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Review

# Non-native fish invasions of a Neotropical ecoregion with high endemism: a review of the Iguaçu River

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## Abstract

The freshwater fish fauna of the Neotropics comprises one of the most diverse ichthyofaunas globally. The Iguaçu ecoregion of the Neotropics includes about 100 described species, of which ≈70% are endemic and the majority of these are considered to be threatened with extinction. As is the case in freshwaters worldwide, the Iguaçu ecoregion has been strongly impacted by a variety of factors, including urbanization, agriculture, the construction of dams and the introduction of non-native species. There is, however, a paucity of information on fish invasions and their impacts in the Iguaçu ecoregion. To address this knowledge gap an exhaustive literature review was conducted to determine the extent of introductions, the main vectors of introductions and the major risks associated with the introduction of non-native fish into the Iguaçu ecoregion. A total of 41 studies concerning non-native fish in the Iguaçu ecoregion were found, the majority (56.1%) from lists of species and first records of non-native species; while 29.3% of the studies only mentioned possible negative impacts of non-native species and 14.6% of studies evaluated, indirectly, the impacts of non-native species. The Iguaçu ecoregion has a long history of fish introductions, beginning with the first record of the "common carp" *Cyprinus carpio* in 1944, and continuing to the recent record, in 2012, of *Steindachnerina brevipinna.* Since 1944, 29 non-native species have been introduced, 19 from different ecoregions of the Neotropics, and 10 introduced from other zoogeographic regions (*Ctenopharyngodon idella, C. carpio, Hypophthalmichthys molitrix, H. nobilis* and *Misgurnus anguillicaudatus* from Palearctic region; *Clarias gariepinus, Oreochromis niloticus* and *Tilapia rendalli* introduced from Ethiopian region, and *Ictalurus punctatus* and *Micropterus salmoides* from Nearctic region). The main vector of introduction was aquaculture, with the aquarium trade, baiting, sport fishing and stocking also playing roles. Studies indirectly investigating the establishment and spread of the introduced species in the Iguaçu ecoregion found nine non-native species which were considered established. Moreover, studies evaluating the impact of non-native species have investigated changes in the feeding habits of non-native species, suggesting competition with native species for food resources, and the increase in the number of fish species introduced over time. The impacts of non-native fishes, often associated with other environmental changes, such as the construction of dams and pollution in the Iguaçu ecoregion, may have severe consequences for the endemic fish fauna, resulting in the further decline and potential extinction of native species.

**Key words:** exotic species, biological invasions, extirpation of native species, habitat alteration, endemic species, reservoirs

## Introduction

Human activities are the main vector transforming aquatic environments, in part by promoting the movement of aquatic organisms worldwide (Welcomme 1988; Cambray 2003; Gozlan 2008; Havel et al. 2015), and reducing the earlier isolation imposed by biogeographic barriers (Kolar and Lodge 2001; Rahel 2007). The result of these human actions has been the intentional and unintentional introduction of countless species in aquatic ecosystems (e.g. McKinney 2006; Leprieur et al. 2008; Gozlan et al. 2010), resulting in a loss of biodiversity around the globe (Vitule et al. 2012a; Dirzo et al. 2014; Dornelas et al. 2014; Jeschke et al. 2014; Ricciardi and Simberloff 2014). Athough some studies have failed to identify impacts from non-native species (e.g. Havel et al. 2015) and some introduced species are not successful at establishing new populations and spreading into new environments (Williamson 1996), many introduced non-native species have become invasive, harming both human interests and the environment, beyond any economic damage they may cause (Lövei 1997; Parker et al. 1999; Pimentel et al. 2001, 2005; Simberloff et al. 2013; Havel et al. 2015).

Human mediated impacts have resulted in freshwater ecosystems losing a greater proportion of their species and habitats than terrestrial and oceanic environments (Dudgeon et al. 2006; Johnson et al. 2008), demonstrating that fish are among the most threatened faunas around the world (Gozlan 2008; Olden et al. 2010; Winemiller et al. 2016). These losses are primarily due to an increase in dam construction and the introduction of non-native species (e.g. Agostinho et al. 2005; Johnson et al. 2008; Vitule et al. 2012b; Ferrareze et al. 2014; Winemiller et al. 2016), thus leading to negative effects on community structure and ecosystem functioning (e.g. Parker et al. 1999; Pelicice and Agostinho 2009; Vitule et al. 2012a; Alexander et al. 2014; Ellender and Weyl 2014). Under particularly threat from human mediated impacts is the freshwater fish fauna of the Neotropics, which comprises one of the most diverse ichthyofaunas in the world (e.g. Schaefer 1998; Reis et al. 2003; Albert and Reis 2011; Pereira et al. 2012). In this region, Brazil stands out for having the highest freshwater fish diversity, including several endemic genera and species (e.g. Reis et al. 2003; Agostinho et al. 2005; Winemiller et al. 2008). Brazil has also recorded a large number of non-native species introduced from other zoogeographic regions (Agostinho and Júlio Jr. 1996; Figueredo and Giani 2005; Vitule 2009; Vitule et al. 2012a; Pelicice et al. 2014); such introductions are more likely to become pests than non-native species transported beyond their native range within the continent (Hassan and Ricciardi 2014). In addition, several extralimital introductions have occurred from adjacent ecoregions (e.g. Agostinho et al. 2008; Vitule 2009; Orsi and Britton 2014), for example Amazonas lowlands natives have been moved to the northeast, southeast and south of Brazil (Agostinho and Júlio Jr. 1996; Agostinho et al. 2008).

In such context, a region particularly vulnerable to non-native fish introductions is the Iguaçu ecoregion of the Neotropics, located in southern Brazil and northern Argentina, which comprises the Iguaçu River, an important tributary of the left margin of the Paraná River (Garavello et al. 1997; Abilhoa et al. 2013; Gubiani and Horlando 2014) (Figure 1). This river basin is considered a global biodiversity ecoregion, as its fishes exhibit high degrees of endemism (Severi and Cordeiro 1994; Garavello et al. 1997; Abell et al. 2008; Ingenito and Duboc 2014), with the proportion of endemics estimated at ≈70% (Zawadzki et al. 1999; Agostinho et al. 2005; Pavanelli and Bifi 2009; Baumgartner et al. 2012). The degree of endemism has been attributed to its geographic isolation from the rest of the Paraná River basin, most probably as a consequence of geological characteristics such as the formation of the Iguaçu Falls approximately 22 million years ago, since these falls serve as an effective barrier to fish dispersal (Garavello et al. 1997; Agostinho et al. 1999; Baumgartner et al. 2006; Alcaraz et al. 2009). The Iguaçu ecoregion contains about 100 described species of fish; however, several as yet undescribed species are also present (Garavello et al. 1997; Baumgartner et al. 2012). This is therefore a distinct and highly relevant ecoregion for conservation of freshwater fish diversity.

Given the importance of this freshwater ecoregion, the frequent threats caused by the introduction of non-native species (Agostinho et al. 1999; Daga et al. 2015) may lead to negative impacts on the endemic fish fauna, thereby increasing the risk of extinctions (Ingenito et al. 2004; Vitule 2009; Gubiani et al. 2010; Daga and Gubiani 2012). Indeed, there is an increasing need for empirical research on the invasion process in the Iguaçu ecoregion. Therefore, here we present an overview of the literature concerning the non-native fish fauna of this region. We performed an exhaustive literature review with the aims of: (*i*) identifying prior studies concerning non-native fish in the Iguaçu ecoregion; (*ii*) assessing temporal trends in the introduction of non-native fish, as indicated by the first records of non-native species within this ecoregion; (*iii*) identifying the biogeographical origin of non-native species and the vectors of their introductions; (*iv*) identifying factors that allow the establishment of fishes introduced into Iguaçu ecoregion, as well as evaluating the data on the spread of non-native fishes; (*v*) assessing the impacts of non-native species in the Iguaçu ecoregion; and, (*vi*) providing insights for the control of non-native fish and the conservation of the endemic fish fauna.

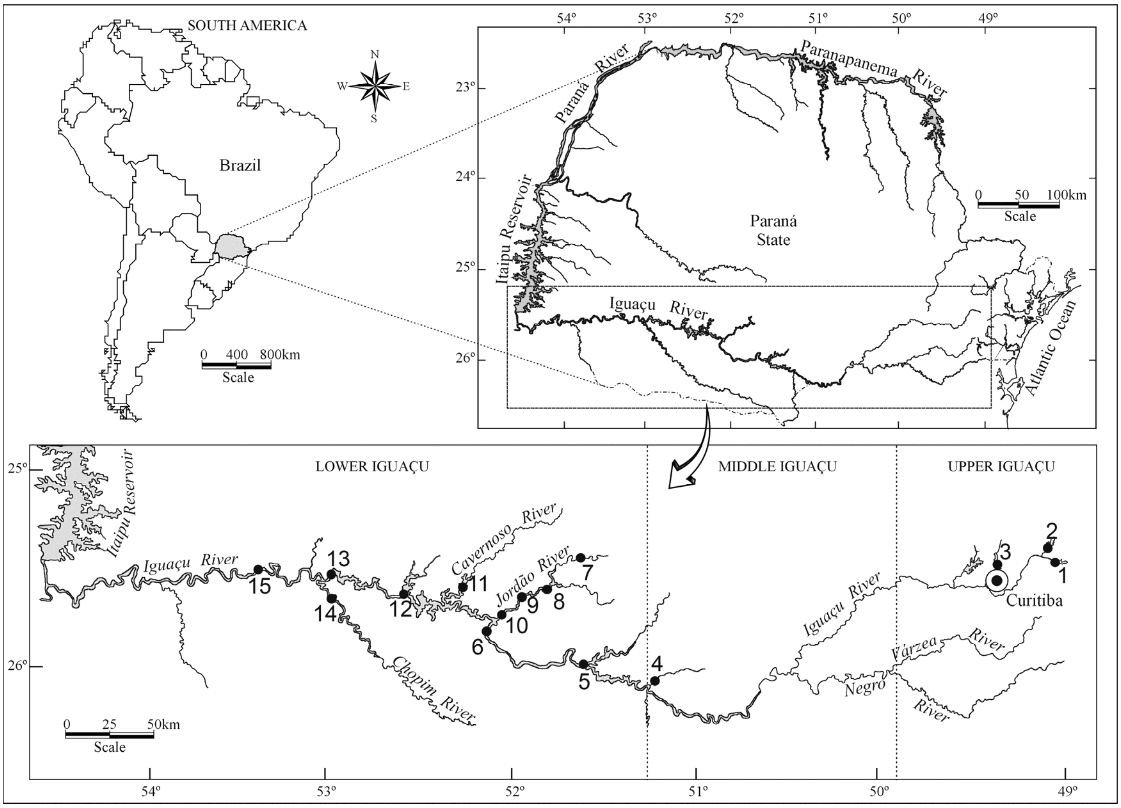



**Figure 1.** Location of the Iguaçu ecoregion in the South America and in the Brazil, showing the boundaries of the upper, middle and lower sub-regions of the Iguaçu River. The black circles represent the reservoirs built in this ecoregion. Reservoirs: 1) Piraquara, 2) Iraí, 3) Passaúna, 4) Salto do Vaú, 5) Foz do Areia, 6) Segredo, 7) Curucaca, 8) Santa Clara, 9) Fundão, 10) Derivação do Rio Jordão, 11) Cavernoso, 12) Salto Santiago, 13) Salto Osório, 14) Chopim and 15) Salto Caxias.

## Materials and methods

The Iguaçu River basin encompasses the largest drainage basin in the State of Paraná (approximately 72 000 $km^2$; Maack 2012), of which 79% belongs to the State of Paraná, 19% to the State of Santa Catarina and 2% to Argentina (Eletrosul 1978). The river basin covers 104 municipalities and includes almost 5 million inhabitants, of which approximately 80% are urbanized (Ipardes 2010). The formation of the basin has been associated with the uplift of the Serra do Mar, which took place during the Mesozoic Era and Early Paleozoic Era, and the creation of the three Paraná Plateaus (e.g. Garavello 2005; Baumgartner et al. 2012; Maack 2012). The particular characteristics of the region, chiefly its geomorphological features and climate patterns (Severi and Cordeiro 1994; Garavello et al. 1997; Maack 2012), result in the Iguaçu River being subdivided into three major sub-regions: *i)* the upper Iguaçu consisting of the segment extending from the source of the river in the metropolitan region of Curitiba to the beginning of its rapids in Porto Amazonas (Ingenito et al. 2004); *ii)* the middle Iguaçu, consisting of the stretch between Porto Amazonas and União da Vitória, and including the river's main tributary, the Rio Negro (Júlio Jr. et al. 1997); and *iii)* the lower Iguaçu, characterized by the presence of numerous waterfalls, including the Salto Grande (13 m), Salto Santiago (40 m), Salto Osório (30 m) and Iguaçu Falls (72 m) (Maack 2012), and providing high potential for hydroelectric power generation (Júlio Jr. et al. 1997; Baumgartner et al. 2012) (Figure 1).

The upper Iguaçu covers a region of high population density, with predominantly industrial and commercial activities (Júlio Jr. et al. 1997; Baumgartner et al. 2012). Therefore, this region receives a large influx of chemical pollutants, primarily from urban/industrial sources in the metropolitan region of Curitiba (Barddal 2006; Gubiani et al. 2008; Freire et al. 2015). However, the tributaries along this stretch of the river drain populated regions less affected by human activities, thereby decreasing the degree of contamination of its waters (e.g. Barddal 2006). In the middle and lower Iguaçu regions, agriculture is the predominant human activity (Júlio Jr. et al. 1997; Baumgartner et al. 2012); however, aquacultural activities (especially fish farming in cages) also occur (Agostinho et al. 1999).

The review comprised an exhaustive literature search, which aimed to cover all studies, published and unpublished, on non-native species introduced into the Iguaçu ecoregion. Studies were included in this review if they met the following criteria: (*i*) non-native species: the first records of species transported beyond their native range limits, which were introduced either directly or indirectly into the Iguaçu ecoregion; (*ii*) establishment and spread of the introduced species: studies identifying (even indirectly) the factors that have allowed the establishment of non-native populations into Iguaçu ecoregion, or studies that have evaluated data on the spread of non-native fishes; (*iii*) ecological impacts: studies that investigated any changes in the recipient ecoregion associated with the presence of non-native fish. All above criteria are direct linked to invasion processes, phases and impacts (e.g. Lockwood et al. 2007; Blackburn et al. 2011).

Non-native species were defined as those occurring outside of their known natural range, including fish from other freshwater ecoregions of South America, as well as other countries, continents or zoogeographical regions, which were introduced either directly or indirectly through a variety of pathways (e.g. aquaculture, sport fishing and stocking) (Agostinho and Julio Jr. 1996; Vitule 2009; Jeschke et al. 2014; Havel et al. 2015). Established species were considered as those recorded in subsequent studies (after the first record), for which there was evidence of survival and reproduction data, indicating that introduced populations have become self-sustaining (e.g. Blackburn et al. 2011). Here, we consider only studies available for the stretch of the Iguaçu River extending from its headwaters to the Iguaçu Falls.

### *Data analysis*

For this review, the studies were identified and quantified according to the main sources of information about the non-native species. In order to assess the temporal trend of the introductions of non-native fish in the Iguaçu ecoregion, we identified the studies according to information about the first records of non-native species. In addition, we counted the total number of studies or articles that met the selection criteria, concerning the establishment, spread and ecological impacts of non-natives.

We calculated the percentage of non-native species captured over time, with the relative frequency based on the number of non-native species registered as a proportion of the total number of non-native species in the Iguaçu ecoregion. In this case, we considered only the first records of introduction into the Iguaçu ecoregion. The cumulative number of non-native species over time was also calculated. In addition, non-native species diversity was expressed as species richness (number of species), based on their biogeographical origin, according to the zoogeographic regions proposed by Wallace (1876): Nearctic, Palearctic, Neotropical, Ethiopian, Oriental and Australian. Finally, richness of non-native species were also assessed according to the major vectors of introductions, following Ingenito et al. (2004) and Baumgartner et al. (2012).

## Results and discussion

### *Studies in the Iguaçu ecoregion*

The literature review identified a total of 41 studies that included non-native species introduced into Iguaçu ecoregion (Tables S1 and S2). The majority of these studies (56.1%) were composed of lists of species and information about the composition of the fish fauna, while 29.3% of studies only mentioned possible negative impacts of introduced species and 14.6% evaluated, indirectly, the impacts of non-native species. Information about the proportion of non-native species that have successfully established or spread from the original point of introduction was scarce in this ecoregion. However, studies often reported other basic ecological information (e.g. reproduction rates of non-native species), or the consecutive catch of non-natives after the first record. Non-native species that have caused severe impacts in the Iguaçu ecoregion were only indirectly studied. As reported by Vitule (2009), studies that focus on the impacts of non-native species are rare or even nonexistent and this pattern is similar throughout the Neotropics.

The majority of the studies included in this review were articles (20 papers), followed by technical reports (11 studies), book chapters (five studies) and theses/dissertations (five studies) (Table S2). We found 29 first records of non-native

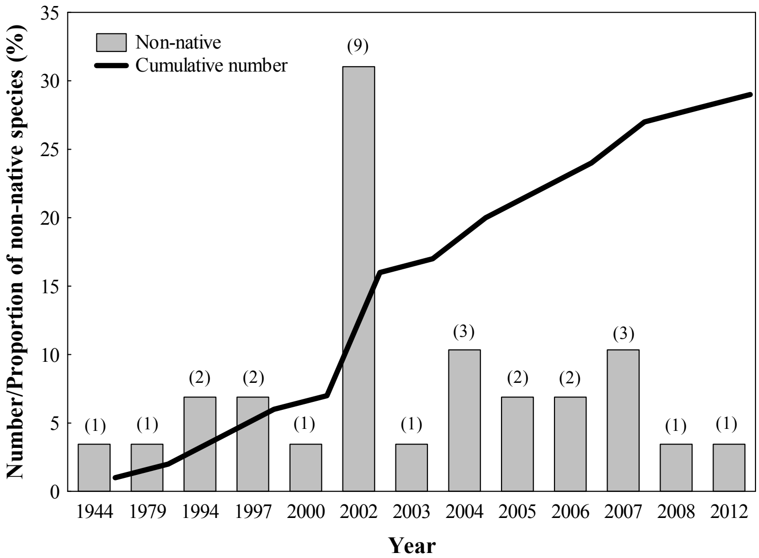



**Figure 2.** Variation in the percentage of non-native fish species introduced into the Iguaçu ecoregion between 1944 and 2012. The number in parenthesis above of the bars indicates the number of non-native species recorded in each year. The black line represents the cumulative number of non-native species over time.

species (Table S1). The majority of these were technical reports (18 non-native species), followed by book chapters (six non-native fishes), and articles (four non-native species).

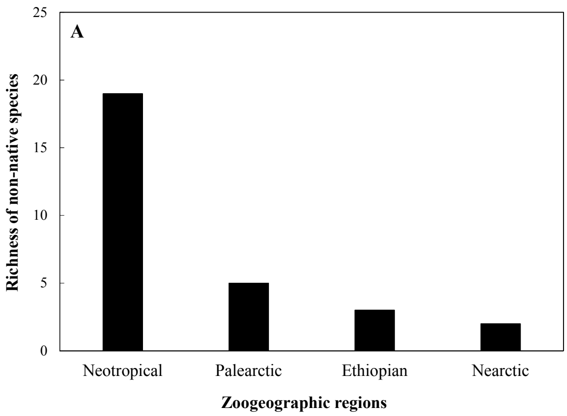
*First records of non-native fish in the Iguaçu ecoregion*

The Iguaçu ecoregion has a long history of introductions. Since 1944, 29 non-native species have been introduced (Table S1). The first record of the introduction of a non-native species was the report of the occurence of the "common carp" *Cyprinus carpio* Linnaeus, 1758, in Porto União, middle Iguaçu region, which occurred seventy-two years ago, and was formally reported by George S. Myers in 1947, who related it to the carp ponds scattered over southern Brazil. This report also refers to the negative impacts of *C. carpio* perceived by local people prior to the construction of the existing reservoirs in this basin. It is probable that the "common carp" was introduced into the Iguaçu River after the disruption of ponds located close to the river channel due to a heavy rain (Myers 1947).

The first recorded introductions were of non-native species from other zoogeographic regions, including *C. carpio, Tilapia rendalli* (Boulenger, 1897) and *Micropterus salmoides* (Lacépède, 1802); all previously reported by studies that aimed to identify the fish fauna of this ecoregion, since there were no specific studies or reports about non-natives (Table S1). The first records of non-native species introduced from other ecoregions in South America were of *Gymnotus inaequilabiatus* (Valenciennes, 1839) in 1994, and *Astyanax altiparanae* Garutti & Britski, 2000, and *Odontesthes bonariensis* (Valenciennes, 1835) in 1997 (Table S1). On the other hand, the most recent first record of non-native species was of *Steindachnerina brevipinna* (Eigenmann & Eigenmann, 1889) in 2012 (Table S1).

The introduction of non-native species from other zoogeographic regions has been a common occurrence since the 1970's. This is especially true of the introduction of North American fishes (e.g. Chamberlain 1947; Myers 1947; Agostinho and Julio Jr. 1996). Apparently, one way to minimize the impacts of non-native species from other zoogeographic regions, was the introduction of species from adjacent ecoregions of the Neotropical region (e.g. Agostinho and Julio Jr. 1996). However, no assessment of possible impacts was conducted prior to the introductions. In addition, the impact of invasions on native biota has often been underestimated, because invasions of non-native fish from adjacent ecoregions are generally not considered in the metrics (Matsuzaki et al. 2013).

Our results demonstrated that there was an increase in the number of first records of non-native fish over time, especially after the year 2000, coincident with the beginning of the monitoring phase of reservoirs, especially those built along the main channel of the Iguaçu River (Figure 2). The increase in the number of non-native species in 2002 was due to the intensive investment in



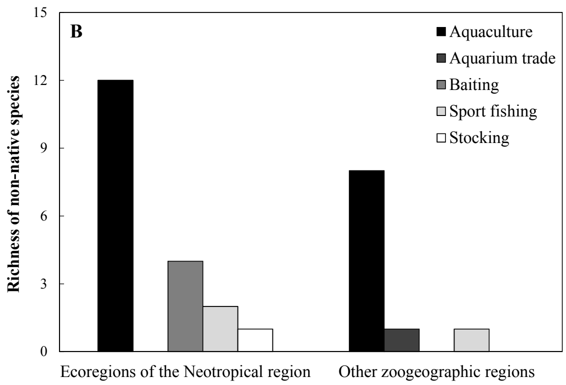




**Figure 3.** (A) Spatial variation of the richness of non-native species according to zoogeographic regions. (B) Richness of non-native species according to the vector of introduction from different ecoregions of the Neotropical region and other zoogeographic regions.

investigations, in order to elaborate the technical report concerning the Salto Caxias reservoir (Figure 2). The largest number of non-native species was recorded in the lower Iguaçu, at least in part due to the larger number of studies, primarily technical reports based on monitoring projects in reservoirs, and from stocking and the use of cages for farming fish in reservoirs (Table S1).

*Origin of non-native fish in the Iguaçu ecoregion*

Non-native fish belonged to six orders, 17 families, 22 genera and 29 species. Nineteen non-native species were considered to have been introduced from different ecoregions of the Neotropical region (Figure 3A; Table S1). The other ten non-native species were originated from other zoogeographic regions: five species, *Ctenopharyngodon idella* (Valenciennes, 1844), *C. carpio, Hypophthalmichthys molitrix* (Valenciennes, 1844), *H. nobilis* (Richardson, 1845) and *Misgurnus anguillicaudatus* (Canton, 1842), introduced from Palearctic region; three species, *Clarias gariepinus* (Burchell, 1822), *Oreochromis niloticus* (Linnaeus, 1758) and *T. rendalli*, introduced from Ethiopian region; and two species, *Ictalurus punctatus* (Rafinesque, 1818) and *M. salmoides*, introduced from Nearctic region (Figure 3A). The main pathway or vector of introduction both from the different ecoregions of the Neotropical region and the other zoogeographic regions was aquaculture (Figure 3B). However, non-native species were also introduced through aquarium trade, the baiting, sport fishing and stocking activities (Figure 3B; Table S1).

The majority of the introductions of non-native species into the Iguaçu ecoregion were from 14 ecoregions of the Neotropics (Figure 3B; Table S1), with most of the fish species, including *Apteronotus ellisi* (Alonso de Arámburu, 1957), *Leporinus macrocephalus* Garavello & Britski, 1988 and *Piaractus mesopotamicus* (Holmberg, 1887), introduced from three ecoregions: the Upper Paraná, the Lower Paraná, and Paraguay. Additional species from these regions include *A. altiparanae*, introduced from the Upper Paraná ecoregion, *Brycon hilarii* (Valenciennes, 1850), introduced from the Paraguay ecoregion; and *G. inaequilabiatus, Salminus brasiliensis* (Cuvier, 1816) and *S. brevipinna*, introduced from the Lower Paraná. These three main ecoregions occur in areas of high population density, in which there is a predominance of industrial and agriculture activity. Consequently, there is a higher demand for electricity (e.g. Agostinho et al. 2007). In order to meet this need there are already a large number of reservoirs in these ecoregions, with additional reservoirs planned or under construction (Agostinho et al. 2007; Ferrareze et al. 2014). In addition to increasing demand for electricity, there is concern about the food supply; for this reason, the fastest growing sector of food production is aquaculture, accounting for almost half of all aquatic species consumed by humans (e.g. Bartley 2011).

The non-native species originating from other ecoregions in the Neotropics and introduced into the Iguaçu basin for aquaculture were species of the genera *Leporinus* and *Pseudoplatystoma*, as well as *A. altiparanae*, *B. hilarii, P. mesopotamicus* and *Prochilodus lineatus* (Valenciennes, 1837).

Most of these species are farmed in cages located in reservoirs. Recently, Brazil's Congress proposed a law that would allow the rearing of non-native fish in cages installed in reservoirs (Lima Jr. et al. 2012; Pelicice et al. 2014). Reservoirs are altered environments that create appropriate conditions for the establishment of introduced non-native species, especially the tolerant and opportunistic fish species commonly used in aquaculture (e.g. Johnson et al. 2008). Furthermore, the increased connectivity of aquatic environments due to the construction of dams, especially the construction of a cascade of reservoirs (Petesse and Petrere Jr. 2012; Casimiro et al. 2015) as are found in the Iguaçu ecoregion (Daga and Gubiani 2012), can homogenize the physical conditions of the environment, thereby facilitating the invasion process (e.g. Havel et al. 2005; Lima Jr. et al. 2012; Daga et al. 2015). Additionally, in areas of greater industrial and urban development in Brazil there has been an increase in the number of recreational fishing ponds on private domains, which are usually located near rivers and serve to commercialize non-native species (e.g. Agostinho and Júlio Jr. 1996; Orsi and Agostinho 1999; Vitule et al. 2006). Because escapes are inevitable, aquaculture, both in ponds and in cages, can therefore provide an intensive and constant flow of non-native species into the ecosystem (Agostinho and Júlio Jr. 1996; Agostinho et al. 1999; Orsi and Agostinho 1999; Azevedo-Santos et al. 2011; Pelicice et al. 2014).

The non-native species introduced from the Palearctic region: *C. idella*, *C. carpio*, *H. molitrix*, *H. nobilis* and *M. anguillicaudatus*, have been introduced into more than twenty countries. In particular, the “common carp” has been introduced into 59 countries and “grass carp” have been introduced into 49 countries (Welcomme 1988; Rahel 2007). The non-native species introduced from the Ethiopian region are species known to have the capacity to tolerate extreme environmental conditions (e.g. McKaye et al. 1995; Canonico et al. 2005; Vitule et al. 2006; Zambrano et al. 2006; Arthur et al. 2010; Esselman et al. 2013; Gutierre et al. 2014). The “tilapia” species have been widely introduced (Welcomme 1988; Agostinho and Júlio Jr. 1996; Esselman et al. 2013) in order to develop smallholder fish farming (Agostinho et al. 1999), and are currently reared at a higher rate in Asia and the Americas than in their native continent (Bartley 2011). The non-native species introduced from the Nearctic region were *I. punctatus*, which can tolerate a variety of habitats, adapting easily to new environmental conditions, such as those encountered in the creation of new ponds for aquaculture (Townsend and Winterbourn 1992; Cruz et al. 2012); and *M. salmoides*, which has been introduced into more than 49 countries (Welcomme 1988; Rahel 2007) as a result of its economic value in the sport fishing industry (e.g. García-Berthou 2002; Britton and Orsi 2012; Petesse and Petrere Jr. 2012; Ribeiro et al. 2015). Moreover, *C. carpio* and *M. salmoides* are listed among the “100 worst invasive alien species” (Lowe et al. 2000).

Overall, aquacultural activity is considered to be the main vector for the introduction of non-native freshwater fish on a global scale (e.g. Welcomme 1988; Agostinho and Júlio Jr. 1996; Gozlan 2008; Vitule 2009; Bartley 2011; Pelicice et al. 2014). In the present study, the main non-native fish introduced from other zoogeographical regions were released as result of aquaculture (eight of the 10 species recorded). These species, *C. carpio*, *C. idella*, *C. gariepinus*, *H. nobilis*, *H. molitrix*, *I. punctatus*, *O. niloticus* and *T. rendalli*, are widespread and have been associated with the homogenization of fish faunas around the world (Rahel 2000, 2007; Clavero and García-Berthou 2006; Clavero and Hermoso 2011; Petesse and Petrere Jr. 2012; Vitule et al. 2012a; Daga et al. 2015).

The aquarium trade is also an important source of the direct release of unwanted organisms, i.e., fish that had been kept as pets, or via escapes from ornamental fish farming (e.g. Padilla and Williams 2004; Abilhoa et al. 2013). Moreover, the aquarium trade is vector for the introduction of other organisms as hitchhikers; these include plants, invertebrates and frogs (e.g. Padilla and Williams 2004; Magalhães and Jacobi 2008; Maceda-Veiga et al. 2013). Likewise, non-native species frequently carry parasites and while they are often adapted to their parasitic cargo, native species are frequently unprepared (i.e. naïve) for such invasions, since they have not co-evolved with the non-native parasites (Gozlan 2008). In our study, the aquarium trade was responsible for the introduction of the “pond loach” *M. anguillicaudatus*, released into the upper Iguaçu region from the Palearctic region. This species is widespread around the world (e.g. Ingenito et al. 2004; Freyhof and Korte 2005; Ribeiro et al. 2008). It can be commonly found in aquarium stores, and its introduction in the Iguaçu ecoregion is probably due to unintentional or deliberate release (Abilhoa et al. 2013).

The introduction of non-native species for sport fishing has been concentrated primarily in reservoirs (Welcomme 1988; Cambray 2003; Gozlan

2008; Clavero et al. 2013). Government agencies and the media in general frequently encourage the development of recreational sport fishing, in addition to illegal introductions by anglers (Vitule 2009; Vitule et al. 2014a). Non-native species introduced for this purpose are usually aggressive predators that have high economic value due to their qualities as fighting fish (Espínola et al. 2010; Britton and Orsi 2012). In our study, *Cichla kelberi* Kullander & Ferreira, 2006, *M. salmoides* and *S. brasiliensis* were introduced into reservoirs in order to enhance sport fishing in the ecoregion. Moreover, the number of individuals of *S. brasiliensis* recently recorded in the monitoring projects in this ecoregion has increased, which may promote the successful invasion of this species. These species are top predators and exercise strong predation pressure on native communities, causing severe impacts (García-Berthou 2002; Latini and Petrere Jr. 2004; Pelicice and Agostinho 2009; Espínola et al. 2010; Gubiani et al. 2010; Ellender and Weyl 2014; Garcia et al. 2014; Pelicice et al. 2015; Vitule et al. 2014a). Apart from the use of non-native fish in sport fisheries, the introduction of companion species as bait is common (Agostinho and Júlio Jr. 1996); many non-native species are introduced either because they escaped from fishing hooks or were released as a part of the remnants of live bait at the end of a sport fishing excursion (Agostinho and Júlio Jr. 1996; Vitule 2009). In our study, the species *A. ellisi*, *G. inaequilabiatus*, *G. sylvius* Albert & Fernandes-Matioli, 1999 and *S. brevipinna* were released in this way, primarily by fishermen trying to capture the biggest fish of the Iguaçu River system, the *Steindachneridion melanodermatum* Garavello, 2005; this endemic species was recently considered to be endangered.

Stocking of non-native species in reservoirs has long been a common practice carried out by government agencies and the hydropower sector (Agostinho and Julio Jr. 1996; Vitule 2009; Agostinho et al. 2010). However, stocking has often been conducted without defined objectives, scientific support, or any subsequent evaluation or monitoring of the results (Agostinho et al. 2010). Despite the huge efforts applied to stocking, using a variety of techniques and species, there are no known cases of stocking which have successfully avoided causing enormous negative, though often not immediately obvious, impacts (e.g. Vitule 2009). In the Iguaçu ecoregion *O. bonariensis* was introduced through this activity in 1997 (Suzuki and Agostinho 1997; Cassemiro et al. 2003). Currently, this species has been considered established in the lower Iguaçu region (Baumgartner et al. 2012; Santa Fé 2015).

### *Establishment and spread of non-native fish in the Iguaçu ecoregion*

Data on the spread and establishment of non-native species in the Iguaçu ecoregion were limited to indirect studies. Although records of the occurrence of non-native species in multiple studies (after the first record) were considered evidence of spread and establishment of non-native species, repeated introductions are likely to occur since in this ecoregion there is high pressure propagule due mainly to aquaculture. In addition, studies evaluating the spread stage of non-native species, from the original point of introduction, were scarce in this ecoregion. Nonetheless, the consecutive catch after the first record for some non-native species, like *C. carpio*, *A. altiparanae*, *O. bonariensis*, *O. niloticus* and *T. rendalli*, have increasingly been reported.

A few studies have indirectly reported on the establishment phase, inferring other basic ecological information like survival and reproduction of non-native populations. Thus, we can strongly infer that some non-native species, such as *A. altiparanae, C. carpio, G. inaequilabiatus, O. niloticus* and *T. rendalli*, could already be established and are spreading in this ecoregion. For example, *A. altiparanae* was found in all the reservoirs of this basin, while *G. inaequilabiatus* and *T. rendalli* were both present in 78% of the reservoirs, in a study considering the main reservoirs in the Iguaçu ecoregion (Daga et al. 2015). In addition, a common group of non-native species, including *C. carpio*, *O. niloticus* and *T. rendalli*, have been repeatedly released into most of the reservoirs of the Iguaçu basin: these species have become established in the major basins of the State of Paraná and also in many regions around the world (Clavero and Hermoso 2011; Petesse and Petrere Jr. 2012; Vitule et al. 2012a; Daga et al. 2015). On the other hand, some non-native species may be established in different reservoirs of this ecoregion, for example *M. salmoides* and *M. anguillicaudatus* in reservoirs in the upper Iguaçu, and *P. lineatus* and *O. bonariensis* to reservoirs in the lower Iguaçu (Cassemiro et al. 2003; Frana 2011; Baumgartner et al. 2012; Sartori 2014; Santa Fé 2015). *Prochilodus lineatus* was among the 10 most captured species in the Foz do Areia reservoir, and its preferential zone was the reservoir margin (Frana 2011), while for

**Table 1.** Origin and vectors of the non-native fish species introduced and established in the Iguaçu ecoregion.

| Origin/Vectors | Introduced | Established | References |
|---|---|---|---|
| **Neotropical** | | | |
| Aquaculture | 12 | 2 | Cassemiro et al. 2003; Frana 2011; Baumgartner et al. 2012; Sartori 2014; Daga et al. 2015; Santa Fé 2015 |
| Baiting | 4 | 1 | |
| Sport fishing | 2 | 0 | |
| Stocking | 1 | 1 | |
| **Palearctic** | | | |
| Aquaculture | 4 | 1 | Myers 1947; Abilhoa et al. 2013 |
| Aquarium trade | 1 | 1 | |
| **Ethiopian** | | | |
| Aquaculture | 3 | 2 | Daga et al. 2015 |
| **Nearctic** | | | |
| Aquaculture | 1 | 0 | Ingenito et al. 2004; Ribeiro et al. 2015 |
| Sport fishing | 1 | 1 | |
| Sum | 29 | 9 | |

*O. bonariensis*, the multiple size classes of the individuals caught were a strong indication of the establishment of this species in the Salto Santiago reservoir (Santa Fé 2015).

According to the studies found in this review, only four of the 19 non-native species introduced from Neotropical regions were considered established in the Iguaçu ecoregion, mainly due to aquaculture, baiting and stocking. From the Palearctic region, two of the five non-native species introduced were considered established in the Iguaçu ecoregion, due to aquaculture and aquarium trade. Of the three species introduced through aquaculture from the Ethiopian region; two were considered established. From the Nearctic region, just one of the two non-native species introduced was able to establish in the Iguaçu ecoregion, through sport fishing (Table 1).

Some species may show a 'lag' phase between the first records of introduction and their subsequent establishment success, and even when an introduced fish species becomes established, this does not mean that it is able to become self-sustaining in all regions of the river basin (e.g. Ellender and Weyl 2014). However, non-native species can cause severe impacts immediately after introduction, even if they are not established or widespread in the recipient region (i.e. invasive) (e.g. Blackburn et al. 2011; Ricciardi et al. 2013; Jeschke et al. 2014).

### *Impacts of non-native fish in the Iguaçu ecoregion*

The establishment of the non-native species reported above, by itself, may be considered an impact, which has caused negative effects on species composition and native community structure (Daga et al. 2015).

In the Iguaçu ecoregion, quantification of negative impacts of non-native species on native fishes was restricted to only six studies, all only indirectly measuring impacts. One study reported that the non-native species *A. altiparanae* has changed its feeding habits from herbivore to omnivore (Cassemiro et al. 2002). Two studies have suggested a gradual increase in the abundance and growth rates of *O. bonariensis* in different reservoirs of this ecoregion, mainly due to the high abundance and availability of zooplankton in the dammed environment, and the ability of the species to exploit this resource (Cassemiro et al. 2003; Santa Fé 2015). The changes reported in these studies were associated with the construction of dams, and these species are well adapted to lentic ecosystems, thus enabling them to increase their abundance after the damming. Dams may also facilitate biological invasions by providing favorable conditions which determine the number of non-native species in the reservoirs, for example higher values of temperature and conductivity (Sartori 2014). Moreover, these non-native species may compete with native ones for the same food resource, reducing the food spectrum of the native fish fauna (e.g. Cassemiro et al. 2002, 2003; Delariva et al. 2013).

Some studies reported the progressive increase of non-native species over time in this ecoregion, which may negatively affect the diversity of endemic species (e.g. Daga and Gubiani 2012; Daga et al. 2015). These increases include instances where the same non-native species was introduced into several reservoirs (leading to biotic homogenization) and/or instances where different non-native species were introduced into different reservoirs (leading to biotic differentiation); the presence of both types of introductions makes it difficult to make predictions of long-term trends for this ecoregion (Daga et al. 2015). However, when considered the 20 reservoirs of the three major basins in the State of Paraná, the precence of non-native fishes into sevaral reservoirs of this ecoregion contributed to biotic homogenization detected at the interbasin scale (Daga et al. 2015). Moreover, the native fish fauna may also be adversely affected by the dispersal of non-native species (e.g. Agostinho et al. 1999; Gubiani et al. 2010; Daga and Gubiani 2012). Additionally, positive interactions among non-native species are still underexplored in this ecoregion (Ribeiro, 2013), however, such interactions could increase the chances of survival, establishment, spread and the invasion rates, as well as the magnitude of the ecological impact (Simberloff and Von Holle 1999). For example, it appears that the introduction and establishment of *M. salmoides* was facilitated by the highly abundant non-native preys ("tilapia" species) in a reservoir of the upper Iguaçu (Ribeiro 2013).

*Management recommendations*

The negative effects on the endemic fish fauna have been poorly studied (e.g. Raghavan et al. 2008), even though the impacts of the non-native fish species associated with environmental modification are well documented in other parts of the world, and often include the decline of native fish (e.g. Rahel 2002; Clavero and García-Berthou 2006; McKinney 2006; Gozlan 2008; Olden et al. 2008; Pelicice and Agostinho 2009; Vitule et al. 2009, 2012b; Woodford et al. 2013; Alexander et al. 2014; Pelicice et al. 2015). Therefore, studies aimed at determining the factors leading to the success or failure of the establishment of non-native species in the recipient region are necessary (e.g. Skóra et al. 2015).

Management practices and population control measures of non-native fishes are scarce in this ecoregion (Ribeiro et al. 2015). However, these actions are needed to reduce the establishment rates, spreading and impacts of non-native species. Management options should include local eradication attempts (e.g. concentrating sport fishing in reservoirs thus non-native fishes could be eradicted from elsewhere), population control techniques (e.g. based on removal programs, such as those using electrofishing) and containment of existing non-native populations to avoid their further spread (e.g. Lockwood et al. 2007; Britton et al. 2011; Ribeiro et al. 2015).

For the Iguaçu ecoregion, the first step should be dissemination of the 'Lista Oficial de Espécies Exóticas Invasoras do Estado do Paraná' (Portaria 059/2015/IAP/GP; http://www.iap.pr.gov.br) as the majority of the non-native fish species recorded in our study were included in this list. In addition, a national integrated database and an illustrated guide to non-native species should be created and made available to stakeholders (e.g. managers and policy makers). This would assist in identification and provide biological information about the non-native species, helping to determine the potential impacts of the listed fish on threatened endemic fish fauna. In addition, it would provide information concerning the potential risks of aquaculture and to public health or safety.

Given the reduced inspection by the country's environmental agencies (e.g. Magalhães and Vitule 2013; Magalhães 2015; Vitule et al. 2014b), it is our responsibility as citizens to denounce wrongful actions and to secure compliance with public policies, including the interception of non-native aquatic species through the inspection of local pet shops and aquarium stores. Some of the confiscated illegal animals could be relocated to public aquariums that possess permits for them. In addition, we need to raise public awareness to encourage individuals to donate their unwanted pets to universities, aquarium hobbyists or other aquarium facilities, instead of opting for release into a local drainage system. Moreover, the abandonment of pets, such as aquarium dumping, is an environmental crime (Oliveira et al. 2014).

In the Iguaçu River, as well as in rivers of other ecoregions in Neotropics, those rearing fish in cages, especially those installed in reservoirs, should be encouraged to use native species (e.g. Agostinho et al. 1999; Lima Jr. et al. 2012). Those developing ponds for aquaculture or ornamental fish farming, especially those building ponds near streams, should also be encouraged to opt for native species, thereby avoiding increased propagule pressure and the risk of invasion by non-native species (e.g. Orsi and Agostinho 1999; Vitule 2009). Cultivating these attitudes, in combination with an educational awareness program, efficient supervision by the appropriate public agencies and adoption of appropriate management practices (e.g. Azevedo-Santos et al. 2015; Ribeiro et al. 2015), will enable increase compliance with current legislation, and improve the monitoring and effective control of non-native species.

## Conclusions

Our study highlights the importance of the Iguaçu ecoregion, which exhibits a high degree of endemism, and which also faces the imminent and actual risk of invasion by non-native fish, thereby representing a major challenge for the conservation of biodiversity. The majority of the records of non-native species were derived from technical reports, illustrating the importance of the basic ecological information generated in these studies. Such information indicates major gaps and biases nationally that should be the focus for future studies. Additionally, it is also important that scientific collections and museums register non-native species and maintain them in their collections, thus ensuring greater accuracy in identifying the early stages of the invasion process. We also highlight the need for surveys and experiments focusing on specific hypothesis and/or species interactions (i.e. empirical research about invasional meltdown, biotic homogenization and/or propagule pressure), in order to inform on impacts of non-natives and invasion biology.

In addition, our study emphasizes the need for further fieldwork in the headwaters of the river, since several native species are considered to be vulnerable or endangered. New species are currently being studied or have only recently been described in this ecoregion, highlighting the high degree of endemism of the fish fauna. We also emphasize the importance and urgency of studies supervised by ichthyologists, which should assume the extirpation of some native species that have only one record and are no longer caught in this ecoregion. This is especially true now, since recent extinctions may have been ignored because the species disappeared before we could discover that they existed.

Finally, the use of native species in aquaculture, ornamental fish farming, sport fishing and other activities should be encouraged, as well as increased educational awareness among the population and compliance with current legislation. This should be coupled with the adoption of management practices and population control measures for non-natives, thereby reducing the ecological impact caused by non-native fish on endemic fish fauna, as the total eradication of any given non-native species is probably impractical.

## Author contributions

V.S.D. and J.R.S.V. conceived the ideas. V.S.D. created the database. T.D. and V.A. assisted on database preparation and taxonomic revision of the species. V.S.D., E.A.G. and J.R.S.V. conducted the data analysis. All authors contributed equally to writing of the last version of the manuscript.

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The following supplementary material is available for this article:

**Table S1.** List of the non-native fish species introduced into the Iguaçu ecoregion between 1944 and 2012.

**Table S2.** List of studies/articles retained for analysis from exhaustive literature search

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