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INVASIVE SPECIES II

Abundance of invasive peacock bass increases with water residence time of reservoirs in southeastern Brazil

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Abstract Neotropical freshwater ecosystems are experiencing a great expansion in the number of invasive species, which is especially alarming since this region harbours 30% of the world's fish biodiversity with high levels of endemism. We aimed to evaluate the main predictors of peacock basses (*Cichla* spp.) abundance outside their native range, which are the Amazon and Tocantins-Araguaia river basins. We used multivariate ordination techniques and multimodel inference to analyse peacock basses abundance in twelve reservoirs of the Paraíba do Sul river basin, southeastern Brazil. Interestingly, reservoirs at higher (southernmost) latitudes, located in more populated areas, had higher water temperature and lower turbidity, due to increased water residence time, and these three variables were also positively correlated with abundance of this warm-water invasive fish. Habitat structure was less important in explaining peacock basses abundance, which was not significantly related to biotic factors (fish species richness and time since peacock basses introduction). We hypothesize that the observed effects of reservoir management on limnological features and peacock bass abundance, particularly water residence time (as a mediator of temperature and turbidity), may apply to other Neotropical basins and could influence the impact of this invader.

Keywords Cichlidae · *Cichla ocellaris* · Invasive species · Neotropical reservoir · Paraíba do Sul river basin · Reservoir limnology

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Introduction

Non-native invasive species are considered as one of the major threats to biodiversity conservation and ecosystem integrity, with ecological effects ranging from behavioural shifts to extinction of native species (Clavero & García-Berthou, 2005; Cucherousset & Olden, 2011). These deleterious effects of alien species generally co-occur with other anthropogenic disturbances, such as fragmentation of populations, habitat loss or degradation, hydrologic alteration, overexploitation, and climate change (Brook et al., 2008; Cucherousset & Olden, 2011; Liew et al., 2016). Traits of the introduced species (invasiveness) and also characteristics of the invaded ecosystem (invasibility) are related to a successful invasion process and shape the distribution of a non-native species, which can provide insights to predict its impacts (Quist et al., 2005). Comprehension of the regulatory factors of an invasive species distribution and abundance is an urgent need, due to the high ecological and economic costs that they cause (Bulleri et al., 2008).

In freshwater ecosystems, reservoirs are one of the ecosystems most prone to biological invasions (Byers, 2002; Liew et al., 2016). Reservoirs often act as stepping-stones for the dispersal of invasive species through riverscapes and non-native species are much more likely to occur in reservoirs than in natural lakes (Havel et al., 2005; Johnson et al., 2008). This conversion of lotic ecosystems into lentic habitats, which involve several alterations in hydrology, results in the extirpation of some species and creation of vacant niches that can be occupied by alien species more adapted to the new environmental conditions (Havel et al., 2005; Liew et al., 2016). These alterations are not instantaneous and generally impair the biota, with gradual species decreases and homogenization since construction until a community accommodation (sensu Agostinho et al., 1999) to the novel hydrological regime. The ageing of a reservoir influences downstream silt deposition and nutrient dynamics, which consequently shift the composition and biomass of planktonic and macrophytes communities; and can also induce the deterioration of habitats, especially in the littoral zone (Straškraba et al., 1993; Agostinho et al., 1999). These changes often result in impacts on fish faunas, causing alterations in species composition, such as declines of top predators, dominance of pelagic species and increases in the number of invasive species (Agostinho et al., 1999; Irz et al., 2002; Liew et al., 2016). Besides the age of a reservoir, which indirectly impacts fish fauna, another important determinant of reservoir functioning is water residence time, which is the average time that water remains within the boundaries of an aquatic system (Rueda et al., 2006). Water residence time is one of the key parameters controlling limnological properties of reservoirs, including thermal stratification, nutrient concentration, primary production, and ecological communities (Kennedy & Walker, 1990; Straškraba et al., 1993; Richardson & Bartsch, 1997; Rueda et al., 2006). The increase in residence time may have indirect effects on fish assemblage composition by creating conditions of high conductivity in reservoirs, increased thermal stratification, and low dissolved oxygen resulting in cyanobacterial blooms, and delays in organic matter decomposition, which ultimately impair water quality. Overall, the consequences of the increase in water residence time favour the dominance of lacustrine species (Straškraba et al., 1993).

Peacock basses or “tucunarés” (*Cichla* spp.) are piscivorous fish native to the Amazon and Tocantins-Araguaia river basins, which have been introduced throughout the lower latitudes of Americas, Africa and Asia (Shafland, 1996; Hickley et al., 2008; Yeo & Chia, 2010; Marques et al., 2016). These voracious, large-sized predators are prized game fish for food and sport fishing in both native and invaded areas (Winemiller, 2001). In their native range, peacock basses are mostly found in shallow littoral habitats of rivers and lakes, requiring high water transparency, warm temperatures, and access to lentic habitats for both feeding (diurnal visual predator) and reproductive purposes (territorial nest guarding) (Winemiller, 2001; Hoeinghaus et al., 2003). Invasive populations of peacock basses have been found to be positively correlated with reservoir area and water depth, transparency and temperature (Espínola et al., 2010), and noxious impacts over native fish fauna have been reported (Zaret & Paine, 1973; Latini & Petrere, 2004; Pelicice et al., 2015; Sharpe et al., 2017).

We sampled twelve reservoirs of the Paraíba do Sul river basin in Brazil where introduced *Cichla* spp. have been recorded (Fig. 1; Table S1), in order to analyse the variation in limnological features among them and the relationship of peacock basses relative abundance with these limnological features (e.g. temperature and transparency), habitat complexity, reservoir features (e.g. water residence time and reservoir age), introduction time and species richness. We hypothesized that the peacock basses abundance in reservoirs of the Paraíba do Sul river basin would increase with higher water temperature and transparency, more lentic conditions (measured as longer water residence time), and more complex habitats, in agreement with other studies descriptions (Winemiller, 2001; Espínola et al., 2010). We also considered as alternative hypotheses: (i) biotic resistance, which is the ability of resident species in a community to reduce the success of exotic invasions, for instance through competition or predation, and is often measured as species richness (Levine et al., 2004); and (ii) time since the introduction of peacock basses, since it can also be expected to influence the abundance of invasive species (Carol et al., 2009).

Materials and methods

Study site and fish sampling

The Paraíba do Sul river basin has a drainage area of 62,074 km^2 and provides water supply and hydroelectricity to around 14 million inhabitants of Rio de Janeiro, Minas Gerais and São Paulo states, southeastern Brazil (Fig. 1; Pinto, 2008; Cavalcanti & Marques, 2016; CEIVAP, 2017). Its climate is tropical humid, with a mean air temperature ranging from 18 to 24°C and precipitation ranging from 50 to 250 mm/month throughout the year (Marengo & Alves, 2005). In southeastern Brazil, the Paraíba do Sul river basin hosts several reservoirs for both water supply and hydroelectricity with surface areas ranging from 0.001 to 224 km^2 (Agostinho et al., 2007). Those systems, located in a gradient of altitude, are characterized by different ages, operational regimes, environmental conditions and time since the introduction of peacock basses. The Paraíba do Sul river basin,

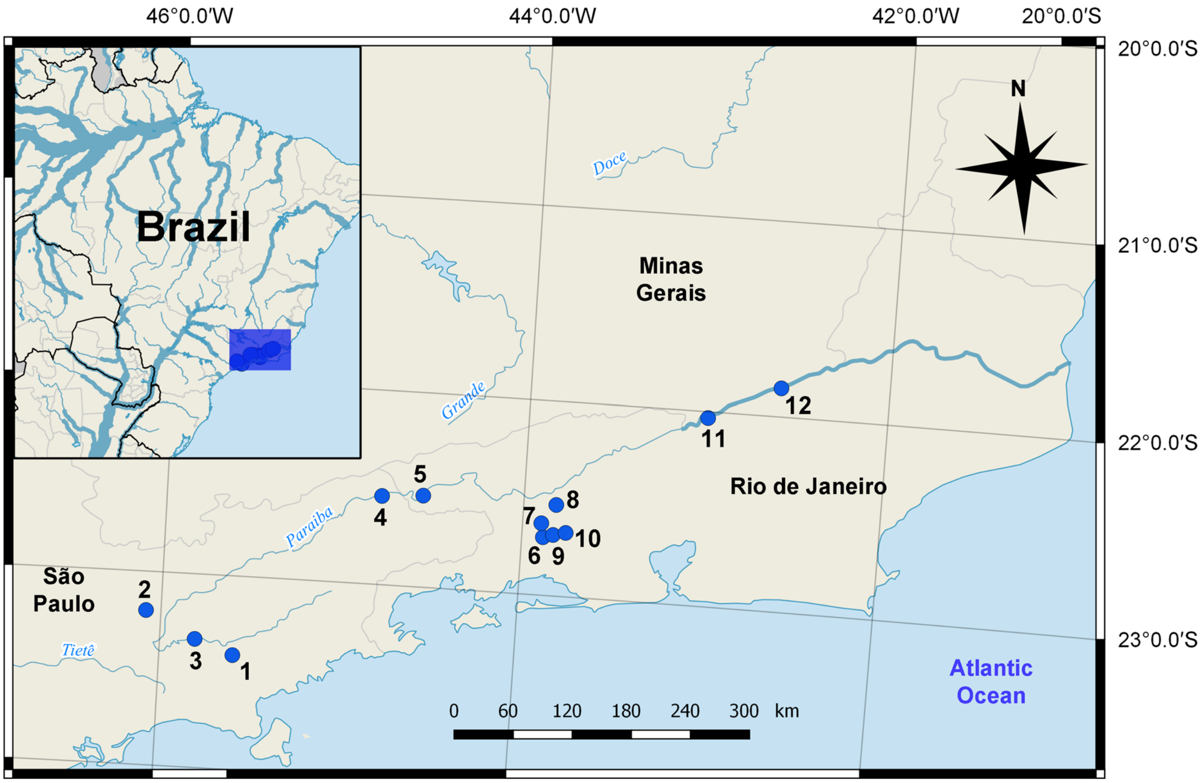

Fig. 1 Geographical location of the twelve studied reservoirs of the Paraíba do Sul river basin

together with the Doce, Jequitinhonha and a few other smaller river basins that drain southeastern Brazil towards the Atlantic Ocean, compose the East Atlantic hydroregion.

Fish samplings were carried out once in each reservoir between April and June of the years 2014 and 2016 through two complementary sampling methods. Angling was performed over two consecutive days (ca. 14 total hours of angling effort per reservoir, to have a constant sampling effort) and gillnets (60 m × 1.5 m; 15, 30 and 45 mm mesh size) were installed in the early afternoon and retrieved the next morning in three sites in the lentic zone of each reservoir. Numerical abundance was expressed as catch per unit of effort (CPUE) of gillnets (specimens/m^2 in 24 h) and by angling (individuals/h). All specimens were maintained on ice until arrival at the laboratory, where they were measured (standard and total length, mm) and weighed (to the nearest g).

We initially identified the peacock basses using the morphological criteria of Kullander & Ferreira (2006), which resulted in some individuals of blue peacock bass *Cichla piquiti* Kullander & Ferreira 2006 and mostly two species of yellow peacock basses, *Cichla kelberi* Kullander & Ferreira 2006 and *Cichla monoculus* Spix & Agassiz 1831. However, we collected some individuals with intermediate characteristics of both *C. kelberi* and *C. monoculus*, as in Santos et al. (2016a). Therefore, we followed Willis et al. (2012), who after genetic analyses suggested that all yellow peacock basses (i.e. *C. kelberi*, *C. monoculus*, *C. pleiozona*, *C. nigromaculata* and *C. ocellaris*) are, in fact, one species complex (*Cichla ocellaris* sensu lato). Moreover, since *C. piquiti* was found in only one of the twelve reservoirs (Santos et al., 2016b) and in low abundance, we analysed the relative abundance of all peacock basses together.

Limnological features were recorded on gillnet sampling sites using a multiparameter probe (temperature, pH, conductivity, turbidity, total dissolved solids (TDS), dissolved oxygen, and chlorophyll *a*), whereas water transparency was measured with a Secchi disk. On these sites, the structural complexity of littoral and submerged habitats was expressed as percent coverage of grass, shrubs, logs, leaves, macrophytes, gravel, sand, and mud. A boarded observer carried out this evaluation visually in a 100-m stretch of the shoreline. Reservoir features (altitude, age, surface area, and water residence time) were obtained from websites of hydroelectricity companies and technical reports. Year of the introduction of peacock basses in each reservoir was estimated through information obtained from local anglers and sparse scientific literature (e.g. Marques et al., 2016).

Statistical analysis

Preliminary analyses of the relationship between the two sampling methods (angling and gillnets) showed that, although significantly correlated ($r_s = 0.42$; $P = 0.011$; Fig. S1) and thus suggesting that they indeed reflect abundance, gillnets failed to record the peacock bass in 67% of samples, while angling had only 11% of absences. Furthermore, variation partitioning (VP) considering CPUE from both angling and gillnets had much more residual variance than when using information from angling alone. Therefore, we only used peacock basses angling data for further analyses.

All statistical analyses were performed with the R statistical software version 3.3.3 (R Core Team, 2016). We used principal component analysis (PCA) to understand the variation in limnological features (temperature, pH, and $\log_{10}$ transformations of conductivity, total dissolved solids (TDS), turbidity, oxygen, transparency and chlorophyll *a*; mean values per reservoir) among systems, using function “rda” in the “vegan” package (Oksanen et al., 2016). PCA is an ordination method suitable for quantitative variables, which preserves the Euclidean distance among sites based on eigenvectors (Borcard et al., 2011). We used the function “PCAsignificance” to estimate the number of significant axes based on the broken-stick criterion, as available in package “BiodiversityR” (Kindt, 2017). The broken-stick criterion provides an accurate estimation of the dimensionality of the data, retaining only components of the PCA with eigenvalues greater than those given by a null model (Jackson, 1993).

A redundancy analysis (RDA) was performed to test the relationship between limnological features and reservoirs characteristics (altitude, area, age, residence time, time since introduction; all of them $\log_{10}$ transformed), using function “rda”. In this analysis, we used reservoir characteristics as explanatory variables and limnological features as the response matrix. RDA is an ordination method similar to PCA but allows evaluations of simultaneous relationship between two multivariate data sets (Legendre & Legendre, 2012). A forward model selection was performed with vegan's function "ordiR2step" (200 permutations; Blanchet et al., 2008), in order to select for a parsimonious model with the highest adjusted R^2.

We used variation partitioning (VP), with function "varpart" of the "vegan" package, to quantify the relative importance of different sets of predictors in explaining relative abundance of *Cichla* spp. ($\log_{10}$–transformed angling CPUE). In the case of single response variables, VP uses partial regression analyses to measure how much of variation is explained by unique or joint effects of groups of predictors (Borcard et al., 1992; Legendre & Legendre, 2012). To reduce collinearity and improve the VP solution, as recommended by Borcard et al. (2011), we used a forward selection procedure, with the "forward.sel" function of package "packfor" (Dray et al., 2016), within three subsets of abiotic predictors: limnological features (temperature, pH, and $\log_{10}$ transformed [conductivity, TDS, turbidity, oxygen, transparency and chlorophyll *a*)], habitat complexity (grass, shrub, log, leaves, macrophytes, gravel, sand, and mud; percentage covered by each habitat arcsine square root transformed), and reservoir characteristics (altitude, area, age, and residence time; all of them $\log_{10}$ transformed). The forward selection procedure of the limnological features selected TDS and water transparency as significant variables that explained as much variance as the whole subset, whereas the procedure for habitat structure and reservoir features selected only macrophyte cover and water residence time, respectively. Since the "varpart" function only allows a maximum of four sets of predictors, we performed two separate VPs. The two VPs used the same three sets of abiotic predictors: limnological features (TDS and water transparency), macrophyte cover, and water residence time. As biotic predictors, one of the VPs used species richness (number of fish species, as a measure of biotic resistance) and the other used years since introduction of *Cichla* spp. ($\log_{10}$ transformed) at the time of sampling (to test for the importance of introduction age for peacock basses abundance). In this analysis, three replicates (gillnet sampling sites) for each reservoir were used to compare the importance of habitat features with the other predictors; for all other analyses in this paper we used the average values per reservoir. Significance of the testable fractions (i.e. unique and overall, but not shared effects) was determined using permutation tests (10,000 permutations), using function "anova.rda" in "vegan".

Multiple regression models of peacock bass CPUE (response variable) and reservoir characteristics (age, area, and residence time), temperature, turbidity, and introduction time as explanatory variables, were used to identify which specific characteristics were the best predictors of the abundance of the peacock basses, using a multimodel inference approach (Burnham & Anderson, 2002) and the "MuMIn" package (Bartón, 2016) in R. All variables (including the response), except temperature, were $\log_{10}$ transformed. We tested model assumptions using residual plots and the "gvlma" package (Peña & Slate, 2006) and all assumptions were met. In multimodel inference, the models are ranked according to Akaike information criteria for small sample size ($\mathrm{AIC_c}$), delta $\mathrm{AIC_c}$ (Δ_i) and Akaike weights (w_i) (Burnham & Anderson, 2002). $\mathrm{AIC_c}$ considers not only the goodness-of-fit of a model, but also its complexity (number of parameters), and the models with the lowest $\mathrm{AIC_c}$ values are the most likely. We used the delta $\mathrm{AIC_c}$ (Δ_i) to select the most likely models, which were those with differences lesser than 7 among the AIC value of the given model *i* and the model with the lowest AIC ($\Delta_i < 7$). The Akaike weights (w_i) can be interpreted as probability that a certain model is the best among the set of models.

Results

Limnological features

The reservoirs of the Paraíba do Sul river basin ranged from oligo- to eutrophic, with observed chlorophyll *a* concentrations from 2.0 to 12.5 $\mu g\ l^{-1}$, high temperatures and low conductivities (Table S2 in Supplementary Material). Several limnological variables were intercorrelated (Fig. S4). The first two axes of principal component analysis (eigenvalues = 4.33 and 1.70) jointly explained 75.4% of the variance of the limnological features and were significant according to broken-stick criteria. The first axis separated systems with low conductivity and turbidity and higher pH and temperature, mostly located upstream (Paraibuna, Igaratá, Santa Branca, and Lajes) from reservoirs with opposite characteristics, mostly downstream (e.g. Anta; Fig. 2). The second axis expressed an effect of trophic status, splitting eutrophic systems (i.e. Santana and Queluz; Table S1), from oligo-mesotrophic systems (e.g. Paracambi, Pereira Passos, Ilha dos Pombos and Vigário).

A forward selection model applied to the redundancy analysis (RDA) of limnological variables with reservoir characteristics (altitude, reservoir area, age, water residence time and introduction time) (Fig. S3) identified water residence time as the best predictor (Fig. 3; adjusted $R^2 = 0.63$; $P = 0.004$). The first RDA axis (66.7%; eigenvalue = 2.8) distinguished reservoirs with long water residence time (> 150 days, Table S1), such as Paraibuna, Igaratá and Lajes, which are large southern reservoirs at upstream reaches, from those with very short residence times (< 2 days), which are small reservoirs at low elevations (e.g. Pereira Passos, Paracambi and Ilha dos Pombos). Water temperature was the limnological feature more influenced by water residence time, indicating that more lentic systems had warmer waters, but conductivity, TDS, and turbidity decreased significantly with residence time as well (Fig. S3). The second unconstrained RDA axis mostly distinguished Queluz reservoir, which despite having a very short residence time had relative warm waters.

Cichla abundance

The first variation partitioning (VP) of *Cichla* abundance showed that limnological features (TDS and transparency, selected by the forward procedure as significant and the best predictors) and water residence time had significant overall effects ($P < 0.05$; Fig. 4A) and also explained the greatest amounts of variation (36 and 21%, respectively). The unique effects were all small and much of the variation was jointly due to limnological, habitat, and reservoir features. Macrophyte cover had overall significant effects (20%; $P = 0.003$), in contrast to species richness. The VP replacing species richness with time since introduction of *Cichla* yielded similar results, with limnological characteristics, water residence time, and macrophyte cover also explaining, jointly but not uniquely, most variation in *Cichla* abundance (Fig. 4B). Time since introduction had no significant unique effects on *Cichla* abundance and both variables were not significantly correlated (Fig. S2).

Multimodel inference suggested many linear models to explain abundance of peacock basses as equally plausible but that most of the models had turbidity and water temperature as predictors (Table 1). Turbidity was negatively related to abundance of peacock basses in nine of the thirteen models, whereas temperature was positively related in five of them. The most likely

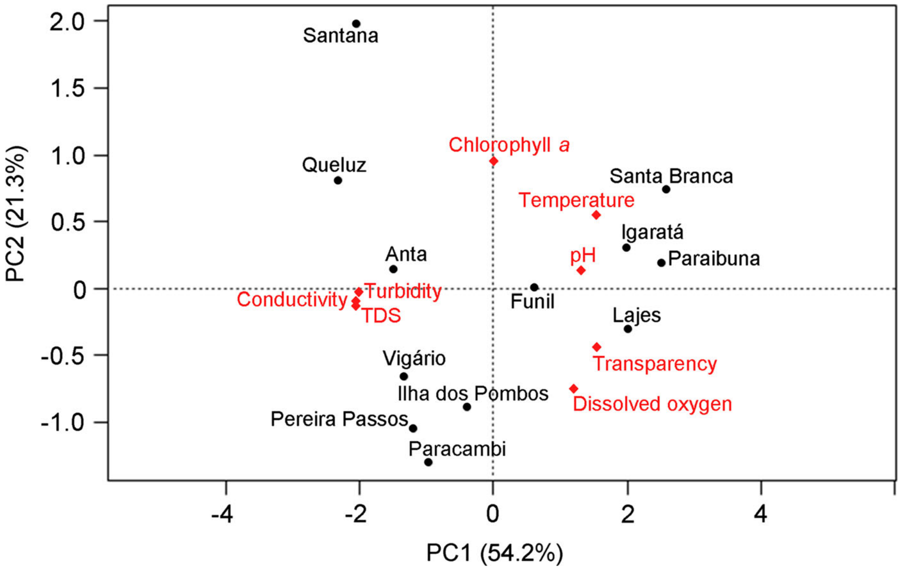

Fig. 2 Ordination of the twelve reservoirs from Paraíba do Sul river basin according to a principal component analysis (PCA) of the limnological features. All variables, except temperature and pH, were $\log_{10}$-transformed

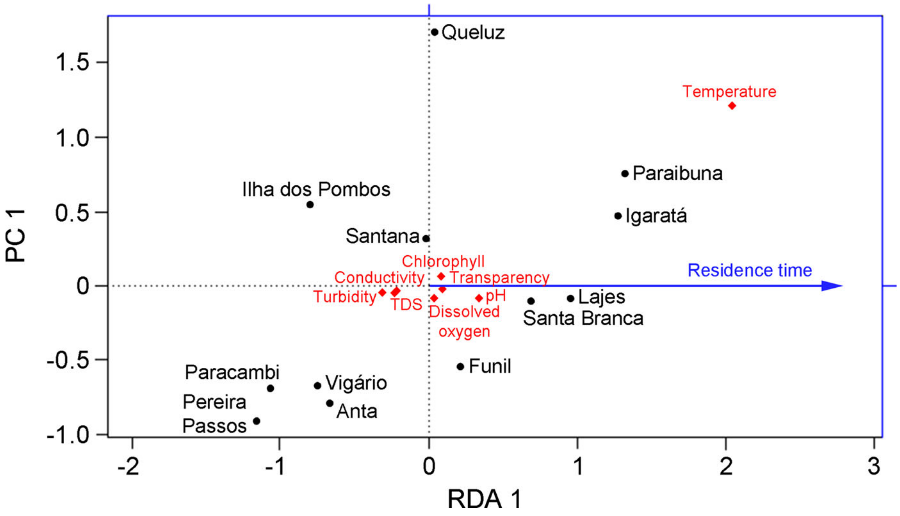

Fig. 3 Ordination of the twelve reservoirs from Paraíba do Sul river basin according to a redundancy analysis (RDA) of limnological features with water residence time as a constraint (explanatory variable). All variables, except temperature and pH, were $\log_{10}$-transformed

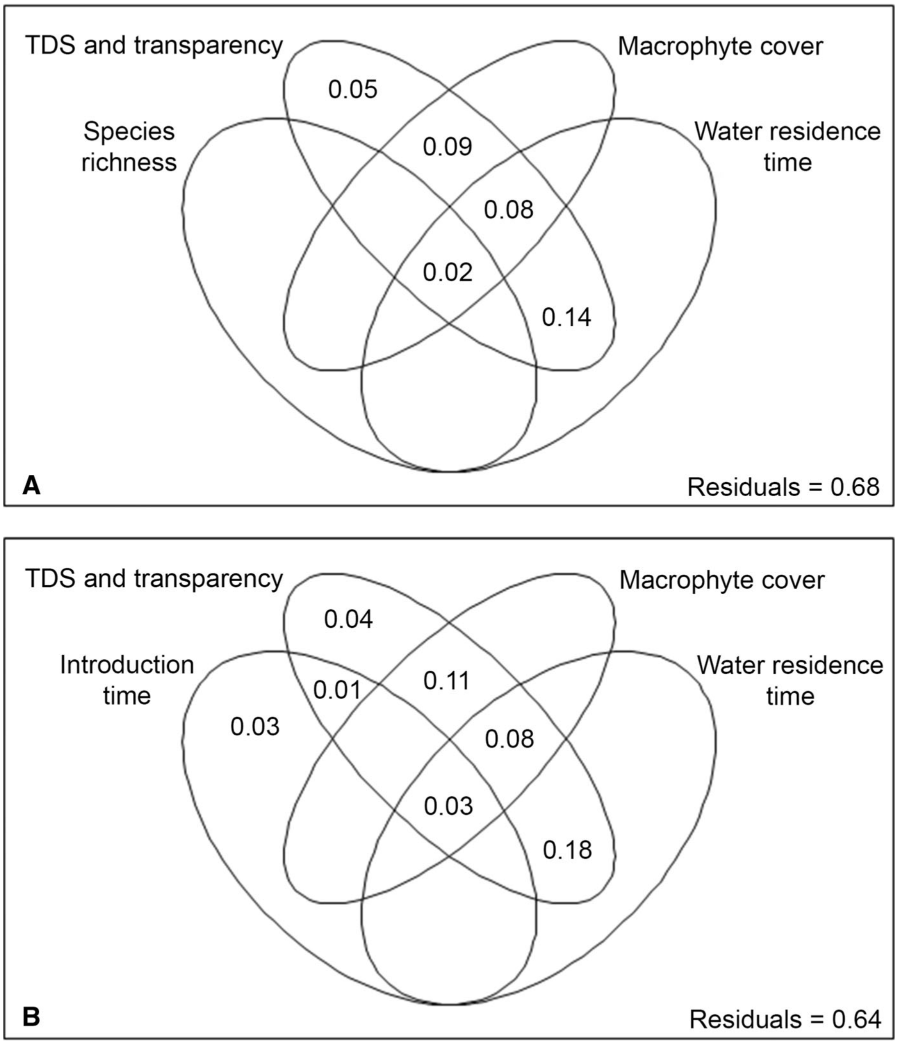

Fig. 4 Variation partitioning of the abundance of peacock basses (angling CPUE) using limnology (total dissolved solids and transparency), macrophyte cover, water residence time, and species richness (**A**) or introduction time (**B**) as explanatory sets. Values ≤ 0.005 are not shown

Table 1 Information criteria analysis of the linear models of the abundance of peacock basses (angling CPUE) with water temperature, turbidity, transparency and reservoir characteristics ($n = 12$ reservoirs)

Model	Variables in the model	Log-likelihood	Number of parameters (k)	AIC$_c$	Delta AIC$_c$ (ΔAIC$_c$)	Akaike weight (w_i)
1	− Turbidity	4.307	1	0.4	0	0.384
2	− Turbidity − reservoir age	5.591	2	2.5	2.15	0.131
3	Temperature − turbidity	5.262	2	3.2	2.81	0.094
4	− Turbidity − introduction time	5.191	2	3.3	2.95	0.088
5	Temperature	2.815	1	3.4	2.98	0.086
6	− Turbidity + residence time	4.394	2	4.9	4.54	0.04
7	− Turbidity − transparency	4.358	2	5.0	4.61	0.038
8	− Turbidity + reservoir area	4.308	2	5.1	4.71	0.036
9	Transparency + temperature	4.143	2	5.4	5.04	0.031
10	− Residence time	1.625	1	5.7	5.36	0.026
11	Temperature − turbidity − reservoir age	6.689	3	6.6	6.24	0.017
12	Temperature − turbidity − introduction time	6.572	3	6.9	6.47	0.015
13	Transparency	0.822	1	7.4	6.97	0.012

A minus sign (" − ") indicates a negative relationship between the predictor and the response variable; otherwise the relation is positive

model considered only turbidity, which covaried with some other variables such as latitude and water residence time (Figs. 5, S3). Similarly to the RDA, this analysis indicated that systems with warmer and less turbid waters (and longer water residence time) had higher abundances of peacock basses (Fig. S4). Introduction time, reservoir area, reservoir age, and transparency only appeared in a few models, with much lower likelihood. Although not considered in the analyses, latitude was highly correlated with temperature, turbidity and water residence time, as shown in Fig. 5.

Discussion

Our findings indicate that the abundance of the peacock basses in the Paraíba do Sul river basin is more influenced by reservoir features, such as water temperature, turbidity and residence time, than other local (habitat availability) or biotic (species richness) factors. Unexpectedly, higher abundances of peacock basses were found at high latitudes (the southernmost reservoirs), but this was due to the more lentic conditions (i.e. long water residence time) found in those systems, which also resulted in warmer and less turbid waters. Those conditions in southerly reservoirs coincide with those in the native range of peacock basses, i.e. lentic, warmer and transparent water conditions (Winemiller, 2001). Overall, headwater reservoirs had warmer, transparent and more oxygenated waters, which were strongly mediated by longer water residence time, resulting in higher peacock basses abundance.

Peacock basses are diurnal piscivorous that consume a variety of prey, with reported native species extirpation through predation and competition in introduced areas (Zaret & Paine, 1973; Winemiller et al., 1997; Santos et al., 2001). These generalist piscivorous rely on vision to capture its prey, and are rarely found in turbid or cold waters (Lowe-McConnell, 1969; Winemiller, 2001). Accordingly, invasive populations of *Cichla* spp. have been suggested to benefit from reservoirs, especially those with larger areas, high water temperature and transparency, and greater maximum depth (Espínola et al., 2010, 2015). Our findings indicate that many of these predictors are correlated with water residence time, which when longer creates more lentic conditions, and consequently warmer and less turbidity waters (Winemiller, 2001; Espínola et al., 2010, 2015).

Water residence time consists of the amount of time that water and transported substances introduced into a reservoir take to flow out of the system, and it is

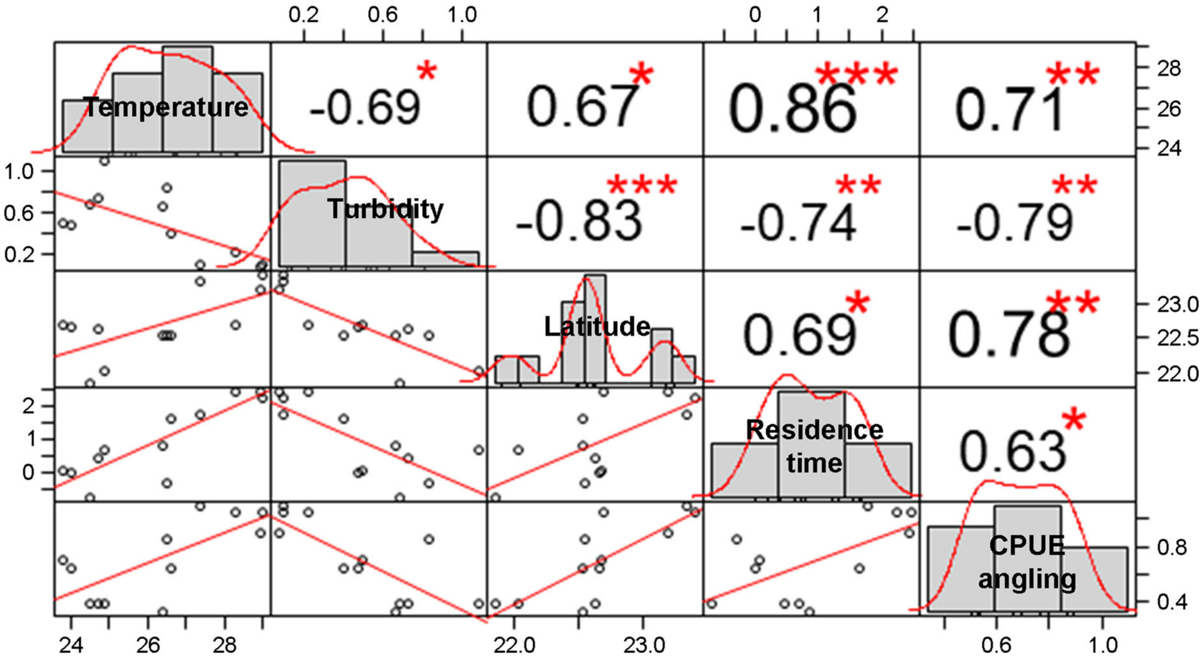

Fig. 5 Pairwise relationships between the abundance of the peacock basses (angling CPUE) and each of the main predictors selected by the multimodel inference. Below the diagonal, the bivariate scatterplots with the linear regression function are shown; the diagonal shows the histogram with an estimated kernel density function; above the diagonal, the Pearson correlation coefficients with significance levels (■$P < 0.10$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$)

generally manipulated to fit human demands and secondarily to maintain water quality requirements (Straškraba, 1999). This variable is related to the phytoplankton community and nutrient availability, influencing the overall biotic community, especially its behaviour in response to hydrological alterations (Soballe & Kimmel, 1987; Kennedy & Walker, 1990; Gomes et al., 2008). It is expected that the longer residence time may provide hydrological stability, which may favour species reproduction, especially for nest-constructors. In fact, reproduction of *Cichla* species was described as related not only to higher water stability (expressed as longer residence time), but also to warmer (23–28°C) and transparent water conditions for native Amazonian and introduced populations (Winemiller, 2001; Espínola et al., 2010). We identified water residence time as a key predictor of the limnological features of Paraíba do Sul reservoirs and, due to its effects on temperature and turbidity, also of the abundance of peacock basses.

Differing from expectations, since the peacock basses thrive in complex habitats (Winemiller, 2001; Espínola et al., 2010), coverage of habitats was not the main driver of abundance variation in this study. However, the importance of this variable raised when combined with others. As far as we know, there is no other study that directly measured habitat availability and its relationship with the abundance of peacock basses, but a positive relationship between these two variables is expected, since *Cichla* spp. rely on shallow, vegetated habitats to build their nests and to prey. Kovalenko et al. (2010) experimentally evaluated the role of aquatic plants in mediating direct and indirect effects of *Cichla kelberi* predation over native prey, and found that in the absence of vegetation, predation was even greater. A better assessment of the influence of structural complexity on the establishment, distribution and impact of *Cichla* spp. should be addressed by designing manipulative experiments of diverse habitat architecture (e.g. Santos et al., 2011), or making use of a combination of time and space-for-time approaches as indicated by Thomaz et al. (2012), since there is evidence that native assemblages may not recover from the impacts of introduced peacock basses (e.g. Sharpe et al., 2017).

The process of invasion begins with the translocation of a determined number of propagules to a novel region, but before the progression from immigrant to invader the process involves a lag phase, followed by rapid exponential increase in the species abundance and distribution (Mack et al., 2000). So, we used the time since the peacock basses were introduced in each reservoir as a potential predictor of the abundance of these species, expecting that systems with old introductions would have evolved from lag phase and therefore would present greater abundance. However, in our study, introduction time had no significant unique or overall relation with the abundance of the peacock basses, despite varying markedly among reservoirs (3–69 years). Further studies should monitor temporally the invasion dynamics of peacock basses, with data from before and after the introduction, although we acknowledge that this is often unavailable. In these cases, comparisons of sites with different ages of introduction arise as realistic evaluations to assess information on invasive species without previous data, as made by Carol et al. (2009).

A negative relationship between species richness and invasibility is often found in ecological studies, but this relation seems to be context dependent. Several studies have been performed in order to evaluate this relationship but they have found both rich and poor communities with increased vulnerability to invasion (Levine & D'Antonio, 1999; Colautti et al., 2006). In our study, the lack of a strong relationship between fish richness and abundance of peacock basses suggests that biotic resistance or facilitative interactions among the invader and the native community are less important than other features of reservoirs, which may impose stronger constraints to the establishment and population increase of this invasive species.

The impacts of an impoundment are cumulative and their effects over local fish faunas depend on species-specific characteristics, such as trophic specialization, reproductive strategy, patterns of migration, and habitat use. These cumulative impacts can be evaluated through the reservoir age, and reductions in the abundance of top predators, lotic-adapted species, mean size of species, and overall species richness, due to several environmental changes that occur since the filling phase, can be expected (Agostinho et al., 1999; Gido et al., 2000). Although conceptual frameworks of the effects of reservoir ageing over fish faunas are well developed, it is still difficult to prove them through empirical evidence (e.g. Bailly et al., 2016). In our case, reservoir age appeared in just two of the thirteen likely models (Table 1) and was barely correlated with peacock basses abundance (Fig. S2). Our study provides information on the main predictors of the abundance of invasive peacock basses in a set of Brazilian reservoirs. Contrary to what could be expected for this tropical, warm-water invasive fish, reservoirs at higher (southernmost) latitudes had higher abundances of peacock basses because the increased water residence times that are necessary in more populated regions raised water temperature and decreased turbidity. Other studies have also shown that freshwater ecosystems often display unexpected latitudinal patterns of water temperature (Hawkins et al., 1997; Carmona-Catot et al., 2014). We hypothesize that residence time may boost peacock basses abundance, when combined with warmer and transparent waters, in other regions, also influencing its impact. If general, water residence time may not only be used as a proxy of other variables more directly related to peacock basses (i.e. water temperature and turbidity) but could also be used to change thermal regimes, control peacock basses populations, and reduce their impact.

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