

# From the headwaters to the Iguassu Falls: Inventory of the ichthyofauna in the Iguassu River basin shows increasing percentages of nonnative species

#### Luciano Mezzaroba<sup>1,</sup> 🐀, Tiago Debona<sup>2</sup>, Augusto Frota<sup>3,4</sup>, Weferson Júnio da Graça<sup>1,5</sup> & Éder André Gubiani<sup>1,2</sup>

<sup>1</sup>Universidade Estadual do Oeste do Paraná, Programa de Pós-Graduação em Recursos Pesqueiros e Engenharia de Pesca, Rua da Faculdade, CEP 85903000, Toledo, PR, Brasil.

<sup>2</sup>Instituto Neotropical de Pesquisas Ambientais, Grupo de Pesquisas em Recursos Pesqueiros e Limnologia, Rua da Faculdade, Jardim La Salle, 85903-000, Toledo, PR, Brasil.

<sup>3</sup>Universidade Estadual de Maringá, Coleção Ictiológica do Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Av. Colombo, CEP 87020-900, Maringá, PR, Brasil.

<sup>4</sup>Universidade Estadual de Maringá, Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais, Av. Colombo, CEP 87020-900, Maringá, PR, Brasil.

<sup>5</sup>Universidade Estadual de Maringá, Centro de Ciências Biológicas, Departamento de Biologia e Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Av. Colombo, CEP 87020-900, Maringá, PR, Brasil. \*Corresponding author: Luciano Mezzaroba, e-mail: mezzarobaluciano@gmail.com

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Abstract: Knowledge of the ichthyofauna of a hydrographic basin is the minimum necessary condition for the implementation of any measures for the exploration, management or preservation of water and fishing resources. Despite its relevance, the number of fish species across the Iguassu River basin is still uncertain. Thus, the objective of this study was to compile the fish species that occur in the extensive stretch of the basin above the Iguassu Falls. In addition, we recorded the level of threat of extinction for native species, the origin of nonnative species, and their main vectors of introduction. To achieve this goal, a survey was carried out through consultations with ichthyological collections as well as online databases. Also, a literature review was conducted using the search platforms Thomson Reuters, SciELO and Elsevier's ScienceDirect to locate all articles published by March 2020 that addressed the topic "ichthyofauna in the Iguassu River basin". The survey compiled a total of 133 fish species distributed in nine orders, 29 families and 72 genera. Seventy-nine fish species were recorded that occur throughout the entire length of the basin, 119 species that occur in the hydrographic units of the middle and lower Iguassu River (40 exclusive) and 93 species that occur in the hydrographic unit of the upper Iguassu River (14 exclusive). The endemism rate shown here for the Iguassu River basin (approximately 69%) contrasts with the 40 nonnative fish species recorded (approximately 30% of the total species in the basin). Successive impoundments, reductions in habitat quality and the increase in the number of nonnative species are the main threats to native species, especially to the endemic species; approximately 20% of these species were listed in some category of threat of extinction. We emphasize that constant monitoring of ichthyofauna is necessary to discover putatively undescribed species, as well as for the application of management strategies to mitigate the negative effects and promote the control of the spread of nonnative species.

Keywords: Extinction, risk; Fish; Introduced, species; List of species; Paraná, State.

# Das cabeceiras às Cataratas do Iguaçu: inventário da ictiofauna da bacia do rio Iguaçu mostra aumento na porcentagem de espécies não nativas

**Resumo:** Conhecer a ictiofauna de uma bacia hidrográfica compreende condição mínima necessária para que se possam implantar quaisquer medidas de exploração, manejo ou preservação dos recursos hídricos e pesqueiros. Apesar de sua relevância, o número de espécies de peixes de toda a bacia hidrográfica do rio Iguaçu ainda é incerto. Assim, o objetivo deste estudo foi compilar as espécies de peixes que ocorrem no extenso trecho da bacia acima das Cataratas do Iguaçu. Além disso, registramos o nível de ameaça de extinção às espécies nativas, a origem das espécies não nativas e suas principais vias de introdução. Para isso foi realizado um levantamento por meio de consultas a coleções ictiológicas, bem como aos bancos de dados online, além de revisão de literatura por meio do uso das plataformas de buscas Thomson Reuters, Scielo e Elsevier – ScienceDirect, que abordavam o tópico "ictiofauna da bacia do rio Iguaçu" e o período de tempo incluiu todos os trabalhos publicados até março de 2020.

O levantamento compilou ao todo 133 espécies, distribuídas em nove ordens, 29 famílias e 72 gêneros. Em toda a extensão da bacia foram registradas 79 espécies de peixes. Nas unidades hidrográficas do médio e baixo rio Iguaçu foram registradas 119 espécies (40 exclusivas) e na unidade hidrográfica do alto rio Iguaçu foram registradas 93 espécies (14 exclusivas). A taxa de endemismo para a bacia do rio Iguaçu (aproximadamente 69%) contrasta com as 40 espécies de peixes não nativos registradas (aproximadamente 30% do total de espécies na bacia). Os sucessivos barramentos, a perda de qualidade de habitats e o aumento no número de espécies não nativas são ameaças às espécies autóctones, especialmente às endêmicas, as quais apresentam aproximadamente 20% listadas em alguma categoria de ameaça ao risco de extinção. Ressaltamos que o monitoramento constante da ictiofauna é necessário para a descoberta de espécies supostamente não descritas, bem como para a aplicação de estratégias de manejo para mitigar os efeitos negativos e promover o controle da disseminação de espécies não nativas. *Palavras-chave: Risco de extinção; Peixes; Espécies, introduzidas; Lista de espécies; Estado do Paraná.* 

# Introduction

The increase in human population and, consequently, human activities has increasingly changed ecosystems around the world, especially aquatic ones (Azevedo-Santos et al. 2019). Aquatic environments form a mosaic of habitats, from headwaters in mountainous regions to estuaries, shallow coastal habitats, reefs and seas (Arthington et al. 2016). For these environments, more than 30,000 fish species have already been described (Nelson et al. 2016), many of which are in danger of becoming locally or globally extinct (Darwall & Freyhof 2015). In this way, for the human use of natural resources from aquatic ecosystems, knowledge of the local ichthyofauna is the minimum necessary condition for the implementation of any measures of exploration, management or preservation for water and fish resources (Cavalli et al. 2018).

In different freshwater environments from different hydrographic basins, ichthyofaunal sampling has been performed and improved over the years; however, several species are still unknown to science (Langeani et al. 2007, Ota et al. 2015). Thus, these species are in danger of disappearing even before they are described and their real geographic distributions are known (Hortal et al. 2015). For the Iguassu River basin, which is one of the main tributaries of the left margin of the Paraná River, new inventories have revealed possible new species (Frota et al. 2016a, for example), many of which are endemic and could fall into categories with a marked risk of extinction.

The high endemism of the ichthyofauna in the hydrographic basin of the Iguassu River makes it a freshwater 'ecoregion' (Zawadzki et al. 1999, Abell et al. 2008, Baumgartner et al. 2012). This characteristic was possibly due to the isolation promoted by the formation of the Iguassu Falls during the Cretaceous (c. 22 Ma), which separated the ichthyofauna upstream of the Iguassu Falls from those downstream (Parolin et al. 2010). In addition, there are several waterfalls and rapids along the main channel and tributaries that contributed to the isolation of fish populations and, consequently, to the speciation process (Garavello et al. 1997, Baumgartner et al. 2012, Maack 2012, Frota et al. 2016a). As the area has high species richness with a high proportion of endemic fish species, the Iguassu River basin comprises a crucial site for preservation, since local extinctions would certainly result in global species extinctions (Baumgartner et al. 2012). The first studies on fish in the Iguassu River were carried out by Haseman (1911a, b), who described 13 fish species. Despite their significance, the ichthyofauna of the entire hydrographic basin of the Iguassu River are still little known when compared to the ichthyofauna of other large hydrographic systems, for example, the upper Paraná River basin (Delariva et al. 2018). In addition, the construction of dams and the introduction of nonnative fish species, mainly from sport fishing (Ribeiro et al. 2017) and aquaculture (Agostinho et al. 1999, ICMBio 2018), have threatened the native fish species of the Iguassu River (Agostinho et al. 1999, Daga & Gubiani 2012, Daga et al. 2016, Gubiani et al. 2018).

Ichthyofaunal surveys have been carried out in a segmented manner in the Iguassu River basin, especially in the upper and lower stretches of the basin (Baumgartner et al. 2012). In a catalog, Severi & Cordeiro (1994) registered 47 fish species for the Iguassu River basin, while Garavello et al. (1997) recorded 52 fish species only for the Segredo reservoir region. Ingenito et al. (2004), in an ichthyofaunal survey carried out in the upper Iguassu River, recorded the occurrence of 41 fish species that had not previously been mentioned, increasing the total number of species recorded for the entire Iguassu River basin to 84. Baumgartner et al. (2006) registered 41 fish species in the area of influence of the Salto Osório Reservoir, and Baumgartner et al. (2012) increased the number of fish in the region corresponding to the lower Iguassu River to 106 fish species. Therefore, it is noted that there is still no compilation of all studies and sampling efforts carried out that make it possible to report the total number of known fish species for the Iguassu River basin, especially in the extensive stretch of the basin above the Iguassu Falls.

In view of the above, the present study aimed to compile the fish species that occur in the entire Iguassu River basin, from the headwaters to the Iguassu Falls, by reviewing the species lists published in scientific articles and books, as well as the species registration in ichthyological collections. In this study, we recorded the endemic fish species for the middle/lower and upper Iguassu River basin, as well as the nonnative fish species and their origin. We investigated the threat level of the native fish species according to the categories of the International Union for Conservation of Nature (IUCN 2012), and we established the main vectors of introduction of the nonnative fish species. In this way, we hope to provide support for strategies for the conservation of ichthyofauna in the Iguassu River basin.

## **Material and Methods**

#### 1. Study area

The Iguassu River is formed by the junction of the Iraí and Atuba rivers on the border between the municipalities of Curitiba and Pinhais on the first of the Paraná plateaus, from where it flows over 1,320 km until flowing into the Paraná River close to the city of Foz do Iguaçu in the Paraná State (SEMA 2010). This river is considered one of the main tributaries of the left margin of the Paraná River, and its mouth is located downstream of the Itaipu Dam (Baumgartner et al. 2006). In addition, the Iguassu River is considered the largest river in the Paraná State as well as the river with the largest drainage basin, with an area of 72,000 km<sup>2</sup>, of which 79% belongs to the Paraná State, 19% to the Santa Catarina State and 2% to Argentina (Eletrosul 1978).

Although the limits are not well established, the hydrographic basin of the Iguassu River can be subdivided into three hydrographic units (Figure 1): the upper, middle and lower Iguassu, which represent the first, second and third Paraná plateaus, respectively (Baumgartner et al. 2012, Maack 2012). The Iguassu Falls (Figure 1) are located in Iguassu National Park (hydrographic unit of the lower Iguassu River) and are considered the largest falls on the planet in terms of water volume, which flows at approximately 1,551 m<sup>3</sup>.s<sup>-1</sup> (SEMA 2010). In this region, the Iguassu River reaches an approximate width of 1,200 m, running in a deep canyon for the rest of its course until its mouth on the Paraná River (Maack 2012). Thus, due to ichthyofaunal isolation promoted by the formation of the Iguassu Falls, our compilation considered the occurrence of fish species from the headwaters of the upper Iguassu River to the Iguassu Falls.

Land use is quite diverse across the basin. In the upper Iguassu River, there is a large resident population that is mainly occupied by industrial, commercial, and service activities. In its course in the interior of the Paraná State, agriculture is predominant, with some areas of intensive agriculture in the region of the municipality of Guarapuava up to the border with the Santa Catarina State to the south of the basin.



Figure 1. Map of the Iguassu River basin, Paraná State, Brazil. Yellow dots indicate the sampling sites within the basin that were georeferenced and cataloged in the ichthyological collections. Each point may correspond to more than one sampling site. The boundaries between the middle/lower and upper hydrographic units are represented by red diamonds. The red star indicates the location of the Iguassu Falls.

In the middle and lower stretches of the Iguassu River, there is a high concentration of forest cover (SEMA 2010), and the unevenness of this region favors hydroelectric use. There are 12 large reservoirs in the middle/lower and another three in the upper Iguassu River basin (Daga et al. 2016). As it is located in an area of rugged relief with several rivers, rapids, and waterfalls, the hydrographic basin of the Iguassu River has greatly influenced the geographical distribution of several groups of organisms, promoting a high degree of endemism of the fish species that inhabit it (Baumgartner et al. 2012).

## 2. Database

The survey of the fish species found in the hydrographic basin of the Iguassu River, in the long stretch above the Iguassu Falls, was carried out by consulting the ichthyological collections of the following institutions: Londrina State University Museum in Londrina (MZUEL), the Museum of Zoology of the University of São Paulo in São Paulo (MZUSP), the Capão da Imbuia Natural History Museum in Curitiba (MHNCI), the PUCRS Museum of Science and Technology in Porto Alegre (MCP), the Nupélia Ichthyology Collection of the State University of Maringá in Maringá (NUP), National Museum of Rio de Janeiro in Rio de Janeiro (MNRJ), and the Ichthyology Collection of GERPEL of the Western Paraná State University in Toledo (CIG). The species records (Figure 1) of these collections came from the online databases Species Link (http://www.splink.org.br/), Fishnet2 (http://www.fishnet2.net/search. aspx) and SiBBr (https://ala-hub.sibbr.gov.br/ala-hub/occurrences/ search), which were accessed in May 2020. Personal communications with the professionals responsible for the ichthyological collections were also carried out. In addition, to complement the information, bibliographical research was performed in March 2020 using articles in the Thomson Reuters (ISI Web of Knowledge, apps.isiknowledge. com), Elsevier's ScienceDirect (http://www.sciencedirect.com), and SciELO (http://www.scielo.org) databases that addressed the topic of "ichthyofauna of the Iguassu River basin". The search terms in the "topic" field were "fish\* OR ichthyo\* OR checklist AND Iguassu River basin", and the searched timespan included all years up to the date of the search. The search was then refined according to the following research areas: environmental sciences, ecology, zoology, freshwater biology, biodiversity, conservation, and fisheries and water resources. In addition, all articles that included lists of fish species of the Iguassu River basin that were published in the journal Check List: Journal of Species Lists and Distributions, which is not indexed in the aforementioned databases, were also included in our review. For this, the search was carried out using the option "search for articles" on the journal website (http://www.checklist.org.br/search), and all categories and volumes were searched. The studies included in this bibliographical research contained a list of fish species caught in the Iguassu River or in its tributaries in the stretch above the Iguassu Falls. Nonrelated articles were excluded based on their title, abstract or, if necessary, after a careful reading of the entire text.

To identify the origin, the fish species were classified as autochthonous (endemic or naturally occurring fish species in the Iguassu River basin) and nonnative. For the classification of nonnative fish species, the recommendation of Ellender & Weyl (2014) was adopted, which separates them into extralimital species (from other hydrographic basins in the Neotropical region) and alien species (from other biogeographic regions). Nonnative fish species were classified according to the possible vectors of introduction into five groups: aquaculture (species widely used in fish farms in the region, introduced intentionally or accidentally); aquarism (ornamental fish species, introduced intentionally or accidentally); stocking (species from stocking in reservoirs); baiting (species used as bait in fishing activities, introduced intentionally or accidentally) and sport fishing (species introduced for sport fishing). The threat level for each autochthonous fish species was set according to the Portaria do Ministério do Meio Ambiente, nº 445 (December 17, 2014) (BRASIL 2014), which was amended by Decree nº 98 (April 28, 2015) (BRASIL 2015) and by the Red Book of Endangered Brazilian Fauna (ICMBio 2018). These regulations classify the endangered species of fish and aquatic invertebrates from the Brazilian fauna with the following categories: extinct in the wild (EW), critically endangered (CR), endangered (EN), and vulnerable (VU). Finally, considering that the middle stretch of the Iguassu River basin is short, with weakly established limits and presents a similar fish species composition with the lower stretch (Ingenito et al. 2004, Baumgartner et al. 2012), we compartmentalized the species distribution inventoried for the middle/ lower and upper stretches of the basin.

#### 3. Fish identification

Identification follows Ingenito et al. (2004), Baumgartner et al. (2012), Garavello et al. (2012), and by comparison of the specimens with original descriptions. Whenever possible, the determinations of the fish species were checked by specialists of each taxonomic group. Fish species were classified based on Van der Laan et al. (2020), except for Astyanax and Psalidodon that follow Terán et al. (2020). Species names validity was based on Fricke et al. (2020). Some species recorded in the collections or literatures analyzed were reexamined and identifications were corrected: Astyanax fasciatus (Cuvier, 1819) is *Psalidodon bifasciatus* (Garavello & Sampaio, 2010); A. aff. scabripinnis (Eigenmann, 1921) is A. totae Ferreira Haluch & Abilhoa, 2005 (see Haluch & Abilhoa 2005) or A. eremus Ingenito & Duboc, 2014 (see Ingenito & Duboc 2014); Bryconamericus sp. and Diapoma aff. alburnum (Hensel, 1870) are Diapoma sp.; Characidium sp. 2 is C. travassosi Melo, Buckup & Oyakawa 2016; Corydoras aff. paleatus (Jenyns, 1842) is Corydoras sp.; Crenicichla yaha Casciotta, Almirón & Gómez, 2006 is C. tesay Casciotta & Almirón, 2009 (see Piálek et al. 2015); C. tesay from Jordão and Areia river basins (sensu Frota et al. 2016a) is Crenicichla sp. (see Říčan et al. 2017); Geophagus brasiliensis (Quoy & Gaimard, 1824) is Geophagus iporangensis Haseman, 1911 (see Argolo et al. 2020); Glandulocauda melanopleura Eigenmann, 1911 is G. caerulea Menezes & Weitzman, 2009 (see Menezes & Weitzman 2009); Gymnogeophagus setequedas Reis, Malabarba & Pavanelli, 1992 is G. taroba Casciotta, Almirón, Piálek & Říčan, 2017 (see Casciotta et al. 2017); Hisonotus sp. is H. yasi (Almirón, Azpelicueta & Casciotta, 2004); some individuals identified as Hoplias aff. malabaricus (Bloch, 1794) are H. misionera Rosso, Mabragaña, González-Castro, Delpiani, Avigliano, Schenone & Díaz de Astarloa, 2016; Megaleporinus aff. elongatus (Valenciennes, 1850) is M. obtusidens (Valenciennes, 1837); M. obtusidens is M. piavussu (Britski, Birindelli & Garavello, 2012), Pareiorhaphis sp. is P. parmula Pereira, 2005, and *Phalloceros caudimaculatus* (Hensel, 1868) is P. harpagos Lucinda, 2008 or P. spiloura Lucinda, 2008.

# Results

The survey on the ichthyofaunal diversity of the Iguassu River hydrographic basin, from its sources to the Iguassu Falls, revealed a total of 133 fish species distributed in nine orders, 29 families and 72 genera (Table 1). Siluriformes (51 species) and Characiformes (48 species) were the most representative orders, comprising approximately 74% of the total species recorded in the basin (Figure 2). The families that showed the highest species richness were Characidae (28 species), Loricariidae (17 species), Cichlidae (13 species), Trichomycteridae (12 species), Anostomidae and Heptapteridae (seven species each), which composed approximately 63% of all species (Figure 2).

The fish species distribution in the middle/lower and upper stretches of the Iguassu River basin revealed that 79 fish species (approximately 59% of the total) were present across the entire length of the basin (Table 1). Of the total species, 119 fish species occurred in the middle/lower Iguassu (approximately 89% of the total fish species), and 40 of these fish species (approximately 30% of the total) were exclusive to this stretch of the basin (Table 1). In the upper Iguassu River, 93 fish species were recorded (approximately 70% of the total fish species), and 14 of these fish species (approximately 11% of the total) were exclusive to this stretch of the basin (Table 1).

The species origin classification revealed that of the 133 recorded fish species, 93 were considered autochthonous (approximately 70% of the total fish species) and 40 were nonnative (approximately 30% of the total fish species). Among the nonnative fish species, 30 species were classified as extralimital (approximately 23% of total fish species and 75% of nonnative fish species), and the other 10 species were classified as aliens (approximately 8% of total fish species and 25% of the nonnative fish species). The main vector of introduction of nonnative fish species was aquaculture.

Table 1. Iguassu River basin ichthyofauna recorded above the Iguassu Falls according to species, voucher specimens, the origin of each species, threat level, introduction vector, and distribution along the middle/lower and upper sections of the basin. Abbreviations are: CAS, California Academy of Sciences; CIG, Coleção Ictiológica do Gerpel; FMNH, Field Museum of Natural History; MACN, Museo Argentino de Ciencias Naturales; MCP, Museu de Ciências e Tecnologia da Pontificia Universidade Católica do Rio Grande do Sul; MHNCI, Museu de História Natural do Capão da Imbuia; MLP, Museo de La Plata; MNRJ, Museu Nacional do Rio de Janeiro; MZUEL, Museu de Zoologia da Universidade Estadual de Londrina; MZUSP, Museu de Zoologia da Universidade de São Paulo; NUP, Coleção Ictiológica do Nupélia; CR: Critically Endangered species; EN: Endangered species; VU: Vulnerable species. Autochthonous\*: Endemic species from Iguassu River basin; Nonnative: Extralimital species; Nonnative\*: Alien species. The symbol # refers to species added to the list due to personal observation of the authors and that do not have material registered in the consulted ichthyological collections.

	Species	Voucher	Origin/Threat level	Introduction vector	Middle/ Lower Iguassu	Upper Iguassu
	CYPRINIFORMES					
	Cobitidae					
1	Misgurnus anguillicaudatus (Cantor, 1842)	MHNCI 9076	Nonnative <sup>•</sup>	Aquarism		Х
	Cyprinidae					
2	Cyprinus carpio Linnaeus, 1758	NUP 1811	Nonnative <sup>•</sup>	Aquaculture	Х	Х
	Xenocyprididae					
3	Ctenopharyngodon idella (Valenciennes, 1844)	NUP 11141	Nonnative <sup>•</sup>	Aquaculture	Х	Х
4	Hypophthalmichthys molitrix (Valenciennes, 1844)	NUP 2383	Nonnative <sup>®</sup>	Aquaculture	Х	Х
5	Hypophthalmichthys nobilis (Richardson, 1845)	NUP 2056	Nonnative <sup>®</sup>	Aquaculture	Х	Х
	CHARACIFORMES					
	Anostomidae					
6	Leporinus amae Godoy, 1980	CIG 3094	Nonnative	Aquaculture	Х	
7	Leporinus friderici (Bloch, 1794)	NUP 11872	Nonnative	Aquaculture	Х	Х
8	Leporinus octofasciatus Steindachner, 1915	NUP 12787	Nonnative	Aquaculture	Х	Х
9	Megaleporinus macrocephalus (Garavello & Britski, 1988)	NUP 3252	Nonnative	Aquaculture	Х	Х
10	Megaleporinus obtusidens (Valenciennes, 1837)	NUP 12788	Nonnative	Aquaculture	Х	Х
11	Megaleporinus piavussu (Britski, Birindelli & Garavello, 2012)	MZUEL 15983	Nonnative	Aquaculture	Х	Х
12	Schizodon borellii (Boulenger, 1900)	MZUEL 17941	Nonnative	Aquaculture	Х	
	Bryconidae					
13	Brycon hilarii (Valenciennes, 1850)	NUP 3245	Nonnative	Aquaculture	Х	Х
14	Brycon orbignyanus (Valenciennes, 1850)	CIG 3516	Nonnative	Aquaculture	Х	
15	Salminus brasiliensis (Cuvier, 1816)	MZUEL 13302	Nonnative	Sport-fishing	Х	Х
	Characidae					
16	Astyanax dissimilis Garavello & Sampaio, 2010	NUP 17791	Autochthonous*		Х	Х
17	Astyanax eremus Ingenito & Duboc, 2014	NUP 13501	Autochthonous*/CR			Х
18	Astyanax jordanensis Vera Alcaraz, Pavanelli & Bertaco, 2009	NUP 5252	Autochthonous*/VU		Х	

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	Species	Voucher	Origin/Threat level	Introduction vector	Middle/ Lower Iguassu	Upper Iguassu
19	Astyanax lacustris (Lütken, 1875)	NUP 17521	Autochthonous		Х	Х
20	Astyanax minor Garavello & Sampaio, 2010	NUP 16888	Autochthonous*		Х	Х
21	Astyanax serratus Garavello & Sampaio, 2010	NUP 16030	Autochthonous*		Х	Х
22	Astyanax totae Ferreira Haluch & Abilhoa, 2005	MHNCI 10305	Autochthonous*			Х
23	Astyanax varzeae Abilhoa & Duboc, 2007	MCP 40535	Autochthonous*			Х
24	Astyanax sp. 1	NUP 3706	Autochthonous*		Х	
25	Astyanax sp. 2	NUP 3048	Autochthonous*		Х	
26	Bryconamericus ikaa Casciotta, Almirón & Azpelicueta, 2004	NUP 15987	Autochthonous*		Х	Х
27	Bryconamericus pyahu Azpelicueta, Casciotta & Almirón, 2003	NUP 19031	Autochthonous*		Х	Х
28	Charax stenopterus (Cope, 1894)	NUP 16033	Nonnative	Aquaculture		Х
29	Diapoma sp.	NUP 6620	Autochthonous*		Х	Х
30	Glandulocauda caerulea Menezes & Weitzman, 2009	MNRJ 5642	Autochthonous*/EN			Х
31	Hasemania maxillaris Ellis, 1911	FMNH 54303	Autochthonous*		Х	Х
32	Hasemania melanura Ellis, 1911	FMNH 54384	Autochthonous*		Х	Х
33	Hyphessobrycon bifasciatus Ellis, 1911	MHNCI 10621	Autochthonous			Х
34	Hyphessobrycon griemi Hoedeman, 1957	MHNCI 10622	Autochthonous		Х	Х
35	Hyphessobrycon reticulatus Ellis, 1911	NUP 15684	Autochthonous		Х	Х
36	Hyphessobrycon taurocephalus Ellis, 1911	FMNH 54389	Autochthonous*			Х
37	Oligosarcus longirostris Menezes & Géry, 1983	NUP 15881	Autochthonous*		Х	Х
38	Roeboides descalvadensis Fowler, 1932	MZUEL 16357	Nonnative	Aquarism	Х	
39	Mimagoniates microlepis (Steindachner, 1877)	NUP 15549	Autochthonous		Х	Х
40	Psalidodon bifasciatus (Garavello & Sampaio, 2010)	MHNCI 12340	Autochthonous		Х	Х
41	Psalidodon gymnodontus Eigenmann, 1911	NUP 6843	Autochthonous*		Х	Х
42	Psalidodon gymnogenys (Eigenmann, 1911)	FMNH 54707	Autochthonous*/EN		Х	Х
43	Undescribed genus sp.	NUP 12783	Autochthonous*		Х	
	Crenuchidae					
44	Characidium travassosi Melo, Buckup & Oyakawa, 2016	MCP 22605	Autochthonous		Х	
45	Characidium sp.	NUP 15876	Autochthonous*		Х	Х
	Curimatidae					
46	Cyphocharax cf. santacatarinae (Fernández - Yépez, 1948)	NUP 11205	Autochthonous		Х	
47	Steindachnerina brevipinna (Eigenmann & Eigenmann, 1889)	NUP 11487	Nonnative	Baiting	Х	
	Erythrinidae					
48	Hoplias intermedius (Günther, 1864)	#	?		Х	Х
49	Hoplias aff. malabaricus (Bloch, 1794)	NUP 11855	Autochthonous		Х	Х
50	Hoplias misionera Rosso, Mabragaña, González-Castro, Delpiani, Avigliano, Schenone & Díaz de Astarloa, 2016	NUP 2074	Autochthonous		Х	
	Parodontidae					
51	Apareiodon vittatus Garavello, 1977	NUP 12097	Autochthonous*		Х	Х
	Prochilodontidae					
52	Prochilodus lineatus (Valenciennes, 1837)	NUP 3251	Nonnative	Reservoir	Х	Х
	Serrasalmidae					
53	Piaractus mesopotamicus (Holmberg, 1887)	NUP 21149	Nonnative	Aquaculture	Х	Х

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	Species	Voucher	Origin/Threat level	Introduction vector	Middle/ Lower Iguassu	Upper Iguassu
	GYMNOTIFORMES					
	Apteronotidae					
54	Apteronotus ellisi (Alonso de Arámburu, 1957)	NUP 3253	Nonnative	Baiting	Х	Х
	Gymnotidae					
55	Gymnotus inaequilabiatus (Valenciennes, 1839)	NUP 3752	Nonnative	Baiting	Х	Х
56	Gymnotus sylvius Albert & Fernandes-Matioli, 1999	NUP 19035	Nonnative	Baiting	Х	Х
	SILURIFORMES					
	Auchenipteridae					
57	Glanidium ribeiroi Haseman, 1911	NUP 2443	Autochthonous*		Х	Х
58	Tatia jaracatia Pavanelli & Bifi, 2009	MZUSP 98248	Autochthonous*		Х	Х
	Callichthyidae					
59	Callichthys callichthys (Linnaeus, 1758)	NUP 5490	Nonnative	Baiting	Х	Х
60	Corydoras carlae Nijssen & Isbrücker, 1983	NUP 19034	Autochthonous*		Х	Х
61	Corydoras ehrhardti Steindachner, 1910	NUP 15802	Autochthonous		Х	Х
62	Corydoras cf. longipinnis Knaack, 2007	NUP 12809	Autochthonous		Х	
63	Corydoras sp.	NUP 709	Autochthonous		Х	Х
64	Hoplosternum littorale (Hancock, 1828)	NUP 11201	Nonnative	Baiting	Х	Х
	Clariidae					
65	Clarias gariepinus (Burchell, 1822)	NUP 3246	Nonnative <sup>•</sup>	Aquaculture	Х	
	Heptapteridae					
66	Heptapterus stewarti Haseman, 1911	MHNCI 10343	Autochthonous*			Х
67	Heptapterus sp.	NUP 15925	Autochthonous*		Х	Х
68	Imparfinis hollandi Haseman, 1911	NUP 2976	Autochthonous*		Х	Х
69	Rhamdia branneri Haseman, 1911	NUP 2448	Autochthonous*		Х	Х
70	Rhamdia voulezi Haseman, 1911	NUP 1659	Autochthonous*		Х	Х
71	<i>Rhamdia</i> sp.	NUP 5284	Autochthonous*		Х	Х
72	Rhamdiopsis moreirai Haseman, 1911	MHNCI 8929	Autochthonous		Х	Х
	Ictaluridae					
73	Ictalurus punctatus (Rafinesque, 1818)	NUP 584	Nonnative <b>■</b>	Aquaculture	Х	Х
	Loricariidae					
74	Ancistrus abilhoai Bifi, Pavanelli & Zawadzki, 2009	MZUSP 104116	Autochthonous*		Х	Х
75	Ancistrus agostinhoi Bifi, Pavanelli & Zawadzki, 2009	MZUSP 104118	Autochthonous*		Х	
76	Ancistrus mullerae Bifi, Pavanelli & Zawadzki, 2009	MZUSP 104121	Autochthonous*		Х	
77	Hisonotus yasi (Almirón, Azpelicueta & Casciotta, 2004)	NUP 8720	Autochthonous*		Х	Х
78	Hypostomus agna (Miranda-Ribeiro, 1907)	NUP 21922	Autochthonous		Х	Х
79	Hypostomus albopunctatus (Regan, 1908)	NUP 593	Autochthonous		Х	Х
80	Hypostomus commersoni Valenciennes, 1836	NUP 552	Autochthonous		Х	Х
81	Hypostomus derbyi (Haseman, 1911)	NUP 677	Autochthonous		Х	Х
82	Hypostomus myersi (Gosline, 1947)	NUP 680	Autochthonous		Х	Х
83	Hypostomus nigropunctatus Garavello, Britski & Zawadzki, 2012	NUP 5082	Autochthonous*		Х	

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	Species	Voucher	Origin/Threat level	Introduction vector	Middle/ Lower Iguassu	Upper Iguassu
84	Loricariichthys cf. melanocheilus Reis & Pereira, 2000	NUP 10791	Nonnative	Aquarism	Х	
85	Loricariichthys cf. rostratus Reis & Pereira, 2000	MHNCI 11044	Nonnative	Aquarism	Х	
86	Neoplecostomus sp.	NUP 11087	Autochthonous*		Х	
87	Otothyropsis biamnicus Calegari, Lehmann A. & Reis, 2013	NUP 16004	Autochthonous		Х	
88	Pareiorhaphis parmula Pereira, 2005	NUP 15928	Autochthonous		Х	Х
89	Rineloricaria langei Ingenito, Ghazzi, Duboc & Abilhoa, 2008	MCP 42506	Autochthonous*			Х
90	Rineloricaria maacki Ingenito, Ghazzi, Duboc & Abilhoa, 2008	NUP 3059	Autochthonous*		Х	
	Pimelodidae					
91	Pimelodus britskii Garavello & Shibatta, 2007	NUP 1786	Autochthonous*		Х	Х
92	Pimelodus ortmanni Haseman, 1911	NUP 1664	Autochthonous*		Х	Х
93	Pseudoplatystoma corruscans (Spix & Agassiz, 1829)	NUP 11142	Nonnative	Aquaculture	Х	Х
94	Pseudoplatystoma reticulatum Eigenmann & Eigenmann, 1889	NUP 3247	Nonnative	Aquaculture	Х	Х
95	Steindachneridion melanodermatum Garavello, 2005	NUP 11903	Autochthonous*/EN		Х	
	Trichomycteridae					
96	Cambeva castroi (de Pinna, 1992)	NUP 3127	Autochthonous*		Х	Х
97	Cambeva crassicaudata (Wosiacki & de Pinna, 2008)	NUP 10827	Autochthonous*/EN		Х	
98	Cambeva davisi (Haseman, 1911)	NUP 19054	Autochthonous		Х	Х
99	Cambeva igobi (Wosiacki & de Pinna, 2008)	NUP 9866	Autochthonous*/EN		Х	
100	Cambeva mboycy (Wosiacki & Garavello, 2004)	NUP 19051	Autochthonous*/EN		Х	Х
101	Cambeva naipi (Wosiacki & Garavello, 2004)	MZUSP 38788	Autochthonous*			Х
102	Cambeva plumbea (Wosiacki & Garavello, 2004)	NUP 1614	Autochthonous*		Х	
103	Cambeva stawiarski (Miranda Ribeiro, 1968)	NUP 19049	Autochthonous		Х	Х
104	Cambeva taroba (Wosiacki & Garavello, 2004)	NUP 3125	Autochthonous*		Х	
105	<i>Cambeva</i> sp. 1	NUP 12660	Autochthonous*		Х	
106	<i>Cambeva</i> sp. 2	NUP 12661	Autochthonous*		Х	
107	Trichomycterus papilliferus Wosiacki & Garavello, 2004	NUP 17363	Autochthonous*/EN		Х	Х
	ATHERINIFORMES					
	Atherinopsidae					
108	Odontesthes bonariensis (Valenciennes, 1835)	NUP 1610	Nonnative	Reservoir	Х	
	CYPRINODONTIFORMES					
	Anablepidae					
109	Jenynsia diphyes Lucinda, Ghedotti & Graça, 2006	NUP 606	Autochthonous*/EN		Х	
110	Jenynsia eigenmanni (Haseman, 1911)	NUP 2862	Autochthonous*		Х	Х
	Poeciliidae					
111	Cnesterodon carnegiei Haseman, 1911	MHNCI 7609	Autochthonous*/VU			Х
112	Cnesterodon omorgmatos Lucinda & Garavello, 2001	MCP 22742	Autochthonous*/EN		Х	
113	Phalloceros harpagos Lucinda, 2008	NUP 19040	Autochthonous		Х	Х
114	Phalloceros spiloura Lucinda, 2008	MCP 27446	Autochthonous			Х
115	Poecilia reticulata Peters, 1859	NUP 19041	Nonnative	Aquarism	Х	
116	Xiphophorus hellerii Heckel, 1848	NUP 21119	Nonnative	Aquarism	Х	
	Rivulidae					
117	Austrolebias araucarianus Costa, 2014	MNRJ 9798	Autochthonous*		Х	
118	Austrolebias carvalhoi (Myers, 1947)	CAS 41178	Autochthonous*/CR			X

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	Species	Voucher	Origin/Threat level	Introduction vector	Middle/ Lower Iguassu	Upper Iguassu
	SYNBRANCHIFORMES					
	Synbranchidae					
119	Synbranchus marmoratus Bloch, 1795	NUP 19047	Nonnative	Baiting	Х	Х
	CICHLIFORMES					
	Cichlidae					
120	Australoheros angiru Říčan, Piálek, Almirón & Casciotta, 2011	NUP 11190	Autochthonous		Х	Х
121	Australoheros kaaygua Casciotta, Almirón & Gómez, 2006	NUP 1839	Autochthonous		Х	Х
122	Cichla kelberi Kullander & Ferreira, 2006	NUP 19171	Nonnative	Sport-fishing	Х	Х
123	Cichlasoma paranaense Kullander, 1983	NUP 9758	Nonnative	Aquarism	Х	
124	Coptodon rendalli (Boulenger, 1897)	NUP 3749	Nonnative <sup>•</sup>	Aquaculture	Х	Х
125	Crenicichla iguassuensis Haseman, 1911	FMNH 54159	Autochthonous*		Х	Х
126	<i>Crenicichla tapii</i> Piálek, Dragová, Casciotta, Almirón & Říčan, 2015	MLP 10560	Autochthonous*		Х	
127	Crenicichla tesay Casciotta & Almirón, 2009	NUP 3731	Autochthonous*		Х	Х
128	Crenicichla tuca Piálek, Dragová, Casciotta, Almirón & Říčan, 2015	MLP 10818	Autochthonous*		Х	
129	Crenicichla sp.	NUP 11288	Autochthonous*		Х	
130	Geophagus iporangensis Haseman, 1911	NUP 704	Autochthonous		Х	Х
131	Gymnogeophagus taroba Casciotta, Almirón, Piálek & Říčan, 2017	MLP 11258	Autochthonous*		Х	
132	Oreochromis niloticus (Linnaeus, 1758)	NUP 19048	Nonnative <sup>•</sup>	Aquaculture	Х	Х
	CENTRARCHIFORMES					
	Centrarchidae					
133	Micropterus salmoides (Lacepède, 1802)	NUP 11898	Nonnative <sup>•</sup>	Sport-fishing	Х	Х



**Figure 2.** Number of species per family of ichthyofauna recorded in the hydrographic basin of the Iguassu River. The colors indicate the order to which each family belongs.

Twenty-one species (52.5% of the total nonnative fish species) were introduced into the basin through this vector, with emphasis on alien species of Asian - *Ctenopharyngodon idella* (Valenciennes, 1844), *Cyprinus carpio* Linnaeus, 1758, *Hypophthalmichthys molitrix* (Valenciennes, 1844) and *Hypophthalmichthys nobilis* 

(Richardson, 1845) – and African origin - *Oreochromis niloticus* (Linnaeus, 1758) and *Coptodon rendalli* (Boulenger, 1897). Fishing was another important vector of introduction of nonnative fish species since seven species (17.5% of the total nonnative fish species) were introduced as bait and three other species (7.5%) by sport fishing. Aquarium activities were responsible for the introduction of seven more species and stocking in reservoirs responsible for the introduction of two other species (5%) (Table 1, Figure 3).



Figure 3. Nonnative fish species according to their introduction vectors into the Iguassu River basin, Paraná State, Brazil.

Of the 93 autochthonous fish species of the Iguassu River, 64 were listed as endemic, which revealed an endemism rate of approximately 69%. Thirteen endemic fish species (approximately 10% of total species, 14% of total native fish species and 20% of endemic fish species) are listed as being under some level of threat (Table 1). Astyanax eremus and Austrolebias carvalhoi (Myers, 1947) were listed at the highest threat level (CR). Nine fish species, or approximately 69% of the species under some level of threat (Cambeva crassicaudata (Wosiacki & de Pinna, 2008); C. igobi (Wosiacki & de Pinna, 2008); C. mboycy (Wosiacki & Garavello, 2004); Cnesterodon omorgmatos Lucinda & Garavello, 2001; Glandulocauda caerulea; Jenynsia diphyes Lucinda, Ghedotti & Graça, 2006; Psalidodon gymnogenys (Eigenmann, 1911); Steindachneridion melanodermatum Garavello, 2005 and Trichomycterus papilliferus Wosiacki & Garavello, 2004), were listed in category EN. Astyanax jordanensis Vera Alcaraz, Pavanelli & Bertaco, 2009 and Cnesterodon carnegiei Haseman, 1911 were listed in the category VU.

Finally, we recorded the occurrence of at least 13 putatively undescribed species of autochthonous fish (listed as "sp." or with the suffix "aff.") for the Iguassu River basin above the Iguassu Falls (Table 1), which represented approximately 10% of the total number of fish species and 14% of the total number of native fish species. Of these species, all occurred in the middle/lower Iguassu River basin, and seven (*Cambeva* sp. 1, *Cambeva* sp. 2, *Crenicichla* sp., *Neoplecostomus* sp., *Astyanax* sp. 1, *Astyanax* sp. 2, and undescribed genus sp.) were considered exclusive to this stretch of the basin.

# Discussion

Our compilation of data increased the number of fish species in the Iguassu River basin to 133 in the stretch above the Iguassu Falls. Our results revealed that 52 more species have been registered than mentioned by Ingenito et al. (2004) for the upper Iguassu River and 13 species more than recorded by Baumgartner et al. (2012) for the lower Iguassu River. It is important to highlight that most of the ichthyofaunal surveys available for the Iguassu River basin occurred in areas influenced by dams built on the main channel of the Iguassu River, since there is a greater financial incentive for research on this modality due to the need of hydroelectric companies to comply with environmental laws (Baumgartner et al. 2012, Frota et al. 2016a). However, in the last decade, the ichthyofauna in the Iguassu River basin has been increasingly studied for ecological and biogeographic purposes. This increase in sampling has revealed, especially at the headwaters of the basin, interesting or alarming new records of native and nonnative fish species (see Abilhoa et al. 2013, Frota et al. 2016a, Larentis et al. 2016, 2019, Delariva et al. 2018), promoting an increase in the number of fish species registered.

In comparing the species richness of the Iguassu River basin with that of other large basins in the Paraná State, it is noted that the hydrographic basins of the Piquiri, Tibagi and Paranapanema rivers, with 152 (Cavalli et al. 2018), 151 (Raio & Bennemann 2010) and 225 (Jarduli et al. 2020) fish species, respectively, exceeded the absolute species richness found in the Iguassu River basin. However, although it has numerically lower species richness, the high endemism rate of the ichthyofauna in the Iguassu River basin, which was estimated at 69% by this study, highlights the environmental importance of conservation of this basin, which is increasingly threatened by environmental degradation and by the introduction of nonnative fish species.

The Iguassu River ecoregion is known for the high rates of endemism among its ichthyofauna (Agostinho et al. 1997, Zawadzki et al. 1999, Baumgartner et al. 2012, Frota et al. 2016a, Daga et al. 2016, Delariva et al. 2018). In the 1990s, the rate of endemism was estimated by Agostinho et al. (1997) to be 80% and by Zawadzki et al. (1999) to be 75%. Our results show that there has been a decrease in the rate of endemism in the Iguassu River basin over the years. This fact is mainly due to the increase in collections in bordering basins, which has shown some cases of sharing of ichthyofaunal species previously considered endemic to the Iguassu River basin, for example, Psalidodon bifasciatus (see Frota et al. 2016a, 2019, 2020, Neves et al. 2020) and Cambeva stawiarski (see Cavalli et al. 2018, Morais-Silva et al. 2018). However, the rate of endemism in the Iguassu River basin, in the stretch above Iguassu Falls, remains an outlier when compared to those of other hydrographic basins that make up the Platina Basin system, for example, the Uruguay River basin (endemism rate estimated at 28%, Bertaco et al. 2016) and the Ivaí River basin (endemism rate estimated at 12%, Frota et al. 2016b).

In addition, 40 fish species (approximately 30%) were introduced into the Iguassu River basin, which is extremely worrying due to the possibility for future decline and potential extinction of autochthonous species (Daga et al. 2016, Ruaro et al. 2018), especially endemic species. The occurrence and establishment of nonnative fish species in aquatic environments often leads to their permanent presence, making subsequent eradication unlikely (Pérez et al. 1997). Representing serious risks to native fish species due to interspecific competition for resources and predation and potentially generating harmful hybridizations (Agostinho et al. 2007, Vitule et al. 2009), the introduced individuals may also contain intrinsic pathogens, larval phases of crustaceans and associated mollusks, which can also cause catastrophic effects on the native ichthyofauna (Casimiro et al. 2010, Vitule et al. 2009).

In Brazil, the introduction of nonnative fish species is common, and the only existing measure to solve this problem is the normative (laws and inspections) and educational approaches. However, this strategy has been failing due to the difficulty of enforcing the laws in a country with such extensive territory and with a society that lacks knowledge of the risks caused by these introductions (Azevedo-Santos et al. 2015). In general, the arrival of a new species in an aquatic environment due to anthropic action results from deliberate releases or escapes from confined environments due to the inefficiency of confinement or even due to accidents (Agostinho et al. 2007). Our compilation pointed to approximately 43% more nonnative fish species than recorded by Daga et al. (2016) for the Iguassu River basin. According to these authors, the Iguassu River basin has a history of species introduction since 1944, when the 'common carp' (Cyprinus carpio) was introduced in the region of the middle Iguassu River, possibly accidentally after the disruption of cultivation nurseries near to the river channel (Casimiro et al. 2018). Our survey corroborates the study of Daga et al. (2016) by revealing that the main vector of introduction of fish species in the Iguassu River was aquaculture, followed by the introduction from aquarism, fishing and stocking in reservoirs. The same vectors were also considered significant in the introduction of species in the hydrographic basin of the Piquiri River (Cavalli et al. 2018), although in smaller proportions than those reported here.

The main areas of introduction in the Iguassu River basin were concentrated in sites with high population density and high industrial activity, which requires the construction of dams and the establishment of aquaculture activities due to the greater need for electricity generation and food production (Daga et al. 2016). Although considered an important source of protein and income production worldwide, aquaculture is also one of the main vectors for the introduction of nonnative fish species in the Neotropical region and in the world (Gubiani et al. 2018, Lima et al. 2018). Considering that the cultivation of nonnative fish species in Brazil occurs mainly in cage nets (Lima et al. 2018), it is possible to infer that escapes are inevitable; therefore, each cage net is a continuous source of nonnative propagules for the environment (Azevedo-Santos et al. 2011). Damage such as alteration the diets of native fauna, alteration of the quality of the habitat due to eutrophication (Lima et al. 2018), invasion of genotypes, increased production of interspecific hybrids and the introduction and transmission of nonnative parasites (Nobile et al. 2020) are also reported to be due to the inopportune invasions associated with aquaculture.

Other activities, such as the release of aquarium fish and sport fishing, also stood out as important vectors of introduction into the Iguassu River basin. The ease of obtaining nonnative ornamental species from various parts of the world makes aquarium one of the main routes responsible for the introduction of these species into Brazilian watersheds (Agostinho et al. 2007, Azevedo-Santos et al. 2015). In general, individuals are introduced to natural or artificial environments by aquarists themselves, who give up this practice when they encounter some adversity, for example, with the excessive growth of individuals and the aggressiveness of some species (Magalhães & Jacobi 2013). Notably, aquarism was responsible for the introduction of the Palearctic fish, the 'dojo loach' (Misgurnus anguillicaudatus (Cantor, 1842)), which was released in the upper Iguassu River, probably unintentionally or deliberately (Abilhoa et al. 2013). Neotropical species have also been introduced due to this activity. This is the case of the 'dentudo' (Roeboides descalvadensis Fowler, 1932), of the 'espadinha' (Xiphophorus hellerii Heckel, 1848), of the 'cará' (Cichlasoma paranaense Kullander, 1983), of the 'barrigudinho' (Poecilia reticulata Peters, 1859), and of the 'cascudos-chinelo' (Loricariichthys cf. melanocheilus Reis & Pereira, 2000 and L. cf. rostratus Reis & Pereira, 2000). Two of the species introduced by aquarism belong to Poeciliidae (Poecilia reticulata and Xiphophorus hellerii), one of the main ornamental fish families marketed in Brazil (Magalhães & Jacobi 2013). Poecilids, in general, have a high invasion capacity and have caused different damages to local fauna (see Stockwell & Henkanaththegedara 2011). In addition to the fact that the species in this group are viviparous animals with high performance in urbanized environments (Ganassin et al. 2020), poecilids have clear advantages that are not observed in native fish (Deacon et al. 2011), representing a high risk to native and endemic populations, especially in aquatic environments in the vicinity of urban centers in the Iguassu River basin.

Sport fishing and the release of live bait are popular in Brazil and are practices that can stimulate species translocations between basins (Azevedo-Santos et al. 2015). In the Iguassu River hydrographic basin, sport fishing was responsible for the introduction of the 'tucunaréamarelo' (*Cichla kelberi* Kullander & Ferreira, 2006), which is native to the basins of the Araguaia and lower Tocantins rivers, and several other species, many of which are carnivorous and piscivorous (Agostinho et al. 2007), with high economic value (Britton & Orsi 2012) and whose life habits can destabilize the local ichthyofauna when they become established in the basin. Our results also revealed the presence of *Micropterus salmoides* (Lacepède, 1802) and *Salminus brasiliensis* (Cuvier, 1816), which were introduced in reservoirs to enhance sport fishing in the region (Daga et al. 2016; Ribeiro et al. 2017).

Hook escapes, as well as the intentional release of the remaining live bait at the end of the fishing trip, were possibly the mechanism for the introduction of some of the fish species found in the Iguassu River basin (Agostinho & Júlio Jr. 1996, Agostinho et al. 2007). *Gymnotus inaequilabiatus* (Valenciennes, 1839), *G. sylvius* Albert & Fernandes-Matioli, 1999, *Callichthys callichthys* (Linnaeus, 1758), and *Hoplosternum littorale* (Hancock, 1828) are widely used as bait in the capture of the 'Surubim-do-Iguaçu' (*Steindachneridion melanodermatum*), which is the largest species in the basin (Daga et al. 2016) and is currently threatened with extinction risk (ICMBio 2018).

The stocking of fish species in reservoirs, also called fishing or restocking, is a very common breeding and releasing practice (Casimiro et al. 2010). Mainly carried out by politicians and the hydroelectric sector (Vitule 2009, Agostinho et al. 2010), stocking can cause serious environmental damage, especially when carried out without adequate technical support and knowledge, which causes disregard for the environmental risks (Agostinho et al. 2010). Fingerlings of low genetic quality and often of nonnative fish species are deliberately introduced into the aquatic environment (Agostinho et al. 2010), Vitule 2009, Casimiro et al. 2010, Agostinho et al. 2010).

The several dams along the main course of the Iguassu River (Garavello et al. 1997, Baumgartner et al. 2012) and the fragmentation of habitats due to agricultural and urban activities (Baumgartner et al. 2012) add to the introductions of nonnative fish species, intensifying the threats to the endemic ichthyofauna in this ecoregion. According to the classification criteria of the IUCN, 20% of the endemic fish species of the Iguassu River basin are endangered. Among them, Astyanax eremus and Austrolebias carvalhoi need more attention because they are in the category of the greatest threat level (CR). Fragmentation and loss of habitat quality also threaten species with limited geographic distributions within the basin, especially those known only to their standard locations (ICMBio 2018). Populations of species that exhibit migratory behavior and that need stretches of rivers free of dams to complete their reproductive cycles, such as Steindachneridion melanodermatum, are also at serious risks due to the cascade of reservoirs along the Iguassu River and tributaries.

In summary, we recommend constant monitoring and increased collection efforts in the Iguassu River basin, especially in the regions that have not been sampled (Figure 1), which over the years have shown important contributions to the knowledge of their ichthyofauna. Our results highlight the gap between evolutionary knowledge and scientific knowledge of ichthyofauna in the Iguassu River basin, characterizing an expressive biodiversity deficit (see Hortal et al. 2015) in relation to possible new species and the accuracy of the geographic distributions of their species. Thus, efforts to apply management strategies to mitigate the negative effects of dam construction, loss of habitat quality and control of the spread of nonnative species must be better supported for this Neotropical hydrographic system with a high degree of endemism.

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# **Author Contributions**

Luciano Mezzaroba: Substantial contribution in the concept and design of the study; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Tiago Debona: Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Augusto Frota: Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Weferson Júnio da Graça: Contribution to data collection; Contribution to manuscript preparation; Contribution to critical revision, adding intelectual content.

Éder André Gubiani: Substantial contribution in the concept and design of the study; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

# **Conflict of Interest**

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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