November	0.120	0.580	0.651	0.895	0.618	0.741
Salto Caxias	July	0.007	0.542	0.001	0.697	0.345	0.376
	November	0.001	0.429	0.001	0.752	0.311	0.422
Salto Grande	July	0.042	0.502	0.108	0.963	0.269	0.649
	November	0.084	0.411	0.171	0.936	0.414	0.643

Salto do Meio	July	0.027	0.415	0.132	0.894	0.547	0.595
	November	0.135	0.415	0.390	0.833	0.497	0.610
Salto Osório	July	0.020	0.500	0.161	0.967	0.541	0.657
	November	0.017	0.454	0.199	0.924	0.699	0.656
Salto Santiago	July	0.024	0.424	0.202	0.957	0.386	0.625
	November	0.034	0.471	0.330	0.969	0.398	0.632
Salto Segredo	July	0.029	0.448	0.154	0.893	0.494	0.618
	November	0.037	0.471	0.236	0.963	0.477	0.624
Salto do Vau	July	0.012	0.707	0.176	0.844	0.217	0.638
	November	0.165	0.707	0.208	0.855	0.408	0.620
Taquarucu	July	0.042	0.425	0.000	0.891	0.295	0.649
	November	0.039	0.382	0.006	0.799	0.561	0.600
Vossoroca	July	0.004	0.482	0.604	0.914	0.444	0.636
	November	0.385	0.487	0.667	0.956	0.485	0.633

APPENDIX S2 - Model construction details: correlation between variables used as model predictors

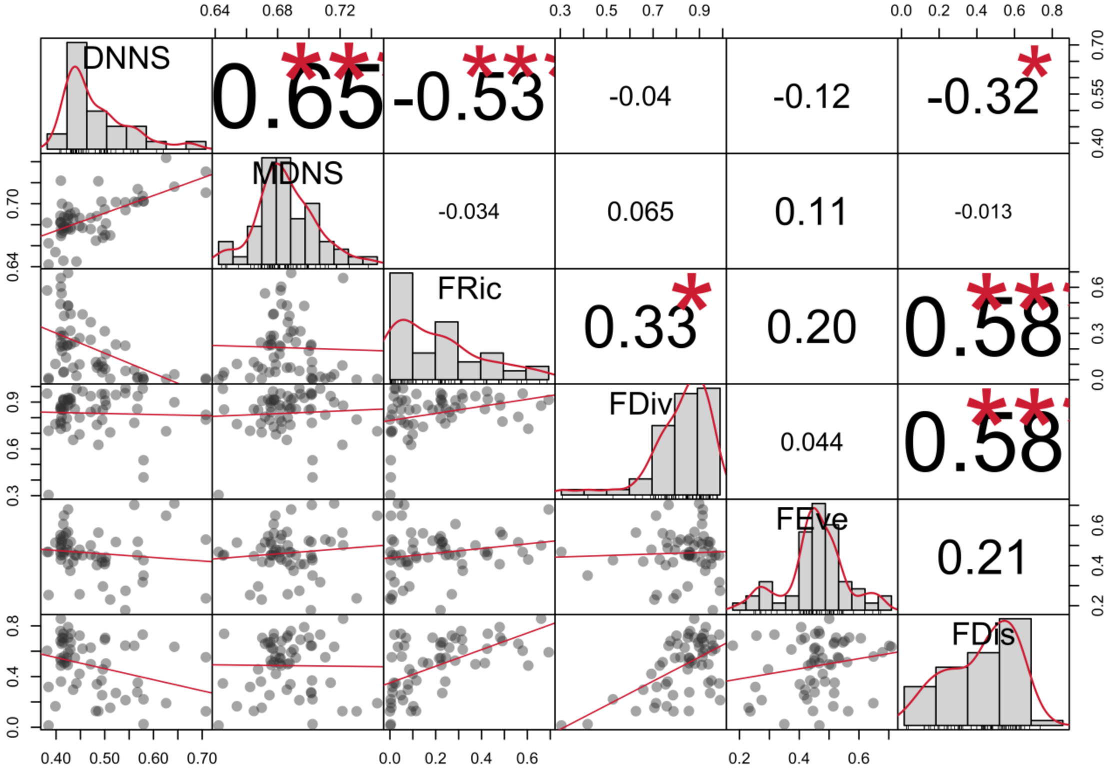

Figure S1- Pairwise relationships between the functional indices of native community. Below the diagonal, the bivariate scatterplots with the linear regression function are shown; the diagonal shows the histogram with an estimated kernel density function; above the diagonal, the Pearson correlation coefficients with significance levels (<P < 0.10; *P < 0.05; **P < 0.01; ***P < 0.001)

APPENDIX S3 - Details of the construction of adapted DNNS (distance of the nearest native species) and MDNS (mean distance to de native species) variables.

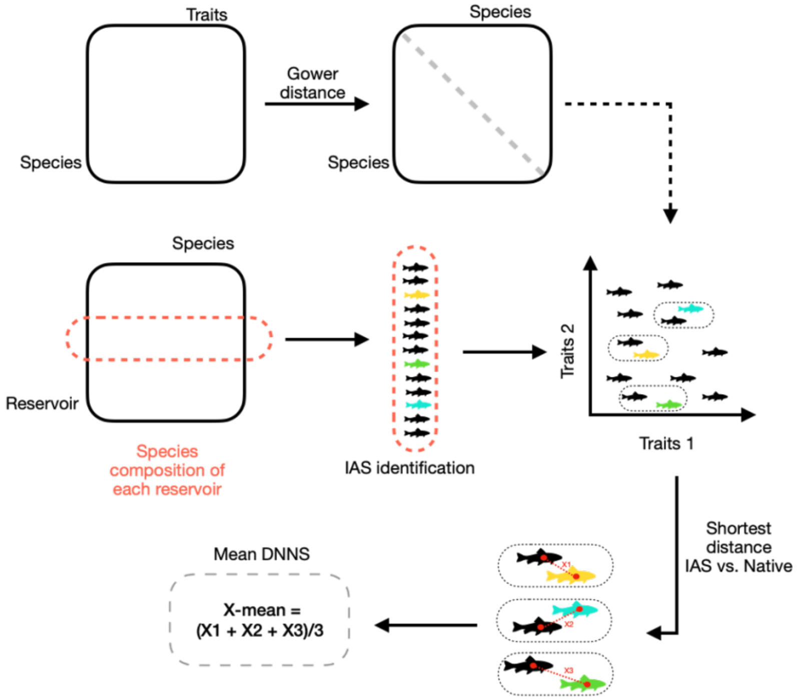

Figure S2 - Conceptual model of the construction of the metric adapted from DNNS. First, the trait distance matrix was calculated for the entire species pool, using the Gower distance. Subsequently, the species composition of each reservoir was used to calculate the mean DNNS. The DNNS calculation consists of defining the distance between each IAS and the nearest resident species. In the case of reservoirs with more than one IAS, the mean was calculated.

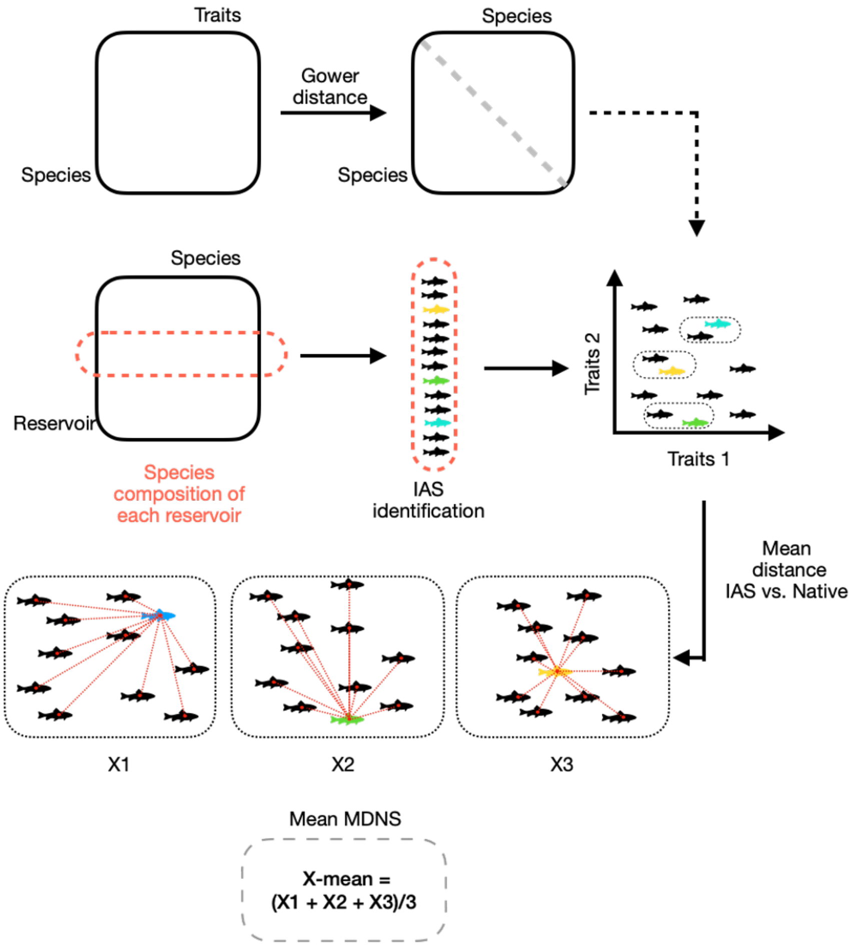

Figure S3 - Conceptual model of the construction of the metric adapted from MDNS. First, the trait distance matrix was calculated for the entire species pool, using the Gower distance. Subsequently, the species composition of each reservoir was used to calculate the mean MDNS. The MDNS calculation consists of defining the mean distance between each IAS and all resident species. In the case of reservoirs with more than one IAS, the mean was calculated.

APPENDIX S4 - List of species identified in the study samples

Table S2 - List of non-native species recorded in the 29 reservoirs in the four basins analyzed in Neotropical region during July and November 2001. Invasive alien species has two asterisk symbols after the name.

ORDER
Family
Species
CYPRINIFORMES
Cyprinidae
Ctenopharyngodon idella (Valenciennes, 1844) **
Cyprinus carpio Linnaeus, 1758 **
Hypophthalmichthys molitrix (Valenciennes, 1844)
Hypophthalmichthys nobilis (Richardson, 1845)
CHARACIFORMES
Characidae
Characidium travassosi Melo, Buckup & Oyakawa, 2016 **
Erythrinidae
Hoplias lacerdae Miranda Ribeiro, 1908 **
Hoplias aff. *malabaricus* (Bloch, 1794)
Parodontidae
Apareiodon affinis (Steindachner, 1879)
Apareiodon ibitiensis Amaral Campos, 1944
Apareiodon piracicabae (Eigenmann, 1907)
Apareiodon vittatus Garavello, 1977
Cynodontidae
Rhaphiodon vulpinus Spix & Agassiz, 1829
Serrasalmidade
Colossoma macropomum (Cuvier,1816) **
Metynnis lippincottianus Cope, 1870
Piaractus mesopotamicus (Holmberg, 1887)
Serrasalmus maculatus Kner, 1858
Serrasalmus marginatus Valenciennes, 1837
Anostomidae
Leporellus vittatus (Valenciennes, 1850)
Leporinus amblyrhynchus Garavello & Britski, 1987
Leporinus friderici (Bloch, 1794)
Leporinus lacustris Amaral Campos, 1945
Leporinus octofasciatus Steindachner, 1915
Leporinus sp. 1
Leporinus sp. 2
Megaleporinus macrocephalus (Garavello & Britski, 1988) **
Megaleporinus piavussu (Britski, Birindelli & Garavello, 2012)
Schizodon borellii (Boulenger, 1900)
Schizodon nasutus Kner, 1858
Curimatidae
Cyphocharax modestus (Fernández-Yépez, 1948)
Steindachnerina brevipinna (Eigenmann & Eigenmann, 1889)
Prochilodontidae
Prochilodus lineatus (Valenciennes, 1837)
Triportheidae
Triportheus nematurus (Kner, 1858)

Bryconidae
Salminus brasiliensis (Cuvier, 1816)
Acestrorhynchidae
Acestrorhynchus lacustris (Lütken, 1875)
Characidae
Aphyocharax anisitsi Eigenmann & Kennedy, 1903
Aphyocharax dentatus Eigenmann & Kennedy, 1903
Astyanax bifasciatus Garavello & Sampaio, 2010
Astyanax bockmanni Vari & Castro, 2007
Astyanax dissimilis Garavello & Sampaio, 2010
Astyanax aff. *fasciatus* (Cuvier, 1819)
Astyanax gymnodontus (Eigenmann, 1911)
Astyanax gymnogenys Eigenmann,1911
Astyanax lacustris (Lütken, 1875)
Astyanax laticeps (Cope 1894)
Astyanax minor Garavello & Sampaio, 2010
Astyanax aff. *paranae* Eigenmann, 1914
Astyanax serratus Garavello & Sampaio, 2010
Astyanax sp. 1
Astyanax sp. 2
Astyanax sp. 3
Astyanax sp. H
Astyanax sp. I
Astyanax sp. L
Astyanax sp. M
Astyanax sp. N
Bryconamericus aff. *iheringii* (Boulenger, 1887)
Bryconamericus ikaa Casciotta, Almirón & Azpelicueta, 2004
Bryconamericus pyahu Azpelicueta, Casciotta & Almirón, 2003
Bryconamericus sp.c
Bryconamericus sp.d
Deuterodon iguape Eigenmann, 1907
Deuterodon sp.
Galeocharax gulo (Cope, 1870)
Hyphessobrycon eques (Steindachner, 1882)
Mimagoniates microlepis (Steindachner, 1877)
Moenkhausia cf. *gracilima* Eigenmann, 1908
Moenkhausia aff. *intermedia* Eigenmann, 1908
Oligosarcus longirostris Menezes & Géry, 1983
Oligosarcus paranensis Menezes & Géry, 1983
Piabarchus stramineus (Eigenmann, 1908)
Roeboides descalvadensis Fowler, 1932
Serrapinnus heterodon (Eigenmann, 1915) **
GYMNOTIFORMES
Gymnotidae
Gymnotus cf. *carapo* Linnaeus, 1758
Gymnotus sylvius Albert & Fernandes-Matioli, 1999
Rhamphichthyidae
Rhamphichthys hahni (Meinken, 1937)
Sternopygidae
Eigenmannia sp.
Sternopygus macrurus (Bloch & Schneider, 1801)
Apteronotidae

Apteronotus ellisi (Alonso de Arámburu, 1957)
SILURIFORMES
Auchenipteridae
Ageneiosus militaris Valenciennes, 1836
Auchenipterus osteomystax (Miranda Ribeiro, 1918)
Glanidium ribeiroi Haseman, 1911
Tatia jaracatia Pavanelli & Bifi, 2009
Tatia neivai (Ihering, 1930)
Trachelyopterus galeatus (Linnaeus, 1766)
Doradidae
Pterodoras granulosus (Valenciennes, 1821)
Rhinodoras dorbignyi (Kner, 1855)
Heptapteridae
Pimelodella gracilis (Valenciennes, 1835)
Rhamdia branneri Haseman, 1911
Rhamdia aff. *quelen* (Quoy & Gaimard, 1824)
Rhamdia voulezi Haseman, 1911
Pimelodidae
Hypophthalmus oremaculatus Nani & Fuster, 1947
Iheringichthys labrosus (Lütken, 1874)
Pimelodus britskii Garavello & Shibatta, 2007
Pimelodus maculatus Lacepède, 1803
Pimelodus microstoma Steindachner, 1877
Pimelodus ornatus Kner, 1858
Pimelodus ortmanni Haseman, 1911
Pinirampus pirinampu (Spix & Agassiz, 1829)
Clariidae
Clarias gariepinus (Burchell, 1822) **
Callichthyidae
Callichthys callichthys (Linnaeus, 1758)
Corydoras ehrhardti Steindachner , 1910
Corydoras aff. *paleatus* (Jenyns, 1842)
Corydoras sp.
Hoplosternum littorale (Hancock, 1828)
Loricariidae
Hypostomus ancistroides (Ihering, 1911)
Hypostomus cf. *aspilogaster* (Cope 1894)
Hypostomus cf. *auroguttatus* Kner, 1854
Hypostomus commersoni Valenciennes, 1836
Hypostomus derbyi (Haseman, 1911)
Hypostomus hermanni (Ihering, 1905)
Hypostomus margaritifer (Regan, 1908)
Hypostomus myersi (Gosline, 1947)
Hypostomus nigromaculatus (Schubart, 1964)
Hypostomus regani (Ihering, 1905)
Hypostomus strigaticeps (Regan, 1908)
Hypostomus sp. 1
Hypostomus sp. 2
Loricariichthys platymetopon Isbrücker & Nijssen, 1979
Megalancistrus parananus (Peters, 1881)
Proloricaria prolixa (Isbrücker & Nijssen, 1978)
Proloricaria sp.
Rhinelepis aspera Spix & Agassiz, 1829

Rineloricaria kronei (Miranda Ribeiro, 1911)
Rineloricaria latirostris (Boulenger, 1900)
Rineloricaria maacki Ingenito, Ghazzi, Duboc & Abilhoa, 2008
Ictaluridae
Ictalurus punctatus (Rafinesque, 1818) **
ATHERINIFORMES
Atherinopsidae
Odontesthes bonariensis (Valenciennes, 1835) **
CICHLIFORMES
Cichlidae
Astronotus crassipinnis Heckel, 1840 **
Australoheros cf. *facetus* (Jenyns, 1842)
Australoheros kaaygua Casciotta, Almirón & Gómez, 2006
Cichla kelberi Kullander & Ferreira, 2006 **
Coptodon rendalli (Boulenger, 1897) **
Crenicichla britskii Kullander, 1982
Crenicichla jaguarensis Haseman, 1911
Crenicichla iguassuensis Haseman, 1911
Crenicichla sp. (Holmberg, 1891)
Crenicichla tesay Casciotta & Almirón, 2009
Geophagus aff. *brasiliensis* (Quoy & Gaimard, 1824) **
Geophagus iporangensis Haseman, 1911
Oreochromis niloticus (Linnaeus, 1758) **
Satanoperca sp.
CYPRINODONTIFORMES
Poeciliidae
Phalloceros harpagos Lucinda, 2008
PERCIFORMES
Sciaenidae
Plagioscion squamosissimus (Heckel, 1840) **
Centrarchidae
Micropterus salmoides (Lacepède, 1802) **

APPENDIX S5 - Model results details

Table S3 - Summary of model selection statistics applied to select the overlap and interaction predictor variable that allowed to fit the most parsimonious model explaining IAS community metrics. The most parsimonious model presented the lowest AICc value (in bold). For each response variable analyzed, we apply two types of models. Model1: add MDNS as a predictor variable; Model2: add DNNS as a predictor variable;

Models	Response variable	Overlap and Interaction IAS vs. native	AICc	Δ AICc	weight
Model1	IAS relative	MDNS	-190.00	3.02	0.18
Model2	abundance	**DNNS**	**-193.00**	**0.00**	**0.82**
Model1	%IAS	**MDNS**	**-86.80**	**0.00**	**0.76**
Model2	biomass	DNNS	-84.50	2.32	0.24

APPENDIX S6 – Results details

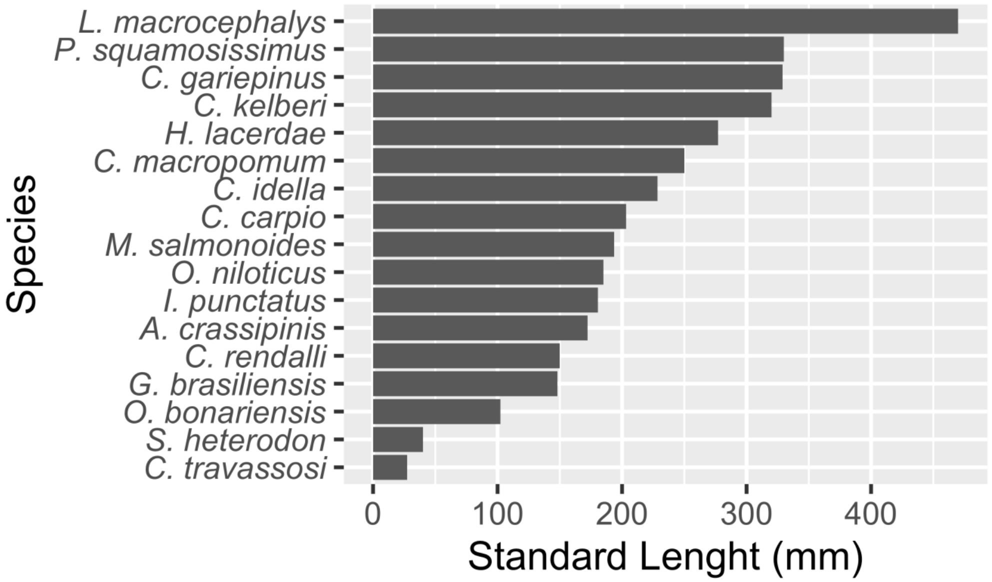

Figure S4 - Standard length recorded for alien invasive species (IASs) found in the studied reservoirs

4 CONCLUIDING REMARKS

In the first approach, the results showed that alien and native fish species from these neotropical reservoirs respond similarly to limnological variations, providing support for the hypothesis of increased resource availability and biotic acceptance. The abundance and richness of native and alien species tends to increase with reservoir productivity, which is mainly related to nutrient concentration and water temperature. In contrast, biotic resistance and propagule and colonization pressures appear to play a minor role in fish invasions in these systems, perhaps in part because of their downstream connectivity. Therefore, many other kinds of IAS can be envisioned to establish and preventing this can be the focus of management.

In the second approach, the results showed that the distribution of the niche in the functional space of native species (i.e., availability of resources) proved to be a determining factor for the dominance of the IAS: i) reservoirs that showed lower dominance of native species in the occupation of the niches, that is, more equitable use of resources, showed greater dominance of IAS; ii) the greater the niche complementarity between the more abundant native species, the smaller the dominance of native species over the use of the most available resources and the greater the dominance of IAS; and iii) the greater the interdependence between native species, the greater the probability of IAS becoming dominant. Thus, the results obtained provide evidence that the patterns of dominance of IASs in reservoirs are related to the unsaturated niche space of the native community, which is a result of reservoir formation that apparently increases as the reservoirs age.

Considering the ongoing biotic homogenization due to fish invasions and the considerable ecological impacts of the region, identifying the causes and processes of invasion is essential for management programs. Therefore, analyzing the importance of these hypotheses in tropical reservoirs can provide more conceptual and practical understanding to assist decision makers in environmental policy and better ecosystem management.