Accepted for publication in Biological Invasions, 05/11/17

Introductions of non-native fishes into a heavily modified river: rates, patterns and management issues in the Paranapanema River (Upper Paraná Ecoregion, Brazil)

Diego Azevedo Zoccal Garcia[1], John Robert Britton[2], Ana Paula Vidotto-Magnoni[3], Mário Luís Orsi[3]

[1]Programa de Pós-Graduação em Ciências Biológicas, Universidade Estadual de Londrina, Rodovia Celso Garcia Cid, Laboratório de Ecologia de Peixes e Invasões Biológicas, Londrina, PR, CEP 86.057-970, Brazil

e-mail: diegoazgarcia@hotmail.com, Tel +55 43 3371 4477

[2]Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Poole, Dorset. BH12 5BB, United Kingdom

[3]Laboratório de Ecologia de Peixes e Invasões Biológicas, Universidade Estadual de Londrina, Rodovia Celso Garcia Cid, Londrina, PR, CEP 86.057-970, Brazil

Abstract

Understanding the pathways and impacts of non-native species is important for helping prevent new introductions and invasions. This is frequently challenging in regions where human activities continue to promote new introductions, such as in Brazil, where aquaculture and sport fishing are mainly dependent on non-native fishes. Here, the non-native fish diversity of the Paranapanema River basin of the Upper Paraná River Ecoregion, Brazil was quantified fully for the first time. This river has been subject to considerable habitat alteration through hydroelectric dam construction and concomitant development of aquaculture and sport fishing. Through compilation of a non-native fish inventory by literature review, with complementary records from recent field studies, analyses were completed on the timings of introduction, and the taxonomy, origin and introduction vectors of the fishes. A total of 47 non-native fish are now present across the basin. Of these, 24 invaded from the Lower Paraná River following construction of Itaipu Dam that connected previously unconnected fish assemblages. Activities including fish stocking, aquaculture and sport angling continue to result in new introductions. Discounting Itaipu invasions, the introduction rate between 1950 and 2014 was approximately one new introduction every three years. Introduced fish were mainly of the Cichlidae and Characidae families; most species were from other South American ecoregions, but fishes of African, Asian, North American and Central American origin were also present. These introductions have substantially modified the river's fish fauna; when coupled with altered lentic conditions caused by impoundment, this suggests that the river's native fishes are increasingly threatened.

Keywords: Biodiversity; Invasion; Aquaculture; Hydroelectric dams; Hydropower.

Introduction

Quantifying the extent of introductions of non-native species into different biogeographic regions is important for identifying how anthropogenic activities modify natural patterns of biodiversity (Villéger et al. 2011; Magurran et al. 2015). As introductions of non-native species result in global biotic homogenization (Rahel 2000; Olden et al. 2004), it is important to understand the pathways and rates of introductions between biogeographic regions, especially in this era of globalization (Jackson and Grey 2013). Introductions of non-native species are often coincident with the anthropogenic modification of natural habitats that can increase invasion risk (McKinney 2006; Poff et al. 2007). Thus, the interaction of introduction pressure and environmental change frequently exacerbates the issues faced by managers when attempting to limit new introductions and then prevent invasions (Britton et al. 2011).

In freshwaters, river basins are frequently considered as biogeographic islands in which opportunities for new species to invade are primarily from introductions resulting from anthropogenic activities, such as aquaculture (Gozlan et al. 2010). Introduction rates into river basins can be high with, for example, 96 introduced species now present in the River Thames, England (Jackson and Grey 2013). In developing inventories of non-native species, the identification of vectors and pathways enables identification of proactive management approaches that can focus efforts on preventing further introductions via greater surveillance and regulation. In some countries, pro-active approaches to prevent and manage non-native species are, however, confounded by environmental and societal factors that promote the likelihood of new invasions, albeit often unintentionally. In Brazil, for example, a combination of measures to increase hydropower provision via river impoundment, the promotion of the aquarium trade using ornamental fish, and the use of intensive aquaculture is substantially increasing the rate of introduction and establishment of non-native species (Britton and Orsi 2012; Lima Junior et al. 2015; Xiong et al. 2015; Padial et al. 2016; Tófoli et al. 2016). Indeed, there is a long legacy of introductions of non-native fishes into many Brazilian river basins (Agostinho et al. 2007; Pelicice et al. 2015; Frehse et al. 2016), including numerous translocations between South American ecoregions that are diverse in species richness (Reis et al. 2016). Therefore, understanding the respective contributions of these human activities (vectors) to the non-native fish fauna of specific Brazilian river basins and ecoregions is important in determining how future introductions could be prevented (Britton and Orsi 2012; Ortega et al. 2015).

The vectors responsible for the introduction of non-native freshwater fish in Brazil, in areas such as the Upper Paraná freshwater ecoregion, include aquaculture (Azevedo-Santos et al. 2011; Ortega et al. 2015), fish stocking to support sport angling (Britton and Orsi 2012), releases of live-bait fishes used by anglers (Garcia et al. 2015), the aquarium trade (Magalhães and Jacobi 2013; Magalhães and Vitule 2013), and the use of fish as biological control agents (Azevedo-Santos et al. 2016). Moreover, the elimination of a natural barrier to fish movement via construction of the Itaipu Dam has already resulted in a mass invasion of the Upper Paraná from the Lower Paraná basin (Júlio Júnior et al. 2009; Vitule et al. 2012; Daga et al. 2015). The Upper Paraná ecoregion is in one of the most inventoried areas of Brazil (Graça and Pavanelli 2007; Langeani et al. 2007), facilitating analysis of the origin and vectors of the non-native fishes. These data then provide more precision and quality on extant knowledge of the introduced species that can then be applied to developing policy and practice for their management.

The Paranapanema River is a major tributary of the Upper Paraná River that has undergone considerable hydro-geomorphological alteration via the construction of 11 hydropower reservoirs. Correspondingly, the river is a highly representative habitat in South America where the interactions of human activities and environmental changes are substantially altering the composition of the fish fauna. Such profound hydro-geomorphological disturbances to rivers tend to promote the likelihood of invasions (Johnson et al. 2008; Britton and Orsi 2012). Correspondingly, the aim here was to investigate the non-native fishes that are now present in the Paranapanema River, with compilation of an inventory of the species present, and analysis of their timings of introduction, current distribution, origins and vectors. Their taxonomy was also determined, with analysis of the orders and families of non-native fishes most frequently introduced.

Methods

Study area

The Upper Paraná Freshwater Ecoregion is located upstream of the Itaipu Reservoir and Lower Paraná River, with the Rivers Paranapanema, Grande, Paranaíba and Tietê being its main tributaries (Castro et al. 2003). The ecoregion is almost entirely in Brazil, except for its southwest region in Paraguay, and it is the most industrialized and urbanized region of Brazil, with large number of cities with over 1 million inhabitants. Originally, this area contained the Atlantic Rainforest and Brazilian Savannah biomes that have now largely been converted to agriculture and livestock. In addition, the Upper Paraná River basin had its watercourses transformed into reservoirs, primarily for electricity production (Agostinho et al. 2007, 2016).

The Paranapanema River basin extends from the southwest of the state of São Paulo (SP) to the northwest of the state of Paraná (22º - 26ºS and 47 - 54ºW) (Fig. 1). Its sources are in the Serra de Paranapiacaba at 900 m altitude, and it flows 930 km to the west before its confluence with the Paraná River. Its course is subdivided into three main stretches: Upper Paranapanema, formed from the sources to the confluence of the Apiaí-Guaçu River, which together with the Itapetininga River are the main tributaries of this section; Middle Paranapanema, where the main tributaries are Itararé and Pardo rivers; and Lower Paranapanema, with the Rivers Cinzas, Tibagi and Pirapó being the main tributaries (Sampaio 1944) (Fig. 1). The hydroelectric development of the Paranapanema River began in 1936, with 11 dams now present that have modified the main river channel into a succession of cascading reservoirs (Fig. 1; Orsi et al. 2016). Cage and tank aquaculture is practised in and around some reservoirs (Orsi and Agostinho 1999; Ramos et al. 2013). The naturally high fish species richness of the basin (127 species, e.g. Castro et al. 2003; Duke Energy 2008) is threatened by these reservoirs, with considerable declines in native fish species richness being recorded in, for example, the Capivara Reservoir (Orsi and Britton 2014). For the purposes of this study, the presence of non-native fishes within the basin was considered across 11 locations that covered the major hydroelectric reservoirs, the main river channel and river tributaries (Fig. 1; Table1).

Fish species inventory and data analysis

In the study, a species was considered to be non-native in the Paranapanema River if literature suggested it should not have naturally occurred in the river due to biogeographical factors. The non-native fishes in the river thus included species from other ecoregions of South America, as well as from other continents. They also included species from the Lower Paraná River that, prior to construction of the Itaipu Dam, were biogeographically isolated from the Upper Paraná River (Vitule et al. 2012).

To compile the inventory list of non-native fishes, the principal method was literature review. The review was based on searches completed in Web of Science, and supplemented by Google Scholar, starting with the river name (‘Paranapanema’) or ecoregion (‘Upper Paraná’) in ‘title’ searches, and then using these within Boolean logic search terms with words including ‘alien’, ‘non-native’, ‘invasive’, ‘non-indigenous’, ‘introduced’, ‘allodiversity’, and their combinations. Searches were then completed using the same terms but searching for ‘topic’ to provide any additional material that would otherwise have been missed. These searches provided an overall list of literature that, following review, provided a reduced number of papers from which information relevant to the study were extracted. In addition to these published sources, grey literature was also sourced. This grey literature primarily comprised documents published by power companies in charge of the hydroelectric dams and often provided details on intentional introductions of non-native fish into the reservoirs that were not available from any other source (e.g. CESP 1997). This review thus provided a list of non-native fishes that have been introduced into the Paranapanema River. Some of the papers and reports also provided complementary information on the timing of detection of the non-native fish (and their introduction in some cases), plus their taxonomy, native origin and introduction vector. Where taxonomic and native origin information was not available then it was collated from other literature sources; these were primarily Reis et al. (2003), Britski et al. (2007), and Eschmeyer et al. (2016).

The introduction vector of each species was assessed from information provided in the original literature source; when this information was not present, then the vector was interpreted from subsequent literature on that species (e.g. whether it is primarily a species used in aquaculture or sport angling). Where this information was lacking then author knowledge was used. The vectors that were identified were: (i) fish stocking via sport-angling; (ii) live-bait fishes used in sport angling; (iii) aquaculture ('fish farming'); (iv) biological control (primarily of mosquito); (v) Itaipu Dam, where the non-native fish was present in the river only as a direct consequence of their upstream movement that was enabled by the dam flooding the natural biogeographic barrier of the Sete Quedas Falls; and (vi) the aquarium trade (Júlio Júnior et al. 2009; Britton and Orsi 2012; Vitule et al. 2012; Azevedo-Santos et al. 2016).

To provide an up-to-date inventory of non-native species in the river, the literature review was complemented by field samples. These samples had been collected quarterly between 2012 and 2014 as part of a monitoring project within the Paranapanema River basin to detect natural fish spawning and nursery areas. Data from these samples were used here only to provide new information on the presence of non-native fishes that represented a new introduction as they had yet to be reported in the literature. The samples were collected from the major habitats of the Rosana, Taquaruçu, Capivara, Canoas I, Canoas II and Salto Grande reservoirs, and their river tributaries (Fig. 1). Adult and juvenile fishes were captured by seine nets (6.0 m^2, 2.0 mm of mesh) and complemented by samples of juvenile and larval fishes collected by sieves (0.4 m^2, 0.5 mm of mesh). As any identified new species would have no supporting information on their native origin and vector, these were determined through literature review and author opinion, as described above.

Following compilation of the inventory list of the non-native fishes and their associated information (taxonomy, timing of introduction, native origin, and vector), these data were evaluated to determine their main patterns. To assess the temporal and spatial pattern of non-native fish introductions, the year of their first detection/introduction was identified (where detection was used as a proxy of the year of introduction). This enabled calculation of the proportion of non-native species that were introduced over time, their introduction rate per year, the cumulative number present, and the spatial variation in the number of species present in the different reservoirs (Fig. 1). If the introduced species was South American, then their geographic origin was given as the donor freshwater ecoregion (Abell et al. 2008); if its origin was from outside of South America then their continent was used (e.g. Africa, Asia, North America and Central America). Analysis of the vectors of introduction was determined as the proportion of species that were introduced via that vector. In addition, information on fish stockings rates in the reservoirs was provided where this was available. Note that the species lists and associated information used in these analyses are provided in full in Appendices 1 and 2 of the Supplementary Material.

Results

Literature review

Initial searches of the river and ecoregion names were used to identify the temporal pattern in the literature of the region. 'Paranapanema' returned 86 papers in Web of Science, published between 1992 and 2017, of which 58 (67 %) have been published in the last decade (taken as 2008 to 2017). 'Upper Paraná' returned 328 papers in Web of Science, published between 1968 and 2017, of which 208 (63 %) have been published in the last decade. Of these peer-reviewed papers, information on the introduced fishes of the Paranapanema River basin was extracted from 20. This information was then supplemented by searched in Google Scholar that provided a further 10 papers in non-ISI journals from which information was extracted. Finally, a combination of online searches and sourced documents from power companies (e.g. providing stocking records) and universities (e.g. PhD theses) provided a further 15 literature sources from which data were extracted. Thus, the literature review aspect of the study is based on 30 peer-reviewed papers and 15 items of grey literature (*cf*. Supplementary Material).

Initial non-native fish introductions

Literature review revealed that the first recorded non-native fish in the Paranapanema River occurred in the 1950s, with the North American largemouth bass, *Micropterus salmoides* Lacepède, 1802, reported (Fig. 2; Appendix 2). Further deliberate introductions of non-native fishes occurred between 1978 and 1992 through fish stocking programmes conducted by 'Companhia Energética de São Paulo' (CESP 1997), with seven non-native species released (Table 1; Appendix 2). A major introduction event was then the flooding of the natural biogeographic barrier of the Sete

Quedas Falls during the formation of the Itaipu Reservoir. This enabled 24 fishes originating from the Lower Paraná Ecoregion to disperse upstream into the Paranapanema River (Júlio Júnior et al. 2009; Vitule et al. 2012; Daga et al. 2015), with these new species resulting in a major peak in the introduction rate (Fig. 2).

Non-native fish composition and distribution

A total of 45 non-native fish species have been recorded in the literature as being introduced into the Paranapanema River between 1950 and 2014 (Table 2; Appendix 1). The field sampling conducted between 2012 and 2014 in a number of reservoirs and their tributaries (*cf*. Methods) increased this total to 47 non-native fishes (Table 2; Appendix 1). This represents an overall rate of 0.72 new species per year; if the 24 fishes associated with the construction of the Itaipu Dam are removed from the data then this reduces to 0.35 new species per year. The 47 non-native fishes belong to eight orders and 21 families. The orders are primarily Characiformes (8 families, 13 species), Siluriformes (6 families, 12 species), and Perciformes (3 families, 12 species) (Appendix 1).

The two new non-native fishes added to the non-native fish inventory from the field sampling were *Ossancora eigenmanni* (Boulenger, 1895) and *Laetacara araguaiae* Ottoni & Costa, 2009. Note that although *O. eigenmanni* has previously been recorded in the basin, it had only been recorded as unidentified Doradidae (Duke Energy 2008), with these new samples now enabling their identification to species level. Conversely, *L. araguaiae* has not reported previously but was present in field samples collected from the Rosana Reservoir in 2013 and was subsequently identified to species level in the laboratory.

Information gathered from the published literature revealed that in terms of distribution in the Paranapanema River, the species that have been detected in at least 9 of the 11 evaluated habitats of the basin were *Hyphesobrycon eques* (Steindachner, 1882) (mato-grosso), *Metynnis lippincottianus* (Cope, 1870) (pacu-cd), *Plagioscion squamosissimus* Heckel, 1840 (corvina), and *Oreochromis niloticus* (Linnaeus, 1758) (Nile tilapia) (Fig. 1; Table 2; Appendix 1). Most of the non-native fishes were recorded within the hydropower reservoirs, whereas only a small proportion were recorded as being present in the main river channel (Fig. 3). Of the reservoirs, the Rosana, Taquaruçu, and Capivara reservoirs had the highest numbers of introduced non-native fishes (Fig. 3).

Native origin and vectors

Nine South American freshwater ecoregions provided 38 of the 47 non-native fishes present in the basin (83% of all introductions) (Fig. 4a). The regions of native origin of these species were primarily Paraguay and the Lower Paraná ecoregions, the Amazonas, Orinoco, Guianas, and Uruguay River basins. The importance of the Lower Paraná ecoregion as a donor region is reflected in the main introduction vector being the flooding of the Sete Quedas Falls via Itaipu Dam construction that enabled 24 species to invade (Fig. 4b). The native origins of species outside of South America were Africa, Asia, North America and Central America, with their vectors mainly being aquaculture, fish stocking and release of ornamental fish (aquarium trade) (Fig. 4b).

Discussion

The number of non-native fishes in the reservoirs and tributaries of the Paranapanema River basin of the Upper Paraná Ecoregion has continued to increase over time, with at least 47 non-native fishes now present. When the influence of the Itaipu Dam is removed from the data, there was a new fish species recorded in the river approximately every three years. These results represent the highest numbers of non-native fish recorded in the Paranapanema River basin to date. In the riverine habitats, three non-native fishes have been recorded previously (Castro et al. 2003), whereas in reservoirs and the tributaries, previous recordings were 13 species (Carvalho et al. 2005) through to 27 (Orsi et al. 2016), 31 (Duke Energy 2008), and finally up to 39 species (Ortega et al. 2015). The families now contributing most to the introduced fish fauna are the Cichlidae and Characidae; of the 10 cichlids present, five have been recorded as *Cichla* spp. (peacock basses).

Across the wider literature review, it was apparent that the Paranapanema River has a relatively low native fish species richness compared to other rivers of the Upper Paraná Ecoregion (e.g. compared to the Paraná, Paranaíba, Grande and Tietê rivers) (Agostinho et al. 1997). However, it was also apparent that the Paranapanema now has a relatively high number of introduced fishes compared with some of these other rivers (Ortega et al. 2015). In other areas of the world that have been studied for their non-native taxa, 15 non-native fish species were recently recorded in the River Thames, England (of 96 non-native species recorded in total) (Jackson and Grey 2013) and in Lake Naivasha, Kenya, 11 non-native fish were introduced between the 1920s and 2000s (Gherardi et al. 2011). Kolar and Lodge (2002) identified 45 non-native fishes in the North American Great Lakes for development of their invasion predictions and risk assessment. As each of these freshwater systems were described as highly invaded (Kolar and Lodge, 2002; Gherardi et al. 2011; Jackson and Grey 2013) then the

Paranapanema River can thus also be considered as a highly invaded freshwater system at the global scale.

The construction of the Itaipu Dam was responsible for over 50% of the non-native fish present in the Paranapanema River basin. The construction of this dam flooded the Sete Quedas Falls in 1982 that comprised of a sequence of 19 groups of waterfalls that physically separated the fish fauna of Upper and Lower Paraná basins (Bonetto 1986; Vitule et al. 2012). Its flooding enabled the upstream dispersal of a number of fishes from the Lower Paraná basin into the Upper Paraná basin where they were non-indigenous (Júlio Júnior et al. 2009). The movement of these fishes through the Paranapanema River was restricted by the Capivara Dam that was built in 1978 without fish passage. However, species such as *Pterygoplichthys ambrosettii* (Holmberg, 1893) and *Loricariichthys platymetopon* Isbrücker & Nijssen, 1979 have since moved above this dam following their rescue from its hydropower turbines and their subsequent translocation into the upstream reservoir (Casimiro et al. 2017). In addition, the 11 hydroelectric reservoirs now present dam along the Paranapanema River have enabled increased cage aquaculture and the creation of sport fisheries (Britton and Orsi 2012). Both activities are heavily reliant on non-native fishes such as *O. niloticus* and *Cichla* spp. respectively (Britton and Orsi 2012). In addition, at least 13 million fish across seven non-native species were released in the reservoirs in stocking events between 1978 and 1992, with these fishes now having established populations (CESP 1997). This number of released fishes could be considered as representing high propagule pressure, an important factor that tends to increase the probability of introduced species establishing (Lockwood et al. 2005, 2009). It is thus suggested that the major engineering of the Paranapanema basin specifically, and the Paraná River more generally, has been the primary driver for the increased non-native fish diversity, and thus all other introduction vectors may be considered secondary and/or supplementary to this.

Although this study has documented 47 introduced fish in the basin, the invasion status of these fish (for example, whether they are established or invasive) was not always apparent. However, with their repeated reporting in the literature and/or their recording in field samples, it was apparent that most of these fishes have, at the very least, established sustainable populations. The high proportion of these fishes within the reservoirs, rather than the main river channel, suggests that these are important habitats for the establishment of these fishes. Indeed, studies generally suggest that impoundments enhance the probability of non-native fishes establishing populations (e.g. Johnson et al. 2008). The high proportion of invasive cichlids in the Paranapanema reservoirs is also supported by other studies that suggest Neotropical impoundments are prone to dominance by introduced cichlids (e.g. Agostinho et al. 2007; Langeani et al. 2007; Ortega et al. 2015). The dominance of cichlid fishes, such as *Cichla*, in the altered hydro-geomorphic conditions of the reservoirs might also relate to the shift in abiotic conditions in the reservoirs, for example, their reduced turbidity. This is because increased water clarity can assist sight feeding piscivores in prey detection and capture, even in the presence of macrophytes that usually provide prey refugia (Pelicice and Agostinho 2009). A potentially important factor in the establishment of *Cichla* spp. in the reservoirs is also their reproductive plasticity. The spawning of *Cichla piquiti* Kullander & Ferreira, 2006 is seasonal in their native Amazonian rivers, with increased reproductive activity at the beginning of the rainy season (Muñoz et al., 2006). In their invasive population of the Itumbiara Reservoir (Paranaíba River basin, Southeast

Brazil), however, reproduction occurred throughout the year (Vieira et al. 2009). This shift in reproductive behaviour, that was asynchronous with rainfall and peak water temperatures, potentially conferred considerable invasion advantages via elevated recruitment (Vieira et al. 2009). Plasticity in life history traits is a feature of many successful invaders, as it usually enables rapid adaptive responses to new conditions (Gozlan et al. 2010). For example, demographic bottlenecks relating to low founding population sizes can be overcome through the introduced individuals growing faster and maturing earlier in order to be able to establish populations more rapidly (Britton and Gozlan 2013).

The high number of non-native fishes introduced into the Paranapanema River means it is important to consider their ecological impacts, especially as the river also has a relatively high native fish species richness at global levels (at least 127 fishes; Castro et al. 2003; Duke Energy 2008). In the reservoirs, there has been an increased number and abundance of invasive piscivorous fishes, especially of the *Cichla* genus (Orsi and Britton 2014). The impacts of introduced *Cichla* fishes have already received considerable attention in the Paraná basin more generally, where they have reportedly substantially increased predation pressure, resulting in deleterious impacts on native fish species richness (e.g. Pelicice and Agostinho 2009; Menezes et al. 2012; Pelicice et al. 2015). A study documenting temporal changes in the fish assemblage of the Capivara Reservoir between 1992 and 2010 revealed that of 50 native fishes present in the initial samples, there were only 23 present in final samples, with an additional 11 non-native fish by 2010 (Orsi and Britton 2014). However, as this native diversity started to decrease prior to *Cichla* establishment, then it was most likely driven initially by the substantial alterations to the hydro-geomorphology of the river, with losses then exacerbated by high *Cichla* predation pressure (Orsi and Britton 2014).

The importance of vectors such as the Itaipu Dam for non-native fish introductions in the Paranapanema River was reflected in the origin of most introduced fishes being other Neotropical basins and South American ecoregions. Indeed, this is typical of the non-native fish fauna of Neotropical reservoirs more generally (Ortega et al. 2015; Latini et al. 2016). However, non-native fishes were also present in the Paranapanema River from four other continents, revealing how globalization of activities such as the ornamental fish trade and aquaculture has resulted in some fishes, such as *Cyprinus carpio* Linnaeus, 1758 and *O. niloticus*, achieving a worldwide distribution (Gozlan et al. 2010; Britton and Gozlan 2013). Moreover, given the propensity of fish farmers to diversify their cultured fishes using fish from different countries and continents (Gozlan 2008), it is probable that more non-South American fish will be introduced into the Paranapanema basin via aquaculture in future.

From a management perspective, the increased non-native fish diversity and decrease in native diversity in the Paranapanema River basin raises substantial conservation concerns. These results suggest that strategies that prevent new introductions via better regulation of the important introduction vectors should be considered. For example, the aquaculture sector is an important economic activity in the Paranapanema basin and is an important introduction vector in the Upper Paraná ecoregion (Agostinho et al. 2007; Ortega et al. 2015; Latini et al. 2016). Non-native fishes, including *Clarias gariepinus* (Burchell, 1822) and *O. niloticus* are cultured (Orsi and Agostinho 1999); both are global invaders and harmful to native fish diversity (Forneck et al. 2016; Latini et al.

2016; Padial et al. 2016). Brazilian aquaculture also tends to prefer cultivating non-native species (Agostinho et al. 2007), with a proposed bill (Law 5989/09) encouraging this further (e.g. Pelicice et al. 2014). In combination, this suggests there is a pressing requirement for increased education of fish farmers on the risks their activities can pose to native fish diversity. This should be allied with enhanced biosecurity of aquaculture sites to prevent fish escapes, with a concomitant shift towards farming native fishes (Britton and Orsi 2012; Forneck et al. 2016). It is also recommended that all policies that promote introducing non-native fishes in reservoirs (e.g. for sport angling) are terminated, with increased regulation and supervision on the keeping and release of ornamental fishes by the public. Unfortunately, given the large spatial distribution of many of the extant non-native fishes that have been introduced into the Paranapanema River basin, there are few management options available that would be effective at preventing their further dispersal and impact (Britton et al. 2011). Consequently, management priorities could aim to prevent new introductions and implement mitigation actions that protect native fish diversity.

In summary, the Paranapanema River is a highly altered river system due to the construction of hydroelectric reservoirs. These altered conditions, in conjunction with human activities such as aquaculture and sport angling, have facilitated the introduction and subsequent invasion of many non-native fishes. Thus, it is apparent that the fish fauna of this river within the Upper Paraná Ecoregion has been heavily modified due to a range of human activities that have altered its physical and biological characteristics, and facilitated the introduction and invasion of many non-native fishes.

Acknowledgements

We thank Fernando Jerep and José Birindelli (MZUEL), Carla S. Pavanelli (Nupelia-UEM), and Heraldo A. Britski (MZUSP) by the clarification about the origin of some non-native species; Sandro G. Britto by provided reports; and Lepib co-workers by provided help in field samples.

References

Abell R, Thieme ML, Revenga C, Bryer M, Kottelat M, Bogutskaya N, Coad B, Mandrak N, Balderas SC, Bussing W, Stiassny MLJ, Skelton P, Allen GR, Unmack P, Naseka A, Ng R, Sindorf N, Robertson J, Armijo E, Higgins JV, Heibel TJ, Wikramanayake E, Olson D, López HL, Reis RE, Lundberg JG, Sabaj Pérez MH, Petry P (2008) Freshwater Ecoregions of the World: a new map of biogeographic units for freshwater biodiversity conservation. BioScience 58:403-414. doi: 10.1641/B580507

Agostinho AA, Júlio Jr. HF, Gomes LC, Bini LM, Agostinho CS (1997) Composição, abundância e distribuição espaço-temporal da ictiofauna. In: Vazzoler AEAM (ed) A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e socioeconômicos. Eduem, Maringá, pp 179-208

Agostinho AA, Gomes LC, Pelicice FM (2007) Ecologia e manejo de recursos pesqueiros em reservatórios do Brasil. Eduem, Maringá

Agostinho AA, Gomes LC, Santos NCL, Ortega JCG, Pelicice FM (2016) Fish assemblages in Neotropical reservoirs: colonization patterns, impacts and management. Fish Res 173:26-36. doi: 10.1016/j.fishres.2015.04.006

Azevedo-Santos VM, Rigolin-Sá O, Pelicice FM (2011) Growing, losing or introducing? Cage aquaculture as a vector for the introduction of nonnative fish in Furnas Reservoir, Minas Gerais, Brazil. Neotrop Ichthyol 9:915-919. doi: 10.1590/S1679-62252011000400024

Azevedo-Santos VM, Vitule JRS, García-Berthou E, Pelicice FM, Simberloff D (2016) Misguided strategy for mosquito control. Science 351:675. doi: 10.1126/science.351.6274.675

Bonetto AA (1986) The Paraná river system. In: Davies BR, Walker KF (eds) The ecology of river systems. Dr. Junk, Dordrecht, pp 541-556

Britski HA, Silimon KZS, Lopes BS (2007) Peixes do Pantanal: manual de identificação. Embrapa Informação Tecnológica, Brasília

Britton JR, Gozlan RE, Copp GH (2011) Managing non-native fish in the environment. Fish Fish 12:256-274. doi: 10.1111/j.1467-2979.2010.00390.x

Britton JR, Orsi ML (2012) Non-native fish in aquaculture and sport fishing in Brazil: economic benefits versus risks to fish diversity in the upper River Paraná basin. Rev Fish Biol Fisher 22:555-565. doi: 10.1007/s11160-012-9254-x

Britton JR, Gozlan RE (2013) How many founders for a biological invasion? Predicting introduction outcomes from propagule pressure. Ecology 94:2558-2566.

Carvalho ED, Britto SGC, Orsi ML (2005) O panorama das introduções de peixes na bacia hidrográfica do rio Paranapanema, Alto Paraná, Brasil. In: Rocha O, Espíndola ELG, Fenerich-Verani N, Verani JR, Rietzler AC (eds) Espécies invasoras em águas doces: estudos de caso e propostas de manejo. Editora da Universidade Federal de São Carlos, São Carlos, pp 253-273

Casimiro ACR, Garcia DAZ, Costa ADA, Britton JR, Orsi ML (2017) Impoundments facilite a biological invasion: dispersal and establishment of non-native armoured catfish *Loricariichthys platymetopon* (Isbrücker & Nijssen, 1979) in a neotropical river. Limnologica 62:34-37. doi: 10.1016/j.limno.2016.11.001

Castro RMC, Casatti L, Santos HF, Ferreira KM, Ribeiro AC, Benine RC, Derdis GZP, Melo ALA, Stopiglia R, Abreu TX, Bockmann FA, Carvalho M, Gibran FZ, Lima FCT (2003) Estrutura e composição da ictiofauna de riachos do rio Paranapanema, Sudeste e Sul do Brasil. Biota Neotropica 3:1-31. doi: 10.1590/S1676-06032003000100007

CESP (1997) Produção de alevinos, povoamento/repovoamento nos reservatórios da CESP, CPFL e outros. Companhia Energética de São Paulo, São Paulo

Daga VD, Skóra F, Padial AA, Abilhoa V, Gubiani EA, Vitule JRS (2015) Homogenization dynamics of the fish assemblages in Neotropical reservoirs: comparing the roles of introduced species and their vectors. Hydrobiologia 746:327-347. doi: 10.1007/s10750-014-2032-0

Duke Energy (2008) Peixes do rio Paranapanema. Horizonte Geográfico, São Paulo

Eschmeyer WN, Fricke R, Van der Laan R (2016) Catalog of fishes: genera, species, references. http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp. Accessed 13 April 2016

Forneck SC, Dutra FM, Zacarkim CE, Cunico AM (2016) Invasion risks by non-native freshwater fishes due to aquaculture activity in a Neotropical stream. Hydrobiologia 773:193-205. doi: 10.1007/s10750-016-2699-5

Frehse FA, Braga RR, Nocera GA, Vitule JRS (2016) Non-native species and invasion biology in a megadiverse country: scientometric analysis and ecological interactions in Brazil. Biol Invasions 18:1-13. doi: 10.1007/s10530-016-1260-9

Garcia DAZ, Hernandes MC, Silva-Souza ÂT, Orsi ML (2015) Establishment of non-native predator (Pisces, Erythrinidae) in a tributary of the Upper Paraná River basin, south Brazil. Neotrop Biol Conserv 10:177-181. doi: 10.1111/jai.12468

Gherardi F, Britton JR, Mavuti KM, Pacini N, Grey J, Tricarico E, Harper DM (2011) A review of allodiversity in Lake Naivasha, Kenya: Developing conservation actions to protect East African lakes from the negative impacts of alien species. Biol Conserv 144:2585-2596. doi: 10.1016/j.biocon.2011.07.020

Gozlan RE (2008) Introduction of non-native freshwater fish: is it all bad? Fish Fish 9: 106-115. doi: 10.1111/j.1467-2979.2007.00267.x

Gozlan RE, Britton JR, Cowx IG, Copp GH (2010) Current knowledge on non-native freshwater fish introductions. J Fish Biol 76:751-786. doi: 10.1111/j.1095-8649.2010.02566.x

Graça WJ, Pavanelli CS (2007) Peixes da planície de inundação do alto rio Paraná e áreas adjacentes. Eduem, Maringá

Jackson MC, Grey J (2013) Accelerating rates of freshwater invasions in the catchment of the River Thames. Biol Invasions 15:945-951. doi: 10.1007/s10530-012-0343-5

Johnson PT, Olden JD, Vander Zanden MJ 2008. Dam invaders: impoundments facilitate biological invasions into freshwaters. Front Ecol Environ 6:357-363. doi: 10.1890/070156

Júlio Júnior HF, Dei Tós C, Agostinho AA, Pavanelli CS (2009) A massive invasion of fish species after eliminating a natural barrier in the upper rio Paraná basin. Neotrop Ichthyol 7:709-718. doi: 10.1590/S1679-62252009000400021

Kolar CS, Lodge DM 2002. Ecological predictions and risk assessment for alien fishes in North America. Science 298: 1233-1236. doi: 10.1126/science.1075753

Langeani F, Castro RMC, Oyakawa OT, Shibatta OA, Pavanelli CS, Casatti L (2007) Diversidade da ictiofauna do Alto Rio Paraná: composição atual e perspectivas futuras. Biota Neotropica 7:181-197

Latini AO, Resende DC, Pombo VB, Coradin L (2016) Espécies exóticas invasoras de águas continentais no Brasil. Ministério do Meio Ambiente, Brasília

Lima Junior, DP, Magalhães ALB, Vitule JRS (2015) Dams, politics and drought threat: the march of folly in Brazilian freshwaters ecosystems. Nat Conservação 13:196-198. doi: 10.1016/j.ncon.2015.11.003

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trend Ecol Evo 20: 223-228. doi: 10.1016/j.tree.2005.02.004

Lockwood JL, Cassey P, Blackburn TM (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Div Distrib 15: 904-910. doi: 10.1111/j.1472-4642.2009.00594.x

Magalhães ALB, Jacobi CM (2013) Asian aquarium fishes in a Neotropical biodiversity hotspot: impeding establishment, spread and impacts. Biol Invasions 15:2157-2163. doi: 10.1007/s10530-013-0443-x

Magalhães ALB, Vitule JRS (2013) Aquarium industry threatens biodiversity. Science 341:457. doi: 10.1126/science.341.6145.457-a

Magurran AE, Dornelas M, Moyes F, Gotelli NJ, McGill B (2015) Rapid biotic homogenization of marine fish assemblages. Nature Comm. 6:8405. doi: 10.1038/ncomms9405

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127:247-260.

Menezes RF, Attayde JL, Lacerot G, Kosten S, Coimbra e Souza L, Costa LS, Van Nes EH, Jeppesen E (2012) Lower biodiversity of native fish but only marginally altered plankton biomass in tropical lakes hosting introduced piscivorous *Cichla* cf. *ocellaris*. Biol Invasions 14:1353-1363. doi: 10.1007/s10530-011-0159-8

Muñoz H, Van Damme PA, Duponchelle F (2006) Breeding behaviour and distribution of the tucunaréCichla aff. monoculus in a clear water river of the Bolivian Amazon. J Fish Biol 69: 1018-1030.

Olden JD, Poff NL, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. Trend Ecol Evol 19:18-24.

Orsi ML, Agostinho AA (1999) Introdução de espécies de peixes por escapes acidentais de tanques de cultivo em rios da bacia do rio Paraná, Brasil. Rev Bras Zool 16:557-560.

Orsi ML, Britton JR (2014) Long-term changes in the fish assemblage of a Neotropical hydroelectric reservoir. J Fish Biol 84:1964-1970. doi: 10.1111/jfb.12392

Orsi ML, Almeida FS, Swarça AC, Claro-García A, Vianna NC, Garcia DAZ, Bialetzki A (2016) Ovos, larvas e juvenis da bacia do rio Paranapanema, uma avaliação para conservação. Triunfal Gráfica e Editora, Assis

Ortega JCG, Júlio Jr. HF, Gomes LC, Agostinho AA (2015) Fish farming as the main driver of fish introductions in Neotropical reservoirs. Hydrobiologia 746:147-158. doi: 10.1007/s10750-014-2025-z

Padial AA, Agostinho AA, Azevedo-Santos VM, Frehse FA, Lima Junior DP, Magalhães ALB, Mormul RP, Pelicice FM, Bezerra LAV, Orsi ML, Pretere Junior M., Vitule JRS (2016) The “Tilapia Law” encouraging non-native fishes threatens Amazonian River basins. Biodivers Conserv 25:1-4. doi: 10.1007/s10531-016-1229-0

Pelicice FM, Agostinho AA (2009) Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir. Biol Invasions 11:1789-1801. doi: 10.1007/s10530-008-9358-3

Pelicice FM, Vitule JRS, Lima Júnior D, Orsi ML, Agostinho AA (2014) A serious new threat to Brazilian freshwater ecosystems: the naturalization of nonnative fish by decree. Conserv Lett 7:55-60. doi:10.1111/conl.12029

Pelicice FM, Latini JD, Agostinho AA (2015) Fish fauna disassembly after the introduction of a voracious predator: main drivers and the role of the invader's demography. Hydrobiologia 746:271-283. doi: 10.1007/s10750-014-1911-8

Poff NL, Olden JD, Merritt DM, Pepin DM. (2007) Homogenization of regional river dynamics by dams and global biodiversity implications. Proc Nat Acad Sci 104: 5732-5737.

Rahel FJ (2000) Homogenization of fish faunas across the United States. Science 288: 854-856.

Ramos IP, Brandão H, Zanatta AS, Zica ÉOP, Silva RJ, Rezende-Ayroza MM, Carvalho ED (2013) Interference of cage fish farm on diet, condition factor and numeric abundance on wild fish in a Neotropical reservoir. Aquaculture 414:56-62. doi: 10.1016/j.aquaculture.2013.07.013

Reis RE, Kullander SO, Ferraris Jr. CJ (2003) Check list of freshwater fishes of South and Central America. Edipucrs, Porto Alegre

Reis RE, Albert JS, Di Dario F, Mincarone MM, Petry P, Rocha LA (2016) Fish biodiversity and conservation in South America. J Fish Biol 89:12-47. doi: 0.1111/jfb.13016

Sampaio T (1944) Relato sobre os estudos efetuados nos rios Itapetininga e Paranapanema. Revista do Instituto de Geografia e Geologia 2:30-81

Tófoli RM, Alves GHZ, Dias RM, Gomes LC (2016) Brazil’s Amazonian fish at risk by decree. Science 353:229. doi: 10.1126/science.aag2922

Vieira AB, Melo R, Santos GB, Bazzoli N (2009) Reproductive biology of the peacock bass *Cichla piquiti* (Perciformes: Cichlidae), an exotic species in a Neotropical reservoir. Neotropical Ichthyol 7:745-750.

Villéger S, Blanchet S, Beauchard O, Oberdorff T, Brosse S (2011) Homogenization patterns of the world’s freshwater fish faunas. Proceedings of the National Academy of Sciences 108:18003-8. doi: 10.1073/pnas.1107614108

Vitule JRS, Skóra F Abilhoa V (2012) Homogenization of freshwater fish faunas after the elimination of a natural barrier by a dam in Neotropics. Divers Distrib 18:494-499. doi: 10.1111/j.1472-4642.2011.00821.x

Xiong W, Sui X, Liang SH, Chen Y (2015) Non-native freshwater fish species in China. Rev Fish Biol Fish 25:651-687. doi: 10.1007/s11160-015-9396-8

Table 1 Number of individuals of non-native fish species stocked in reservoirs of the Paranapanema River between 1978 and 1992, from stocking programs conducted by 'Companhia Energética de São Paulo' (CESP 1997).

	Reservoir					
Species	Rosana	Capivara	Salto Grande	Chavantes	Jurumirim	Total
Astronotus crassipinnis	0	26,300	34,000	17,000	24,000	101,300
Cyprinus carpio	0	390,000	135,000	265,646	819,557	1,610,203
Sorubim lima	10,000	9,000	0	0	0	19,000
Schizodon borellii	0	30,000	38,000	60,144	90,000	218,144
Triportheus angulatus	0	1,075,000	52,642	80,000	305,000	1,512,642
Oreochromis niloticus	0	1,935,000	615,000	1,243,000	5,694,200	9,487,200
Hoplias lacerdae	0	188,280	27,800	50,000	169,300	435,380
Total	10,000	3,653,580	902,442	1,715,790	7,102,057	13,383,869

Table 2 Composition and distribution of the non-native fish species introduced into the Paranapanema River basin between 1950 and 2014, where 'X' denotes introduced and '-' denotes absence in that location. Locations are shown in Fig. 1 and are represented here as: Ros = Rosana Reservoir; Taq = Taquaruçu Reservoir; Cap = Capivara Reservoir; Tib = Tibagi River; Can I = Canoas I Reservoir; Can II = Canoas II Reservoir; Sgr = Salto Grande Reservoir; Our = Ourinhos Fish Ladder; Cha = Chavantes Reservoir; Jur = Jurumirim Reservoir; Upper = Tributaries of the Upper Paranapanema River. For taxonomic details by species and the sources of information on the introduction, please see Appendix 1 of Supplementary Material.

	Location within the Paranapanema River basin										
Species	**Ros**	**Taq**	**Cap**	**Tib**	**Can I**	**Can II**	**Sgr**	**Our**	**Cha**	**Jur**	**Upper**
Aphyocharax dentatus	X	X	X	-	X	X	-	-	-	-	-
Apteronotus caudimaculosus	-	-	X	-	-	-	-	-	-	-	-
Astronotus crassipinnis	X	-	X	-	X	X	X	X	-	-	-
Auchenipterus osteomystax	X	X	-	-	-	-	-	-	-	-	-
Brachyhypopomus pinnicaudatus	-	-	-	-	-	-	X	-	-	-	-
Bryconamericus exodon	-	-	-	X	-	-	-	-	-	-	-
Catathyridium jenynsii	X	X	-	-	-	-	-	-	-	-	-
Cichla kelberi	X	-	X	-	-	-	X	-	X	-	-
Cichla monoculus	-	-	X	-	X	X	-	-	-	X	-
Cichla ocellaris	-	-	-	-	-	-	-	X	-	-	-

Cichla piquiti	-	-	-	-	-	-	X	-	X	-	-
Cichla temensis	-	-	-	-	-	-	-	X	-	-	-
Clarias gariepinus	-	X	X	X	-	-	-	-	-	-	-
Coptodon rendalli	X	-	X	X	-	-	-	X	-	X	-
Ctenopharyngodon idella	-	-	-	X	-	-	-	-	-		-
Cyprinus carpio	-	-	X	X	-	-	-	-	-	X	X
Erytrhinus erythrinus	X	-	X	-	-	-	-	-	-	-	-
Hoplias lacerdae	-	-	-	-	-	-	-	-	-	X	-
Hyphessobrycon eques	X	X	X	X	X	X	X	X	-	X	-
Hypophthalmus edentatus	X	X	-	-	-	-	-	-	-	-	-
Ictalurus punctatus	-	-	X	-	-	-	-	-	X	-	-
Laetacara araguaiae	X	-	-	-	-	-	-	-	-	-	-
Leporinus macrocephalus	-	-	X	X	X	-	X	-	-	-	-
Loricariichthys platymetopon	X	X	X	X	X	X	-	-	-	-	-
Metynnis lippincottianus	X	X	X	X	X	X	X	-	-	X	-
Micropterus salmoides	-	-	-	X	-	-	-	-	-	-	-
Misgurnus anguillicaudatus	-	-	-	-	-	-	-	-	-	-	X
Oreochromis niloticus	X	X	X	X	X	X	X	-	X	X	X
Ossancora eigenmanni	X	X	-	-	-	-	-	-	-	-	-
Pimelodus ornatus	X	X	-	-	-	-	-	-	-	-	-

Plagioscion squamosissimus	X	X	X	X	X	X	X	X	X	-	-
Poecilia reticulata	X	X	X	X	-	-	X	X	-	-	-
Potamotrygon cf. *motoro*	X	X	-	-	-	-	-	-	-	-	-
Pterodoras granulosus	X	X	-	-	-	-	-	-	-	-	-
Pterygoplichthys ambrosettii	X	-	X	-	-	-	-	-	-	-	-
Rhamphichthys hahni	X	X	-	-	-	-	-	-	-	-	-
Roeboides descalvadensis	X	X	-	-	-	-	-	-	-	-	-
Satanoperca pappaterra	X	-	-	-	-	-	-	-	-	-	-
Schizodon borellii	X	X	X	-	-	-	-	-	-	-	-
Serrasalmus marginatus	X	X	-	-	-	-	-	-	X	-	-
Sorubim lima	X	X	X	X	-	X	-	-	-	-	-
Steindachnerina brevipinna	X	-	-	-	-	-	-	-	-	-	-
Trachelyopterus galeatus	X	X	-	-	-	-	-	-	-	-	-
Trachydoras paraguayensis	X	X	-	-	-	-	-	-	-	-	-
Triportheus angulatus	-	-	X	X	-	-	-	-	-	-	-
Triportheus nematurus	-	X	X	-	-	-	X	-	X	X	-
Xiphophorus hellerii	X	-	-	-	-	-	-	-	X	-	-
Total number of species by location	30	23	22	15	9	9	11	7	8	8	3

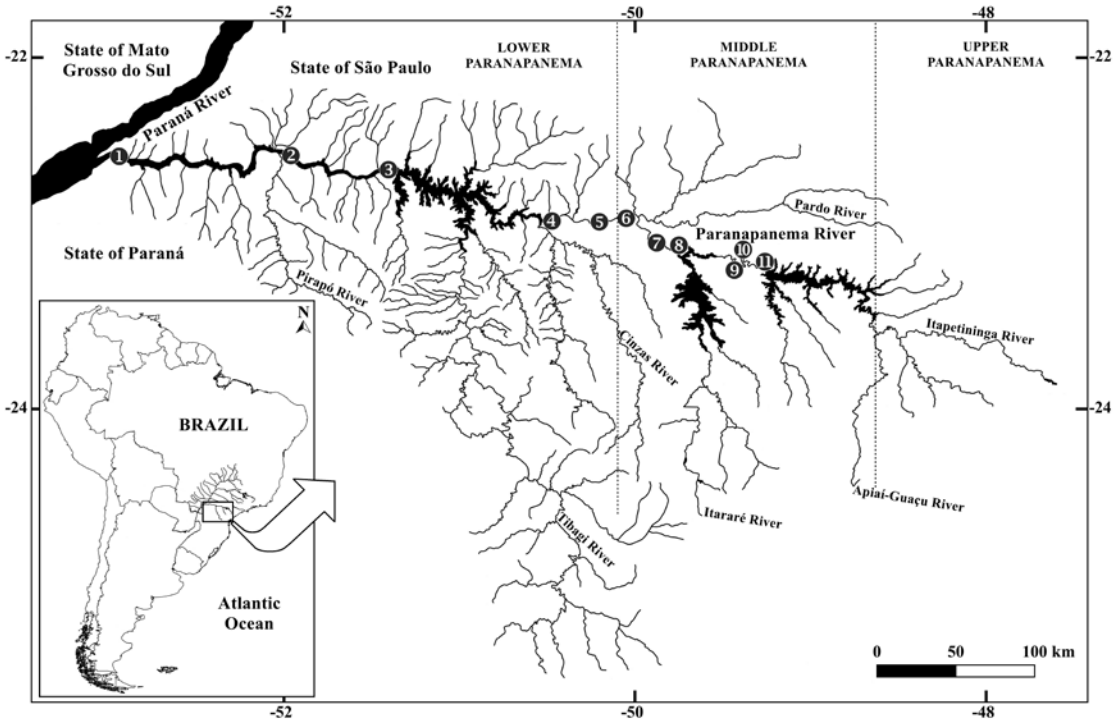

Fig. 1 Inset: Location of the study area in Brazil. Main: the Paranapanema River basin located in the Upper Paraná Ecoregion, where the numbers represent the locations of the hydroelectric reservoirs: 1) Rosana; 2) Taquaruçu; 3) Capivara; 4) Canoas I; 5) Canoas II; 6) Salto Grande; 7) Ourinhos; 8) Chavantes; 9) Paranapanema; 10) Piraju; and 11) Jurumirim.

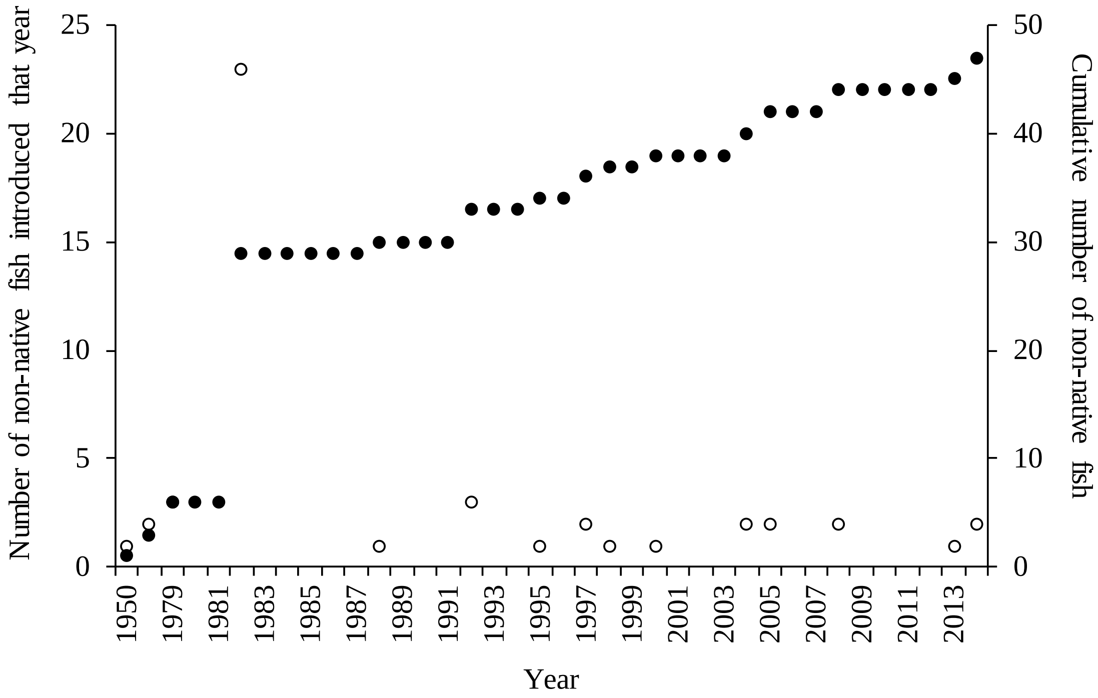

Fig. 2 Number of non-native fish species introduced in the Paranapanema River basin per year between 1950 and 2014 (clear circles) and the cumulative number of non-native fishes that have been introduced (filled circles).

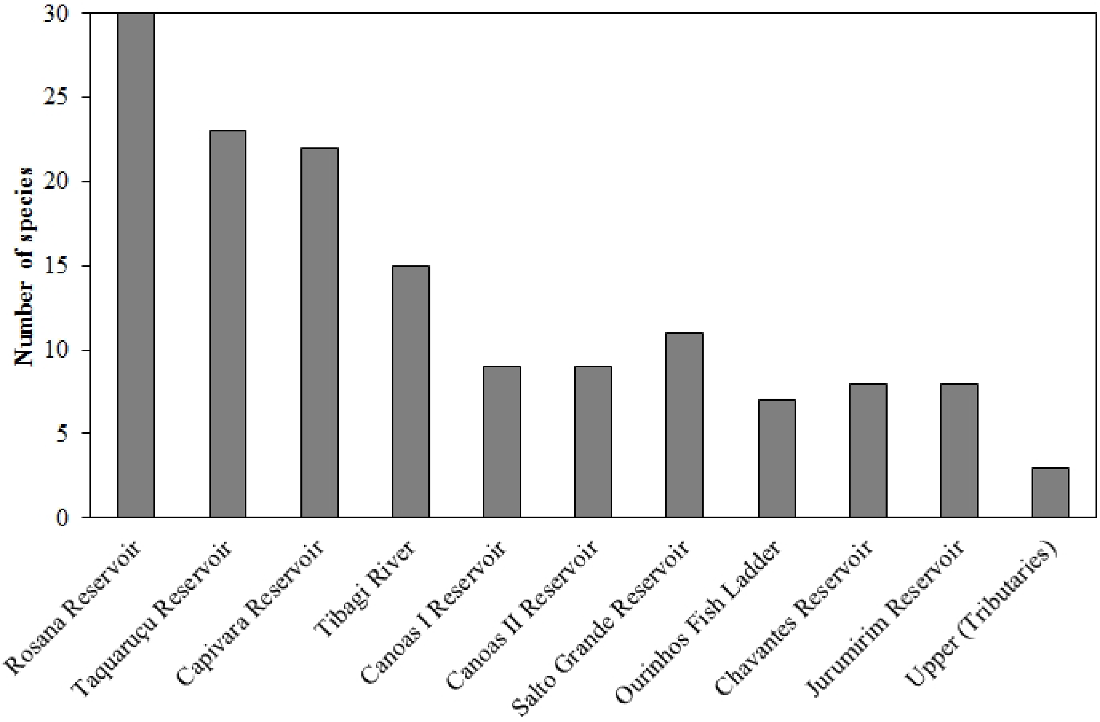

Fig. 3 The number of non-native fish present in each hydroelectric reservoir and river tributary of in the Paranapanema River basin. Information gathered from literature and field samples.

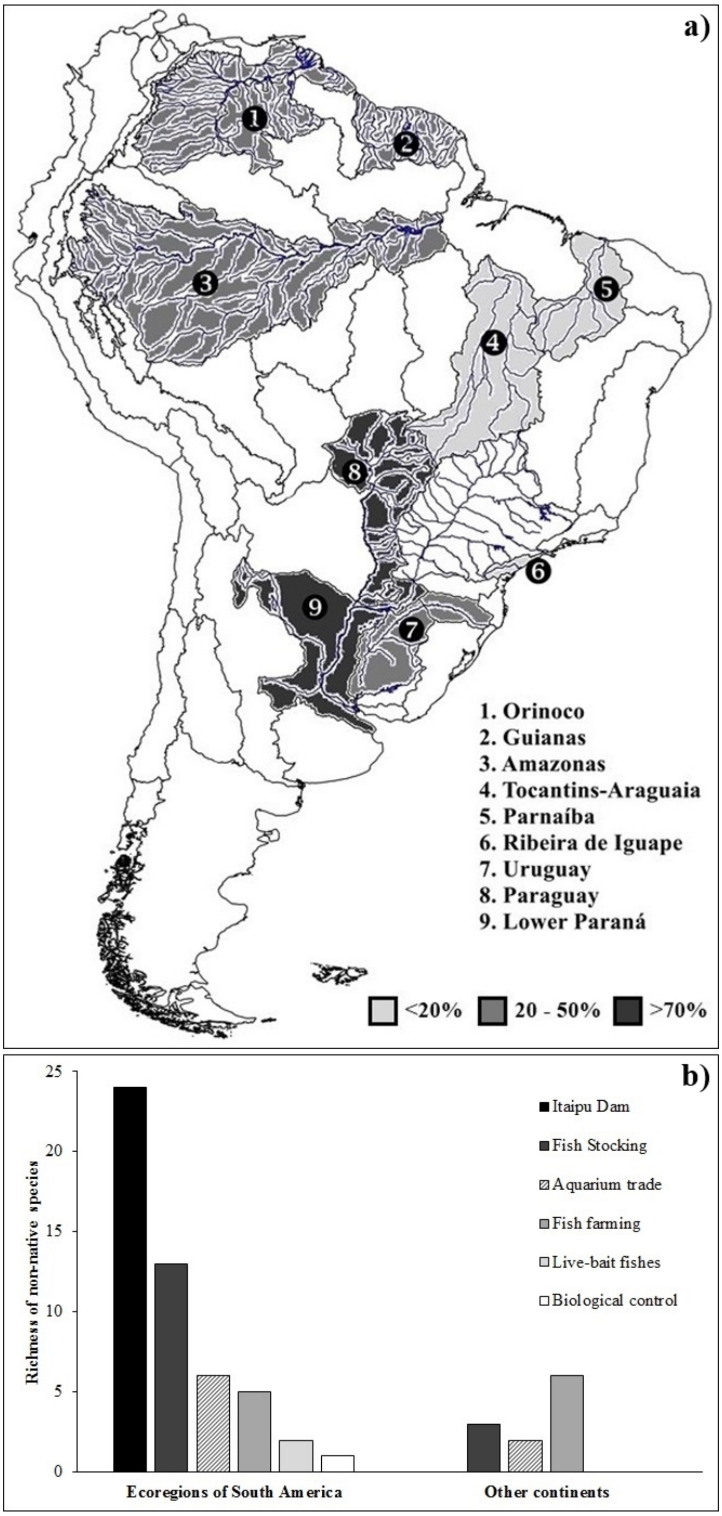

Fig. 4 (a) Origin of the non-native fish species (N = 47) introduced into the Paranapanema River according to South American ecoregions (Abell et al. 2008); (b) Origins of the non-native fish species introduced into the Paranapanema River according to the vector of introduction.