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Ecological impacts of an invasive top predator fish across South America



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HIGHLIGHTS

GRAPHICAL ABSTRACT

- Fish species richness decreases with greater invader abundance in reservoirs.
 Greater abundance of the top predator is
- found in human-modified systems.
- Maximum depth, population status and ecosystem type were the best predictors.
- Introduction year showed invasion pathways not related to geographical proximity.
- Older introductions in reservoirs had less native and more introduced species.

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ABSTRACT

Peacock bass Cichla ocellaris is a piscivorous cichlid native from the Amazon and Orinoco river basins, which has been broadly introduced into tropical areas worldwide, leading to several adverse local effects. However, predictors of its invasibility and assessments of its ecological impacts over large spatial scales are still lacking. The importance of different environmental factors in explaining the relative abundance of peacock bass in 62 sites across South America (30 native and 32 invaded systems) was investigated. The impacts of peacock bass on fish assemblages were appraised, using years since introduction as a proxy of its cumulative impacts and modern statistical techniques, such as random forests, and negative binomial regression models. Random forests highlighted maximum depth, introduced status, and ecosystem type as the best predictors of the peacock bass relative abundance, which ranged 0.01-26.0%, increased with maximum depth, was highest in invaded reservoirs but decreased with depth in native riverine populations. Other factors such as climate or limnological features were less important in explaining C. ocellaris abundance, which did not vary markedly with years since introduction. Introduction year was not related to latitude but varied among hydrographic regions, indicating invasion pathways not linked to geographical proximity. Variation partitioning of different fish assemblage metrics showed that hydrographic region followed by limnological and reservoir features accounted for most explained variation, indicating a strong historical and local influence. Introduction time accounted for 5–8% of variation in species composition and diversity, independently of limnological features. Our results suggest that the ecological effects of introduced C. ocellaris on native fish fauna are likely but small compared to large geographical and environmental gradients. Although experiments and before-after designs are probably more sensitive in detecting the ecological impacts of invasive species, large-scale compilations of available data are more feasible and can provide invaluable information, especially for large-sized invaders that are often illegally introduced.

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1. Introduction

Invasive alien species continue to impact ecosystems and biodiversity despite of worldwide commitments (such as the Aichi biodiversity targets) and legislation to prevent and mitigate these threats (Dick et al., 2013a, 2017; Ricciardi et al., 2012). There has been much progress in describing species characteristics related to invasiveness (Kolar and Lodge, 2001; van Kleunen et al., 2010; Howeth et al., 2015) and also in determining the invasibility of a community or habitat (Ilhéu et al., 2014; Ellender et al., 2015; Franco et al., 2018). However, few effective strategies are still applied to controlling invasive species in aquatic systems, especially in large and species-rich Neotropical environments.

Determining whether single or multiple environmental factors shape the distribution and ecological impacts of invasive alien species is crucial for risk assessment and also for developing control and eradication strategies, especially when these invaders are top predators (Salo et al., 2007; Dick et al., 2013b; Sharpe et al., 2017). Introduced predators are considered as one of the leading causes of declines and extirpations of species worldwide, with adverse effects cascading on food webs and scaling up to entire ecosystems (Pinto-Coelho et al., 2008; Bezerra et al., 2017). These predators often induce changes in the composition and structure of invaded systems, with consequences on both native biodiversity and provision of ecosystem services (Zaret and Paine, 1973; Latini and Petrere, 2004; Salo et al., 2007; Pelicice and Agostinho, 2009).

Impacts of invasive species are more conclusive through both laboratory or field experiments, but this is often not feasible when dealing with large ecosystems or scales and large species, such as the cases for instance of the temperate largemouth bass (Micropterus salmoides, Pereira and Vitule, 2019) or the tropical peacock basses (Cichla spp.), top predators widely introduced worldwide for sport fisheries (Carol et al., 2009; Garcia et al., 2014; Espínola et al., 2015). The recreational and economic interests lead some sport fishermen to often, albeit illegally, introduce target and bait species throughout systems, probably increasing their chances of establishment through high and constant propagule pressures (Simberloff, 2009; Britton and Orsí, 2012). Longterm assessments might also be used to follow an introduction from its beginning and compare the temporal dynamics with control sites or before-introduction periods, but such large temporal databases are generally unavailable, especially for tropical freshwater systems (Parker et al., 1999; Agostinho et al., 2007). The most available and feasible approach for large freshwater ecosystems arguably is to compare sites with different times since introduction, attempting to account for other environmental gradients with robust modelling (Lodge et al., 1998; Brändle et al., 2008; Carol et al., 2009). Time since introduction (referred to residence time for species introduced into a region but not necessarily in the wild, Pyšek and Jarošík, 2005) has been shown to predict the ranges (Pyšek and Jarošík, 2005; Williamson et al., 2009), abundance (Bennett et al., 2013), severity of impacts (Carol et al., 2009) or degree of enemy release (Hawkes, 2007) of invasive species, although the evidence mostly comes from terrestrial plants.

In the Neotropics, the mediating factors of species invasive ability are still barely known, even with the increasing threat posed by nonnative fish species, which is especially alarming, since this region holds ~30% of the world's fish diversity (Reis et al., 2003; Lévêque et al., 2008). Many non-native fish species are continuously introduced throughout the Neotropical region, despite the several impacts described at local levels, especially peacock basses Cichla sp., and the tilapia Oreochromis niloticus (Figueiredo and Giani, 2005, Pelicice et al., 2015). Peacock basses (Cichla spp.) comprise 15 species of cichlids native from the Amazon and Orinoco river basins (Kullander and Ferreira, 2006) that have been widely introduced into several reservoirs throughout the Americas, but especially in south and southeastern Brazil (Espínola et al., 2010; Marques et al., 2016). Within the genus Cichla, the group commonly known as yellow peacock basses (Cichla ocellaris Bloch and Schneider 1801, C. monoculus Spix and Agassiz 1831, and C. kelberi Kullander and Ferreira, 2006) is the most widespread, being also introduced in northeastern Brazil (Dourado and Davies, 1978), Panamá (Zaret and Paine, 1973), Florida, US (Shafland, 1996), and more recently Africa and Asia (Concepcion and Nelson, 1999; Hickley et al., 2008; Yeo and Chia, 2010; Rahim et al., 2013; Guerrero, 2014; Golani et al., 2019). They are voracious diurnal piscivores often causing adverse local effects on native fishes when introduced (Zaret and Paine, 1973; Pinto-Coelho et al., 2008; Pelicice and Agostinho, 2009; Sharpe et al., 2017). However, we are not aware of any study addressing how spatial, limnological and reservoir features, and fish species composition of the native and invaded ecosystems interact to explain the abundances of peacock basses through large spatial scales. Besides, the apparent local and regional ecological impacts attributed to peacock basses were not assessed or even supported at broader spatial scales before. Therefore, the aims of our study were: i) to assess the importance of different factors in explaining the relative abundance of Cichla ocellaris across South America (the region that harbours most of the studies on this group, Franco et al. in prep.); and ii) to assess the variation of fish assemblages with time since peacock bass introduction, relative to environmental factors, as proxies of ecological impacts of Cichla ocellaris at large geographical scales. Here, the molecularbased classification of Willis et al. (2012) was followed, and thus the five phenotypes of yellow peacock basses showing high levels of introgressive hybridization were regarded as a single species, namely Cichla ocellaris sensu lato. In addition to sharing many morphological, functional and ecological similarities, the five phenotypes of Cichla ocellaris sensu lato (C. kelberi, C. monoculus, C. nigromaculata, C. ocellaris, and C. pleiozona) comprise the most frequently introduced peacock basses, representing thus the most widespread biological entity of this genus. We hypothesized that peacock bass abundances would be related to some environmental and fish community attributes, but this relationship would be different regarding the ecosystem type (lentic versus lotic) and distribution status (native versus introduced). We expected greater impacts of Cichla ocellaris in lentic systems where this species has been introduced, especially those with warmer and more transparent waters, in accordance to previous studies for both native Cichla intermedia, C. orinocensis, and C. temensis populations (Winemiller, 2001) and introduced C. kelberi populations (Espínola et al., 2010).

2. Methods

The online databases of Web of Science, Scopus and Google Scholar were searched until July 2016 using "Cichla" AND "fish assemblage" OR "community" OR "native" OR "invasive" OR "alien" OR "introduced" OR "non-native" as keywords. We retained studies with abundance (raw or percentage) data of fish species, in which the yellow peacock basses - Cichla ocellaris sensu lato (C. ocellaris, C. monoculus, C. kelberi, C. pleiozona, and C. nigromaculata) following Willis et al. (2012; see also Espínola et al., 2015) was present, either as a native or alien species. A further search was performed to compile abiotic variables (when they were not already available from the references previously obtained), using as keywords: the name of the system; AND limnology OR hydrography OR water quality; and often the referred variable (e.g. water temperature). Studies for which limnological data were not available were discarded, leading to 62 study populations (30 native and 32 introduced), mostly in Brazil but also in Guyana, Peru, Bolivia and Paraguay (Fig. 1). The following information was finally compiled from the retained studies: relative abundance of all fish species, features from the study system (e.g. hydrographic region, coordinates, reservoir age, residence time, maximum depth, and altitude), some limnological variables (e.g. temperature, pH, total phosphorus and dissolved oxygen concentrations, transparency, and conductivity), year of Cichla ocellaris introduction (if applicable), and sampling year. Gillnets were used in most (~90%) of the retained studies, but other fishing gears (i.e. seines, cast nets, long-lines) were also used and gillnet dimension and effort were variable among studies. Therefore, relative abundance (percent proportion of the total fish abundance) of peacock basses and the



Fig. 1. Map showing the location of the studied lakes, reservoirs and rivers across South America. Symbol size is proportional to the relative abundance of peacock bass. Green symbols are located in the native distribution of peacock bass, while red symbols are at the invaded range.

other fish species were calculated and used in our analyses instead of raw abundances. Although such standardisation might potentially attenuate the responses among fish species and abiotic conditions within a given ecosystem, we expected that relative abundance was robust enough to be used as a proxy for comparisons among systems and to detect peacock bass effects over native assemblages and the relationship of this invader with environmental variables. As in some previous studies (e.g. Carol et al., 2009; Franco et al., 2018), because for most aquatic invasive species data before introductions are seldom available, we used time since introduction as a proxy of the accumulated potential impacts of peacock bass, assuming that the effects on native assemblages (e.g. species declines or extirpations) are not yet fully realized in recent introductions and increase with time. The compiled data are given in the Supplementary information (Tables S1 and S2).

2.1. Data analyses

We used Random forests (RF) to evaluate the importance of predictors of relative abundance of peacock bass, both in the native and introduced areas. Random forest (RF) is a machine-learning technique increasingly used in many scientific areas due to their high accuracy and ability to characterize complex interactions among predictors (Breiman, 2001; Strobl et al., 2008). RF have many advantages over other more conventional statistical techniques: run efficiently on large databases with many correlated predictors, give estimates of what variables are the most important, allow missing data, and handle particularly well nonlinearities and interactions (Prasad et al., 2006; Cutler et al., 2007). We used the 'cforest' function in the 'party' package (Hothorn et al., 2006) of the R software (R Core Team, 2016) to estimate what are the most important variables to explain the relative abundance of peacock bass. Conditional variable importance was assessed through the 'varimp' function, available in the 'party' package (Hothorn et al., 2006), which adjusts for correlations between predictor variables (Strobl et al., 2008). We used as predictors: hydrographic region, latitude, ecosystem type, area, maximum water depth, altitude,

transparency, conductivity, precipitation, pH, dissolved oxygen, phosphate, and mean and minimum water temperatures. We used the 'party' rather than the more widely used 'randomForest' R package (Liaw and Wiener, 2002) to avoid the biased variable selection and variable importance for predictor variables when they are of different types (e.g. scales, categories) or in the case of correlated predictors (Strobl et al., 2007, 2008, 2009). We used 1000 trees to build the RF because increasing this number did not substantially change the results of variable importance or explained variation (Strobl et al., 2008). As the number of variables randomly sampled as candidates at each split, we used the recommended default of the square root of number of predictors (Liaw and Wiener, 2002). Note that the out-of-bag estimate of variance used in RF is as accurate as using a test set of the same size as the training set and thus removes the need for a set aside test set in standard applications (Breiman, 2001; Prasad et al., 2006). Moreover, our aim was not to develop a predictive model but to rank the importance of variables and understand their effects. RF partial dependence plots (Friedman, 2001) were obtained for the most important predictors. These plots give a graphical depiction of the marginal effect of a predictor on the response variable, after partialing out the effects of the other predictors in the model (see Tuulaikhuu et al., 2017 for similar analyses). The relationship of relative abundance of *C. ocellaris* with maximum depth by ecosystem type and native/introduced status, and time since introduction in rivers and reservoirs was illustrated through generalized additive models (GAM) with the beta regression family.

For introduced populations, we used variation partitioning (Borcard et al., 1992) to quantify the relative importance of different descriptor sets and years since *Cichla's* introduction (as a proxy of the cumulative impacts of peacock bass) in explaining fish assemblage metrics. Variation partitioning (VP) computes the adjusted R^2 based on linear regression (or redundancy analyses for multiple response variables) to estimate the unique and joint fractions explained by a set of explanatory variables (Borcard et al., 2011). We performed four different VP analyses, using as responses: the matrix of relative abundances (286 species \times 32 sites) with Hellinger transformation (Legendre and Gallagher,

2001), the Shannon's index of diversity, observed native fish richness, and Pielou's evenness. We used four predictors sets for each of the VP analyses: 1) limnological and reservoir features (minimum and mean temperatures, pH, absolute value of latitude, and log-transformations of elevation, maximum depth, oxygen, transparency and oxygen and total phosphorous concentrations); 2) ecosystem type (10 rivers vs. 22 reservoirs); 3) years since introduction of peacock bass at the study time; and 4) hydrographic region (five regions as dummy variables). VPs were obtained using function "varpart" in the "vegan" package (Oksanen et al., 2016) of the R statistical software. The different unique and overall fractions in VP were tested with permutation tests (10,000 permutations), using function "anova.cca".

We further used negative binomial (generalized linear) models (NBM) to test for effects of hydrographic region, ecosystem type (reservoir, lake or river) and time since the introduction of C. ocellaris (predictors) on species richness, because this response variable is less well modelled with the linear models used in VP. We used the function "glm.nb" as available in the package "MASS" (Ripley et al., 2017) of R statistical software and scripts modified from Magellan and García-Berthou (2015). NBMs are an extension of GLMs which account for overdispersion, which is frequent in ecological data and was also present in our study, with an extra parameter "theta". We compared NBMs with an information theoretical framework (Burnham and Anderson, 1998), i.e. Akaike information criteria (AIC), to compare four models with the abovementioned three predictors: a null model without predictors and models with and without time since the introduction both with additive and multiplicative effects of hydrographic region and ecosystem type. The Akaike's Information Criterion (AICc) combines goodness-of-fit with parsimony (number of parameters) of models, with the best fitting model having the lowest AICc. The relative plausibility of each candidate model was assessed by calculating Akaike weights (w_i) , which range from 0 to 1 and are interpreted as the probability that the model is the best among those evaluated given the data.

3. Results

3.1. Relative abundance of Cichla ocellaris

The relative abundance (RA) of *C. ocellaris* ranged 0.01-26.0% in the studies considered (mean = 2.1%; Fig. 1) with higher mean values in invaded (3.3%) than in native areas (0.8%). Random forest analyses explained 20.4% of this response variable and suggested that maximum depth of the system, native vs. introduced status, and ecosystem type (rivers, lakes, and reservoirs) were the best predictors of RA (Fig. 2).

Other factors such as climate (temperatures and latitude) or physical and chemical water features (transparency, oxygen and phosphate concentrations, pH, and conductivity) were less important predictors. *Cichla ocellaris* increases in abundance with the maximum depth of the system, although mainly in reservoirs in the introduced area (Fig. 3A). The smooth terms of GAM models of RA and maximum depth were significant for reservoirs in the introduced area and rivers in the native area (P < 0.001) but followed opposing trends (i.e. positive for introduced reservoirs, negative for native rivers). Higher RA was recorded in native rivers (1%) than in native reservoirs (0.3%) and lakes (0.4%); by contrast, the opposite pattern was found for invaded systems, with 1% in rivers, and reservoirs reaching the highest RA (4.3%) (Figs. 1 and 3).

Among introduced populations, GAM models suggested no relationship (smooth term) between RA and years since introduction (introduction age) in either rivers or reservoirs, despite the higher abundance in the latter (Fig. 3B); therefore, RA of peacock bass did not increase markedly in older introductions. Year of introduction, which was highly correlated with introduction age (r = -0.96, n = 32, P < 0.001), was not related to latitude of the study system (r = 0.19, P = 0.30) but varied significantly among hydrographic regions (ANOVA, P = 0.005) because introductions started earlier in the more populated states of southeastern Brazil (SE Atlantic, e.g. Rio de Janeiro State) and are more recent in the Paraná river basin (Fig. S1).

3.2. Effects of introduction age on fish assemblages

Variation partitioning of fish assemblage characteristics (Fig. 4) showed that: i) except for fish species evenness, hydrographic region followed by physical and chemical water features had higher percentages of explained variation; ii) the differences between reservoirs and rivers were in general less important although its unique effects were significant for species diversity (permutation test, P = 0.042); iii) the unique effects of hydrographic region were significant for species composition and richness (permutation tests, P < 0.05) and marginally significant for species diversity (P = 0.083); iv) the unexplained variation was higher for fish species evenness, in which none of the four predictor sets had significant unique or overall effects ($P \ge 0.095$).

Except for fish species evenness, the overall effects of years since introduction of peacock bass explained 5–8% of the variation (Fig. 4) and were significant for species composition (P = 0.005) and marginally significant for species richness (P = 0.087). However, the unique effects of introduction age were never significant (P > 0.05) because most of its variation was jointly explained with hydrographic region (Fig. 4) given



Fig. 2. Variable importance of predictors of relative abundance of peacock bass according to the random forest technique (explained variation = 20.4%). Predictors with variable importance to the left of the dashed red line can be considered uninformative.



Fig. 3. Relationship of relative abundance of *Cichla ocellaris* with maximum depth by ecosystem type and native/introduced status (top) and time since introduction in rivers and reservoirs (bottom). A generalized additive model with the beta regression family is shown.

the marked differences in introduction year or age among hydrographic regions (Fig. 5). Fish species richness in reservoirs decreased with years since peacock bass introduction (Fig. 5A) and the same pattern is independently observed in three hydrographic regions (Fig. 5B). Information criteria of negative binomial models showed that although models with only hydrographic region and ecosystem type were the most likely, the models with years since introduction had about 28% of the likelihood and were $<2 \Delta AICc$ (Table 1). Heat maps (Fig. 6) suggest that in reservoirs with older introductions, e.g. reservoirs in Rio de Janeiro state, i.e. SE Atlantic hydrographic region, such as Lajes, with Cichla introduced ca. 63 years before the study period (Santos et al., 2001) or Vigário, 48 years (Marques et al., 2016), several native species (e.g. Astyanax fasciatus, Gymnotus carapo, Hoplias malabaricus, and Rhamdia quelen) disappeared and relative abundances shifted towards a greater dominance of other introduced species (e.g. Plagioscion squamosissimus, Coptodon rendalli, and Oreochromis niloticus), some of them less sensitive to piscivory (e.g. Metynnis lippincotianus).

4. Discussion

Our findings are the first in demonstrating, through a broad spatial coverage (~32 latitudinal degrees; 3500 km of distance range), that peacock bass experienced a noticeable population boom in reservoirs wherein it was introduced. The hypothesis of positive additive effects of river damming on non-native peacock bass populations (i.e. lowering the proportion of native predators and competitors and increasing the predation effects of this invader) is supported by the trend of decreased relative abundances of peacock bass with water depth in rivers within its native range, wherein running waters (and probably more turbulent and turbid conditions) prevailed over lentic conditions (Agostinho et al., 2007; Espínola et al., 2015). The influence of depth on the relative abundance of introduced peacock bass in reservoirs was stronger than geo-graphical, physical, or other limnological features. Using peacock bass



Fig. 4. Variation partitioning of species composition (A), Shannon's diversity index (B), species richness (C), and Pielou's evenness (D) using limnological and reservoir features, ecosystem type, time since introduction, and hydrographic region as predictor sets. The overall variation explained by each predictor set is given between parentheses. Values <0 are not shown.



Fig. 5. Relationship of fish species richness with time since introduction by ecosystem type and hydrographic region. Linear models are shown (note the log-scale for species richness).

relative abundance allowed us to perform robust comparisons of varied systems widespread through South America and of studies using different fishing gears (mostly gillnets) and effort, with no apparent limitations in capturing signals of the major environmental factors and fish assemblage attributes related to shifts of peacock bass abundance. We believe that studies in other continents would have similar results of the predictors for the establishment of peacock basses and the impact on native fish fauna that would follow.

Peacock bass experienced a large demographic growth with increased water depth of reservoirs located outside its native range. Similar predictions were provided in studies spanning only local or regional scales (e.g. Upper Paraná and Paraíba do Sul river basins) and excluding comparisons with less-altered systems (e.g. lakes and rivers) of both native and introduced areas (Pelicice and Agostinho, 2009; Espínola et al., 2010; Franco et al., 2018). These studies focused on presence-absence data (Pelicice and Agostinho, 2009; Espínola et al., 2010) or used raw abundance data (Franco et al., 2018) to infer the environmental features that contributed most to the invasibility of reservoirs by peacock bass.

Table 1

Information criteria of negative binomial models of fish species richness using as predictors ecosystem type (reservoirs vs. rivers), hydrographic region and years since introduction of peacock bass.

Model	Explained deviance (%)	AIC _c	Delta AIC _c (Δ AIC _c)	d. f.	Akaike weight (<i>w_i</i>)
ALL SITES					
Ecosystem type + Region	46.9	254.9	0.0	7	0.714
Ecosystem type + Region + Years	47.1	256.8	1.9	8	0.280
Constant	-	265.1	10.1	2	0.005
$\begin{array}{l} \text{Ecosystem type} \times \\ \text{Region} \times \text{Years} \end{array}$	50.1	267.0	12.1	14	0.002
RESERVOIRS ONLY					
Region	41.4	170.6	0.0	6	0.583
Region + Years	42.8	172.1	1.5	7	0.275
Constant	-	174.1	3.5	2	0.100
Region \times Years	43.3	175.9	5.3	9	0.041

This strong positive effect of water depth on peacock bass abundance could be explained because deep reservoirs are also generally associated with the prevalence of lentic, transparent and warmer waters, and structurally-simple habitat conditions, which altogether favor the predation exerted by this visual piscivore (Winemiller, 2001; Espínola et al., 2015; Franco et al., 2018). Another non-mutually exclusive explanation is that these conditions typical of deeper reservoirs also adversely affected the whole fish assemblage, decreasing the relative abundances of non-adapted native species and strengthening the contribution of peacock bass.

River impoundment leads to environmental disturbances on the whole ecosystem, impacting native communities through critical alterations in the hydrological regime, habitat architecture and energy flow (Bailly et al., 2016; Baumgartner et al., 2017). Shifts on the composition and structure of native fish assemblages caused by river damming also seem to facilitate the establishment and spread of invasive species (Havel et al., 2005; Liew et al., 2016), as predicted for *Cichla* spp. introduced into reservoirs of Upper Paraná river basin and other Brazilian regions (Espínola et al., 2010; Franco et al., 2018). This mechanism apparently occurs through the occupation and exploitation by invasive species of vacant niches, after the extirpation of those native species which could not tolerate the change from lotic to lacustrine conditions, resulting thus in the impoverishment and biotic homogenisation of native fish assemblages (Havel et al., 2005; Liew et al., 2016).

Although the abundances of peacock bass were mostly influenced by the ecosystem type and introduced status, fish assemblage attributes were largely explained by local limnological conditions (i.e. water physical and chemical variables) and historical effects (i.e. hydrographic region, as previously stated by Tedesco et al., 2005 and Franco et al., 2018). Relationships among invasive species and fish assemblages are often confounded by local factors, such as environmental heterogeneity at the landscape, variation in resource availability, human alterations, and also the invasion stage (Fitzgerald et al., 2016). Furthermore, many studies covering large spatial scales face low partitioning among predictors, often sharing much of the explained variation among the predictive variables or accounting for great amounts of unexplained variation (Diniz-Filho and Bini, 2005; Diniz-Filho et al., 2009; Bailly et al., 2016). However, years since introduction of peacock bass accounted for 5-8% of variation in the species composition and fish diversity assessed in our study, regardless of physical and chemical water variables, with information criteria also suggesting negative effects of peacock bass on fish richness.

Cumulative impacts of peacock bass introduction on native fish assemblages have been previously reported, ranging from biotic homogenisation and decreases of native richness and diversity to trophic cascading effects (Zaret and Paine, 1973; Latini and Petrere, 2004; Pelicice and Agostinho, 2009; Menezes et al., 2012). In our study, peacock bass effects were apparently lower than other local or historical predictors of fish assemblages, probably due to the influence of our large-scale approach, but also because peacock bass was present in all systems used in our analyses. The approach used here, although not designed to directly split the synergistic effects of peacock bass introduction and river damming, showed that the cumulative impacts of this invasive species are likely, regardless of ecosystem type. Increased peacock bass abundance can be related to adverse effects on species composition, diversity, and richness, especially for non-native populations in the northeastern and southeastern Atlantic and also in Paraná hydrographic basins, the regions wherein this invader was introduced the earliest.

In this sense, reservoirs with the oldest peacock bass introduction also experienced considerable changes on fish assemblage composition, with increased contributions of other invasive species (i.e. the South American silver croacker *P. squamosissimus*, the tilapias *C. rendalli* and *O. niloticus*, and the silver dollar *M. lippincotianus*) together with the disappearance of native ones (*A. fasciatus*, *G. carapo*, *H. malabaricus*, and *R. quelen*). Further, in addition to stressing the potential impacts through predation on native species of small sizes (< 150 mm TL,



Hypostomus sp. Schizodon nasutus Leporinus friderici Trachelyopterus galeatus Astyanax lacustris Iheringichthys labrosus Crenicichla britskii Serrasalmus maculatus Acestrorhynchus lacustris Galeocharax gulo Leporinus octofasciatus Steindachnerina insculpta Hoplias malabaricus Hypostomus ancistroides Hoplosternum littorale Gymnotus carapo Myloplus tiete Megaleporinus obtusidens Pimelodus maculatus Rhamdia quelen Plagioscion squamosissimus Cichla ocellaris Geophagus brasiliensis Oligosarcus hepsetus Astyanax fasciatus Synbranchus marmoratus Éigenmannia virescens Astyanax bimaculatus Prochilodus brevis Crenicichla menesezi Oreochromis niloticus Astyanax parahybae Metynnis lippincottianus Coptodon rendalli

Fig. 6. Heatmap of species composition (relative abundance) as a function of increasing time since introduction (from left to right) in the study reservoirs. The more reddish color indicates higher relative abundance; light yellow indicates species not recorded in that reservoir. Species appearing in less than ten systems were omitted.

such as the tetra *A. fasciatus*) or slender-bodied (such as the banded knifefish *G. carapo*), our study also stresses the likely negative effects of peacock bass on the native piscivores (South American catfish *R. quelen* and trahira *H. malabaricus*). Although feeding interactions of peacock bass with *H. malabaricus* have been previously reported (Pompeu and Godinho, 2001; Pereira et al., 2015), no study has provided evidence of extirpation of native piscivores through peacock bass effects before, which is still more surprising when considering that *H. malabaricus* is a species fully adapted to lentic systems. Even so, this issue should be more deeply addressed through experimental trials that are able to control for potential confounding effects of dam age on the adverse consequences on native fish.

Finally, taking into account that peacock basses are highly valued as game fish in sport fisheries (Azevedo-Santos et al., 2015; Freire et al., 2016), we anticipate that they will continue to be introduced and thrive, particularly in deep and lentic systems of tropical or subtropical climates, as our findings highlighted. This is of especial concern considering the predictions of increasingly number of reservoirs worldwide, and especially in South America and tropical regions of Africa and Asia (Tollefson, 2011; Zarfl et al., 2015). Although imposing a great threat for native fish species, especially on small sized and slender-bodied species (Santos et al., 2001), but apparently also on native piscivores through competition (Fugi et al., 2008), if the spread of non-native peacock bass populations increases over time, it will be an opportunity to test whether our predictions are accurate. In this sense, further longterm studies using standardized sampling methods and effort and incorporating systems wherein peacock basses are not present or using before-after introduction designs are necessary. We find extremely important that further studies focus on evaluating the impacts on ecosystem functioning level, and also on the functional and phylogenetic diversities of the invaded systems. Despite their little implementation by hydroelectric companies, if management measures that increase

water flow in reservoirs were carried out (thus decreasing water residence time and depth), they would be also an interesting opportunity to test our predictions about the response of peacock bass abundance to water depth and residence time. Educational campaigns should be directed to sport fishermen at risky systems in order to inform them about the adverse effects caused by the peacock bass and also to restrain "catch-and-release" practices to attempt to prevent further introductions of this top predator fish.

Supplementary data to this article can be found online at https://doi. org/10.1016/j.scitotenv.2020.143296.

Data availability statement

The literature review was made using data available online in Google Scholar, Scopus, and Web of Science databases. All occurrence records, systems features, limnological variables and species richness used in the analyses and also to generate the maps are available in the tables and studies listed in Supporting Information. The shapefile used to generate the map are also publicly available in the FEOW database.

CRediT authorship contribution statement

Ana Clara Sampaio Franco: Data gathering, Methodology, Writing -Original draft preparation. Emili García-Berthou: Methodology, Formal analysis, Writing - Review & Editing. Luciano Neves dos Santos: Conceptualisation, Methodology, Writing - Review & Editing.

Declaration of competing interest

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

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Ecological impacts of an invasive top predator fish across South America

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Table S1. Location and features of the study sites compiled and analysed where <i>Cichla</i>
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location, limnological and reservoir features used in analysescsv file
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abundance of the species captured in each systemcsv file

Study site	Latitude	Longitude	Hydrographic region	Ecosystem type	Native status or introduction year	References
Anavilhanas	2° 32' S	60° 47' W	Amazon	lake	native	Petry et al. (2003); Yamamoto et al. (2014)
Araçá	3° 19' 54" S	58°18' 25" W	Amazon	lake	native	Santos (2013); Soares et al. (2014)
Araguaia	13° 15' S	50° 35' W	Tocantins-Araguaia	river	native	Tejerina-Garro et al. (1998)
Cana Brava	13° 24' S	48° 9' W	Tocantins-Araguaia	reservoir	native	Buchmann (2014); Silva et al. (2007)
Capim Branco	18° 47' 22" S	48° 8' 36" W	Paraná	reservoir	2006	Pizetta (2007); Rêgo (2008)
Capivara	22° 40' 44" S	51° 19' 55" W	Paraná	reservoir	1997	Bennemann et al. (2011); Marcucci et al. (2005); Naliato (2009)
Chavantes	23° 07' 50" S	49° 42' 4" W	Paraná	reservoir	1995	Ayroza (2012); Magnoni (2009); Nobile (2010)
Coaracy Nunes	0° 54' 12" N	51° 16' 16" W	Amazon	reservoir	native	Oliveira (2012); Sá-Oliveira et al. (2015)
Curuá-Una	2° 54' S	54° 27' W	Amazon	river	native	Junk et al. (1981); Vieira (2000)
Cuyuní	6° 23' 18" N	58° 41' 39" W	Essequibo	river	native	Machado-Allison et al. (2000); Pisapia et al. (2013)
Edson Queiroz	4° 13′ 27″ S	40° 2′ 08″ W	NE Atlantic	reservoir	1987	Batista et al. (2014); Gurgel- Lourenço et al. (2015)
Gramame	7° 17' 49" S	34° 57' 37" W	NE Atlantic	reservoir	1990	Barbosa (2012); Souza (2013)
Grande	20° 36' 9" S	46° 35' 27" W	Paraná	river	1990	Castro et al. (2004); Rolla et al. (1992); Vono et al. (1997)
Guariba	8° 13' S	60° 28' W	Amazon	river	native	Pedroza et al. (2012)

Table S1. Location and features of the study sites compiled and analysed where *Cichla ocellaris* has been recorded.

Ilha das Onças	1° 26' S	48° 34' W	Amazon	river	native	Silva (2006); Torres (2010)
Ilha dos Pombos	21° 50' 40" S	42° 34' 43" W	SE Atlantic	reservoir	2000	Araújo & Rocha (2012); Uehara et al. (2015)
Ilha Solteira	19° 19' 2'' S	51° 04' 34" W	Paraná	reservoir	1990	Mello (2012); Pagotto & Souza (2006); Vasilio (2006)
Ipixuna-Maici	6° 09' 52" S	61° 46' 4" W	Amazon	river	native	Anjos (2009)
Itaipu	25° 24' 20" S	54° 35' 10" W	Paraná	reservoir	1985	Abes et al. (2001); Baumgartner et al. (2008); Mello (2012); Oliveira et al. (2005); Ribeiro- Filho et al. (2011)
Jacaré-Guaçu	21° 41' 14" S	49° 12' 20" W	Paraná	river	1998	Esguícero & Arcifa (2011); Rodríguez (2001)
Lago Batata	1° 31' 46" S	56° 16' 0" W	Amazon	lake	native	Cardoso (2009); Soares (2015)
Lago Jacaré	2° 19' S	56° 31' W	Amazon	lake	native	Freitas & Garcez (2004); Sousa & Freitas (2008)
Lago Tupé	4° 53' 36" S	64° 0' 22" W	Amazon	lake	native	Soares & Yamamoto (2005); Trevisan & Forsberg (2007)
Lagos do rio Solimões	3° 51' 33" S	62° 35' 8" W	Amazon	lake	native	Freitas et al. (2014); Prado et al. (2009); Trevisan & Forsberg (2007)
Lajes	22° 45' 35" S	43° 55' 24" W	SE Atlantic	reservoir	1945	Araújo & Rocha (2012); Santos et al. (2011); Soares et al. (2008); Uehara et al. (2015)
Madeira	6° 44' 58" S	62° 22' 10" W	Amazon	river	native	Couto (2009); Torrente-Vilara et al (2011)
Mamoré	14° 36' 0" S	65° 0' 16" W	Amazon	river	native	Couto (2009); Pouilly et al (2014)
Marechal Dutra	6° 25' 15" S	36° 36' 1" W	NE Atlantic	reservoir	1965	Duarte (2011); Nascimento et al. (2011)
Nanay	3° 48' S	73° 23' W	Amazon	river	native	Correa & Ortega (2010);

Negro	2° 03' S	60° 24' W	Amazon	river	native
Pandeiros	15° 39' 54" S	44° 38' 7" W	São Francisco	river	1982
Paraíba do Sul	22° 30' 31" S	44° 13' 2" W	SE Atlantic	river	1982
Paraná	22° 46' 13" S	53° 18' 10" W	Paraná	river	1992
Pardo	20° 9' 42" S	48° 37' 37" W	Paraná	river	1990
Paulo Sarasate	4° 14′ 3″ S	40° 27′ 40″ W	NE Atlantic	reservoir	1964
Pereira Passos	22° 41' 1" S	43° 49' 26" W	SE Atlantic	reservoir	1970
Purus	7° 23' S	65° 11' W	Amazon	river	native
Ribeirão Diamante	22° 37' 21" S	52° 50' 59" W	Paraná	river	2004
Rio das Mortes (MT)	12° 32' 45" S	50° 56' 19" W	Tocantins-Araguaia	river	native
Rios do Semi-árido	6° 18' 22" S	37° 10' 44" W	São Francisco	river	1971
Rosana	22° 36' S	52° 52' W	Paraná	reservoir	2004
Rupununi Santa Cruz do Apodi	3° N 5° 46' 1" S	59° 45' W 37° 47' 59" W	Essequibo NE Atlantic	river reservoir	native 2002

Lin	dgren & Röttorp (2009)
Go	ulding et al. (1988); Trevisan
& I	Forsberg (2007)
Ma	scarenhas et al. (2013);
Rez	zende et al. (2012; 2016);
Sar	ntos et al. (2015); Souza
(20	16)
Ara	aújo et al. (2001); Silva (2001)
Me	llo (2012); Baumgartner et al.
(20	08); Petry (2001)
Cas	stagnolli (2008); Meletti et al.
(20	03); Meschiatti et al. (2000)
Bat	ista et al. (2014); Gurgel-
Lou	urenço et al. (2015)
Ara	aújo & Rocha (2012); Uehara
et a	ul. (2015)
Du	arte (2008); Silva et al. (2010)
For	nseca et al. (2009); Granado et
al.	(2009); Morales et al. (2009)
Me	lo (2006); Melo et al. (2007;
200)9); Lima (2009)
Ca	rvalho et al. (2013); Dias
(20	06); Gurgel & Fernando
(19	94); Medeiros et al. (2010);
Sil	va (2012)
Bag	gatini et al. (2007); Feitosa
(20	07); Fonseca et al. (2009);
Me	llo (2012); Pelicice (2007)
Lo	we-McConnell (1964)
No	vaes et al. (2014); Segundo

Salto Grande	22° 54' 13" S	49° 59' 0" W	Paraná	reservoir	1995
Samuel	8° 51' 6" S	63° 21' 26" W	Amazon	reservoir	native
Santa Branca	23° 20' 7" S	45° 47' 56" W	SE Atlantic	reservoir	1980
São Francisco	11° 6' 55" S	43° 11' 40" W	São Francisco	river	1982
Saracá-Araticum	1° 37' S	56° 29' W	Amazon	river	native
Serra da Mesa	14° 5′ 42″ S	48° 17′ 23″ W	Tocantins-Araguaia	reservoir	native
Tapajós	2° 46' 20" S	55° 5' 36" W	Amazon	river	native
Três Irmãos	20° 39' 36" S	51° 17' 38" W	Paraná	reservoir	1985
Três Marias	18° 12' 56" S	45° 15' 55" W	São Francisco	reservoir	1982
Trombetas	7° 24' S	72° 25' W	Amazon	river	native
Tucuruí	3° 50' 3" S	49° 38' 53" W	Tocantins-Araguaia	reservoir	native
UHE Curuá-Una	2° 49' 2" S	54° 18' 4" W	Amazon	reservoir	native
UHE Miranda	18° 54' 29" S	48° 01' 2" W	Paraná	reservoir	2005

(2013); Silva (2013) Brandão (2007); Brandão et al. (2009); Carmo (2000); Dornfeld (2002); Mello (2012) Nascimento et al. (2009); Silva (2007); Viana (2002) Araújo & Rocha (2012); Uehara et al. (2015) Luz et al. (2009; 2012); Mascarenhas et al. (2013); Medeiros et al. (2007); Normando et al. (2014) Cardoso (2009); Reis (2011) Mazzoni et al. (2012); Silva et al. (2014)Galvão-Miranda et al. (2009); Keppeler (2015) Barrella & Petrere (2003); Granado et al. (2009); Liliamtis (2007); Mello (2012) Brito (2010); Brito et al. (2013); Prado & Pompeu (2014) Cardoso (2009); Ferreira (1993); Ropke et al. (2014) Botelho (2007); Mérona et al. (2001)Gunkel et al. (2003); Junk et al. (1981); Vieira (2000) Callisto et al. (2002); Flauzino (2014); Garcia (2005)

UHE Pedra	13° 52' 5" S	40° 14' 15" W	E Atlantic	reservoir	1989	Calado-Neto (2007); Severi et al. (2010)
UHE São Simão	19° 0' 59" S	50° 29' 1" W	Paraná	reservoir	1997	Mello (2012); Neves et al. (2006) Costa & Freitas (2010: 2013:
Urucu	4° 10' S	63° 32' W	Amazon	river	native	2014); Trevisan & Forsberg (2007)
Verde	20° 4' 5" S	53° 10' 41" W	Paraná	river	1987	Almeida & Coelho (2014); Pesoa & Cardoso (2015)
Vigário	22° 37' 56" S	43° 53' 36" W	SE Atlantic	reservoir	1960	Araújo & Rocha (2012); Gomes et al. (2008); Uehara et al. (2015)
Yurimáguas	4° 56' S	74° 21' W	Amazon	river	native	Lindgren & Röttorp (2009); Ortega et al. (2007)

Table S2. Limnological features and observed fish species richness of the study sites compiled and analysed. See Table S1 for location of the sites.

System	Altitud e (m)	Precipitatio n (mm)	Maximu m depth (m)	Minimum water temperatur e (°C)	Mean water temperatur e (°C)	рН	Conductivi ty (µS/cm)	Dissolve d oxygen (mg/L)	Transparenc y (m)	Total phosphorus concentratio n (mg/L)	Observe d fish species richness
Anavilhana s	13	1750	27.6	26.2	29.0	4.2	15.6	3.9	0.8	0.034	95
Araçá	12	2033	9.8	26.9	30.7	6.7	61.5	3.6	0.5	0.168	26
Araguaia	220	1869	6.6	27.0	28.5	6.9	45.5	3.4	0.6	0.113	90
Cana Brava	289	1421	3.5	23.9	27.6	7.5	94.1	5.9	3.8	0.017	93
Capim Branco	597	1566	52.0	22.9	23.0	6.0	30.7	6.4	4.0	0.009	29
Capivara	325	1256	50.0	20.6	24.2	6.3	78.9	7.6	1.5	0.029	33
Chavantes	474	1357	67.0	20.9	23.2	7.3	52.7	7.0	2.9	0.039	35
Coaracy Nunes	45	2500	30.0	26.5	27.7	6.1	20.5	5.2	1.2	0.140	41
Curuá-Una	29	1772	18.0	27.4	28.0	5.9	21.4	6.3	1.9	0.033	59
Cuyuní	1	1650	7.0	23.0	24.0	5.5	27.7	4.4	0.5	0.006	88
Edson Queiroz	193	855	24.0	26.3	27.9	8.0	259.5	3.7	1.0	0.456	13
Gramame	375	1514	35.0	26.0	27.9	6.9	93.4	6.6	4.8	0.250	29
Grande	660	1524	1.15	21.7	25.2	7.4	45.0	7.7	0.8	0.021	35
Guariba	81	2550	5.95	27.1	29.2	5.7	6.7	4.0	1.5	0.035	139
Ilha das Onças	1	2532	17.0	23.5	28.2	6.0	46.1	6.2	0.2	0.015	34
Ilha dos	132	1265	32.0	25.2	25.3	7.6	59.0	8.8	0.1	0.075	20

Pombos											
Ilha Solteira	300	1316	10.0	28.0	29.8	6.3	80.0	5.3	3.0	0.053	32
Ipixuna- Maici	27	2525	0.75	28.0	29.1	6.0	23.0	3.4	0.7	0.052	36
Itaipu	253	1728	220.0	21.9	29.5	7.4	53.0	7.6	1.2	0.031	85
Jacaré- Guaçu	377	1491	1.7	19.9	24.4	6.7	66.6	7.1	0.5	0.255	79
Lago Batata	1	2300	9.5	28.5	29.7	6.1	10.5	5.9	1.6	0.222	157
Lago Jacaré	5	2748	9.5	27.0	30.2	6.6	93.5	2.3	1.1	0.027	45
Lago Tupé Lagos do	45	2290	13.5	27.0	29.0	4.6	15.9	4.5	1.2	0.168	50
rio Solimões	31	2290	10.5	28.2	29.2	6.6	67.0	2.5	0.9	0.168	115
Lajes	423	1362	50.0	24.2	29.1	7.3	33.0	8.0	2.5	0.015	14
Madeira	29	2200	25.0	20.9	25.2	5.9	14.6	5.2	0.7	0.018	170
Mamoré	158	1557	17.0	28.4	29.4	6.7	126.5	4.9	0.4	0.040	139
Marechal Dutra	297	521	25.0	25.0	27.0	8.6	439.5	7.5	0.9	0.254	22
Nanay	88	2857	1.5	28.5	28.9	6.8	7.0	3.8	0.1	0.003	35
Negro	11	2154	10.0	28.6	29.8	4.3	8.6	5.2	1.1	0.027	297
Pandeiros	456	1060	1.2	19.8	24.1	7.3	81.0	4.4	0.8	0.033	22
Paraíba do Sul	384	2250	12.0	20.3	22.8	6.6	13.0	5.8	0.9	0.080	20
Paraná	238	1280	13.0	17.9	23.1	6.8	45.5	6.6	1.3	0.043	34
Pardo	438	1550	5.0	18.0	20.2	6.4	77.0	7.7	0.8	0.029	23
Paulo Sarasate	147	926	34.0	27.6	28.5	7.8	223.5	5.6	1.0	0.166	13

Pereira Passos	91	1454	18.6	24.6	24.9	5.8	108.0	7.5	0.4	0.075	16
Purus	59	2227	9.4	29.3	32.7	6.5	67.8	5.6	0.2	0.098	83
Ribeirão Diamante	252	1300	3.0	20.4	21.3	7.2	46.7	8.0	3.0	0.014	36
Rio das Mortes (MT)	201	1500	39.7	24.4	27.4	6.2	10.4	4.7	0.8	0.137	104
Rios do Semi-árido	118	600	3.0	29.3	30.7	8.0	370.0	3.7	1.3	0.049	34
Rosana	256	1125	25.0	20.5	24.8	6.7	69.3	8.1	1.8	0.030	41
Rupununi	99	1780	8.0	26.0	30.5	6.1	30.8	4.4	0.6	0.006	61
Santa Cruz do Apodi	60	767	57.5	25.0	28.3	8.0	281.7	6.2	4.0	0.034	20
Salto Grande	385	1365	19.8	17.7	20.9	6.6	120.4	4.7	0.5	0.216	30
Samuel	87	2194	87.4	21.0	32.0	6.5	29.7	7.1	2.9	0.013	110
Santa Branca	621	1301	45.0	24.3	28.3	7.5	38.0	7.9	2.1	0.017	18
São Francisco	402	1000	3.5	22.5	23.7	5.9	66.8	7.0	1.5	0.100	61
Saracá- Araticum	173	2000	1.55	28.7	26.0	4.9	11.5	5.8	1.4	0.042	113
Serra da Mesa	474	1638	154.0	24.0	26.0	8.0	100.0	10.0	3.0	0.012	51
Tapajós	6	2460	7.7	29.6	29.7	7.4	45.1	5.8	1.2	0.009	29
Três Irmãos	321	1199	60.0	20.0	25.2	7.6	153.8	7.4	1.3	0.039	13
Três Marias	567	1214	75.0	22.5	24.9	8.2	55.6	6.1	2.7	0.004	29

Trombetas	169	2431	11.0	24.2	29.5	5.7	27.3	7.5	1.5	0.010	143
Tucuruí	70	1600	75.0	29.2	30.3	6.9	55.5	7.0	1.1	0.060	61
UHE Curuá-Una	28	2096	17.0	26.5	27.7	5.3	17.5	7.9	1.8	0.016	30
UHE Miranda	700	1479	80.0	23.0	24.0	7.2	12.3	5.0	4.8	0.040	24
UHE Pedra	228	703	41.0	27.7	30.0	8.5	268.5	6.3	2.6	0.132	14
UHE São Simão	398	1474	127.0	27.14	28.0	7.4	46.4	6.0	2.0	0.015	16
Urucu	16	2290	14.5	27.3	28.3	5.4	44.5	1.9	0.7	0.168	33
Verde	330	1370	3.5	26.8	28.0	7.7	23.3	7.5	0.8	0.039	60
Vigário	418	1362	20.0	24.6	24.6	7.1	83.0	7.0	0.4	0.040	17
Yurimágua s	117	1188	5.0	22.5	27.1	7.3	140.0	5.0	0.3	0.003	52

Fig. S1. Beanplots of the year of the introduction of peacock bass in each hydrographic region. A beanplot is a one-dimensional scatter plot which shows the individual observations as small vertical lines, the estimated density next to that and an average line for the distribution (Kampstra, 2008). The dotted line represents the average for the whole plot.



Fig. S2. Pairwise relationships of selected features of the study sites: minimum and mean water temperature, pH, altitude, maximum depth, conductivity, dissolved oxygen, transparency, total phosphorus concentration and absolute latitude. The histogram and density function of each variable is given in the diagonal, the bivariate scatterplots with the regression line below the diagonal and the Pearson correlation value with the significance level above the diagonal (*, P < 0.05; **, P < 0.01, ***, P < 0.001)



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