



Spatial and environmental factors predict the composition of non-native fish assemblages in Neotropical reservoirs

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Abstract Hydropower dams are one of the largest sources of anthropogenic impacts on freshwater systems in the world. In addition to the modifications in environmental dynamics (i.e., fish migration barrier, water flow reduction, depth increase, flood regulation), the novel environments are favorable to the dissemination of non-native species in the basin. The lack of native species adapted to the changed environment creates occupations opportunity (i.e., available resources) for non-native species, which end up finding in these environments ideal areas to complete their life cycle. Thus, the aim of the work was identify which reservoir characteristics provide as well benefits for non-native fish species. Specifically, we tested the hypothesis that the spatial structure, reservoir productivity and morphology, and chronological characteristics are factors related to the composition and abundance of non-native fish species in

reservoir. Using novel statistical techniques (Principal coordinates of neighbour matrices and Distance-based linear models), it was possible to identify the spatial patterns and to understand how the characteristics of the reservoirs influence the composition of the abundance of these species. Our results show that some reservoir characteristics provide benefits to non-native fish species, thus being localities within the hydrologic basins that can be considered as sources of non-native fish species propagules. In general, our results showed that larger and older reservoirs have a greater abundance of non-native fish species. Also, it was possible to identify spatial patterns, where in smaller scales neighboring reservoir tend to be more similar as to the composition and abundances of non-native fish species and this similarity can reach basin level.

Keywords Freshwater systems · Ichthyofauna · Impoundments · Lentic environments · Invasion process · Reservoir characteristics

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Introduction

Currently, there has been a great deal of discussion on the consequences of the introduction of non-native species in ecosystems (Vitule et al. 2009; Vilà et al. 2011; Gallardo et al. 2016). Impacts of introduced non-native species are context-dependent, ranging

from direct competition with native species to homogenization and extinction of the biota (Wilcove et al. 1998; Ceradini and Chalfoun 2017). There are studies describing shifts in food webs of the fish fauna and changes in the structure of the native community, leading to ecosystem shifts (Olowo and Chapman 1999; Attayde et al. 2007). The introduction and subsequent success in the establishment of non-native species depend on a host of factors such as: distance from water bodies to urban centers (i.e., greater the proximity greater the propagule pressure; Spear et al. 2013; Dostálek et al. 2014); resident native species richness (i.e., the biotic resistance/acceptance; Elton 1958; Fridley et al. 2007); and system productivity (i.e., dynamic equilibrium model; Huston 1979, 2004). Therefore, understanding the mechanisms that lead to success in the establishment of non-native species in environments is a challenge for modern ecologists and many hypotheses have been developed (Catford et al. 2009).

Some studies show that anthropogenic-modified environments are more susceptible to invasion because they have dramatically altered habitats and food web structure, causing extensive environmental changes (Havel et al. 2005; Ortega et al. 2018). Some modifications are so fast that they do not provide enough time for evolutionary responses of native species (Byers 2002). In this context, in freshwater ecosystems, reservoirs are recent anthropogenic-modified environments in the landscape and are in constant biological modification (i.e., biological succession; Agostinho et al. 1999, 2008, 2015). Among the environmental modifications caused by the construction of dams are the alteration in flow regime, sediment retention along the reservoir and remodeling of aquatic communities (Agostinho et al. 1999; Miranda and Krogman 2015). Most native fish species cannot remain in these regions due to lack of pre-adaptation to lentic environments or fail to maintain viable populations over time, due to new system dynamics, for example, long distance migratory species such as *Salminus brasiliensis* and *Pseudoplatystoma corruscans* (Agostinho et al. 2015). Thus, over time, richness and abundance of native species decrease (Bailly et al. 2016; Ortega et al. 2018), which may favor the appearance of “resource gaps” for non-native species (Elton 1958; Davis et al. 2000). In addition to the aging of the reservoirs, other variables such as reservoir area and productivity can influence

the invasion process, because they are related to the amount of resource available in the environment. Larger and more productive reservoirs tend to have greater non-native fish species richness because they have more environmental heterogeneity (e.g., different amount of habitat) and trophic resources availability, respectively (Huston 1979, 2004; Melbourne et al. 2007).

Once established, populations of non-native species represent a constant propagules source for upstream and downstream regions of reservoirs. Because dams are built in regions with high hydropower potential (i.e., to supply the energy demand, water supply and other purposes, these buildings are designed to capture as much water as possible), associated reservoirs have high connectivity with the river networks where they are located, facilitating dispersion of these species (i.e., the configuration of the space has great influence on the dispersion of non-native species; Havel et al. 2005). When reservoirs are in a cascade, this situation can be aggravated because non-native species find favorable regions for their establishment throughout the basin. Thus, the position of the reservoir in space (i.e., distance and/or insertion in the same basin), in relation to the reservoirs that already have established non-native species, influences the probability of the reservoir to suffer with propagule pressure of these species. Neighboring reservoirs that are inserted in the same basin are more likely to have the same composition (i.e., abundance and richness of species) of non-native species than those further away or that are inserted in different basins.

In this context, this paper aims to specify which reservoir characteristics provide benefits for invasive species. Specifically, we tested the hypothesis that the spatial structure, reservoir productivity morphology and chronological characteristics are factors related to the composition of non-native species in reservoir. We expect that the position of the reservoir in the basin (spatial structure) influence non-native species composition and abundance, due to fish dispersion and introduction by humans. Such influence may be restricted to smaller scales (i.e., neighboring reservoirs; close reservoirs with similar non-native species composition and abundance); or to reach larger scales (i.e., reservoirs inserted into the same basin, with similar non-native species composition and abundance). It is also expected that, the chronological age of reservoir has a positive influence in the abundance

of non-native species, once this variable provides insights of the time of propagule-pressure. The same is expected for the reservoir's morphology and productivity, as they are associated with the amount of resource available.

Materials and methods

Study area

We studied 29 reservoirs located in rivers of the Paraná State and neighbouring states (Fig. 1), south Brazil. Seven reservoirs are on the Paranapanema River; two on the Tibagi River, a tributary of the Paranapanema; two on the Ivaí River; two on the Piquiri River; thirteen on the Iguaçu River; and four in the Litorânea basin (Online Resource B). Therefore, out of the 29 studied reservoirs, 25 belonged to the Paraná River basin (Paranapanema, Tibagi, Ivaí, Piquiri and Iguaçu rivers), and four to the Atlantic

basin. However, the Iguaçu basin is separated from the Paraná by an insurmountable barrier for fish, the Iguaçu Falls.

Biological data

Fish assemblages were sampled in the lacustrine region of the reservoirs, in different depth (littoral, surface—pelagic and bottom—bathypelagic) using gill-nets of different mesh sizes (2.4–14.0 cm between opposing knots), exposed for 24 h, the fish were collected in the morning, afternoon and night. The collection were carried out in 2001 in the drought and rain period, which comprise the months of July and November, respectively. The data on numerical abundance of each species captured by sample were indexed by the catch per unit effort (CPUE; number of individuals in 1000 m² of gillnet during 24 h). Taxonomic identification was based on Reis et al. (2003), except for families Clariidae and Ictaluridae, for which we used Burges (1989), Centrarchidae (Singer

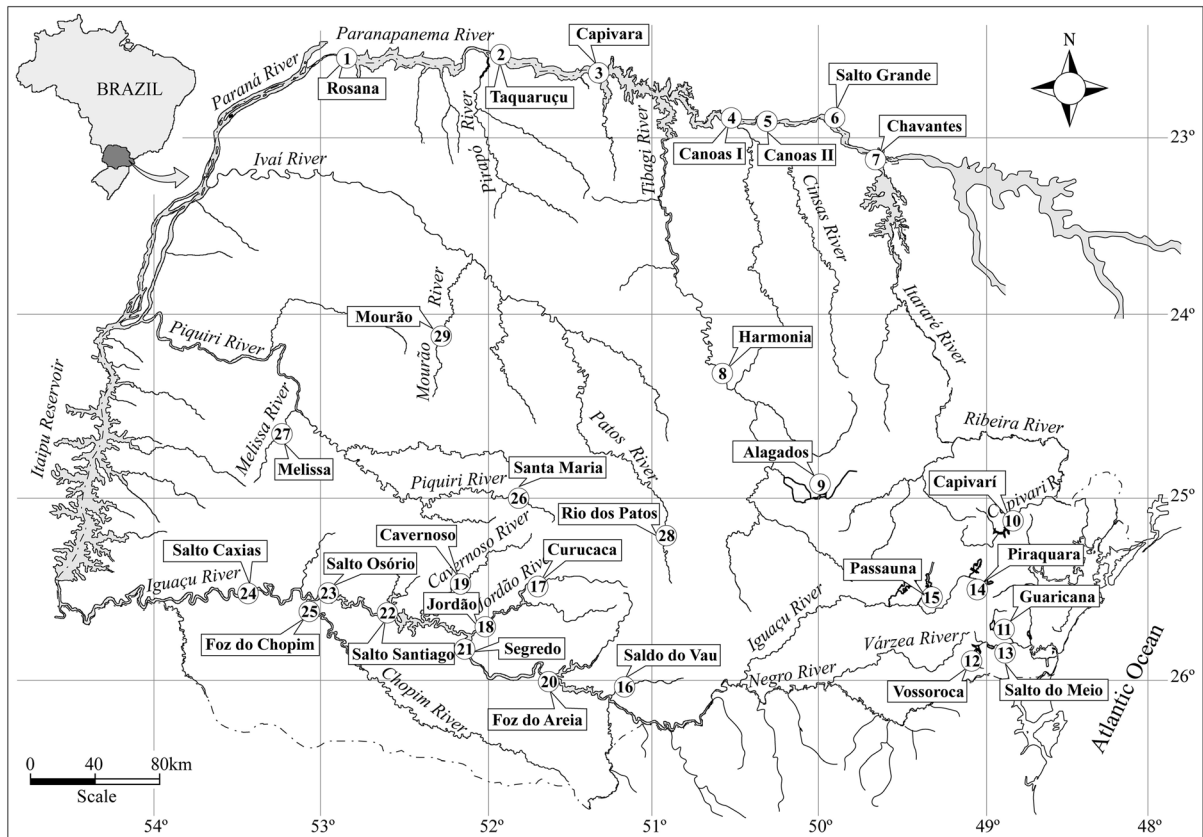


Fig. 1 Map of the Paraná State showing the locations of the study reservoirs

and Singler 1987) and Cyprinidae (Cavender and Coburn 1992).

Environmental data

The environmental variables measured along the fish samplings were used as proxy for productivity, such as: turbidity (NTU), total suspended material (mg/L; Teixeira et al. 1965), total phosphorus ($\mu\text{g/L}$; APHA 2005), orthophosphate ($\mu\text{g/L}$; APHA 2005), total nitrogen ($\mu\text{g/L}$; Mackereth et al. 1978), chlorophyll-*a* ($\mu\text{g/L}$; Nusch 1980), nitrate ($\mu\text{g/L}$; Mackereth et al. 1978), dissolved organic carbon ($\mu\text{g/L}$; Shimazdu TOC-5000A Total Organic Carbon (TOC) Analyzer), phosphate ($\mu\text{g/L}$; APHA 2005), total dissolved phosphorus ($\mu\text{g/L}$; APHA 2005), and biovolume of phytoplankton (mm^3/L). The morphological characteristics (area and depth) of the reservoirs were taken from Gubiani et al. (2011). The reservoirs' age was obtained by the difference between the year of sampling and the year of the formation of the reservoir. Although recognized as important, some variables such as retention time, discharge, variation in water level, were not used because they were not available for several reservoirs.

Spatial data

For the construction of the spatial data matrix we used the hydrological distance between the reservoirs. The hydrologic distance is calculated on a shapefile that represents the hydrographic network, using as starting and finishing points the geographical coordinates of each reservoir (i.e., latitude and longitude). The calculation of the distances is performed with the Dijkstra algorithm, which measures the smallest distances between two points (Dijkstra 1959; Loro et al 2015). We performed the calculation with the QNEAT3 complement (Qgis Network Analysis Toolbox; Raffler 2018), implemented in Qgis 3.0 (QGIS Development Team 2018).

We used PCNM (Principal Coordinates of Neighbour Matrices) to summarize the spatial structure. This method allows ecologists to model spatial structure at multiple spatial scales and to incorporate this representation in statistical analysis (Borcard et al. 2011). The spatial structure, derived from the hydrological distances among reservoirs were summarized in a resemblance matrix (Euclidean distance) and this

matrix was truncate to retain only the distances among close neighbours. Posteriorly, a PCoA (Principal Coordinates Analysis) of the truncated distance matrix was conducted to summarize the spatial structure in PCNMs (axes generated in the PCoA). The eigenvectors were then used as spatial explanatory variables in a model (Online Resource A). The scores of the first PCNM represent the greatest scale in the sample sites, while the last represents the smaller scale (i.e., the PCNM produces a spectral decomposition of space and can model spatial structure at all the spatial scale that can be perceived by the data set; Borcard et al. 2004). This procedure was performed in program R, using the `pcnm` function of the `vegan` package (Online Resource A).

Data analysis

In order to summarize the productivity proxy variables in a single variable, we performed a principal component analysis (PCA) of all the productivity proxies (variables) to use the scores of the first and second axes (the ones that explain most of the variation) as latent variables. We decided to use latent variables because it minimizes the problems caused by collinearity in models (Dormann et al. 2013). Thus, we summarized all productivity variables in two axes (the scores of the first two PCA axes).

Prior to analysis, we transformed the non-native fish assemblage data to express species abundance as square-root transformed proportionate abundances in each sampling site. This transformation reduces the weight of the most abundant species in the analysis. We also transformed the variable area by taking its natural logarithm. Due to the great number of environmental variables and possible correlations among them, we used the variation inflation factor (VIF) between each possible pair of variables to exclude one of those with $\text{VIF} > 10$ (Neter et al. 1996). When VIFs exceeding 10 there is a signal of serious multicollinearity, requiring correction.

In order to choose the most appropriate PCNM scores to include in the general model, twenty four PCNM (and their scores) were generated and summarized the spatial structure of our sampling sites (Resource Online D). After the generation of the scores of the axes, a matrix was created containing the twenty-four axes of PCNMs and the others

environmental variables as area, age, PCA1, PCA2 and sampling month.

To evaluate the influence of environmental and spatial variables on the variability of composition of all non-native fishes and to select the best explanatory model, we applied a DISTLM (Distance-Based Linear Model) using Akaike's information criterion (AIC) (Anderson et al. 2008). The forward selection was performed to select only the PCNMs and environmental variables that had significant influences on the structure of the composition of the non-native fish species (Blanchet et al. 2008). Distance-based redundancy analysis (dbRDA) was used to examine the influence of predictors on the spatial distribution of samples (Anderson et al. 2008). In all analysis, 9999 permutations were made. The variable sampling month (July and November) was included in the model as a dummy variable to quantify the temporal effects in the samplings. Finally, to evaluate which species were most related to the patterns observed in the model, a Spearman correlation was performed between species CPUEs (original composition of non-native fish data matrix) and the first two axes of dbRDA.

Results

We recorded 17 non-native species in the reservoirs of which *Oreochromis niloticus* and *Geophagus brasiliensis* were found in all the basins (Online Resource F). Of the all the basins only Atlantic and Piquiri basins did not present exclusive species. The exclusive species of Iguaçu basins were: *Characidium* sp., *Clarias gariepinus*, *Ctenopharyngodon idella*, *Leporinus macrocephalus*, *Odontesthes bonariensis*; in the Paranapanema basin were found three exclusive species: *Astronotus ocellatus*, *Odontostilbe* sp., *Plagioscion squamosissimus*; in the Tibagi and Ivai only one specie was found: *Colossoma macropomum* and *Hoplias lacerdae*, respectively.

The first PCA axis (eigenvalue = 1.52) was positively correlated with total phosphorus ($r = 0.75$) and total nitrogen ($r = 0.75$), and represented approximately 50.7% of the total variability, while the second PCA axis (eigenvalue = 0.91) was positively correlated with chlorophyll ($r = 0.93$), and represented approximately 30.4% of total variability (Online Resource C). Thus, when the PCA 1 and 2 scores

increased, the values of total phosphorus, total nitrogen and chlorophyll also increase (Fig. 2). Therefore, we consider that higher values of the scores in PCA1 and PCA2 indicate higher productivity.

The linear model selected by DISTLM included PCNM1, PCNM2, PCNM4, PCNM7, PCNM8, PCNM9, PCNM11, PCNM12, PCNM14, PCNM15, PCNM22, PCNM24, area, collection and age as determinants of non-native species composition and abundance in reservoir. Although all variables in the model presented significant relationships, the percentage of variation explained by each of them was different (Table 1). The variable that presented the highest correlation was PCNM1, followed by age, PCNM6, sampling month, PCNM2, PCNM12, PCNM8, PCNM22, Area, PCNM15, PCNM4, PCNM24, PCNM11, PCNM9, PCNM7 and PCNM14. The graphic representation of DISTLM results was represented by a dbRDA. The percentage of total variation in the first axes was 33.15% and the second axes was 11.63% of total variation.

The significant PCNM1, age, PCNM6, sampling month, PCNM2, PCNM12, PCNM8, PCNM22, Area, PCNM15, PCNM4, PCNM24, PCNM11, PCNM9, PCNM7 and PCNM14 effects are visible in the ordination biplot (Fig. 3). The first axis was positively correlated with area (reservoirs of the Paranapanema

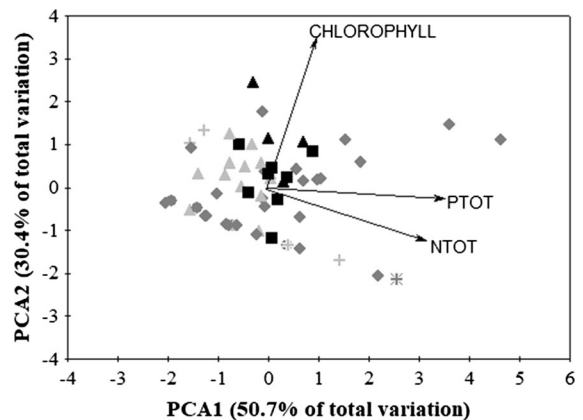


Fig. 2 Result of the principal component analysis with the proxy productivity variables (chlorophyll-*a*, total phosphorus and total nitrogen concentrations). Each point on the graph represents a reservoir at a given collection. Black triangles: Tibagi; light grey triangles: Paranapanema; black squares: Litorânea; dark grey quadrilaterals: Iguaçu; light gray crosses: Ivai; dark grey circles: Piquiri. The arrow represents the direction of the effect (positive correlation) of the summarized environmental variables on an axis

Table 1 Results of sequential tests of DISTLM (distance-based linear modelling) analysis with *P*-value of the permutation and percentage of variation explained for the selected model

Variable	AIC	SS (trace)	Pseudo-F	<i>P</i>	Prop.	Cumul.	Res.df
Area	161.54	2.432	19.519	0.001	0.028	0.028	59
PCNM1	154.59	1.946	15.618	0.001	0.176	0.204	58
Age	151.47	0.991	7.955	0.001	0.087	0.290	57
PCNM6	148.48	0.887	7.117	0.001	0.063	0.353	56
S.M.	146.76	0.615	4.933	0.002	0.043	0.396	55
PCNM24	146.02	0.429	3.446	0.005	0.025	0.421	54
PCNM12	145.19	0.423	3.396	0.007	0.032	0.453	53
PCNM7	144.45	0.391	3.140	0.008	0.021	0.474	52
PCNM2	143.27	0.432	3.468	0.008	0.034	0.508	51
PCNM8	142.17	0.399	3.199	0.012	0.029	0.537	50
PCNM22	141.04	0.383	3.078	0.007	0.029	0.566	49
PCNM15	139.99	0.355	2.849	0.018	0.028	0.594	48
PCNM4	138.67	0.365	2.932	0.025	0.026	0.620	47
PCNM11	137.20	0.362	2.902	0.021	0.025	0.645	46
PCNM9	135.99	0.317	2.543	0.039	0.022	0.667	45
PCNM14	135.03	0.276	2.218	0.033	0.020	0.687	44

$R^2 = 0.687$

AIC, Akaike information criterion; *SS* (trace), the total sum of square of sequential test (of deviations explained with this); *Pseudo-F*, the multivariate analogue of Fisher's ratio, estimates by how much the sum of square deviates from random; *P*, probability of random influence of a factor; *Prop.*, the proportion of variability which explained each factor (in the marginal tests without coaction of factors); *Cumul.*, running cumulative total (percent of the variability explained by the model); *Res.df*, number of degrees of freedom

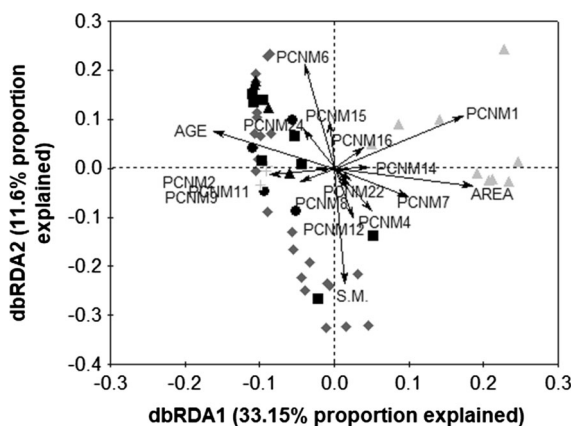


Fig. 3 Result of the distance-based redundancy analysis (dbRDA) with the predictor variables (age, area, sample month and PCNMs) showing the greatest importance for the linear model. Black triangles: Tibagi; light gray triangle: Parapanema; black squares: Litorânea; dark grey quadrilaterals: Iguaçu; light gray crosses: Ivaí; dark gray circle: Piquiri

River have larger areas), PCNM1 and PCNM7 and negatively correlated with age and PCNM2. The second axis was positively correlated with PCNM1,

PCNM6 and PCNM24 and negatively correlated with sampling month, PCNM12 and PCNM4 (Table 2). Some PCNM axes such as PCNM8, PCNM22, PCNM15, PCNM11, PCNM9 and PCNM14 despite having significant relationships in the DISTLM model, showed very low relationship values with the first two axes (> 0.2). The species that showed significant positive correlation with the first axis of the dbRDA was *P. squamosissimus*, while *C. carpio*, *G. brasiliensis* and *C. rendalli* presented significant negative correlations (Table 3). While *G. brasiliensis* and *C. rendalli* were positively correlated with second axis and *O. bonariensis* was negatively correlated with second axis (Table 3).

Discussion

Our results indicate that reservoirs are suitable environments for the establishment of non-native species, and some environmental variables are closely related for this process. Among the species found in the

Table 2 Relationships between the coordinates of the dbRDA (distance-based Redundancy Analysis) axes and the orthonormal X variables (multiple partial correlations)

Variable	dbRDA1	dbRDA2	dbRDA3	dbRDA4	dbRDA5
Area	0.603	− 0.078	− 0.565	0.082	0.061
PCNM1	0.572	0.359	0.256	0.059	0.212
Age	− 0.467	0.178	0.434	0.185	0.025
PCNM6	− 0.114	0.640	0.048	− 0.035	0.114
S.M.	0.065	− 0.471	0.179	0.201	0.281
PCNM24	− 0.099	0.240	− 0.055	0.450	− 0.344
PCNM12	0.064	− 0.212	0.196	− 0.209	− 0.337
PCNM7	0.339	− 0.112	0.155	0.221	− 0.223
PCNM2	− 0.260	− 0.027	0.128	− 0.308	0.161
PCNM8	0.032	− 0.087	− 0.441	0.408	0.292
PCNM22	0.046	− 0.092	0.545	− 0.045	0.238
PCNM15	− 0.019	0.175	0.418	0.142	− 0.018
PCNM4	0.113	− 0.201	0.082	0.266	− 0.256
PCNM11	− 0.021	− 0.004	0.219	0.328	0.043
PCNM9	− 0.168	− 0.030	0.029	− 0.152	0.146
PCNM14	0.149	− 0.001	− 0.024	− 0.149	− 0.471

S.M. Sampling month

Table 3 Values of Spearman correlation coefficients (ρ) between CPUE (catch per unit of effort; number of individuals per 1000 m² of gillnet in 24 h) of nonnative fish species and dbRDA (distance bases Redundancy Analysis) scores

Species	dbRDA1	dbRDA2
<i>Astronotus ocellatus</i>	0.132	0.101
<i>Characidium</i> sp.	− 0.101	0.041
<i>Cichla monoculus</i>	0.198	− 0.161
<i>Clarias gariepinus</i>	− 0.026	0.214
<i>Colossoma macropomum</i>	− 0.032	0.046
<i>Ctenopharyngodon idella</i>	− 0.132	0.162
<i>Cyprinus carpio</i>	− 0.264 ***	− 0.228
<i>Geophagus brasiliensis</i>	− 0.873 ***	0.531 *
<i>Hoplias lacerdae</i>	− 0.056	− 0.034
<i>Ictalurus punctatus</i>	− 0.101	0.049
<i>Leporinus macrocephalus</i>	0.094	− 0.214
<i>Micropterus salmoides</i>	− 0.002	− 0.117
<i>Odontesthes bonariensis</i>	− 0.010	− 0.407 *
<i>Odontostilbe</i> sp.	0.169	0.222
<i>Oreochromis niloticus</i>	0.067	− 0.035
<i>Plagioscion squamosissimus</i>	0.730 ***	0.153
<i>Coptodon rendalli</i>	− 0.445 *	0.588 ***

The values in bold are those that presented significant values (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$)

reservoirs are *Cyprinus carpio* and *Micropterus salmoides*, which fall within the eight most widely-introduced freshwater fishes in Europe (García-Berthou et al. 2005). Among the variables that influence the establishment of species in the reservoirs are the spatial arrangement in fine and broad scales, the area of the reservoir and age.

The space was the variable that together (i.e., broad and fine scale) had the greatest influence on the composition of non-native species in the reservoirs. This influence was detected in most of the study reservoirs (e.g., PCNM1, PCNM2 and PCNM7 were responsible for the separation of the reservoirs in the first axis and the PCNM1, PCNM6, PCNM4, PCNM12 and PCNM24 were responsible for the separation of the reservoirs in the second axis). In the first axis we can observe that the reservoirs of Paranapanema basin were separated from the others and their composition and abundance of the non-native species had a great influence on the broad scale. This result can be explained by the fact that the species *P. squamosissimus*, among the studied basins, is restricted to the Paranapanema basin and it was present and abundant in all reservoirs of this basin (Online Resource E). It was possible to observe an influence of fine and broad scales on our data, since the model selected the first and last axes of the PCNM. These results strengthen the idea that reservoirs act as step-stones for biological invasions (Havel et al.

2005). At fine scales (i.e., represented by PCNM6 PCNM12 and PCNM24), the reservoirs appear to act as a source of propagules for neighboring reservoirs, mainly for *C. rendalli*, *G. brasiliensis*, *C. carpio* and *O. bonariensis*. This propagule pressure can occur “naturally” in the direction downstream a reservoir through the active and passive dispersion of individuals, eggs and larvae, or in an “artificial” way through human introduction. The “artificial” pressure can occur in the reservoir-upstream direction as well. Since the population of the non-native species establishes in the reservoir, the probability of invasion in neighboring reservoirs increases. In contrast, at broad scale, the PCNM1 and 2 (i.e., the variables responsible for the greatest proportion of the variation in the composition of non-native species), separated the Paranapanema sub-basin from the others, while Paranapanema was in the positive side of dbRDA1, Iguaçu, Litorânea, Tibagi, Piquiri and Ivai were in the negative side. The selection of the variable PCNM1 and 2 by the model shows that the dispersion of the non-native species can reach the basin level, especially for *P. squamosissimus* from Paranapanema basin and *G. brasiliensis*, *C. rendalli*, *C. carpio* and *O. bonariensis* for the other basins, especially for Iguaçu and Litorânea basin where their abundance shows the highest values (Online Resource E). Still, this result captures the differences in history of non-native species introduction in the basins. The history of introduction is spatially dependent, and it related to the incentive of public policies (very common in Brazil; see Agostinho et al. 2007, 2010) for the introduction of non-native species along the country.

As expected, the area of the reservoirs presented positive relationships with the composition and abundance of non-native species, particularly the species *P. squamosissimus* had the greatest influence on the results. This relationship is also found for native fish species in these reservoir (Bailly et al. 2016; Ortega et al. 2018) and is related to the size and diversity of available habitats (Drakare et al. 2006). Therefore, larger reservoirs tend to support greater abundance of non-native species (Gido and Brown 1999). Since this relationship is found for both native and non-native species, it is an indication that either there is biotic acceptance in these environments or that interspecific relationships are so weak that the introduction of species in these environments does not interfere with the composition of pre-existing species. Nevertheless,

more work needs to be done to test these hypotheses in these environments.

Another variable that had an influence on the non-native species composition and abundance was reservoir age. There are some studies that reveal that aging is a good predictor of fish assemblages (Bailly et al. 2016; Santos et al. 2017; Ortega et al. 2018). However, age seems to affect composition of native and non-native species in different ways. While, the age had a negative influence on native species (i.e., over time there is a reduction in the richness of native species; Agostinho et al. 2015; Ortega et al. 2018), our results suggest that the same is not true for the main non-native fish species (e.g., *C. rendalli*, *C. carpio* and *G. brasiliensis*). Older reservoirs showed greater abundance of these species. These results may have two possible explanations: older reservoirs suffered more propagule pressure and/or the non-native species had a longer period to increase their populations.

Although our results identify spatial patterns in the composition of non-native fish species in reservoirs, the study presents some limitations. It is important to emphasize that the history of species introduction (i.e., the period between the introduction and collection of data can not be controlled) and the distance of reservoir to urban centers affects our results, because its influence is spatially dependent (e.g., in the 1970s there was great incentive to stocking *P. squamosissimus* in reservoirs of the Paranapanema river) and affects the composition of non-native species in the reservoirs. However, since we used abundance data in the analyses, it was possible to identify some trends regarding the success of establishment of these species. Secondly, the status of some of these species in the environment was not considered, for instance if indeed they can be considered invasive species (i.e., non-native species that spread beyond the introduction site and become abundant; Rejmánek et al. 2002). This requires long-term community monitoring (i.e., temporal analysis). However, some of these species are recognized as one of the most widely introduced aquatic species in the world, as for example: *C. carpio*, *C. idella* and *O. niloticus* (García-Berthou et al. 2007). Another limitation is that the trophic state of reservoirs is very dependent on the water retention time and can vary greatly over the year. Although our results agree with the literature, we believe that more specific studies are needed to test the hypothesis that invasive species became dominant in disturbed and productive

environments (Dynamic equilibrium model; Huston 1979, 2004).

Thus, our results show that some reservoir characteristics provide benefits to non-native species, thus being localities within the hydrologic basins that can be considered as sources of non-native species propagules. In general, our findings showed that larger and older reservoirs have a greater abundance of non-native species. Also, it was possible to identify spatial patterns, where in smaller scales neighboring reservoir tend to be more similar as to the composition and abundance of non-native species and this similarity can reach basin level. Since fish invasive species are characterized by great dispersal ability and tolerance to a wide range of environmental conditions (Moyle 1986; Sakai et al. 2001), reservoirs can act as passports to increase the amplitude of invaded area for these species. Therefore, it is worth emphasizing possible negative synergistic effects of the presence of reservoirs in the basin.

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