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Homogenization of freshwater fish faunas after the elimination of a natural barrier by a dam in Neotropics

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ABSTRACT

Aim We quantify biotic homogenization of fish fauna caused by the elimination of a natural barrier between two freshwater ecoregions. We also evaluated fish introductions by different mechanisms such as aquaculture, angling and the aquarium trade in the homogenization of fish assemblages. The relative importance of native extinctions in the homogenization process was assessed by simulating the exclusion of threatened species in the data set.

Location Paraná River, south-eastern South America.

Methods A fish species list of the Parana River Basin was organized in a subset of species distributions, according to pre- and post-introductions caused by the elimination of the natural barrier and by other mechanisms. Biotic homogenization was verified by the use of Jaccard's and Bray–Curtis's coefficients, Whittaker's beta diversity index, non-metric multidimensional scaling analysis (NMDS) and nonparametric tests.

Results For all subsets of species distributions, we observed an increase in the number of non-native species in common related to the introductions. Between 40 and 52% of the species currently present in the Upper Paraná Basin dispersed upstream from the Lower Paraná after the construction of Itaipu Dam, including at least 1 class, 2 orders, 4 families and 16 genera of fish. Jaccard's coefficient between the Upper and Lower Parana River increased by 6–7.5% only considering the Itaipu Dam influence and 10.5% considering all mechanisms of fish introductions. More than 50% of the increase in similarity was caused by the elimination of the barrier. Our results indicated functional homogenization related to large-bodied Siluriformes (catfish).

Main conclusions Itaipu Lake flooded a natural barrier and allowed hydrologic connectivity between the Upper and Lower Paraná River, and many fishes of the lower part of the river were able to colonize the upper stretches. The homogenization of the two assemblages between these adjacent aquatic regions was an unpredicted result of hydropower implementation. Introductions by dam can also shift longitudinal and latitudinal body size patterns (i.e. Bergmann's rule).

Keywords

Biodiversity crisis, biogeography, dam construction, ecological filter, Parana River, water resources conservation.

INTRODUCTION

Biotic homogenization refers to a decrease in taxonomic, genetic and/or functional differences among previously distinct biota (Olden, 2006). Such homogenization can be caused by the introduction of non-native species that are often cosmopolitan or human-associated, and/or the loss of native species, most of them rare, localized and endemic (Mckinney & Lockwood, 1999; Rahel, 2002). The phenomenon of homogenization is complex and extends across all levels of biological organization and may integrate, in a synergetic way, many aspects of the current global environmental crisis such as the introduction of non-native species, extinction and extirpations of native species, biodiversity loss, climate change, habitat loss

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and habitat alteration (Rahel, 2002, 2007; Olden, 2006; Rahel & Olden, 2008). Therefore, it is a major form of global biotic impoverishment, and biodiversity loss has been considered as an unacceptable environmental change (Rockström *et al.*, 2009; Stigall, 2010).

In general, studies about homogenization have explored the loss of regional biotic integrity or distinctiveness because of the introduction of widespread, cosmopolitan or human-associated species and/or the extirpation of rare, localized and endemic species (e.g. McKinney & Lockwood, 1999; Rahel, 2000). Although many biologists have expressed major concern about this phenomenon, the extension of this process is still poorly documented in developing nations, where like other conservation issues (see Myers *et al.*, 2000; Brooks *et al.*, 2006; Abell *et al.*, 2008), this topic is often misunderstood and underexplored. In aquatic ecosystems of megadiverse countries like Brazil, for example, only recent papers have mentioned it and brought the topic to light (e.g. Vitule, 2009; Gubiani *et al.*, 2010).

In aquatic ecosystems, recent papers have expanded the theoretical framework of biotic homogenization (e.g. Olden & Poff, 2003; Olden *et al.*, 2010; Taylor, 2010; Watanabe, 2010), where introduction has generally increased local richness, as the establishment of non-native species through translocations, stocking, fish-farmers, anglers and engineering installations outpaced the extinction of native species. However, there are exceptions, where the dispersal and establishment of non-native species had destructive impacts on endemic biota (Rahel, 2002, 2007; Vitule *et al.*, 2009).

The level of biotic homogenization may be influenced by a great number of ecological characteristics, such as habitat conditions (Lambdon *et al.*, 2008; Qian *et al.*, 2008), the species involved (Rahel, 2000; Qian & Ricklefs, 2006), time after introduction and human interventions (Olden *et al.*, 2005; Smart *et al.*, 2006). In human-altered ecosystems, the removing of geographic constraints responsible for habitat isolation and dispersal limitations, for example, can provide a variety of pathways by which aquatic species can successfully invade another biota. The establishment of non-native fishes is more probable into altered system, where native assemblages have been disrupted (e.g. Moyle & Light, 1996a,b; Johnson *et al.*, 2008), such as those caused to community structure following river impoundment.

Dams can reduce hydrologic connectivity between neighbouring habitats or conversely enhance connectivity by allowing the dispersal of fish into systems outside of their natural range (Havel *et al.*, 2005; Johnson *et al.*, 2008). Reservoir construction, for example, may contribute to biotic homogenization through habitat homogenization and circumventing natural biogeographical filters (Rahel, 2002, 2007). In South America, the potential elimination of natural obstacles to fish movement has not received sufficient attention during environmental impact studies to date for many planned hydropower dams (Júlio *et al.*, 2009).

This paper aims to quantify biotic homogenization of fish fauna caused by the flooding of an isolation mechanism between the Upper and Lower Paraná River aquatic regions. The Itaipu Reservoir, located in the main channel of the Paraná River between Brazil and Paraguay, was completed in 1982, and it is one of the world's largest power plants. Itaipu inundated Sete Quedas (or Guaira) Falls, a so-called natural barrier between the Upper and Lower Paraná River regions. It is conceivable, however, that this barrier acted as an important 'ecological filter' instead of 'natural barrier', being quite impermeable for most species, but did not represent an absolutely insurmountable obstacle to the dispersion of migratory fish in periods of exceptional floods. According to Agostinho *et al.* (2007) and Júlio *et al.* (2009), in years of very high discharge, individuals of large migratory species such as *Salminus brasiliensis, Pseudoplatystoma corruscans*, *Piaractus mesopotamicus* and *Zungaro jahu* were able to cross the natural barrier in both directions, suggesting that the populations were not isolated to gene flow among regions (e.g. Bignoto *et al.*, 2009). Until now, only Langeani *et al.* (2007), Júlio *et al.* (2009) and Gubiani *et al.* (2010) have accessed the issue of species movement into the Upper Paraná River's aquatic environments after the elimination of the barrier created by the Itaipu impoundment. Although these papers are very relevant, there has not been previous concern about other changes in faunal similarities caused by the elimination of the barrier between the two regions. Further, previous work did not attempt to isolate the effect of the dam construction to that of introductions caused by different mechanisms such as aquaculture, angling and the aquarium trade between the aquatic regions. In other words, there is no framework to holistically understand biotic homogenization and its consequences.

METHODS

Study area

In south-eastern South America, the La Plata River Basin comprises a wide area of over 3.1 million km^2, covering an extensive part of Argentina's continental territory, south-east Bolivia and the southern part of Brazil, Paraguay and Uruguay. The Paraná River is the largest sub-basin, constituting 48.7% of the La Plata Basin's overall surface area. The Paraná River is formed by the joining of the Grande and Paranaíba Rivers, and it is considered the 14th longest river in the world (4695 km).

The Paraná River flows north-south into the La Plata River in northern Argentina, draining most of the south-central part of South America from the Andes to the Serra do Mar near the Atlantic Ocean (Agostinho *et al.*, 2004). According to Bonetto (1986), the Sete Quedas (or Guaira) Falls, now flooded by the Itaipu impoundment, formerly constituted a natural barrier that separated two distinct ichthyofaunistic regions: the Upper Paraná (900,000km^2), almost completely inside Brazilian territory, and the Lower Paraná (or Parano-Platense ichthyofaunistic Province *sensu* Bonetto, 1986), with 1.7×10^6 km^2 (excluding the Uruguay River) (Fig. 1). These two provinces are similar and coherent to the Upper and Lower Paraná ecological units proposed by the 'Freshwater Ecoregions of the

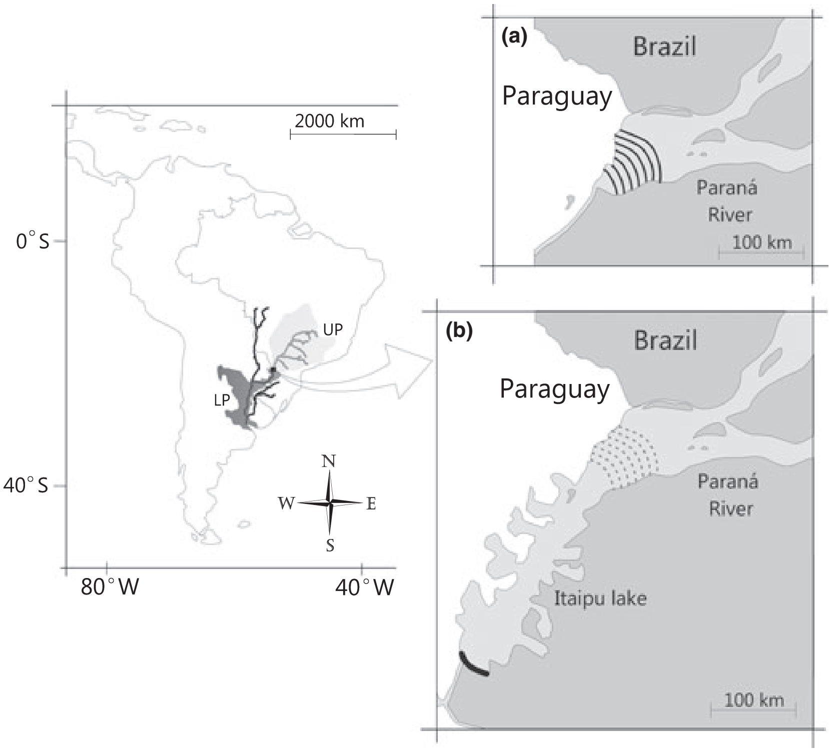

Figure 1 The La Plata River system formed by the Paraná, Paraguay and Uruguay River basins. (a) The Sete Quedas Falls (black lines) formerly constituted a natural barrier separating the Upper (UP) and Lower (LP) Paraná freshwater ecoregions. (b) The Sete Quedas Falls were flooded (slight grey dots) in 1982 by the Itaipu Impounded.

World' project (*sensu* Abell *et al.*, 2008; FEOW – http://www.feow.org).

Data collection

The master fish species list with taxonomic status and distribution data for the freshwater ichthyofauna of the Parana River Basin was generated from Reis *et al.* (2003), López *et al.* (2005), Langeani *et al.* (2007), Júlio *et al.* (2009) and FishBase (Froese & Pauly, 2011). The taxonomic classification of species follows FishBase (Froese & Pauly, 2011). We only consider fish species that have a currently valid scientific name to avoid taxonomic problems and discrepancies, such as hypothetical species and synonyms still in use. Native species were regarded as those that occur in the region as a result of natural processes, whereas non-native species were considered those with established reproducing populations registered outside their natural range because of the direct introduction by different mechanisms (e.g. aquaculture, angling and aquarium trade) or 'natural' dispersal between adjacent aquatic regions after the elimination of the barrier (indirect human influence).

Functional homogenization of fish fauna assemblages was examined through the species most commonly available ecological characteristics: maximum recorded body length, migratory behaviour and trophic level. Data on life history traits of fish species were collected from FishBase (Froese & Pauly, 2011) and available literature.

The assessment of biotic homogenization in fish fauna assemblages between the Upper and Lower Paraná River was calculated separately for the fish data provided by Langeani *et al.* (2007) and Júlio *et al.* (2009), since these authors present some differences in species distribution status (native vs. non-native) and cause of introduction (direct vs. indirect) in the upper parts of Paraná River.

The final species list was reviewed case-by-case, and a subset of species distributions and ecological characteristics was selected according to the following criteria: Lower Paraná River Basin before fish introductions (LBTI), Lower Paraná River Basin after fish introductions (LATI), Upper Paraná River Basin before fish introduction according to Langeani *et al.* (2007) (UBIL), Upper Paraná River basin before introduction according to Júlio *et al.* (2009) (UBIJ), Upper Paraná River after fish introduction (UATI), Upper Paraná River after fish introduction caused only by the Itaipu impoundment, according to Langeani *et al.* (2007) (UAIL) and Upper Paraná River after fish introduction caused only by the Itaipu according to Júlio *et al.* (2009) (UAIJ) (see Appendix S1).

Data analysis

Jaccard's coefficient, which is used for quantifying community similarity and is commonly employed in the quantitative estimates of homogenization (e.g. Rahel, 2000, 2002; Olden & Poff, 2003; Taylor, 2010), was applied among the described subset of species distributions. Jaccard's coefficient of percentage similarity was calculated as follows: $J_{x1,\, x2} = [a/(a+b+c)] \times 100$, where $x1$ and $x2$ symbolize two freshwater sites with specific fish assemblages, a is the total number of species current in both $x1$ and $x2$, b is the number of species that occur in $x1$ and do not occur in $x2$, and c is the number of species absent in $x1$ and present in $x2$. Jaccard's coefficient (expressed as percentage) was quantified as the change (differences) in similarity for each subset pairwise combination over a specified time interval: pre- and post-introductions caused by Itaipu impoundment (i.e. elimination of the barrier) and by the sum of all different mechanisms of non-native species introduction (i.e. aquaculture, stocking – legal or illegal, angling, ornamental/aquarium trade).

Because homogenization can be characterized by species loss as well as species additions (Olden & Poff, 2003), we also assessed the potential effects of species losses in the homogenization process. Effects of species losses were evaluated by simulating the exclusion of all threatened species and recalculating similarities. Even though the categorizations of threatened species (endangered, vulnerable and rare) made by Chebez (1999) and Machado *et al.* (2008) may not accurately reflect actual extinction risks, our intention was to compare the relative importance of introductions vs. extinctions of native species in driving patterns of homogenization to predict the worst possible scenario.

Differences in fish assemblages among each subset pairwise combination were also assessed using Whittaker's beta diversity index (turnover of species across gradients). The index value varies from 0 (identical faunas) to 1 (no species in common). Whittaker's index between pre- and post-introductions was compared by the Wilcoxon signed rank test and by box plots.

Our comparative analysis of fish assemblages' similarities among the subset of species distributions included a non-metric multidimensional scaling analysis – NMDS – (Clarke & Gorley, 2006) to display, in a two-dimensional plane, the variations of similarities among the described subsets. The NMDS multivariate ordination was performed on the presence/absence matrix of the subsets of species distributions and migratory behaviour using Jaccard's coefficient and on the continuous functional ecological characteristics data (maximum body length and trophic level, $\log_{10}$-transformed) using the Bray–Curtis similarity coefficient. We preferred to use the NMDS analysis over other ordination methods because it makes fewer assumptions about the nature of the data, it allows the use of any distance measure of the samples, and it also seeks to preserve the distance relationships among the samples in the low-dimensional ordination space (Clarke, 1993). Minimal connections among subsets of fish distribution were summarized by superimposing a minimum spanning tree on the NMDS ordination. The multivariate ordination analyses were performed using PAST version 1.9 (Hammer *et al.*, 2001).

The effect and magnitude of body length and trophic level were also statistically evaluated through a comparative analysis using Kruskall–Wallis one-way analysis of variance by ranks, the Wilcoxon signed rank test and box plots. All data were $\log_{10}$-transformed prior to analyses. Tests were performed to assess differences in ecological characteristics among fish assemblages and taxonomic orders between the Upper and Lower Paraná River before and after introductions. The effect of migratory behaviour frequencies was assessed using chi-square test. All box plots and nonparametric tests were performed in the R software environment for statistical computing and graphics (R Development Core Team, 2008).

RESULTS

The total data set consisted of 492 species from three classes, 13 orders and 43 families distributed in both aquatic ecoregions. The order with the highest richness was Siluriformes, having 199 species, followed by Characiformes (181 species), Perciformes (40 species) and Gymnotiformes (20 species). Of the total, 332 valid species were found to currently occur in the upper parts of the Paraná River, 264 being native and 68 (21%) non-native; In the Lower Paraná River, 299 occurred, being 292 natives and only 6 (1%) non-natives (Table 1).

Based on Langeani *et al.* (2007), our data showed that 52% of the non-natives species currently present in the Upper Paraná Basin dispersed from the Lower Paraná after the construction of Itaipu Dam. These species were distributed in 31 genera. Eleven (35%) of those already occurred in the Upper Paraná Basin, whereas 20 (65%) were exclusive to the Lower Paraná before the dam. When taking into account higher taxa, 1 class, 3 orders and 6 families that reached the Upper Paraná were also exclusive to the lower region before impoundment. When considering our data set in relation to Júlio *et al.* (2009), 40% of the non-natives species currently present in the upper basin reached the upstream regions after the elimination of the barrier. These species belonged to 25 genera. Nine (36%) already occurred in the Upper Paraná Basin, and 16 (64%) were exclusive to the Lower Paraná before the construction of the dam. Considering higher taxa, 1 class, 2 orders and 4 families that occurred exclusively in the Lower Paraná Region invaded the Upper Paraná (see Table 1 and Appendix S1).

Table 1 Number of fish taxa in the Upper and Lower Paraná basin before and after introductions caused by the elimination of the barrier and by other mechanisms.

	Before introductions		After introductions	
Taxa	Lower Paraná	Upper Paraná	Lower Paraná	Upper Paraná
Class	3	1	3	2
Order	12	6	13	11
Family	40	27	42	38
Genus*	152	$116^{J}/117^{L}$ (115†)	156	154
Species*	292	$258^{J}/259^{L}$ (253†)	299	332

*Numbers and status of native genus and species provided by Langeani *et al.* (2007)^{L} and Júlio *et al.* (2009)^{J} are different because those authors disagree on the identity of several species.

†Number of genera and species in common considering both lists (see Appendix S1).

Table 2 Homogenization measures (ΔJ) among the Lower and Upper Paraná subsets considering all fish taxa (left) and simulating the exclusion of threatened species (right).

		All fish taxa					Scenario excluding threatened species				
Lower subsets		Upper subsets									
After and before introduction		After introduction	*Ja* (%)	Before introduction	*Jb* (%)	ΔJ (1)	After introduction	*Ja* (%)	Before introduction	*Jb* (%)	ΔJ (2)
After	vs.	UAIJ	22.85	UBIJ	16.56	**6.29**	UAIJ	21.27	UBIJ	15.73	**5.54**
Before	vs.	UAIJ	22.88	UBIJ	16.53	**6.35**	UAIJ	21.78	UBIJ	15.79	**5.99**
After	vs.	UAIL	24.48	UBIL	16.77	**7.71**	UAIL	22.98	UBIL	16.06	**6.92**
Before	vs.	UAIL	24.52	UBIL	16.74	**7.78**	UAIL	24.46	UBIL	16.02	**8.44**
Before	vs.	UATI	27.03	UBIL	16.77	10.26	UATI	27.03	UBIL	16.06	10.97
Before	vs.	UATI	27.03	UBIJ	16.56	10.47	UATI	27.03	UBIJ	15.84	11.19
Before	vs.	UATI	27.03	UBIL	16.74	10.29	UATI	27.03	UBIL	16.02	11.01
Before	vs.	UATI	27.03	UBIJ	16.53	10.50	UATI	27.03	UBIJ	15.79	11.24
After	vs.	UATI	28.25	UBIL	16.77	11.48	UATI	26.69	UBIL	16.06	10.63
After	vs.	UATI	28.25	UBIJ	16.56	11.69	UATI	26.69	UBIJ	15.84	10.85

Jaccard's similarity coefficient (expressed as percentage) was calculated between the Lower and Upper subsets after (*Ja*) and before (*Jb*) introductions. ΔJ values are the respective changes in similarities after the event of fish introduction. ΔJ (1) – considering all fish taxa and ΔJ (2) – simulating the exclusion of threatened species. ΔJ bolder values show the homogenization (i.e. increase in similarity) in fish fauna assemblages between the Upper and Lower Paraná River after the elimination of the barrier by the impoundment.

There was an evident and significant increase in the similarity for all subset combinations in our quantifications (Table 2). Considering only fish introduction caused by the Itaipu, the similarity measures among the upper and lower basin increased from 16.53–16.77% to 22.85–24.52%, depending on the reference used (Langeani *et al.*, 2007 or Júlio *et al.*, 2009). In contrast, when evaluating all kinds of species introduction, the increase in similarity was from 16.53–16.77% to 27.03–28.25%, taking account the aquatic environments after the elimination of the barrier by the Itaipu impoundment. In the simulations excluding threatened species, the taxonomic similarities among the Upper and Lower Paraná Basin after impoundment, we found an increase from 15.73–16.06% to 21.27–24.46. When all kinds of species introduction were evaluated, values ranged from 15.84–16.06% to 26.69–27.03%.

As a further index of taxonomic homogenization, the turnover of species distribution subsets before and after incorporating introductions of non-native fishes dropped an average of 0.16 (Fig. 2). The analysis of turnover in fish species composition between pre- and post-introductions clearly showed a significant decrease in the distinctiveness of the fish fauna after introductions ($Z = 45$, $P = 0.0039$) (see Appendix S2).

Ordination revealed a distinct separation among the pre- and post-introduction subsets of species distributions and ecological characteristics, also indicating that similarity increased between the Upper and Lower Paraná Basin. The effect of elimination of the barrier and all mechanisms of fish introductions indicated taxonomical and functional homogenization (Fig. 3).

Nonparametric tests and box plots of ecological traits showed that larger maximum body length was the most important characteristic (or commonality) among the species that successfully colonized the upstream portion of the river. Statistical significance also found the Siluriformes phylogenetic influence on body size (Fig. 4). The effect of trophic level

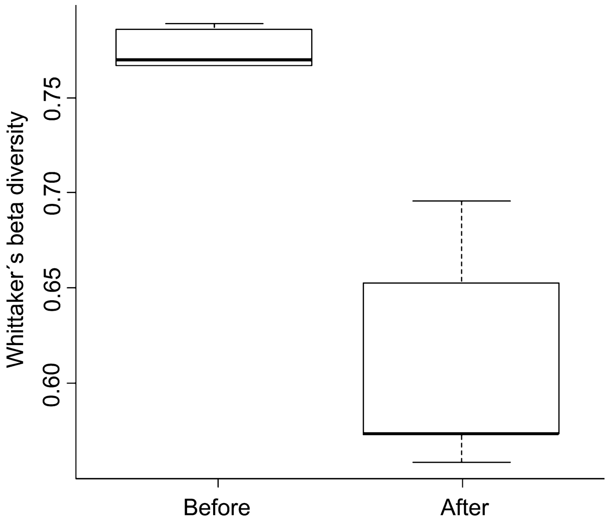

Figure 2 Box plot comparing all subsets of species distribution before and after introductions of non-native fishes using the Whittaker's beta diversity index. Bold lines in the box are the median of the data. Boxes include 50% of the data; 75th percentiles are indicate in the top of the box (upper quartile), and the bottom of the box indicates the 25th percentile (lower quartile) of the data. Vertical lines extend to the upper and lower deciles (90th and 10th percentiles). Wilcoxon signed rank test showed a significant decrease in the distinctiveness of the fish fauna after introductions ($Z = 45$, P-value = 0.0039).

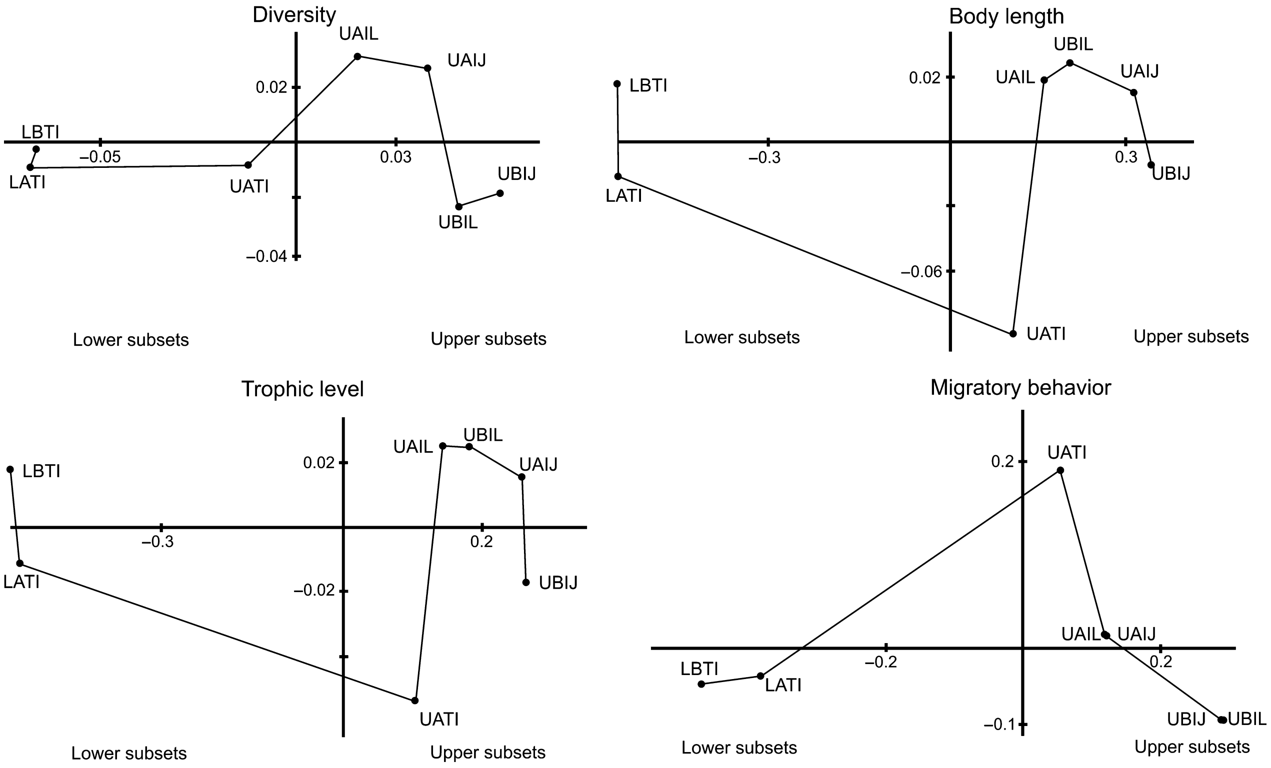

Figure 3 Ordination plot based on the non-metric multidimensional scaling analysis (NMDS, stress < 0.0001) using Jaccard's similarity coefficient of the Lower (LBTI and LATI) and Upper (UAIJ, UAIL, UBIJ, UBIL and UATI) Paraná subsets of the entire assemblage, considering species distributions (diversity), body length, trophic level and migratory behaviour. Each subset is joined using a minimum spanning tree.

($H = 5.84$, $P = 0.56$) and migratory behaviour ($\chi^2 = 0.43$, $P = 0.81$) revealed no statistical difference in all possible comparisons.

DISCUSSION

In south-eastern South America, the Itaipu impoundment flooded a natural barrier between the Upper and Lower Paraná River, and fishes of the lower part of the river basin massively colonized the upper stretches. The homogenization that has been verified was due primarily to the unidirectional fish species advance to upper regions rather than the extirpation of threatened species. The biotic homogenization between these adjacent aquatic regions was an unpredicted and unquantified result of the hydropower implementation.

Notwithstanding the significant decrease in the distinctiveness of the fish fauna after introductions, our results also indicated that similarity between the Upper and Lower Paraná River increased 6–7.5% only because of the Itaipu's influence (which represented more than 50% of the increase in similarity between the upper and lower portions of the river was caused by the elimination of the barrier), and 10.5% was related to various kinds of fish introductions. This degree of homogenization was similar to similarity among 27 areas in Japan that increased an average of 9% (13.6 forms/area Watanabe, 2010) and larger than 7.2% average similarity from 48 states of the United States (18.8 species/area Rahel, 2000), 1.2% average similarity from 13 provinces and territories in Canada (7.8 species/area Taylor, 2004; average similarity that decreased by 0.9% between 2000 and 2005 Taylor, 2010) and 3.0% among major drainages in Australian fish faunas (Olden *et al.*, 2008). Although the geographic scale and original species diversity were different among the studied areas, all results highlighted the magnitude and complexity of the homogenization process, as well as the potential dimension of the previously underexplored impacts.

Since scale can influence the community's degree of saturation (Davies *et al.*, 2011), we believe that our results were greatly affected by the spatial scale used, but they correspond to predicted scenarios at large scales, where homogenization is expected (Olden & Poff, 2003). Although species extirpations following fish introductions have rarely been detected at the large regional scale, population-level extinctions may occur at smaller spatial scales mainly when non-native species reduce the native species to a small population fragments in a few refuges (e.g. Lepprieur *et al.*, 2006; Pelicice & Agostinho, 2008). In this respect, we believe that the underestimation of the real number of many small range extirpations (i.e. local extinctions in reservoirs by environmental change or by invasive species e.g. Pelicice & Agostinho, 2008) is almost certain. On the other hand, our results were very realistic from a biogeographical viewpoint

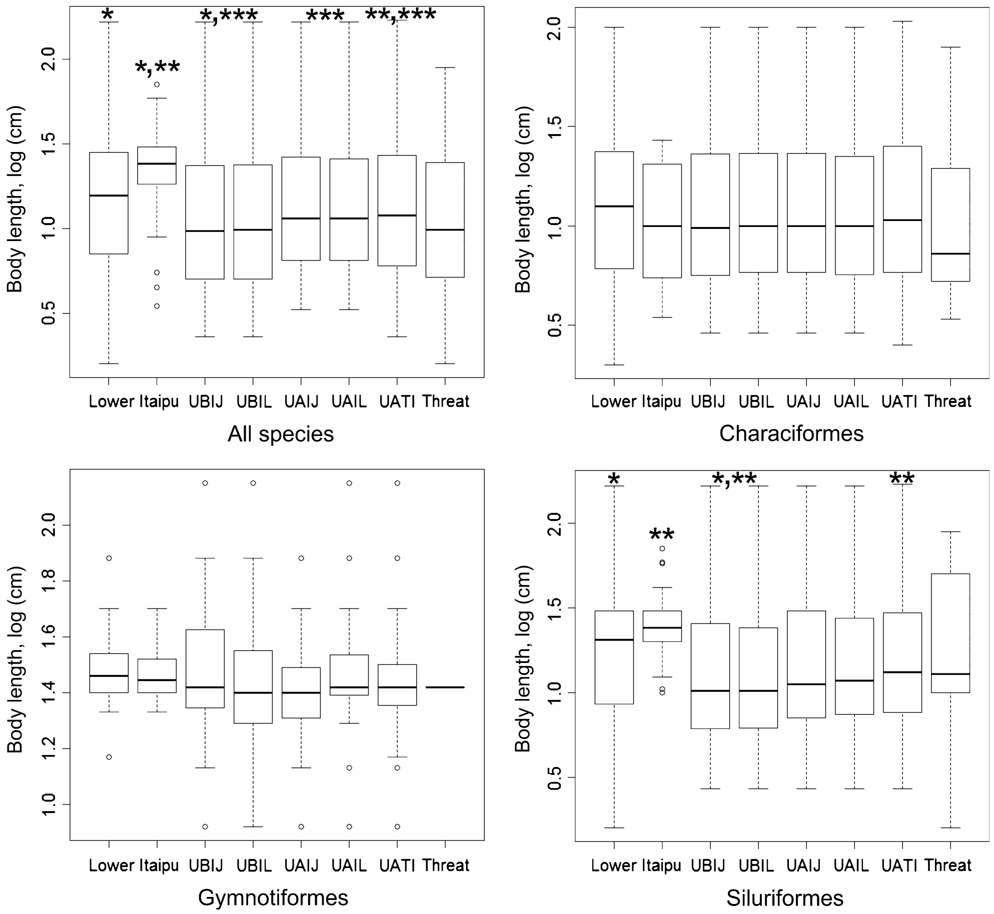

Figure 4 Box plots comparing body length effects for all species (N = 492), Characiformes (N = 181), Gymnotiformes (N = 20) and Siluriformes (N = 199). Subsets organized according to the following criteria: Lower Paraná before introductions (Lower), fish introduced only by Itaipu impoundment (Itaipu), Upper Paraná before (UBIJ and UBIL) and after (UAIJ, UAIL and UATI) introductions, and considering only threatened species (threat). Bold lines in the box are the median of the data. Boxes include 50% of the data; 75th percentiles are indicate in the top of the box (upper quartile), and the bottom of the box indicates the 25th percentile (lower quartile) of the data. Vertical lines extend to the upper and lower deciles (90th and 10th percentiles). Significant differences were observed in all species (H = 17.55, $P < 0.01$), and Siluriformes influence on body size (H = 38.01, $P < 0.01$). Subsets were pairwise compared, and statistical significances were indicated (*$P < 0.001$, **$P < 0.01$, ***$P < 0.05$).

(especially regional) and will stimulate new research in the future about this new paradigm. Even though obtaining accurate small-scale data for these two regions is very difficult and it is beyond the scope of the present study, we believe that this kind of small-scale homogenization investigation needs to be addressed. In general, the human-mediated introduction and extinction processes act at different temporal scales, where species extinctions might take many decades to come to completion, and such time-lags could generate a huge debt in extinctions that will be paid in the future (Sax *et al.*, 2002; Sax & Gaines, 2008).

In addition to the taxonomic homogenization process, our results on the influence of introduced species' ecological traits using multidimensional analysis also revealed that similarity increased between the Upper and Lower Paraná Basin. In contrast, central tendency analysis demonstrated that only body size showed significant differences before and after the massive faunal mixing, and trophic level and migratory behaviour were less likely to predict the functional implications of community changes. Our results also illustrated that those ecological traits were not useful tools to characterize species that were extirpated by simulating the exclusion of all threatened species in the homogenization process. Such observations are related to the fact that environmental threats on small- and large-bodied freshwater fishes are very complex, and it is not easy to predict the real species extinction risk in relation to simple or individual life history traits (Olden *et al.*, 2007).

Large body size was the most important ecological trait that can predict successful colonizers. In general, successfully established non-native fishes tend to have larger sizes than native fish species (Vila-Gispert *et al.*, 2005; Ribeiro *et al.*, 2008), which can be explained by the fact that body size is a crucial ecological characteristic associated with growth, fecundity and age at maturity, competitive success, mortality rates, longevity, trophic position and the functioning of food webs

(Layman *et al.*, 2005; Olden *et al.*, 2007). Our results also showed that size differences were influenced at least in part by phylogeny, due primarily to the unidirectional large-bodied Siluriformes that advance to upper regions after Itaipu impoundment. We believe that Siluriformes were significantly over-represented because they are naturally one of the most diverse groups of vertebrates, especially in the Neotropics. This group also constitutes the main fish component of the Parana River basin, and even before any fish introductions this order already accounted for more than 40% of species. Thus, the natural richness of this group of fish could not prevent new massive catfish invasions. Additionally, our results indicated that indirect human introductions by dam can also shift longitudinal and even latitudinal body size patterns especially in the southern hemisphere (i.e. Bergmann's rule, Blanchet et al., 2010).

Considering the ecological characteristics examined, migratory behaviour and trophic level seem not to be good predictors of invasion success or even represent a real barrier to invasion of the species that colonized upstream reaches. Migratory behaviour frequencies did not differ in both assemblages probably because the same groups of characins (Characiformes) and catfish (Siluriformes) that were evaluated are migratory and require the same kind of spawning, nursery and feeding habitats to complete their life history (Agostinho *et al.*, 2003). Similarly, our trophic level statistical approach did not detect differences among the upper and lower subsets before and after introductions, even though introduced species are expected to occupy an ecological niche unoccupied by the native community (Moyle & Marchetti, 2006), altering the community trophic structure of the area invaded and causing them to become homogenized in functional scale (Olden *et al.*, 2004). This topic clearly deserves further investigation, and different approaches may lead to stronger predictive models of invasion success. Indeed, we believe that comprehensive analyses on the patterns of food resource use (trophic guilds) and partitioning are needed to clarify how the naturalized non-native invaders interact with native species.

Our study is an initial assessment to understand the changes that have occurred in the Parana River Basin after the dispersal of fish into aquatic systems outside of their natural range. We would emphasize that not much effort has gone into looking for homogenization or the elimination of ecological filters and its consequences in the Neotropical region, and only recently dam construction was highlighted as a potential source of homogenization between freshwater ecosystems because of the removal of natural barriers, stocking programs and other sources of human introductions (Agostinho *et al.*, 2010; Torrente-Vilara *et al.*, 2011). How the ongoing homogenization of fish communities will exactly remodel the aquatic community structure and function remains largely unknown. Biotic changes in aquatic ecosystems by aquaculture, aquarium species additions, angling and engineering feats are increasing very fast in developing countries, and their impacts and consequences are still largely underexplored.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of fish species presence–absence data in the aquatic ecoregions of Lower and Upper Paraná River before and after fish introductions.

Appendix S2 Whittaker's beta diversity index (β) comparing all subsets of species distribution before and after introductions of non-native fishes.

BIOSKETCHES

J.R.S. Vitule is interested in ecology and management of invasive species. His research focuses on the conservation of the endemic freshwater fishes of the Atlantic rain forest, and the management of non-native fish species that threaten their survival.

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Authors contributions: J.R.S.V. conceived and developed the idea for the present study; J.R.S.V. and V.A. conducted the data analysis; J.R.S.V., F.S.N. and V.A. made databases compilation and wrote the manuscript.

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