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# Fishes of the upper rio Paraná basin: diversity, biogeography and conservation

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The upper rio Paraná basin drains the most developed and environmentally degraded region in South America: the Brazilian southeast. While it is one of the most well-known Neotropical fish assemblages, it is also one of the most threatened by anthropic activity. Urbanization, deforestation, dam construction, invasive species, and water pollution not only reduce the living area of species but also alter our perception of the basin and its biotic elements. Such changes are so profound and pervasive that raise uncertainties about the native or non-native status of several species. This paper aims to offer a detailed picture of the native diversity and historical biogeography of the fishes in the upper rio Paraná basin, which we hope will offer a solid foundation for future conservation policies. We update the list of native species, analyze geographical distributions, and identify biogeographical patterns, emphasizing areas requiring recognition as distinct biotas for conservation efforts. Over the past 15 years, more than 100 additional species have been described or recorded, expanding the total to 341 native species belonging to six orders and 30 families, making it the richest river basin in Brazil outside the Amazonian region. Unlike most neotropical basins where Characidae dominates, loricariids make up nearly one-fourth of the total fish diversity in the region. Species and clades concentrate in the central basin, while endemics

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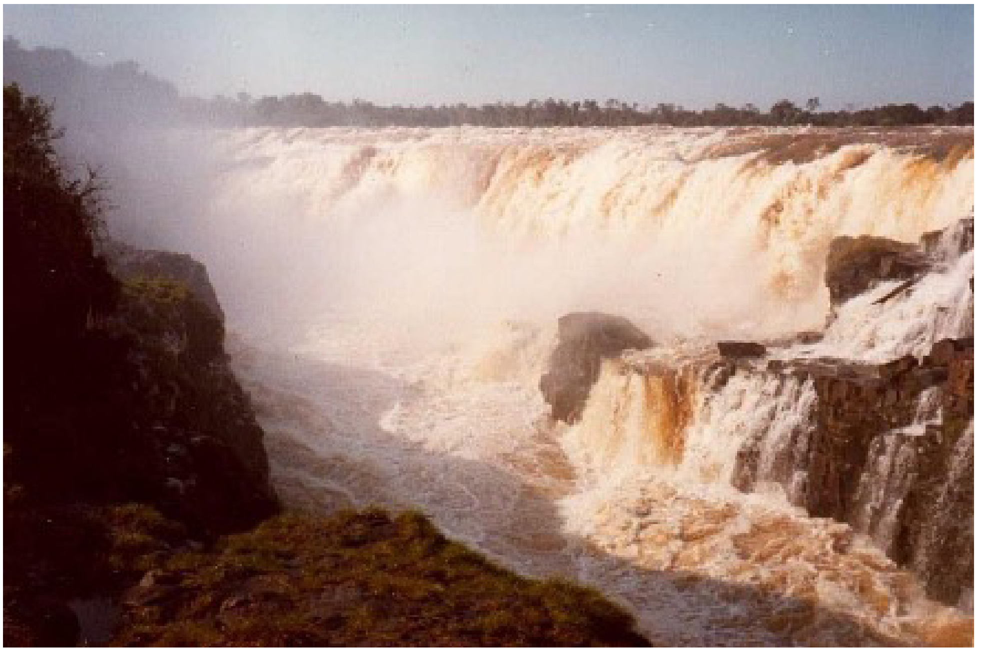
are confined to peripheral areas due to the complex biogeographical history shared with neighboring basins. Eighteen distinct biogeographical regions are identified, discussing their composition, histories, and conservation implications. The upper rio Paraná basin has 10% of its fish fauna ranked as endangered and present 128 non-native species, including three hybrids. This places it as the major drainage with the largest number of endangered taxa in the neotropics and at the same time the one with the most numerous non-native elements. Existing protected areas are deemed ineffective in preserving diverse assemblages and fail to safeguard the majority of threatened and narrowly-endemic species.

Keywords: Biodiversity, Ichthyofauna, Neotropical region, Non-native species, Taxonomy.

A bacia do alto rio Paraná drena a região mais desenvolvida e ambientalmente degradada da América do Sul: o sudeste brasileiro. Ao mesmo tempo que é uma das assembleias de peixes neotropicais mais conhecidas, também é uma das mais ameaçadas pela atividade antrópica. Urbanização, desmatamento, barramentos de usinas, espécies invasoras e poluição da água não apenas reduzem a área de vida das espécies, mas também alteram nossa percepção da bacia e de seus elementos bióticos. Essas mudanças ambientais são tão profundas e abrangentes que geram incertezas sobre a natureza nativa ou não nativa de várias espécies. Este artigo visa oferecer uma visão detalhada da diversidade nativa e da biogeografia histórica dos peixes da bacia do alto rio Paraná, fornecendo uma base sólida para futuras políticas de conservação. Atualizamos a lista de espécies nativas, analisamos distribuições geográficas e identificamos padrões biogeográficos, enfatizando áreas que requerem reconhecimento como biotas distintas para esforços de conservação. Nos últimos 15 anos, mais de 100 espécies adicionais foram descritas ou registradas, expandindo o total para 341 espécies nativas pertencentes a seis ordens e 30 famílias, tornando-a a bacia hidrográfica mais rica do Brasil fora da região amazônica. Ao contrário da maioria das bacias neotropicais em que Characidae domina, os loricariídeos constituem quase um quarto da diversidade total de peixes na região. Espécies e clados se concentram na região central da bacia, enquanto elementos endêmicos estão restritos a áreas periféricas devido à complexa história biogeográfica compartilhada com bacias vizinhas. Dezoito regiões biogeográficas distintas são identificadas, sua composição, biogeografia e conservação são discutidas. A bacia do alto rio Paraná possui 10% de sua ictiofauna classificada como ameaçada e apresenta 128 espécies não nativas, incluindo três híbridos. Isso a posiciona como a drenagem com o maior número de táxons ameaçados nos trópicos ao mesmo tempo que tem a maior riqueza de elementos não nativos. As áreas protegidas existentes são consideradas ineficazes na preservação das diferentes assembleias e falham em proteger a maioria das espécies ameaçadas e as endêmicas.

Palavras-chave: Biodiversidade, Espécies não nativas, Ictiofauna, Região Neotropical, Taxonomia.

## PROLOGUE



Sete Quedas falls, the former geographic barrier that delimited the upper rio Paraná basin as a distinct biogeographic region, was submerged by the construction of the Itaipu dam in 1982. Source: Brazilian government, available at: https://www12.senado.leg.br/noticias/materias/2016/09/21/orfa-do-salto-de-sete-quedas-guaira-podera-receber-mais-royalties-de-itaipu

"*Sete quedas por mim passaram, e todas sete se esvaíram.*

*Cessa o estrondo das cachoeiras, e com ele a memória dos índios, pulverizada, já não desperta o mínimo arrepio.*

*...*

*- E desfaz-se por ingrata intervenção de tecnocratas. Aqui sete visões, sete esculturas de líquido perfil dissolvem-se entre cálculos computadorizados de um país que vai deixando de ser humano para tornar-se empresa gélida, mais nada.*

*...*

*- Sete quedas por nós passaram, e não soubemos, ah, não soubemos amá-las, e todas sete foram mortas, e todas sete somem no ar, sete fantasmas, sete crimes dos vivos golpeando a vida que nunca mais renascerá.*"

**Carlos Drummond de Andrade**

(Rio de Janeiro, Jornal do Brasil, 9 Sep 1982)

## INTRODUCTION

The upper rio Paraná basin corresponds to approximately one-quarter of the La Plata basin, making it one of the largest hydrographic basins in the Brazilian territory. The upper rio Paraná basin is formed by various sub-basins which drain the areas corresponding to the Brazilian States of Goiás, Minas Gerais, São Paulo, Mato Grosso do Sul, Paraná, and the Distrito Federal, having as main tributaries the rivers Paranaíba, Grande, Tietê, and Paranapanema (Bonetto *et al*., 1986; Britski, Langeani, 1988). It is located mostly in the Brazilian southeast, the most heavily urbanized region in South America, with high population density and large urban and industrial centers, comprising *ca*. 40% of the Brazilian population (IBGE, 2023). In addition, agriculture and cattle raising are historic activities in the region and have grown significantly in recent years (Agostinho *et al*., 2007a,b; Pelicice *et al*., 2021). Economically developed regions are usually those where biodiversity is most severely threatened, because investment in conservation is not in proportion to the economic prosperity of those regions (Martinelli *et al*., 2002; Pelicice *et al*., 2017).

The ichthyofauna of the upper rio Paraná basin is relatively rich. The latest compilation lists 236 native species, plus additional still undescribed species (Langeani *et al*., 2007). At least 70 species in the basin were considered non-native, being either exotic or accidental additions caused by the Itaipu hydroelectric dam (Agostinho *et al*., 2004a; Langeani *et al*., 2007; Júlio Júnior *et al*., 2009; Vitule *et al*., 2012). The basin has a high degree of fish endemism (Britski, Langeani, 1988; Castro *et al*., 2003; Menezes *et al*., 2003), with several species restricted to the basin or to parts of its tributaries. This led several authors to consider the upper rio Paraná as an independent biogeographic unit in the neotropics (*e.g*., Ringuelet, 1975; Vari, 1988; Abell *et al*., 2008; Dagosta *et al*., 2021).

Despite being one of the most intensively studied drainages in South America (Langeani *et al*., 2007; Galves *et al*., 2009), little effort has been employed towards minimizing so-called Wallacean shortfall (Lomolino *et al*., 2004; Bini *et al*., 2006), *i.e*., to fill in the gaps in knowledge about the geographic distribution of species in the basin. Despite available ichthyofaunistic lists for the upper rio Paraná (Langeani *et al*., 2007; Ota *et al*., 2018), so far there has been little concerted effort to survey distributional data on its fish species in order to understand their distribution patterns and to employ historical biogeography as a tool to delimit priority areas for conservation. This paper endeavors to compile and organize published knowledge on the diversity of fishes in the upper rio Paraná and to produce an up-to-date species list, to identify biogeographic patterns within the basin, and to use the generated information to define the areas of highest relevance for the conservation of its ichthyofauna. Multiple biogeographic analyses utilizing a range of methodologies (*i.e*., Species richness, Bioregionalization, Phylogenetic Diversity, Beta diversity, and Weight Endemism) were undertaken to acquire a thorough and all-encompassing understanding of the biogeography of fishes living in the upper rio Paraná basin.

## MATERIAL AND METHODS

**Study area.** The rio Paraná basin is divided into four hydrographic regions (Stevaux, 1994, 2000): 1) Upper Paraná: from its headwaters to the Sete Quedas falls, between Guaíra, Brazil and Salto del Guairá, Paraguay (or Guairá Falls, currently submerged by the Itaipu Dam); 2) Middle Paraná: downstream from Sete Quedas to the confluence with the Rio Paraguai, between Isla del Cerrito and Paso de la Patria, Argentina; 3) Lower Paraná: floodplain, downstream from Paraná-Paraguai confluence to the region of Rosario, Argentina; 4) Paraná Delta: from the confluence of río Carcarañá (municipality of Gaboto, Argentina) to río de La Plata estuary. The Itaipu Dam is located 150 km downstream from the Sete Quedas falls, the original natural barrier between the upper and middle-lower rio Paraná (Langeani *et al.*, 2007). The definition of upper Paraná by Abell *et al.* (2008) is different and includes all water bodies upstream from Itaipu Dam. Although herein we follow the definition of Stevaux (2000), for practical reasons the sector from Itaipu upstream to Sete Quedas is also included in our maps and analyses (Fig. 1). Such addition is necessary in order to discuss the major impact that the dam has for the diversity, biogeography and conservation of the entire river basin.


**FIGURE 1** | The upper rio Paraná and its main tributaries. The basin is defined as the entire area drained upstream of the former Sete Quedas Falls. Note that the Itaipu dam is located downstream from Sete Quedas. Numbers indicate capital cities in the basin: 1. São Paulo; 2. Brasília; 3. Goiânia; 4. Campo Grande.

The region drained by the upper rio Paraná has pronounced heterogeneity of phytophysiognomies, including Semidecidual Forests, Cerrados, Mixed Ombrophilous Forests, Campos Rupestres and Gallery Forests (Hueck, Seibert, 1981; Agostinho *et al*., 2007a; Thomaz *et al*., 2007; Agostinho *et al*., 2009). The upper rio Paraná basin has broad altitudinal range, between 200 and 2,000 m a.s.l., with most of its area within the 400–600 m range, in the central portion of the basin (Fig. 2).

Geologically, the upper rio Paraná basin lies mainly within the Paraná sedimentary basin, a Paleozoic-Mesozoic intracratonic sedimentary basin formed in the interior of the Gondwana paleocontinent by successive sequences of sedimentary and intrusive/extrusive magmatic formations over a cratonic basement; its outcropping formations have been shaped by erosion and uplift since the Upper Cretaceous, when its depositional history ceased (Milani, Thomaz Filho, 2000). The eastern portion of the upper rio Paraná basin lies at the Mantiqueira province, an ancient (Neoproterozoic-Paleozoic) folding belt where the highest altitudes within the upper Paraná basin (2,000 m a.s.l.) are reached and where the headwaters of most of the main tributaries of the upper Paraná basin (rio Paranapanema, rio Tietê, and rio Grande) have their sources. The Mantiqueira province is a complex area both physiognomically and historically, as an ancient orogen deeply affected by the opening of the Atlantic Ocean, and which has undergone cycles of upfliting, denudation, and rifting (Almeida, Carneiro, 1998; Hiruma *et al*., 2010; Alkmin, 2015). The northern portions of the upper rio Paraná basin are within the São Francisco craton (Teixeira *et al*., 2000), to the east, and the Brasília fold belt, to the west (Pimentel *et al*., 2000). The Paraná sedimentary basin ends westward in Mato Grosso do Sul State at the Pantanal tectonic basin (see, *e.g*.,

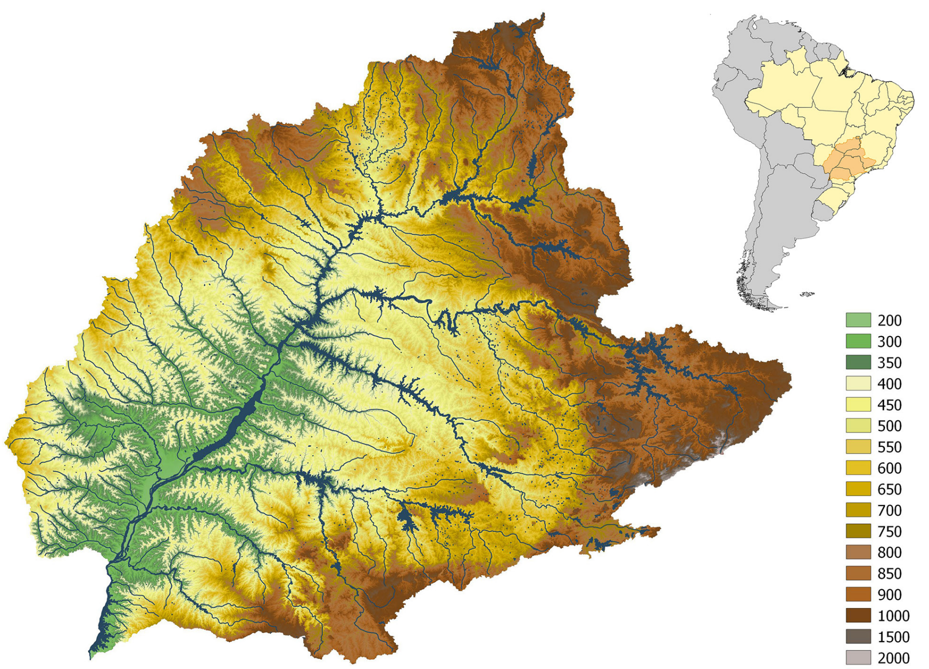



**FIGURE 2** | Topographic map of the upper rio Paraná. In the upper right corner, the location of the basin (highlighted in orange) in Brazil and in the South American continent.

Assine *et al.*, 2015: fig. 1; Sallun Filho, Karmann, 2007: fig. 1), where its boundaries and the ones from the upper rio Paraná basin partially coincides, and more southward the Asuncion arch make the boundaries between the Paraná sedimentary basin and the Chaco basin (and again partially coinciding with the present basin limits) (Milani, Thomaz Filho, 2000). The resulting topography of this relatively complex geological setting is, as expected, very diverse. The eastern portion of the upper rio Paraná within the Mantiqueira region, where the highest altitudes within the basin are reached (2,000 m a.s.l.), present high-gradient rivers. In contrast, the central plateau of the Paraná basin, due to its long history of denudation, present a predominantly gentle slope towards the rio Paraná. The gentle slope of the Paraná sedimentary basin in the upper rio Paraná basin contrasts with the high-gradient, fast-flowing rivers draining the southern portion of the Paraná sedimentary basin, south of the Sete Quedas Falls, *i.e.*, the rio Iguaçu basin and the upper rio Uruguai basins, reflecting the differences in the magmatic and sedimentary formations between these areas (Almeida, 1956). The upper rio Paraná lies on an ancient (pre-Devonian) rift (Milani, 2004). Holocene (8,000 years old to the present) floodplains are present along the stretch downstream Porto Primavera dam, preceded by a dry period (40,000–8,000 years old) when the rio Paraná was a braided river system lacking floodplains (Stevaux, 1994, 2000).

The upper rio Paraná basin has a number of important tributaries, including the Grande, Tietê, Paranaíba, and Paranapanema rivers (Fig. 1), mostly having their headwaters in eastern Brazil. Left-margin tributaries are extensive, up to 1,000 km and many have their headwaters in crystalline rocks of the Serra do Mar, Serra da Paranapiacaba, and Serra da Mantiqueira. Right-margin tributaries (*e.g.*, Ivinhema, Pardo, Verde, and Sucuriú rivers) are under 400 km in length and their sources are in the ranges of Serra de Maracaju and Serra de Carapó (Souza Filho, Stevaux, 1997). The rio Paraná itself is formed by the confluence of the rivers Paranaíba and Grande, on the triple boundary of São Paulo, Minas Gerais, and Mato Grosso do Sul states.

The rio Paranaíba originates in the Serra Mata da Corda in State of Minas Gerais at 1,100 m a.s.l., extending for 120 km in its first stretch to the city of Patos de Minas, later forming the border between the states of Minas Gerais and Goiás (Santos, 2010). The fish fauna of the basin is relatively poorly-known compared with the remainder of the upper Paraná. Fish surveys were published for some of its tributaries, including the rio Corumbá (Pavanelli *et al.*, 2007), upper rio São Bartolomeu (Aquino *et al.*, 2009) and rio Araguari (Langeani, Rego, 2014), Santa Maria, Meia Ponte, and Piracanjuba river basins (Vieira, Tejerina-Garro, 2014), rio Meia Ponte basin (Fialho *et al.*, 2007; Dias, Tejerina-Garro, 2010).

The rio Grande originates in the Serra da Mantiqueira, at the limit between the states of São Paulo and Minas Gerais, 1,500 m a.s.l. and runs for 1,050 km (Ziesler, Ardizzone, 1979). This is the largest subdrainage of the upper Paraná and its longest tributaries draining the left margin. The most important right-margin tributary is the rio Uberaba, previously inventoried by Ribeiro *et al.* (2019). On the left margin, there are many ichthyological surveys of the rio Mogi-Guaçu (*e.g.*, Meschiatti, Arcifa, 2009), of the rio Sapucaí by Oliveira *et al.* (2016) and Azevedo-Santos *et al.* (2019), of the rio Preto by Santos *et al.* (2017), and for the stream fauna in general by Castro *et al.* (2004).

The rio Tietê basin is the second largest in the State of São Paulo. It originates at 840 m a.s.l. at Serra do Mar, municipality of Salesópolis, and crosses the capital of the State, running 1,150 km to join the rio Paraná, at the boundary with State of Mato Grosso do Sul. There are multiple ichthyological inventories of parts of the basin (*e.g*., Northcote *et al*., 1985; Uieda, Barreto, 1999; Castro *et al*., 2005; Silva *et al*., 2006; Esguícero, Arcifa, 2011; Marceniuk *et al*., 2011; Cetra *et al*., 2012; Serra *et al*., 2015; Smith *et al*., 2018; Reia *et al*., 2020).

The rio Paranapanema, which begins in the Serra de Paranapiacaba at an altitude of approximately 900 m a.s.l., is among the largest left-bank tributaries of the upper Paraná. With its main tributaries being the rivers Itararé, Tibagi, Pardo, and Pirapó, it stretches along 500 km before reaching its mouth at the rio Paraná. It is one of the most impacted basins of the Brazilian southeast, with over ten dams along its main channel (Ziesler, Ardizzone, 1979; Henry, 2005). A broad inventory of its fish fauna was recently published (Jarduli *et al*., 2020), as well as the ichthyofauna of one of its main tributaries, the rio Itararé (Frota *et al*., 2020). Other smaller basins south of the Paranapanema, such as the rio Ivaí and rio Piquiri have compiled lists of the ichthyofauna by Frota *et al*. (2016) and Cavalli *et al*. (2018), respectively. The fish fauna occurring in streams of the rio Paranapanema basin was investigated by Castro *et al*. (2003).

Right-margin tributaries of the upper Paraná are smaller and comparatively less well-surveyed, except for the rio Ivinhema. The portion draining the territory of the State of Mato Grosso do Sul had its ichthyofauna compiled by Froehlich *et al*. (2017). The region of the Aporé-Sucuriú complex and the rio Iguatemi basin had its fish fauna inventoried by Froehlich *et al*. (2006) and Súarez, Petrere Júnior (2003), respectively. Few ichthyological studies have been conducted in the rio Verde basin and a brief inventory of the middle portion of the basin was presented by Rosa *et al*. (2020). The rio Pardo and rio Amambai are also poorly known, with some studies on specific aspects of the fish fauna, such as Lima *et al*. (2013) on the distribution of fish eggs and larvae in the rio Pardo and Silva *et al*. (2017) in the rio Amambai, and Pereira *et al*. (2018) on the fish parasites in the rio Amambai.

The main right-margin tributary of the upper Paraná is the rio Ivinhema. One of its main components is the rio Dourados, originating at 700 m a.s.l. and receiving inflows from the rivers Santa Maria, Brilhante, and Vacaria. The rio Ivinhema drains an area of 46,023 km² (Agostinho *et al*., 2000; Vicentin *et al*., 2019). The rio Ivinhema basin is practically free of dams and is the most intensely studied of the right-margin tributaries (*e.g*., Suárez *et al*., 2006, 2007, 2008a,b, 2011; Súarez, Lima-Junior, 2009). A large portion of that basin is within a protected area, the Várzeas do rio Ivinhema State Park.

**List of native species of the upper rio Paraná.** The only previous checklist of the fish species occurring at the upper rio Paraná basin was Langeani *et al*. (2007). We herein update the list including species described since then, newly published records for the basin, and nomenclatural changes that have happened in the intervening period. Only native species from the upper rio Paraná basin are considered in the Tab. 1. The compilation includes all taxa described until 30 April 2023, so it does not include *Eigenmannia catira* Cardoso & Dutra, 2023, which was published after the acceptance of the present article. Undescribed species mentioned in the literature are referred only when biogeographically significant, and are not included either in the quantification for the basin or in the database for analyses. Nomenclatural classification follows Van der Laan, Fricke (2023).

**Non-native species.** The main purpose of this paper is to discuss the biodiversity of fishes native to the upper rio Paraná basin. However, because of the ubiquitous presence and strong impact of invasive species in the river basin, a list of non-native species is also included separately. Such a list is inherently highly transient, because of the dynamic and unpredictable nature of invasion events, and therefore needs constant updating.

In some cases, the identification of a taxon as native or non-native is complex, and in all such instances, we base our decision on available data, consultation with taxonomist specialists and literature (*e.g*., Langeani *et al*., 2007; Ota *et al*., 2018). Complex cases that require further discussion will be addressed in detail in the "Discussion - Questionable native or non-native species" section.

Some non-native species recorded in the literature for the basin were not included in the list. The record of *Cynopotamus kincaidi* (Schultz, 1950) from Langeani *et al*. (2007) is from Foz do Iguaçu municipality, Paraná State, downstream from the Itaipu power plant. To date, the species has only been collected in the "Canal da Piracema", an artificial channel to enable the transposition of fish species through the Itaipu reservoir, which began operating in late 2002. However, *C. kincaidi* has never been collected in or upstream from the Itaipu reservoir. Therefore, the species is considered as non-native to the upper rio Paraná basin. Langeani *et al*. (2007) recorded *Farlowella oxyrhyncha* (Kner, 1853), however, the lot that has based this record (NUP 1496) has been reidentified as *Farlowella hahni* Meinken, 1937. Another record from Langeani *et al*. (2007) excluded here is that of *Odontesthes bonariensis* (Valenciennes, 1835), which occurs in the rio Iguaçu but not in the upper rio Paraná basin. The allochthonous record of *Pimelodus fur* (Lütken, 1874) in Langeani *et al.* (2007) refers to *P. microstoma* Steindachner, 1877. Records in Casimiro *et al.* (2018) of *Salmo trutta* Linnaeus, 1758 and *Brycon falcatus* Müller & Troschel, 1844 appears to be misidentification of *Oncorhynchus mykiss* (Walbaum, 1792), and *B. amazonicus* (Agassiz, 1829), respectively.

**Taxonomic problems.** Some of the species previously recorded for the upper rio Paraná by Langeani *et al*. (2007) are not included herein. *Astyanax goyacensis* Eigenmann, 1908 was excluded following Garutti, Langeani (2009). *Astyanax paranahybae* Eigenmann, 1911 is a junior synonym of a *Piabina argentea* Reinhardt, 1867 (*cf*. Santos, 2014). *Psalidodon eigenmanniorum* (Cope, 1894) from the upper rio Paraná basin was described as *Astyanax bockmanni* Vari & Castro, 2007 (= *Psalidodon bockmanni*). *Apteronotus paranaensis* (Schindler, 1940) is considered here as a species *inquirenda* following Ferraris *et al*. (2017). Morais-Silva *et al*. (2018) and Reis *et al*. (2020) documented the presence of *Cambeva stawiarski* (Miranda Ribeiro, 1968) in the upper rio Paraná basin. However, this record was invalidated by Reis *et al*. (2021), who restricted the distribution of the species to the rio Iguaçu basin. *Pimelodella rudolphi* Miranda Ribeiro, 1918 is a junior synonym of *Pimelodella meeki* Eigenmann, 1910 (Slobodian, 2017). *Psalidodon argentum* (Salgado, 2021) was recently described from the basin, but the publication was later withdrawn by the author. According to the ICZN rules, this does not revert the availability of the name (see Dubois, 2020). So, the taxon is considered as available here, although it is not included in the quantifications of the diversity in the basin because its validity pends confirmation. The species is very similar to *Psalidodon fasciatus* (Cuvier, 1819), a species widely distributed throughout southeastern and northeastern Brazilian drainages.

The taxonomy of the *Gymnotus* species occurring in the upper Paraná is still poorly known. Although some species such as *Gymnotus cuia* Craig, Malabarba, Crampton & Albert, 2018 and *G. sylvius* Albert & Fernandes-Matioli, 1999 have part of their type material or examined material in their original descriptions from the upper rio Paraná basin, but recent taxonomic studies (GMD, pers. obs.) have questioned the validity of these species. Therefore, the record of these species in the basin cannot yet be confirmed and only *Gymnotus pantherinus* (Steindachner, 1908) can unambiguously be assigned to the basin. The identity of the remaining *Gymnotus* species recorded for the basin are still poorly understood and thus were not included either in maps or in biogeographic analyses. Other species with either poorly documented or poorly known taxonomically in the upper rio Paraná are *Cichlasoma dimerus* (Heckel, 1840), *Serrapinnus piaba* (Lütken, 1875), *Synbranchus madeirae* Rosen & Rumney, 1972, and species of the *Hoplias malabaricus* complex group. In all such cases, no distribution map is presented, and their data was not employed in biogeographic analyses. According to Bifi (2013), the distribution considered here for *Hoplias* aff. *malabaricus* encompasses two morphotypes: *Hoplias* cf. *malabaricus* and an undescribed species. Following Mota *et al.* (2018), we are herein considering *Hemigrammus* aff. *marginatus* (*sensu* Ota *et al*., 2015) as not clearly diagnosable from *Moenkhausia bonita* Benine, Castro & Sabino, 2004. The distribution of *M. bonita* considered here refers to the morphotype with a complete lateral line, while records with incomplete lateral lines, more frequent in the eastern portion of the basin, are not considered for analyses or species mapping.

**Geographical coordinates acquisition.** A database containing more than 45,000 geographical coordinates of fish species of the upper rio Paraná basin was compiled using information available in the taxonomic literature, museum collections, and metadata depositories. Personalized Python Scripts with regular expression patterns (*i.e*., regex) were employed to assemble coordinates from the digital literature. Published papers with distribution maps yet lacking georeferenced specimens had their respective coordinates extracted manually using a georeferenced map as a proxy. Species not treated in taxonomic revisions or published maps had their distributions based on inventories and records from online depositories. Additional coordinates were obtained from ichthyological collections (*e.g*., DZSJRP, LBP, MZUEL, MZUSP, NUP, USNM) via SpeciesLink http://splink.cria.org.br, from data made available to the authors by respective curators, and the database published by Tonella *et al*. (2023). Compiled distribution points (Fig. 3) correspond to coordinates digitized from published taxonomic papers and those obtained from ichthyological databases.

**Data validation.** Compiled recorded coordinates were subject to an automated processing routine intended to identify and remove records with georeferencing problems, mainly those from SpeciesLink. The routine included the three steps suggested by Robertson *et al*. (2016). Duplicated coordinates were removed to avoid pseudoreplication. Species distributions were finally inspected visually to identify suspicious records. Those outside of their geographical distributions known from the literature of the upper rio Paraná were removed to assure the reliability of data.

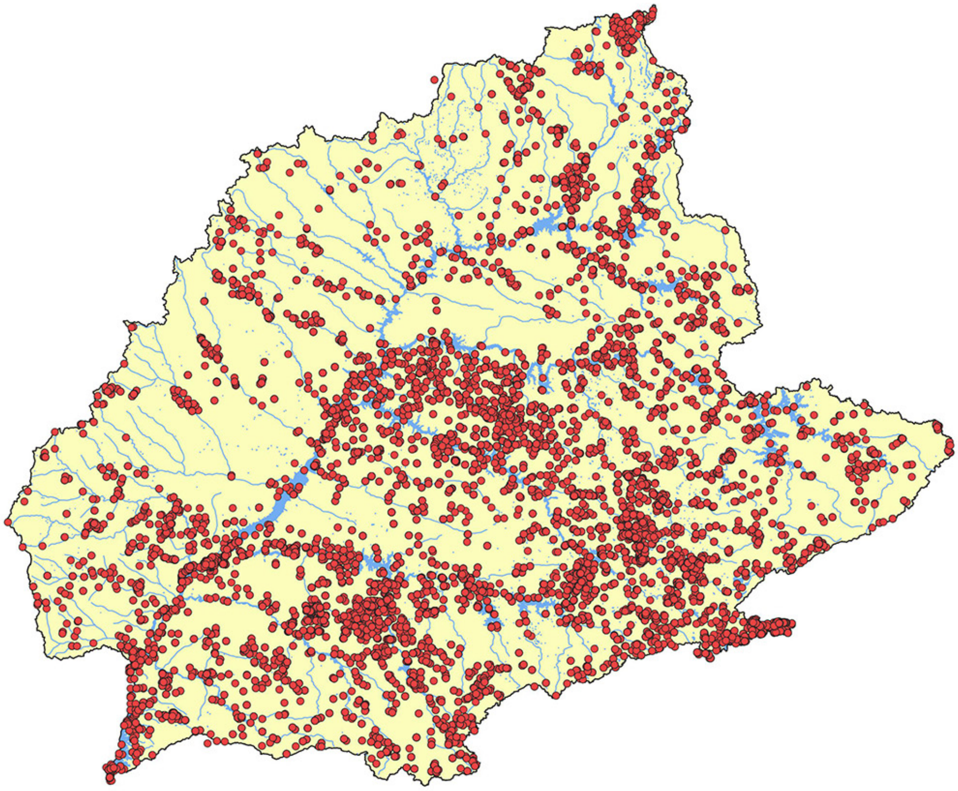


**FIGURE 3 |** Sampling records of fishes in the upper Paraná basin compiled in this study. Most points are concentrated on the left bank, mainly in the regions corresponding to the rios Tietê, Grande, and Paranapanema, where there are concentrations of urban centers and/or research institutions.

**Georeferenced layers.** Distribution of hydroelectric dams was extracted from the Sistema de Informações Geográficas do Setor Elétrico (SIGEL) of Agência Nacional de Energia Elétrica (ANEEL), available at: https://sigel.aneel.gov.br/Down/. Delimitation of biomes are from the Instituto Brasileiro de Geografia e Estatística (IBGE), Mapa de Biomas do Brasil 1/5.000.000, available at: https://www.ibge.gov.br/geociencias/cartas-e-mapas/informacoes-ambientais/15842-biomas.html?=&t=downloads.

**Threatened species.** Categories of threatened fish species in the upper rio Paraná followed Portaria GM/MMA # 300, of December 13, 2022 (MMA, 2022). Although that list was subsequently revoked, for legal reasons, by the Portaria MMA # 354, of January 27, 2023 (MMA, 2023), it remains the most up-to-date document available on threatened fishes of Brazil.

**Biogeographic analyses.** All databases prepared for biogeographic analyses were prepared in R (R Develoment Core Team, 2017). In all cases, the delimitation mask of interpolation was the profile of the hydrographic basin of the upper rio Paraná. Only native species were included in analyses.

**Bioregionalization of the upper rio Paraná basin.** Bioregionalization of the ichthyofauna was prepared with the software Infomap Bioregions2 (Edler *et al*., 2017), Beta version available at https://www.mapequation.org/bioregions2/. That option was chosen because of certain implementations available only in the newest version, such as the use of smaller quadricules (1/128° *vs*. 1/8° in older versions) and the quantity of trials, previously limited to 10 in older versions. InfoMap bioregions subdivides the region and compares the biota within each quadrant, then regrouping the parts and defining bioregions based on the similarity of species composition. The software employs adaptive quadricule resolution, a crucial feature when dealing with uneven sampling efforts, as is the case in the realistic situations addressed here. The analysis applied the following configurations: maximum cell capacity ≥ 300.000 and minimum cell capacity = 5, trials ≥ 100. Changing those parameters does not significantly change resulting patterns. According to Daru *et al*. (2020), recognized patterns of endemism are scale-dependent. To minimize bias, we opted for a result that is less susceptible to cell size variations. Consistent results are obtained when the minimum cell size varies between 1/32 and 1 degree, and the maximum cell size is fixed at 1 degree.

**Species richness.** Species Richness Interpolation (SRI) maps species richness using Spline interpolation algorithm to attribute values which smooth out the curve of collected species between coordinates. Estimates were inferred by the software Biodinamica (Oliveira *et al*., 2019). Parameters used were: hexagon size of sample unit 1.5 (equivalent to 150 km); resolution raster 0.5; minimum of one sample per hexagon; remaining parameters according to default values of the software.

**Concentration of threatened species.** A separate Species Richness analysis using SRI was employed to identify which regions in the basin concentrate records of species in threatened levels. The analysis included only species considered as threatened according to the Lista Nacional de Espécies Ameaçadas de Extinção, Portaria GM/MMA Nº 300/2022 (MMA, 2022). The hexagon size of the sample unit was 0.5 (equivalent to 50 km); resolution raster 0.5; minimum of one sample per hexagon; remaining parameters followed default configurations of the software.

**Phylogenetic diversity.** The method of Phylogenetic Diversity (PD) defines the phylogenetic diversity of a group of species within areas as the summation of all branches of a phylogenetic tree comprising all elements of that group (Faith, 1992). The tree employed was from Cassemiro *et al*. (2023) where exclusively species with occurrence in the upper rio Paraná were utilized. Estimates were inferred by spline interpolator using default parameters of the software Biodinamica (Oliveira *et al*., 2019): hexagon size of sample unit 1.5 (equivalent to 150 km); resolution raster 0.5; and at least one sample per hexagon.

**Weight endemism index.** Endemism indices do not take into account the size of the occurrence area of species. This poses a problem because important regions for geographically restricted species can be considered as equivalent to regions with occurrence of widely distributed endemic species. In order to minimize such distortion, the Weight Endemism Index (WEI) combines endemism and species richness

(Williams, Humphries, 1994). The index is calculated as an inverse function of the species distribution, so that species in smaller areas receive higher scores (Kier, Barthlott, 2001; Oliveira *et al*., 2017). WEI was calculated per cell as the sum of all WEI values calculated independently from each species within 1.5 (equivalent to 150 km) cells of the hexagonal grid, including at least one sample and raster resolution of 0.5. To identify areas with the highest levels of endemism, we utilized the spline interpolator with the default settings of the Biodinamica software (Oliveira *et al*., 2019).

**NMDS analysis.** The Non-Metric Multidimensional Scaling (NMDS) analysis is a multivariate statistical technique employed to explore and visualize patterns of similarity or dissimilarity among regions. In this instance, it is utilized to depict spatial variation in species compositions across diverse areas. NMDS transforms species composition data (Beta diversity), calculated through the Jaccard dissimilarity matrix among grid cells converted into linear estimates of three spatial vectors and utilizing Spline Interpolation (Albert *et al*., 2020). In the graphical representation, similar samples exhibit more comparable colors. This facilitates the visualization of sample clusters based on their biological similarities, thereby providing insights into community structure and species distribution across distinct environments or conditions. Default parameters of the program were employed.

## RESULTS

**A brief history of the taxonomic knowledge of fishes of the upper rio Paraná basin.** In comparison to other regions in South America, ichthyological surveys of the upper rio Paraná basin began relatively late. Although the famous Bavarian naturalists Carl Friedrich Philipp Martius and Johann Baptist Spix have visited areas belonging to the upper rio Paraná basin between 1817–1818, no ichthyological material from this region can be attributed to this expedition. Therefore, the credit for the first ichthyological collection in the basin goes to Johann Natterer, who collected fish specimens at two specific sites, "Ypanema" (currently Ipanema National Forest, in a tributary of the Sorocaba River, itself a tributary of the Tietê River) and "Irisanga" (currently Estiva Gerbi, in the Mogi-Guaçu River basin), both located in São Paulo State, between 1822 and 1823 (*e.g*., Vanzolini, 1993). The relatively few fish species collected by him in the upper rio Paraná basin were reported by Kner (1859, 1860), and includes *Prochilodus vimboides* Kner, 1859 described from "Ypanema", paradoxically a species rather rare in the upper rio Paraná basin, and the bryconid *Brycon nattereri* Günther, 1864 described from Irisanga. A little after Natterer, the Langsdorff Expedition, a Russian-funded expedition organized by Baron Georg Heinrich von Langsdorff, descended the rio Tietê, starting at the city of Porto Feliz, São Paulo state, in 1826, and then upstream in the rio Paraná en route to Mato Grosso State (Vanzolini, 1996). As noticed by Vanzolini (1996), except for the value of the produced drawings and watercolors, the expedition was a failure from the point of view of zoological knowledge, since the material collected (deposited at the Zoological Museum of Saint Petersburg) was never studied. The watercolors, which were only published in the XX century, depict some of the fish collected during the expedition, including *Steindachneridion scriptum* (Miranda

Ribeiro, 1918), a species only described almost one century later, and the pacu, *Piaractus mesopotamicus* (Holmberg, 1887).

These earlier explorations were followed by a hiatus on ichthyological explorations of the upper rio Paraná basin that lasted almost 80 years and only ended at the end of the XIX century with the foundation of the Museu Paulista, on the banks of the rio Ipiranga, in São Paulo city, in 1893 (Pinto, 1945). Hermann von Ihering, the first director (Moraes, 2008), sent some fishes from São Paulo state, including several from the upper rio Paraná basin, to the Indiana University, where they were studied by Eigenmann, Norris (1900). Rodolpho von Ihering, the son of Hermann, started working at the Museu Paulista in 1902 and published several papers describing many fish species from the upper rio Paraná basin, especially catfishes (*e.g*., Ihering, 1905, 1907, 1911), among them *Corydoras flaveolus* Ihering, 1911, *Hypostomus regani* Ihering, 1905, and *Loricaria piracicabae* Ihering, 1907. Subsequently to Hermann von Ihering dismissal from the Museu Paulista in 1916, and Rodolpho voluntary termination of employment in 1917, the fish collections of the Museu Paulista were studied by Alípio de Miranda Ribeiro, who described some species from the upper rio Paraná basin, for example, *Steindachneridion scriptum*.

In 1907, Carl Eigenmann arranged for one of his students, John D. Haseman, to come to South America to collect fishes for the Carnegie Museum at Pittsburgh in regions not sampled by the Thayer Expedition. The collections were made between 1907 and 1910 (Haseman, Eigenmann, 1911). Haseman travelled extensively across the upper rio Paraná in the states of São Paulo and Minas Gerais between July and October 1908, assembling the largest collection of the basin at the time. The material collected was studied both by Haseman himself (*e.g*., Haseman, 1911), by Ellis (1911), and by Eigenmann (*e.g*., Eigenmann, 1915, 1917, 1918, 1921), who described numerous fish species from the basin such as *Coptobrycon bilineatus* (Ellis, 1911), *Crenicichla jaguarensis* Haseman, 1911, *Glandulocauda melanopleura* (Ellis, 1911), *Imparfinis mirini* Haseman, 1911, *Serrapinnus notomelas* (Eigenmann, 1915), *Cambeva paolence* (Eigenmann, 1917), among others.

Rodolpho von Ihering resumed his ichthyological activities in 1927 in the then recently created Instituto Biológico, in São Paulo city, and made pioneering studies about the fish biology in the upper rio Paraná basin, mostly in the rio Piracicaba and the rio Mogi Guaçu in the State of São Paulo (Ihering, 1929). In his last contribution on the systematics of fishes from the upper rio Paraná basin Ihering (1930) described four species for the basins, among them *Bunocephalus larai* Ihering and *Tatia neivai* (Ihering). Ihering was invited in 1937 by the Brazilian government to organize the Estação Experimental de Biologia e Piscicultura, Pirassununga (EEBP; currently CEPTA), on the banks of the rio Mogi Guaçu, which was inaugurated in 1939, the same year that Ihering passed away. The EEBP would have in the subsequent years a leading role in the ichthyological studies in the upper rio Paraná basin.

In 1941, Antônia Amaral Campos was put in charge of the fish collection of the Departamento de Zoologia, a new institution created in 1939 to hold the zoological collections formerly belonging to the Museu Paulista. She remained in this position until 1951 (Dopazo *et al*., 2021) and during that time published some publications dealing with fishes from the upper rio Paraná basin (*e.g*., Amaral Campos, 1944, 1945). She described three valid species from the basin (*Apareiodon ibitiensis* Amaral Campos, 1944, *Leporinus lacustris* Amaral Campos, 1945, and *Oligosarcus pintoi* Amaral Campos, 1945).

From the early decade of 1940 until the mid-1960's, ichthyologists working at the EEBP, namely Otto Schubart and Alcides Lourenço Gomes, made several contributions to the knowledge of the fishes from the upper rio Paraná, especially the ones from the rio Mogi-Guaçu basin (*e.g*., Gomes, 1956; Gomes, Schubart, 1958; Schubart, 1964a,b; Schubart, Gomes, 1959). Schubart (1962) published a checklist of the fishes from the rio Mogi-Guaçu basin, the first checklist ever to be published for any river basin in Brazil. Another pioneering work is Gomes, Azevedo (1960), which was the first published study in the upper rio Paraná basin (and in Brazil) focusing on the stream fish fauna. Ichthyologists working at the Museu Nacional as William Gosline and Haroldo Travassos collaborated with the ichthyologists of the EEBP and published some papers dealing with fishes from the upper rio Paraná basin (*e.g*., Gosline, 1947; Travassos, 1955; 1956; 1960; Travassos, Pinto, 1957). After Schubart's death in 1964 and Gomes' resignation in the early 1960's, Manuel Pereira de Godoy kept working on the fishes from the rio Mogi-Guaçu, making important contributions to the knowledge of fish migrations in the basin, but also some taxonomic contributions (*e.g*., Godoy, 1968, 1969). The small fish collection that was kept at the EEBP still existed in December 1994 (FCTL, pers. obs.) but unfortunately was discarded soon after that date; only a few type specimens preserved in the personal collection of Manuel Pereira de Godoy (see Azevedo-Santos *et al*., 2023) and some specimens deposited at the LIRP and MZUSP collections survived the demise of the EEBP collection.

The study of the ichthyofauna from the upper rio Paraná basin undertook a profound change after the arrival, in the early 1960's, of the ichthyologists Heraldo Britski and Náercio Menezes. Britski and Menezes, who are still actively engaged in research, including being co-authors of the present study, joined the Departamento de Zoologia (which was transferred to the Universidade de São Paulo in 1969 when it got its present name, the Museu de Zoologia da Universidade de São Paulo). With the help of José Lima de Figueiredo, these ichthyologists started a progressive buildup of a large fish collection at the MZUSP, which naturally included large new fish collections from the upper rio Paraná basin (Böhlke *et al*., 1978; Menezes *et al*., 1997). Particularly, Heraldo Britski focused much of his research on fishes from the upper rio Paraná basin (*e.g*., Britski, Luengo, 1968; Britski, 1980; Britski, Garavello, 1978; Britski, Langeani, 1988). These ichthyologists also played a crucial role in training several fish taxonomists who later formed taxonomic research groups and fish collections in other portions of the upper rio Paraná basin (*e.g*., Carla S. Pavanelli, Universidade Estadual de Maringá, Maringá, State of Paraná; Flávio A. Bockmann and Ricardo M. C. Castro, Universidade de São Paulo, Ribeirão Preto; Francisco Langeani, Universidade Estadual Paulista "Júlio de Mesquita Filho", São José do Rio Preto; Júlio César Garavello, Universidade Federal de São Carlos, São Carlos).

Starting in the 1990's, the number of researchers and institutions working with fishes from the rio upper Paraná experienced an exponential growth, making a difficult task any attempt to summarize the history of this still ongoing research program. However, it is worth noting that until the 1990's, ichthyological studies primarily were focused in studying larger water bodies (Galves *et al*., 1999). However, in the subsequent decades, there has been a shift towards conducting inventories in streams that support distinct fish communities and a significant number of small-sized species (Castro, 1999). This approach has led to the identification and characterization of numerous small-sized species within the basin, as well as the documentation of species shared with adjacent basins.

**Ichthyofaunistic composition of the upper rio Paraná basin.** The upper rio Paraná basin contains 341 native fish species (Tab. 1), distributed in six orders (Fig. 4), 30 families (Fig. 5) and 125 genera (Tab. 1). Three genera represent lineages endemic to the basin, the characids *Aphyocheirodon* Eigenmann, 1915, and *Lophiobrycon* Castro, Ribeiro, Benine & Melo, 2003, all monotypic, and *Tembeassu* Triques, 1988 (Apteronotidae) with a recently-described second species (Peixoto *et al*., 2022).

The present list is an update on the previous one by Langeani *et al*. (2007), which compiled 236 native species. In the intervening 15 years, more than 100 species were added to the basin, an increase of almost one-third. The difference is due to new species

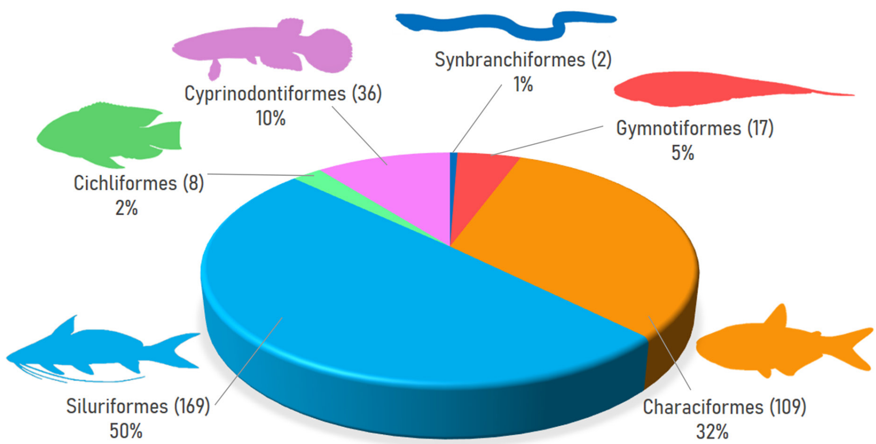



**FIGURE 4** | Diversity of native fish species present in the upper rio Paraná by orders. The value in parentheses corresponds to the number of species in each order.

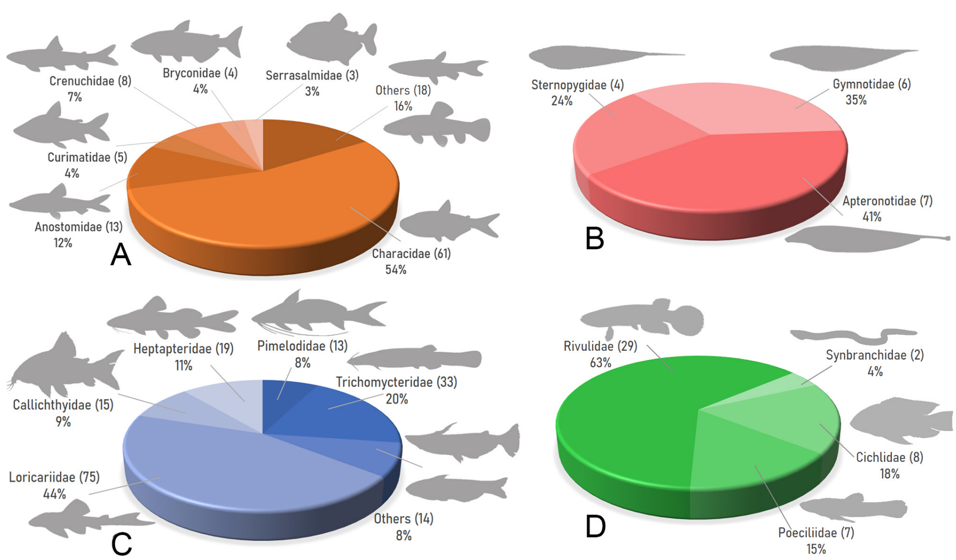



**FIGURE 5** | Diversity of native fish species present in the upper rio Paraná basin by families: **A.** Characiformes; **B.** Gymnotiformes; **C.** Siluriformes; **D.** Other orders.

described in the interim or new records for the basin. Much of the increase represents new species of Loricariidae, a family which practically doubled in number of species since Langeani *et al*. (2007), going from 40 to 75. Another major additions were the Trichomycteridae, which experienced a quadrupling in its species count (from 8 to 33) and the family Rivulidae, which almost tripled its representations, increasing from 11 to 29 species. New records mostly represent fish species typical of neighboring basins which have been recently found also in peripheral reaches of the upper Paraná (*e.g.*, *Astyanax lineatus* (Perugia, 1891), *Hyphessobrycon griemi* Hoedeman 1957, *Jupiaba acanthogaster* (Eigenmann, 1911), *Scleromystax barbatus* (Quoy & Gaimard 1824)).

Langeani *et al*. (2007) projected increments in the known diversity of the basin in a graph of species described per decade. The graph indicated exponential growth with no tendency to stabilization. Data presented herein confirm that prediction and show that the trend of increase continues unabated.

As in most drainages in the neotropics, a majority of the fishes of the upper rio Paraná belong to the Otophysi (Fig. 4), with 86.5% of total species diversity concentrated in the Siluriformes, Characiformes, and Gymnotiformes. Fishes of the Otophysi lineage also dominate the freshwater systems in Africa and in Asia. As in other Neotropical basins, the richest orders are Siluriformes and Characiformes (*cf*. Albert *et al*., 2020). Familial composition also follows a pattern typical of the majority of continental waters in the neotropics, vastly dominated by small body-size species. Six families (Loricariidae, Characidae, Rivulidae, Trichomycteridae, and Heptapteridae) concentrate most of the diversity (218 spp. or 64% of species), with Loricariidae alone comprising nearly a quarter of all fish species of the upper rio Paraná basin.

**TABLE 1** | List of native fish species occurring in the upper rio Paraná basin. Threatened species are followed by the abbreviations: VU - Vulnerable, EN - Endangered, CR - Critically Endangered, CR(PEX) - Possibly Extinct.

| Taxon | Record in the upper rio Paraná / comments |
|---|---|
| **CHARACIFORMES** | |
| **Acestrorhynchidae** | |
| *Acestrorhynchus lacustris* (Lütken, 1875) | Langeani *et al.* (2007) |
| **Anostomidae** | |
| *Leporellus pictus* (Kner, 1858) | *Leporellus vittatus* in Langeani *et al.* (2007), Ramirez (2015) |
| *Leporinus amblyrhynchus* Garavello & Britski, 1987 | Langeani *et al.* (2007) |
| *Leporinus friderici* (Bloch, 1794) | Langeani *et al.* (2007) |
| *Leporinus lacustris* Campos, 1945 | Langeani *et al.* (2007) |
| *Leporinus microphthalmus* Garavello, 1989 | Langeani *et al.* (2007) |
| *Leporinus octofasciatus* Steindachner, 1915 | Langeani *et al.* (2007) |
| *Leporinus paranensis* Garavello & Britski, 1987 | Langeani *et al.* (2007) |
| *Leporinus striatus* Kner, 1859 | Langeani *et al.* (2007) |
| *Megaleporinus obtusidens* (Valenciennes, 1836) | *Leporinus elongatus* in Langeani *et al.* (2007) |
| *Megaleporinus piavussu* (Britski, Birindelli & Garavello, 2012) | Langeani *et al.* (2007) |
| *Schizodon altoparanae* Garavello & Britski, 1990 | Langeani *et al.* (2007) |
| *Schizodon intermedius* Garavello & Britski, 1990 | Langeani *et al.* (2007) |
| *Schizodon nasutus* Kner, 1858 | Langeani *et al.* (2007) |

**TABLE 1** | (Continued)

| Taxon | Record in the upper rio Paraná / comments |
|---|---|
| **Bryconidae** | |
| *Brycon nattereri* Günther, 1864 | Langeani *et al*. (2007) |
| *Brycon orbignyanus* (Valenciennes, 1850) - CR | Langeani *et al*. (2007) |
| *Salminus brasiliensis* (Cuvier, 1816) | Langeani *et al*. (2007) |
| *Salminus hilarii* Valenciennes, 1850 | Langeani *et al*. (2007) |
| **Characidae** | |
| Aphyocharacinae | |
| *Aphyocharax dentatus* Eigenmann & Kennedy, 1903 | Langeani *et al*. (2007). Allochthonous in Ota *et al*. (2018) |
| Characinae | |
| *Galeocharax gulo* (Cope, 1870) | *Galeocharax knerii* in Langeani *et al*. (2007) |
| Cheirodontinae | |
| *Aphyocheirodon hemigrammus* Eigenmann, 1915 | Langeani *et al*. (2007) |
| "*Cheirodon*" *stenodon* Eigenmann, 1915 | Langeani *et al*. (2007) |
| *Kolpotocheirodon theloura* Malabarba & Weitzman, 2000 | Langeani *et al*. (2007) |
| *Odontostilbe avanhandava* Chuctaya, Bührnheim & Malabarba, 2018 | Chuctaya *et al*. (2018) |
| *Odontostilbe weitzmani* Chuctaya, Bührnheim & Malabarba, 2018 | Chuctaya *et al*. (2018) |
| *Serrapinnus heterodon* (Eigenmann, 1915) | Langeani *et al*. (2007) |
| *Serrapinnus notomelas* (Eigenmann, 1915) | Langeani *et al*. (2007) |
| *Serrapinnus piaba* (Lütken, 1875) | New record. MCP 47052 |
| *Spintherobolus papilliferus* Eigenmann, 1911 - EN | Langeani *et al*. (2007) |
| Stethaprioninae | |
| *Astyanax biotae* Castro & Vari, 2004 | Langeani *et al*. (2007) |
| *Astyanax lacustris* (Lütken, 1875) | *Astyanax altiparanae* in Langeani *et al*. (2007) |
| *Astyanax lineatus* (Perugia, 1891) | Ferreira *et al*. (2017) |
| *Astyanax trierythropterus* Godoy, 1970 | Langeani *et al*. (2007) |
| *Coptobrycon bilineatus* (Ellis, 1911) | Langeani *et al*. (2007) |
| *Hasemania crenuchoides* Zarske & Géry, 1999 - EN | Langeani *et al*. (2007) |
| *Hasemania hanseni* (Fowler, 1949) | Langeani *et al*. (2007) |
| *Hasemania nana* (Lütken, 1875) | Souza (2021) |
| *Hasemania uberaba* Serra & Langeani, 2015 - EN | Serra, Langeani (2015) |
| *Hollandichthys multifasciatus* (Eigenmann & Norris, 1900) | Langeani *et al*. (2007) |
| *Hyphessobrycon balbus* Myers, 1927 | Langeani *et al*. (2007) |
| *Hyphessobrycon bifasciatus* Ellis, 1911 | Langeani *et al*. (2007) |
| *Hyphessobrycon boulengeri* (Eigenmann, 1907) | *Hyphessobrycon reticulatus* in Langeani *et al*. (2007) |
| *Hyphessobrycon coelestinus* Myers, 1929 | Langeani *et al*. (2007) |
| *Hyphessobrycon duragenys* Ellis, 1911 - EN | Langeani *et al*. (2007) |
| *Hyphessobrycon griemi* Hoedeman, 1957 | Reis *et al*. (2020) |
| *Hyphessobrycon herbertaxelrodi* Géry, 1961 | New record. DZSJRP 11731 |
| *Hyphessobrycon uaiso* Carvalho & Langeani, 2013 | Carvalho, Langeani (2013) |
| *Jupiaba acanthogaster* (Eigenmann, 1911) | Lopes *et al*. (2020) |
| *Moenkhausia aurantia* Bertaco, Jerep & Carvalho, 2011 | *Moenkhausia* sp. in Aquino *et al*. (2009) |
| *Moenkhausia bonita* Benine, Castro & Sabino, 2004 | Vanegas-Rios *et al*. (2019). Not clearly diagnosable from *Hemigrammus* aff. *marginatus* (*sensu* Ota *et al*., 2015) according to Mota *et al*. (2018) |
| *Moenkhausia* aff. *intermedia* Eigenmann, 1908 | Langeani *et al*. (2007) |
| *Moenkhausia* aff. *sanctaefilomenae* (Steindachner, 1907) | Langeani *et al*. (2007) |
| *Oligosarcus argenteus* Günther, 1864 | Azevedo-Santos *et al*. (2019) |
| *Oligosarcus paranensis* Menezes & Géry, 1983 | Langeani *et al*. (2007) |
| *Oligosarcus pintoi* Campos, 1945 | Langeani *et al*. (2007) |

**TABLE 1** | (Continued)

| Taxon | Record in the upper rio Paraná / comments |
|---|---|
| *Oligosarcus planaltinae* Menezes & Géry, 1983 | Langeani *et al.* (2007) |
| *Psalidodon anisitsi* (Eigenmann, 1907) | *Hyphessobrycon anisitsi* in Langeani *et al.* (2007) |
| *Psalidodon argentum* (Salgado, 2021) | Salgado (2021). Recently described species whose validity is questionable |
| *Psalidodon bifasciatus* (Garavello & Sampaio, 2010) | Neves *et al.* (2020) |
| *Psalidodon bockmanni* (Vari & Castro, 2007) | *Astyanax bockmanni* in Langeani *et al.* (2007) |
| *Psalidodon fasciatus* (Cuvier, 1819) | *Astyanax fasciatus* in Langeani *et al.* (2007) |
| *Psalidodon paranae* (Eigenmann, 1914) | *Astyanax paranae* in Langeani *et al.* (2007) |
| *Psalidodon rioparanaibanus* Alves, Oliveira, Pasa & Kavalco, 2020 | Alves *et al.* (2020) |
| *Psalidodon schubarti* (Britski, 1964) | *Astyanax schubarti* in Langeani *et al.* (2007) |
| Stevardiinae | |
| *Bryconamericus coeruleus* Jerep & Shibatta, 2017 | Jerep, Shibatta (2017) |
| *Bryconamericus* aff. *iheringii* (Boulenger, 1887) | Langeani *et al.* (2007) DZSJRP 7900 |
| *Bryconamericus turiuba* Langeani, Lucena, Pedrini & Tarelho-Pereira, 2005 | Langeani *et al.* (2007) |
| *Creagrutus varii* Ribeiro, Benine & Figueiredo, 2004 | Langeani *et al.* (2007) |
| *Glandulocauda melanopleura* (Ellis, 1911) | *Glandulocauda melanogenys* in Langeani *et al.* (2007) |
| *Lophiobrycon weitzmani* Castro, Ribeiro, Benine & Melo, 2003 | Langeani *et al.* (2007) |
| *Mimagoniates microlepis* (Steindachner, 1877) | Langeani *et al.* (2007) |
| *Piabarchus stramineus* (Eigenmann, 1908) | *Bryconamericus stramineus* in Langeani *et al.* (2007) |
| *Piabina anhembi* Silva & Kaefer, 2003 | Langeani *et al.* (2007) |
| *Piabina argentea* Reinhardt, 1867 | Langeani *et al.* (2007) |
| *Planaltina britskii* Menezes, Weitzman & Burns, 2003 | Langeani *et al.* (2007) |
| *Planaltina glandipedis* Menezes, Weitzman & Burns, 2003 | Langeani *et al.* (2007) |
| *Planaltina kaingang* Deprá, Graça, Pavanelli, Avelino & Oliveira, 2018 | Deprá *et al.* (2018) |
| *Planaltina myersi* Böhlke, 1954 | Langeani *et al.* (2007) |
| *Pseudocorynopoma heterandria* Eigenmann, 1914 | Langeani *et al.* (2007) |
| **Crenuchidae** | |
| *Characidium gomesi* Travassos, 1956 | Langeani *et al.* (2007) |
| *Characidium heirmostigmata* Graça & Pavanelli, 2008 | Graça, Pavanelli (2008) |
| *Characidium lagosantense* Travassos, 1947 | Silveira (2008) |
| *Characidium oiticicai* Travassos, 1967 | Langeani *et al.* (2007) |
| *Characidium onca* Melo, Brito Ribeiro & Lima, 2021 | Melo *et al.* (2021) |
| *Characidium schubarti* Travassos, 1955 | Langeani *et al.* (2007) |
| *Characidium xanthopterum* Silveira, Langeani, Graça, Pavanelli & Buckup, 2008 | Silveira *et al.* (2008) |
| *Characidium* aff. *zebra* Eigenmann, 1909 | Langeani *et al.* (2007) |
| **Curimatidae** | |
| *Cyphocharax corumbae* (Pavanelli & Britski, 1999) | *Steindachnerina corumbae* in Langeani *et al.* (2007) |
| *Cyphocharax modestus* (Fernández-Yépez, 1948) | Langeani *et al.* (2007) |
| *Cyphocharax naegelii* (Steindachner, 1881) | Langeani *et al.* (2007) |
| *Cyphocharax vanderi* (Britski, 1980) | Langeani *et al.* (2007) |
| *Steindachnerina insculpta* (Fernández-Yépez, 1948) | Langeani *et al.* (2007) |
| **Cynodontidae** | |
| *Rhaphiodon vulpinus* Spix & Agassiz, 1829 | Langeani *et al.* (2007) |

**TABLE 1** | (Continued)

| Taxon | Record in the upper rio Paraná / comments |
|---|---|
| **Erythrinidae** | |
| *Hoplias argentinensis* Rosso, González-Castro, Bogan, Cardoso, Mabragaña, Delpiani & Díaz de Astarloa, 2018 | Reis *et al.* (2020) |
| *Hoplias intermedius* (Günther, 1864) | *Hoplias microcephalus* in Langeani *et al.* (2007) |
| *Hoplias* aff. *malabaricus* (Bloch, 1794) | Langeani *et al.* (2007) |
| *Hoplias misionera* Rosso, Mabragaña, González-Castro, Delpiani, Avigliano, Schenone & Díaz de Astarloa, 2016 | Ota *et al.* (2018) |
| **Lebiasinidae** | |
| *Pyrrhulina australis* Eigenmann & Kennedy, 1903 | Langeani *et al.* (2007) |
| **Parodontidae** | |
| *Apareiodon affinis* (Steindachner, 1879) | Langeani *et al.* (2007) |
| *Apareiodon ibitiensis* Campos, 1944 | Langeani *et al.* (2007) |
| *Apareiodon piracicabae* (Eigenmann, 1907) | Langeani *et al.* (2007) |
| *Apareiodon vladii* Pavanelli, 2006 | Langeani *et al.* (2007) |
| *Parodon moreirai* Ingenito & Buckup, 2005 | Langeani *et al.* (2007) |
| *Parodon nasus* Kner, 1859 | Langeani *et al.* (2007) |
| **Prochilodontidae** | |
| *Prochilodus lineatus* (Valenciennes, 1837) | Langeani *et al.* (2007) |
| *Prochilodus vimboides* Kner, 1859 - VU | Langeani *et al.* (2007) |
| **Serrasalmidae** | |
| *Myloplus tiete* (Eigenmann & Norris, 1900) - EN | *Myleus tiete* in Langeani *et al.* (2007) |
| *Piaractus mesopotamicus* (Holmberg, 1887) | Langeani *et al.* (2007) |
| *Serrasalmus maculatus* Kner, 1858 | Langeani *et al.* (2007) |
| **GYMNOTIFORMES** | |
| **Apteronotidae** | |
| *Apteronotus acidops* Triques, 2011 | Ota *et al.* (2018) |
| *Apteronotus brasiliensis* (Reinhardt, 1852) | Allochthonous in Langeani *et al.* (2007) |
| *Apteronotus ellisi* (Arámburu, 1957) | Allochthonous in Langeani *et al.* (2007) |
| *Sternarchella curvioperculata* Godoy, 1968 - EN | Langeani *et al.* (2007) |
| *Sternarchorhynchus britskii* Campos-da-Paz, 2000 - EN | Langeani *et al.* (2007) |
| *Tembeassu marauna* Triques, 1988 CR | Langeani *et al.* (2007) |
| *Tembeassu titanicus* Peixoto, Campos-da-Paz, Menezes, de Santana, Triques & Datovo, 2022 | Peixoto *et al.* (2022) |
| **Gymnotidae** | |
| *Gymnotus* aff. *carapo* Linnaeus, 1758 | Langeani *et al.* (2007) |
| *Gymnotus* aff. *cuia* Craig, Malabarba, Crampton & Albert, 2018 | Craig *et al.* (2018) |
| *Gymnotus* aff. *inaequilabiatus* (Valenciennes, 1839) | Langeani *et al.* (2007) |
| *Gymnotus* aff. *omarorum* Richer-de-Forges, Crampton & Albert, 2009 | Jarduli *et al.* (2020) |
| *Gymnotus pantherinus* (Steindachner, 1908) | Langeani *et al.* (2007) |
| *Gymnotus* aff. *sylvius* Albert & Fernandes-Matioli, 1999 | Albert *et al.* (1999) |
| **Sternopygidae** | |
| *Eigenmannia dutrai* Peixoto, Pastana & Ballen, 2021 | Peixoto *et al.* (2021) |
| *Eigenmannia guairaca* Peixoto, Dutra & Wosiacki, 2015 | Ota *et al.* (2018) |
| *Eigenmannia trilineata* López & Castello, 1966 | Langeani *et al.* (2007) |
| *Sternopygus macrurus* (Bloch & Schneider, 1801) | Langeani *et al.* (2007) |
| **SILURIFORMES** | |
| **Aspredinidae** | |
| *Amaralia oviraptor* Friel & Carvalho, 2016 | Ota *et al.* (2018) |
| *Bunocephalus hertzi* Esguícero, Castro & Pereira, 2020 | Esguícero *et al.* (2020) |
| *Bunocephalus larai* Ihering, 1930 | Langeani *et al.* (2007) |

**TABLE 1** | (Continued)

| Taxon | Record in the upper rio Paraná / comments |
|---|---|
| **Auchenipteridae** | |
| *Ageneiosus militaris* Valenciennes, 1835 | Ota *et al.* (2018). Allochthonous in Langeani *et al.* (2007) |
| *Glanidium cesarpintoi* Ihering, 1928 | Langeani *et al.* (2007) |
| *Tatia britskii* (Sarmento-Soares & Birindelli, 2015) | Sarmento-Soares, Birindelli (2015) |
| *Tatia neivai* (Ihering, 1930) | Langeani *et al.* (2007) |
| *Trachelyopterus coriaceus* Valenciennes, 1840 | Langeani *et al.* (2007) |
| *Trachelyopterus galeatus* (Linnaeus, 1766) | Langeani *et al.* (2007). Allochthonous and as *Parauchenipterus galeatus* in Ota *et al.* (2018) |
| **Callichthyidae** | |
| Callichthyinae | |
| *Callichthys callichthys* (Linnaeus, 1758) | Langeani *et al.* (2007) |
| *Hoplosternum littorale* (Hancock, 1828) | Langeani *et al.* (2007) |
| Corydoradinae | |
| *Aspidoras albater* Nijssen & Isbrücker, 1976 | Tencatt *et al.* (2022) |
| *Aspidoras fuscoguttatus* Nijssen & Isbrücker, 1976 | Langeani *et al.* (2007) |
| *Aspidoras lakoi* Miranda Ribeiro, 1949 | Tencatt *et al.* (2022) |
| *Corydoras aeneus* (Gill, 1858) | Langeani *et al.* (2007) |
| *Corydoras difluviatilis* Britto & Castro, 2002 | Langeani *et al.* (2007) |
| *Corydoras ehrhardti* Steindachner, 1910 | Langeani *et al.* (2007) |
| *Corydoras flaveolus* Ihering, 1911 | Langeani *et al.* (2007) |
| *Corydoras lacrimostigmata* Tencatt, Britto & Pavanelli, 2014 | Tencatt *et al.* (2014) |
| *Corydoras* aff. *longipinnis* Knaack, 2007 | Reis *et al.* (2020) |
| *Scleromystax barbatus* (Quoy & Gaimard, 1824) | Marceniuk *et al.* (2011) |
| *Scleromystax macropterus* (Regan, 1913) - EN | Langeani *et al.* (2007) |
| **Cetopsidae** | |
| *Cetopsis gobioides* Kner, 1858 | Langeani *et al.* (2007) |
| **Doradidae** | |
| *Rhinodoras dorbignyi* (Kner, 1855) | Langeani *et al.* (2007) |
| **Heptapteridae** | |
| *Cetopsorhamdia iheringi* Schubart & Gomes, 1959 | Langeani *et al.* (2007) |
| *Chasmocranus brachynemus* Gomes & Schubart, 1958 - EN | Langeani *et al.* (2007) |
| *Heptapterus carmelitanorum* Azevedo-Santos, Deprá, Aguilera, Faustino-Fuster & Katz, 2022 | Deprá *et al.* (2022) |
| *Heptapterus longicauda* (Borodin, 1927) | *Imparfinis borodini* Mees & Cala, 1989 in Langeani *et al.* (2007) |
| *Heptapterus multiradiatus* Ihering, 1907 - CR(PEX) | Langeani *et al.* (2007) |
| *Imparfinis lepturus* Silva, Reia, Morimoto, Benine & Oliveira, 2023 | Silva *et al.* (2023) |
| *Imparfinis mirini* Haseman, 1911 | Langeani *et al.* (2007). Distribution based on Silva *et al.* (2023) |
| *Imparfinis piperatus* Eigenmann & Norris, 1900 | Langeani *et al.* (2007) |
| *Imparfinis schubarti* (Gomes, 1956) | Langeani *et al.* (2007). Distribution based on Silva *et al.* (2023) |
| *Phenacorhamdia tenebrosa* (Schubart, 1964) | Langeani *et al.* (2007) |
| *Phenacorhamdia roxoi* Silva, 2020 | Silva (2020) |
| *Phenacorhamdia unifasciata* Britski, 1993 | Langeani *et al.* (2007) |
| *Pimelodella avanhandavae* Eigenmann, 1917 | Langeani *et al.* (2007) |
| *Pimelodella boschmai* Van der Stigchel, 1964 | Langeani *et al.* (2007) |
| *Pimelodella gracilis* (Valenciennes, 1835) | Langeani *et al.* (2007) |
| *Pimelodella meeki* Eigenmann, 1910 | Senior-synonym of *P. rudolphi* Miranda Ribeiro, 1918 in Slobodian (2017) |
| *Rhamdia quelen* (Quoy & Gaimard, 1824) | Langeani *et al.* (2007) |
| *Rhamdiopsis microcephala* (Lütken, 1874) | Langeani *et al.* (2007) |
| *Rhamdiopsis moreirai* Haseman, 1911 - VU | Reis *et al.* (2020) |
| *Taunayia bifasciata* (Eigenmann & Norris, 1900) | Langeani *et al.* (2007) |

**TABLE 1** | (Continued)

| Taxon | Record in the upper rio Paraná / comments |
|---|---|
| **Loricariidae** | |
| Hypoptopomatinae | |
| *Corumbataia britskii* Ferreira & Ribeiro, 2007 | Ferreira, Ribeiro (2007) |
| *Corumbataia cuestae* Britski, 1997 | Langeani *et al.* (2007) |
| *Corumbataia liliai* Silva, Roxo, Souza & Oliveira, 2018 | Silva *et al.* (2018) |
| *Corumbataia lucianoi* Silva, Roxo, Souza & Oliveira, 2018 | Silva *et al.* (2018) |
| *Curculionichthys insperatus* (Britski & Garavello, 2003) | *Hisonotus insperatus* in Langeani *et al.* (2007) |
| *Curculionichthys oliveirai* (Roxo, Zawadzki & Troy, 2014) | Roxo *et al.* (2014) |
| *Curculionichthys piracanjuba* (Martins & Langeani, 2012) | Martins, Langeani (2012) |
| *Hisonotus alberti* Roxo, Silva, Waltz & Melo, 2016 | Roxo *et al.* (2016) |
| *Hisonotus depressicauda* (Miranda-Ribeiro, 1918) | Langeani *et al.* (2007). Distribution follows Calegari *et al.* (2017) |
| *Hisonotus francirochai* (Ihering, 1928) | Langeani *et al.* (2007). Distribution follows Calegari *et al.* (2017) |
| *Hisonotus pachysarkos* Zawadzki, Roxo & Graça, 2016 | Zawadzki *et al.* (2016) |
| *Hisonotus paulinus* (Regan, 1908) | Langeani *et al.* (2007). Distribution follows Calegari *et al.* (2017) *Microlepidogaster depressinotus* Miranda Ribeiro, 1918 is regarded as a junior synonym of *H. paulinus* pending further studies |
| *Microlepidogaster arachas* Martins, Calegari & Langeani, 2013 | Martins *et al.* (2013) |
| *Microlepidogaster dimorpha* Martins & Langeani, 2011 | Martins, Langeani (2011b) |
| *Microlepidogaster longicolla* Calegari & Reis, 2010 | Calegari, Reis (2010) |
| *Microlepidogaster perforata* Eigenmann & Eigenmann, 1889 - CR | Langeani *et al.* (2007) |
| *Otothyropsis alicula* Lippert, Calegari & Reis, 2014 | Lippert *et al.* (2014) |
| *Otothyropsis biamnicus* Calegari, Lehmann & Reis, 2013 | Calegari *et al.* (2013) |
| *Otothyropsis marapoama* Ribeiro Carvalho & Melo, 2005 | Langeani *et al.* (2007) |
| *Otothyropsis polyodon* Calegari, Lehmann & Reis, 2013 | Calegari *et al.* (2013) |
| *Pseudotocinclus tietensis* (Ihering, 1907) - EN | Langeani *et al.* (2007) |
| *Pseudotothyris obtusa* (Miranda Ribeiro, 1911) | Reis *et al.* (2020) |
| *Rhinolekos britskii* Martins, Langeani & Costa, 2011 | Martins, Langenai (2011) |
| *Rhinolekos garavelloi* Martins & Langeani, 2011 | Martins, Langeani (2011) |
| *Rhinolekos schaeferi* Martins & Langeani, 2011 | Martins, Langeani (2011) |
| Hypostominae | |
| *Ancistrus* aff. *cirrhosus* (Valenciennes, 1836) | Langeani *et al.* (2007) |
| *Hypostomus albopunctatus* (Regan, 1908) | Langeani *et al.* (2007) |
| *Hypostomus ancistroides* (Ihering, 1911) | Langeani *et al.* (2007) |
| *Hypostomus brevis* (Nichols, 1919) | Langeani *et al.* (2007). Known only from the holotype (Weber, 2003) |
| *Hypostomus crulsi* Soares, Aquino, Bagley, Langeani & Colli, 2021 | Soares *et al.* (2021) |
| *Hypostomus denticulatus* Zawadzki, Weber & Pavanelli, 2008 | Zawadzki *et al.* (2008a) |
| *Hypostomus fluviatilis* (Schubart, 1964) | Langeani *et al.* (2007) |
| *Hypostomus heraldoi* Zawadzki, Weber & Pavanelli, 2008 | Zawadzki *et al.* (2008a) |
| *Hypostomus hermanni* (Ihering, 1905) | Langeani *et al.* (2007) |
| *Hypostomus iheringii* (Regan, 1908) | Langeani *et al.* (2007) |
| *Hypostomus margaritifer* (Regan, 1908) | Langeani *et al.* (2007) |
| *Hypostomus meleagris* (Marini, Nichols & LaMonte, 1933) | Poorly known species, with type locality apparently in upper rio Paraná (Weber, 2003) |
| *Hypostomus multidens* Jerep, Shibatta & Zawadzki, 2007 | Jerep *et al.* (2007) |
| *Hypostomus nigromaculatus* (Schubart, 1964) | Langeani *et al.* (2007) |
| *Hypostomus paulinus* (Ihering, 1905) | Langeani *et al.* (2007) |
| *Hypostomus regani* (Ihering, 1905) | Langeani *et al.* (2007) |
| *Hypostomus robertsoni* Dias & Zawadzki, 2021 | Dias, Zawadzki (2021) |
| *Hypostomus strigaticeps* (Regan, 1908) | Langeani *et al.* (2007) |

**TABLE 1** | (Continued)

| Taxon | Record in the upper rio Paraná / comments |
|---|---|
| *Hypostomus tietensis* (Ihering, 1905) | Langeani *et al.* (2007) |
| *Hypostomus topavae* (Godoy, 1969) | Langeani *et al.* (2007) |
| *Hypostomus variipictus* (Ihering, 1911) | Azevedo *et al.* (2021) |
| *Hypostomus yaku* Martins, Langeani & Zawadzki, 2014 | Martins *et al.* (2014) |
| *Megalancistrus parananus* (Peters, 1881) | Langeani *et al.* (2007) |
| Loricariinae | |
| *Harttia absaberi* Oyakawa, Fichberg & Langeani, 2013 | Oyakawa *et al.* (2013) |
| *Harttia gracilis* Oyakawa, 1993 | Langeani *et al.* (2007) |
| *Loricaria piracicabae* Ihering, 1907 | Langeani *et al.* (2007) |
| *Proloricaria lentiginosa* (Isbrücker, 1979) | *Loricaria lentiginosa* in Langeani *et al.* (2007) |
| *Proloricaria prolixa* (Isbrücker & Nijssen, 1978) | *Loricaria prolixa* in Langeani *et al.* (2007) |
| *Rineloricaria latirostris* (Boulenger, 1900) | Langeani *et al.* (2007) |
| *Rineloricaria pentamaculata* Langeani & Araújo, 1994 | Langeani *et al.* (2007) |
| *Rineloricaria rodriquezae* Costa-Silva, Oliveira & Silva, 2021 | Costa-Silva *et al.* (2021) |
| Neoplecostominae | |
| *Isbrueckerichthys calvus* Jerep, Shibatta, Pereira & Oyakawa, 2006 | Langeani *et al.* (2007) |
| *Isbrueckerichthys saxicola* Jerep, Shibatta, Pereira & Oyakawa, 2006 - EN | Langeani *et al.* (2007) |
| *Neoplecostomus bandeirante* Roxo, Oliveira & Zawadzki, 2012 | Roxo *et al.* (2012) |
| *Neoplecostomus botucatu* Roxo, Oliveira & Zawadzki, 2012 | Roxo *et al.* (2012) |
| *Neoplecostomus canastra* Roxo, Silva, Zawadzki & Oliveira, 2017 | Roxo *et al.* (2017) |
| *Neoplecostomus corumba* Zawadzki, Pavanelli & Langeani, 2008 | Zawadzki *et al.* (2008) |
| *Neoplecostomus jaguari* Andrade & Langeani, 2014 | Andrade, Langeani (2014) |
| *Neoplecostomus langeanii* Roxo, Oliveira & Zawadzki, 2012 | Roxo *et al.* (2012) |
| *Neoplecostomus paranensis* Langeani, 1990 | Langeani *et al.* (2007) |
| *Neoplecostomus selenae* Zawadzki, Pavanelli & Langeani, 2008 | Zawadzki *et al.* (2008) |
| *Neoplecostomus watersi* Silva, Reia, Zawadzki & Roxo, 2019 | Silva *et al.* (2019) |
| *Neoplecostomus yapo* Zawadzki, Pavanelli & Langeani, 2008 | Zawadzki *et al.* (2008) |
| *Pareiorhina carrancas* Bockmann & Ribeiro, 2003 | Langeani *et al.* (2007) |
| *Pareiorhina pelicicei* Azevedo-santos & Roxo, 2015 | Azevedo-Santos, Roxo (2015) |
| *Pareiorhina rosai* Silva, Roxo & Oyakawa, 2016 | New record. DZSJRP 20982 |
| *Pareiorhina* aff. *rudolphi* (Miranda Ribeiro, 1911) | Azevedo-Santos, Roxo (2015) |
| *Pareiorhaphis parmula* Pereira, 2005 | Reis *et al.* (2020) |
| *Pareiorhaphis togoroi* Oliveira & Oyakawa, 2019 | Oliveira, Oyakawa (2019) |
| Rhinelepinae | |
| *Rhinelepis aspera* Spix & Agassiz, 1829 | Langeani *et al.* (2007) |
| **Pimelodidae** | |
| *Hemisorubim platyrhynchos* (Valenciennes, 1840) | Langeani *et al.* (2007) |
| *Iheringichthys labrosus* Lütken, 1874 | Langeani *et al.* (2007). Allochthonous in Ota *et al.* (2018) |
| *Iheringichthys syi* Azpelicueta & Britski, 2012 | Azpelicueta, Britski (2012) |
| *Megalonema platanum* (Günther, 1880) | Ota *et al.* (2018). Allochthonous in Langeani *et al.* (2007) |
| *Pimelodus maculatus* Lacepède, 1803 | Langeani *et al.* (2007) |
| *Pimelodus microstoma* Steindachner, 1877 | Ota *et al.* (2018) |
| *Pimelodus paranaensis* Britski & Langeani, 1988 | Langeani *et al.* (2007) |
| *Pimelodus platicirris* Borodin, 1927 | Langeani *et al.* (2007) |
| *Pinirampus pirinampu* (Spix & Agassiz, 1829) | Langeani *et al.* (2007) |
| *Pseudoplatystoma corruscans* (Spix & Agassiz, 1829) - VU | Langeani *et al.* (2007) |
| *Steindachneridion punctatum* (Miranda-Ribeiro, 1918) | Langeani *et al.* (2007) |
| *Steindachneridion scriptum* (Miranda-Ribeiro, 1918) - EN | Langeani *et al.* (2007) |
| *Zungaro jahu* (Ihering, 1898) | Langeani *et al.* (2007) |

**TABLE 1** | (Continued)

| Taxon | Record in the upper rio Paraná / comments |
|---|---|
| **Pseudopimelodidae** | |
| *Microglanis garavelloi* Shibatta & Benine, 2005 | Langeani *et al.* (2007) |
| *Pseudopimelodus mangurus* (Valenciennes, 1835) | Langeani *et al.* (2007) |
| *Rhyacoglanis paranensis* Shibatta & Vari, 2017 | *Pseudopimelodus* aff. *pulcher* in Langeani *et al.* (2007) |
| **Scoloplacidae** | |
| *Scoloplax empousa* Schaefer, Weitzman & Britski, 1989 | Ota *et al.* (2018) |
| **Trichomycteridae** | |
| *Cambeva davisi* (Haseman, 1911) | *Trichomycterus davisi* in Ota *et al.* (2018) |
| *Cambeva diabola* (Bockmann, Casatti & de Pinna, 2004) | *Trichomycterus diabolus* in Langeani *et al.* (2007) |
| *Cambeva guareiensis* Katz & Costa, 2020 | Katz, Costa (2020) |
| *Cambeva horacioi* Reis, Frota, Fabrin & Graça, 2019 | Reis *et al.* (2019) |
| *Cambeva iheringi* (Eigenmann, 1917) | Marceniuk *et al.* (2011) |
| *Cambeva paolence* (Eigenmann, 1917) - EN | *Trichomycterus paolence* in Langeani *et al.* (2007) |
| *Cambeva pascuali* (Ochoa, Silva, Costa e Silva, Oliveira & Datovo, 2017) - CR | Ochoa *et al.* (2017) |
| *Cambeva perkos* (Datovo, Carvalho & Ferrer, 2012) | Datovo *et al.* (2012) |
| *Ituglanis amphipotamus* Mendonça, Oyakawa & Wosiacki, 2018 | Mendonça, Oyakawa, Wosiacki, 2018 |
| *Ituglanis goya* Datovo, Aquino & Langeani, 2016 | Datovo *et al.* (2016) |
| *Paravandellia oxyptera* Miranda Ribeiro, 1912 | Langeani *et al.* (2007) |
| *Pseudostegophilus paulensis* Miranda Ribeiro, 1918 | Langeani *et al.* (2007) |
| *Scleronema auromaculatum* Costa, Sampaio, Giongo, Almeida, Azevedo-Santos & Katz, 2022 | Costa *et al.* (2022) |
| *Trichomycterus adautoleitei* Costa, Azevedo-Santos & Katz, 2023 | Costa *et al.* (2023) |
| *Trichomycterus araxa* Costa, Mattos, Sampaio, Giongo, Almeida & Katz, 2022 | Costa *et al.* (2022) |
| *Trichomycterus* aff. *brasiliensis* Lütken, 1874 | Allochthonous in Langeani *et al.* (2007) |
| *Trichomycterus candidus* (Miranda-Ribeiro, 1949) | Langeani *et al.* (2007) |
| *Trichomycterus coelhorum* Costa, Azevedo-Santos & Katz, 2023 | Costa *et al.* (2023) |
| *Trichomycterus funebris* Katz & Costa, 2021 | Costa, Katz (2021) |
| *Trichomycterus garbei* Costa, Azevedo-Santos & Katz, 2023 | Costa *et al.* (2023) |
| *Trichomycterus giarettai* Barbosa & Katz, 2016 | Barbosa, Katz (2016) |
| *Trichomycterus humboldti* Costa & Katz, 2021 | Costa, Katz (2021) |
| *Trichomycterus ingaiensis* Katz & Costa, 2021 | Costa, Katz (2021) |
| *Trichomycterus listruroides* Costa, Katz & Azevedo-Santos, 2023 | Costa *et al.* (2023) |
| *Trichomycterus maracaya* Bockmann & Sazima, 2004 | Langeani *et al.* (2007) |
| *Trichomycterus pauciradiatus* Alencar & Costa, 2006 | Langeani *et al.* (2007) |
| *Trichomycterus pirabitira* Barbosa & Azevedo-Santos, 2012 | Barbosa, Azevedo-Santos (2012) |
| *Trichomycterus piratymbara* Katz, Barbosa & Costa, 2013 | Katz *et al.* (2013) |
| *Trichomycterus reinhardti* (Eigenmann, 1917) | Thereza (2018) |
| *Trichomycterus sainthilairei* Katz & Costa, 2021 | Costa, Katz (2021) |
| *Trichomycterus saturatus* Costa, Katz & Azevedo-Santos, 2023 | Costa *et al.* (2023) |
| *Trichomycterus septemradiatus* Katz, Barbosa & Costa, 2013 | Katz *et al.* (2013) |
| *Trichomycterus uberabensis* Costa, Azevedo-Santos & Katz, 2023 | Costa *et al.* (2023) |
| **CYPRINODONTIFORMES** | |
| **Poeciliidae** | |
| *Cnesterodon hypselurus* Lucinda & Garavello, 2001 | Langeani *et al.* (2007) |
| *Phalloceros harpagos* Lucinda, 2008 | Ota *et al.* (2018) |
| *Phalloceros reisi* Lucinda, 2008 | Marceniuk *et al.* (2011) |
| *Phallotorynus fasciolatus* Henn, 1916 - CR(PEX) | Langeani *et al.* (2007) |
| *Phallotorynus jucundus* Ihering, 1930 | Langeani *et al.* (2007) |
| *Phallotorynus pankalos* Lucinda, Rosa & Reis, 2005 | Langeani *et al.* (2007) |
| *Phallotorynus victoriae* Oliveros, 1983 | Langeani *et al.* (2007) |

**TABLE 1** | (Continued)

| Taxon | Record in the upper rio Paraná / comments |
|---|---|
| **Rivulidae** | |
| *Melanorivulus amambaiensis* Volcan, Severo-Neto & Lanés, 2018 | Volcan *et al.* (2018) |
| *Melanorivulus apiamici* (Costa, 1989) | *Rivulus apiamici* in Langeani *et al.* (2007). Distribution follows Costa (2005) |
| *Melanorivulus egens* (Costa, 2005) | *Rivulus egens* in Langeani *et al.* (2007) |
| *Melanorivulus faucireticulatus* (Costa, 2008) | Costa (2008a) |
| *Melanorivulus formosensis* (Costa, 2008) | Costa (2008b) |
| *Melanorivulus giarettai* (Costa, 2008) | Costa (2008c) |
| *Melanorivulus illuminatus* (Costa, 2007) - VU | Costa (2007) |
| *Melanorivulus interruptus* Volcan, Severo-Neto & Lanés, 2018 | Volcan *et al.* (2018) |
| *Melanorivulus ivinhemensis* Volcan, Severo-Neto & Lanés, 2018 | Volcan *et al.* (2018) |
| *Melanorivulus larissae* Ywamoto, Nielsen & Oliveira, 2020 | Ywamoto *et al.* (2020) |
| *Melanorivulus leali* Costa, 2013 | Costa (2013) |
| *Melanorivulus linearis* Costa, 2018 | Costa (2018) |
| *Melanorivulus nigromarginatus* Costa, 2018 | Costa (2018) |
| *Melanorivulus nigropunctatus* Volcan, Klotzel & Lanés, 2017 | Volcan *et al.* (2017) |
| *Melanorivulus ofaie* Volcan, Klotzel & Lanés, 2017 | Volcan *et al.* (2017) |
| *Melanorivulus pictus* (Costa, 1989) | *Rivulus pictus* in Langeani *et al.* (2007). Distribution follows Costa (2005) |
| *Melanorivulus pinima* (Costa, 1989) - EN | *Rivulus pinima* in Langeani *et al.* (2007) |
| *Melanorivulus polychromus* Nielsen, Neves, Ywamoto & Passos, 2016 | Nilsen *et al.* (2016) |
| *Melanorivulus proximus* Costa, 2018 | Costa (2018) |
| *Melanorivulus rossoi* (Costa, 2005) | *Rivulus rossoi* in Langeani *et al.* (2007) |
| *Melanorivulus rutilicaudus* (Costa, 2005) - VU | *Rivulus rutilicaudus* in Langeani *et al.* (2007) |
| *Melanorivulus scalaris* (Costa, 2005) - EN | *Rivulus scalaris* in Langeani *et al.* (2007) |
| *Melanorivulus vittatus* (Costa, 1989) - EN | *Rivulus vittatus* in Langeani *et al.* (2007) |
| *Pituna brevirostrata* Costa, 2007 - CR | Costa (2007) |
| *Simpsonichthys boitonei* Carvalho, 1959 - CR | Langeani *et al.* (2007) |
| *Simpsonichthys margaritatus* Costa, 2012 | Costa (2012) |
| *Simpsonichthys nigromaculatus* Costa, 2007 - VU | Costa (2007) |
| *Simpsonichthys parallelus* Costa, 2002 - EN | Langeani *et al.* (2007) |
| *Simpsonichthys santanae* (Shibata & Garavello, 1992) - EN | Langeani *et al.* (2007) |
| **SYNBRANCHIFORMES** | |
| **Synbranchidae** | |
| *Synbranchus* aff. *marmoratus* Bloch, 1795 | Langeani *et al.* (2007) |
| *Synbranchus* aff. *madeirae* Rosen & Rumney, 1972 | Carvalho, Eduardo (2022) |
| **CICHLIFORMES** | |
| **Cichlidae** | |
| *Australoheros oblongus* (Castelnau, 1855) | *Australoheros facetus* (Jenysn, 1842) in Langeani *et al.* (2007) |
| *Cichlasoma dimerus* (Heckel, 1840) | Carvalho, Eduardo (2022) |
| *Cichlasoma paranaense* Kullander, 1983 | Langeani *et al.* (2007) |
| *Crenicichla haroldoi* Luengo & Britski, 1974 | Langeani *et al.* (2007) |
| *Crenicichla jaguarensis* Haseman, 1911 | Langeani *et al.* (2007) |
| *Crenicichla jupiaensis* Britski & Luengo, 1968 - EN | Langeani *et al.* (2007) |
| *Geophagus iporangensis* Haseman, 1911 | *Geophagus brasiliensis* (Quoy & Gaimard, 1824) in Langeani *et al.* (2007) |
| *Saxatilia britskii* (Kullander, 1982) | *Crenicichla britskii* in Langeani *et al.* (2007) |

**Distribution maps.** The compilation of native species in the upper rio Paraná served as basis for distribution maps of each of the species in the basin (Figs. 6–27), except those mentioned in "Taxonomic problems" (see Material and Methods). The plates that follow include maps in the taxonomic order presented in Tab. 1. The aim of species-specific maps is to demonstrate the general distribution patterns of each species in the basins, and is not an exhaustive map of collections, which would be a taxonomic purpose beyond the scope of the present paper.

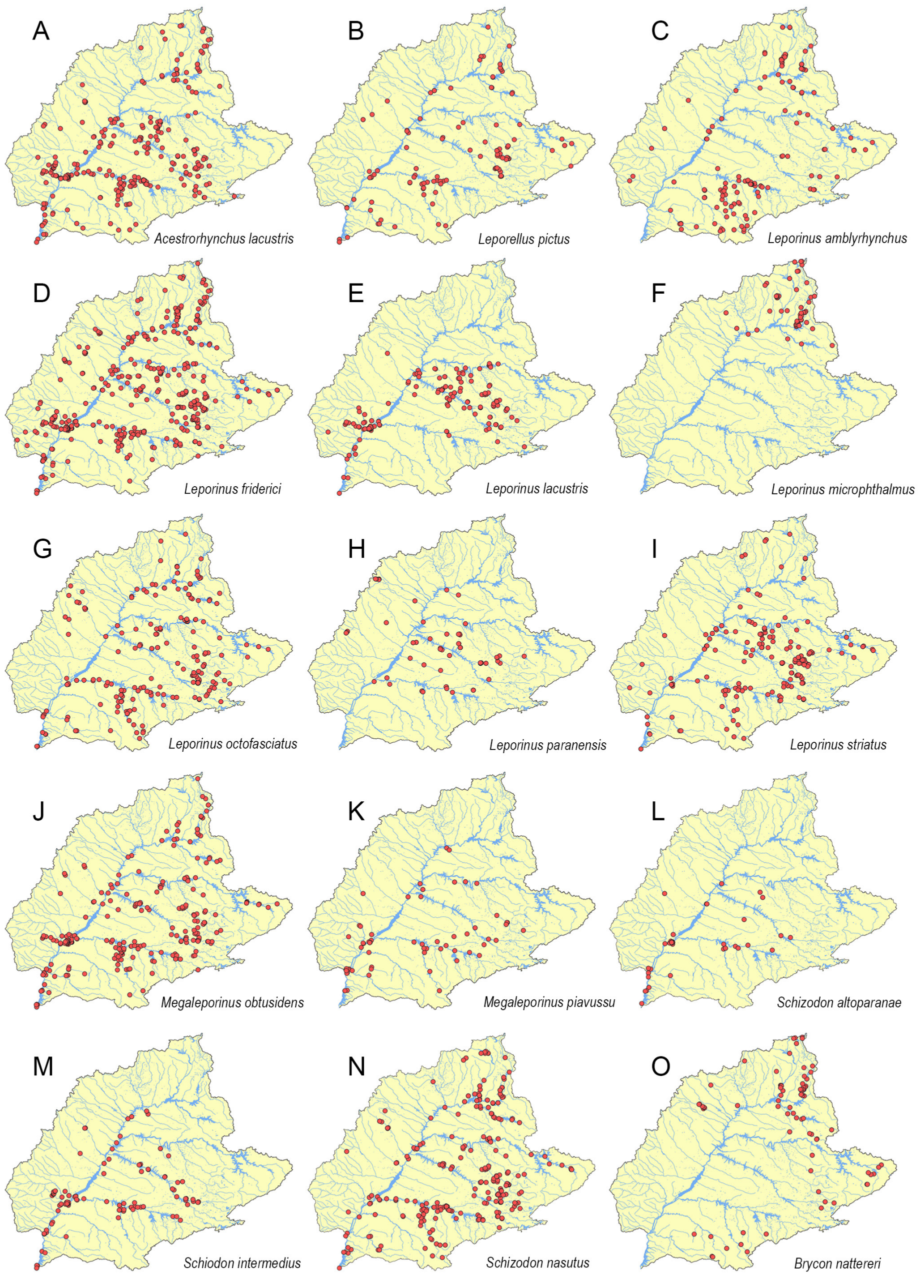



**FIGURE 6** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Acestrorhynchus lacustris*; **B.** *Leporellus pictus*; **C.** *Leporinus amblyrhynchus*; **D.** *Leporinus friderici*; **E.** *Leporinus lacustris*; **F.** *Leporinus microphthalmus*; **G.** *Leporinus octofasciatus*; **H.** *Leporinus paranensis*; **I.** *Leporinus striatus*; **J.** *Megaleporinus obtusidens*; **K.** *Megaleporinus piavussu*; **L.** *Schizodon altoparanae*; **M.** *Schizodon intermedius*; **N.** *Schizodon nasutus*; **O.** *Brycon nattereri*.

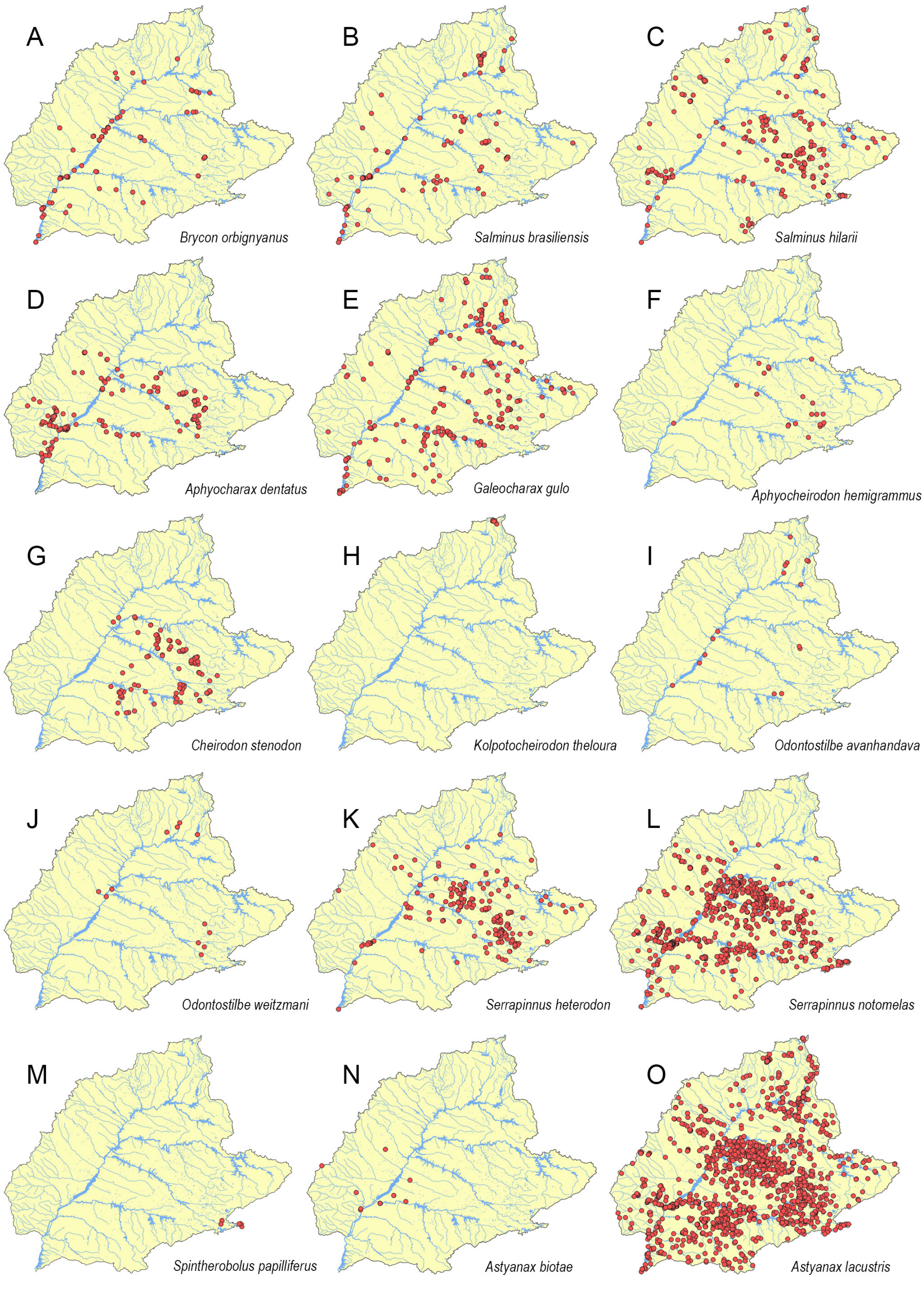



**FIGURE 7** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Brycon orbignyanus*; **B.** *Salminus brasiliensis*; **C.** *Salminus hilarii*; **D.** *Aphyocharax dentatus*; **E.** *Galeocharax gulo*; **F.** *Aphyocheirodon hemigrammus*; **G.** *Cheirodon stenodon*; **H.** *Kolpotocheirodon theloura*; **I.** *Odontostilbe avanhandava*; **J.** *Odontostilbe weitzmani*; **K.** *Serrapinnus heterodon*; **L.** *Serrapinnus notomelas*; **M.** *Spintherobolus papilliferus*; **N.** *Astyanax biotae*; **O.** *Astyanax lacustris*.

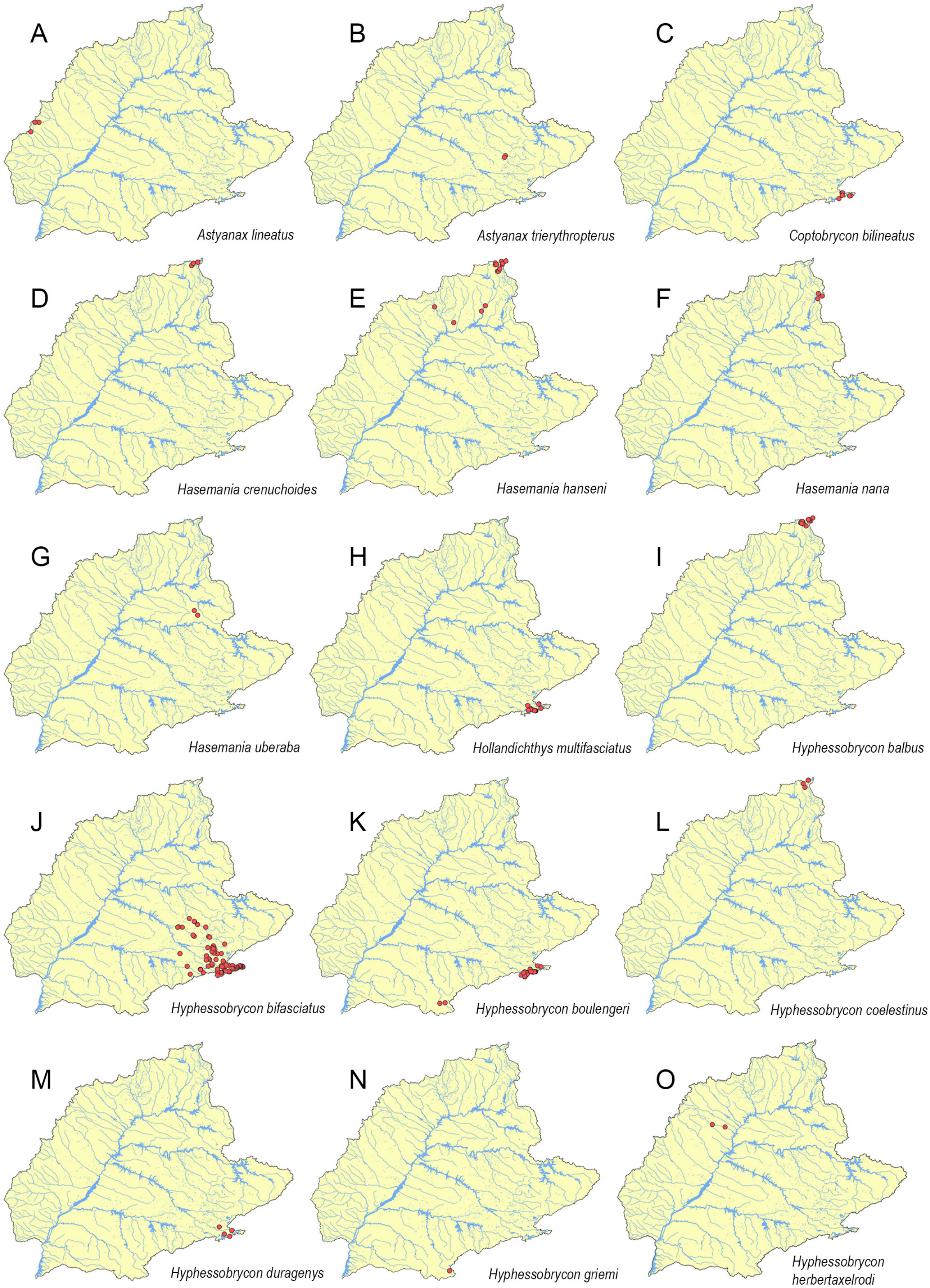



**FIGURE 8 |** Distribution maps of native fishes occurring in the upper Paraná. **A.** *Astyanax lineatus*; **B.** *Astyanax trierythropterus*; **C.** *Coptobrycon bilineatus*; **D.** *Hasemania crenuchoides*; **E.** *Hasemania hanseni*; **F.** *Hasemania nana*; **G.** *Hasemania uberaba*; **H.** *Hollandichthys multifasciatus*; **I.** *Hyphessobrycon balbus*; **J.** *Hyphessobrycon bifasciatus*; **K.** *Hyphessobrycon boulengeri*; **L.** *Hyphessobrycon coelestinus*; **M.** *Hyphessobrycon duragenys*; **N.** *Hyphessobrycon griemi*; **O.** *Hyphessobrycon herbertaxelrodi*.

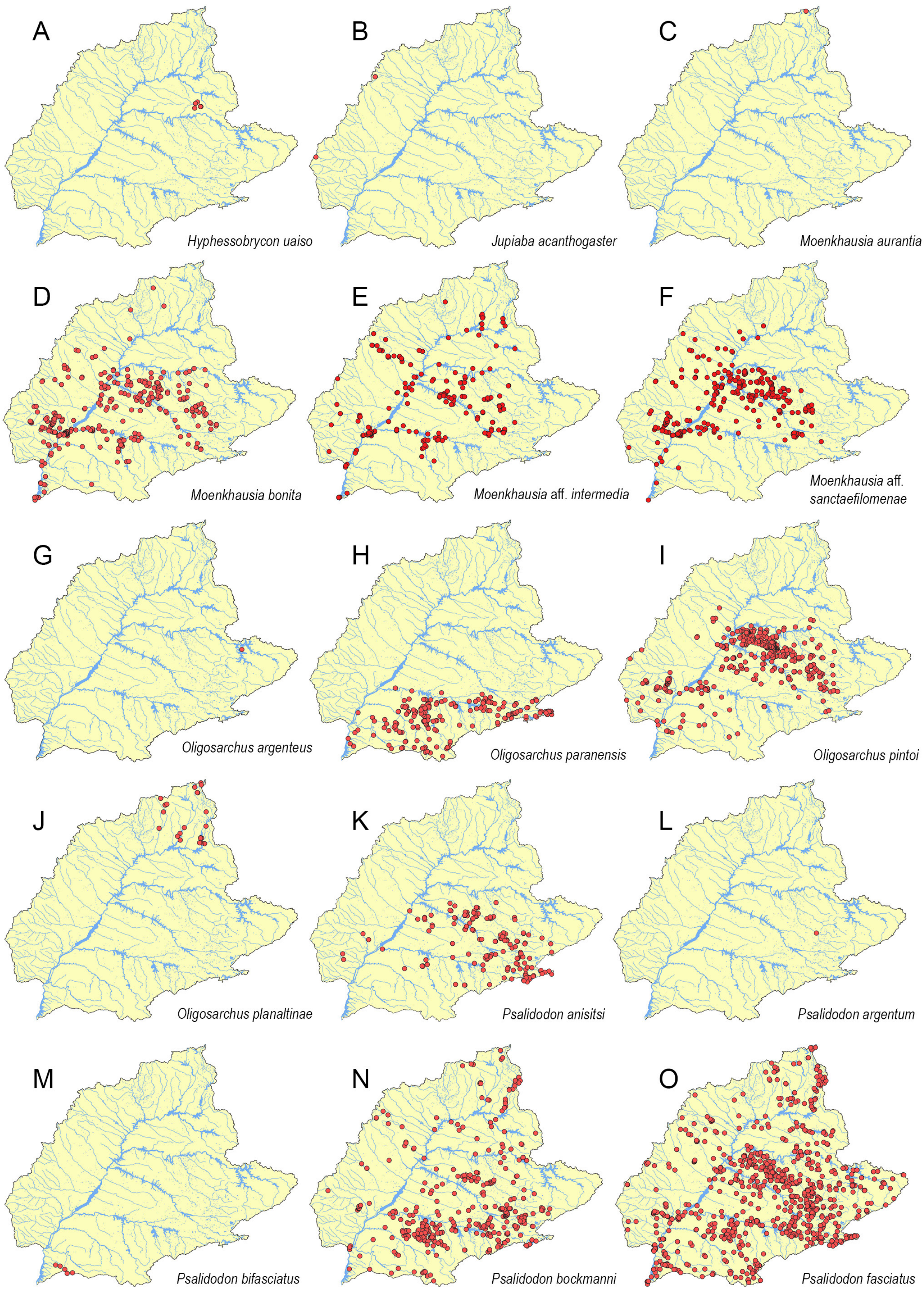



**FIGURE 9** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Hyphessobrycon uaiso*; **B.** *Jupiaba acanthogaster*; **C.** *Moenkhausia aurantia*; **D.** *Moenkhausia bonita*; **E.** *Moenkhausia* aff. *intermedia*; **F.** *Moenkhausia* aff. *sanctafilomenae*; **G.** *Oligosarcus argenteus*; **H.** *Oligosarcus paranensis*; **I.** *Oligosarcus pintoi*; **J.** *Oligosarcus planaltinae*; **K.** *Psalidodon anisitsi*; **L.** *Psalidodon argentum*; **M.** *Psalidodon bifasciatus*; **N.** *Psalidodon bockmanni*; **O.** *Psalidodon fasciatus*.

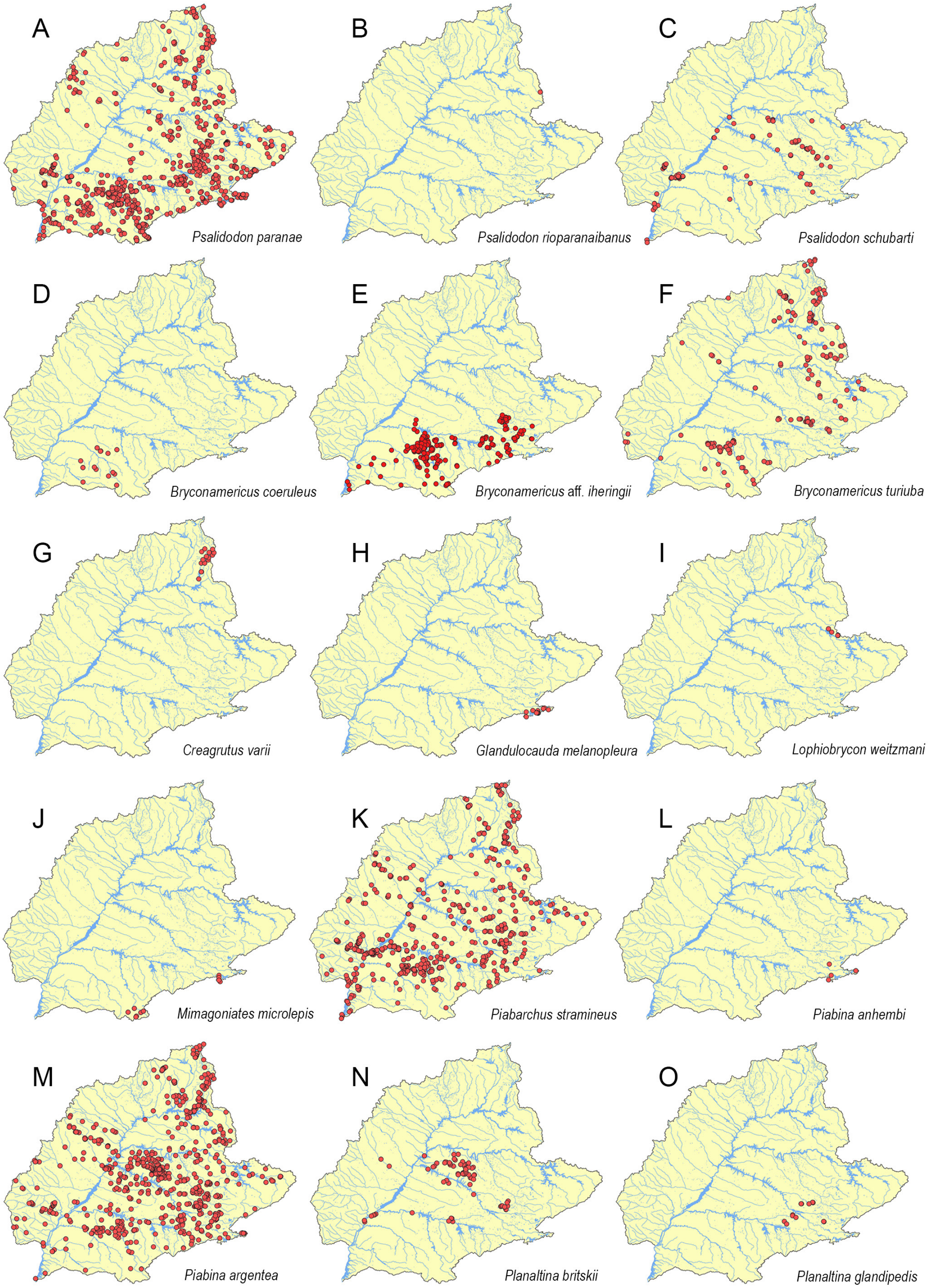



**FIGURE 10|** Distribution maps of native fishes occurring in the upper Paraná. **A.** *Psalidodon paranae*; **B.** *Psalidodon rioparanaibanus*; **C.** *Psalidodon schubarti*; **D.** *Bryconamericus coeruleus*; **E.** *Bryconamericus* aff. *iheringii*; **F.** *Bryconamericus turiuba*; **G.** *Creagrutus varii*; **H.** *Grandulocauda melanopleura*; **I.** *Lophiobrycon weitzmani*; **J.** *Mimagoniates microlepis*; **K.** *Piabarchus stramineus*; **L.** *Piabina anhembi*; **M.** *Piabina argentea*; **N.** *Planaltina britskii*; **O.** *Planaltina glandipedis*.

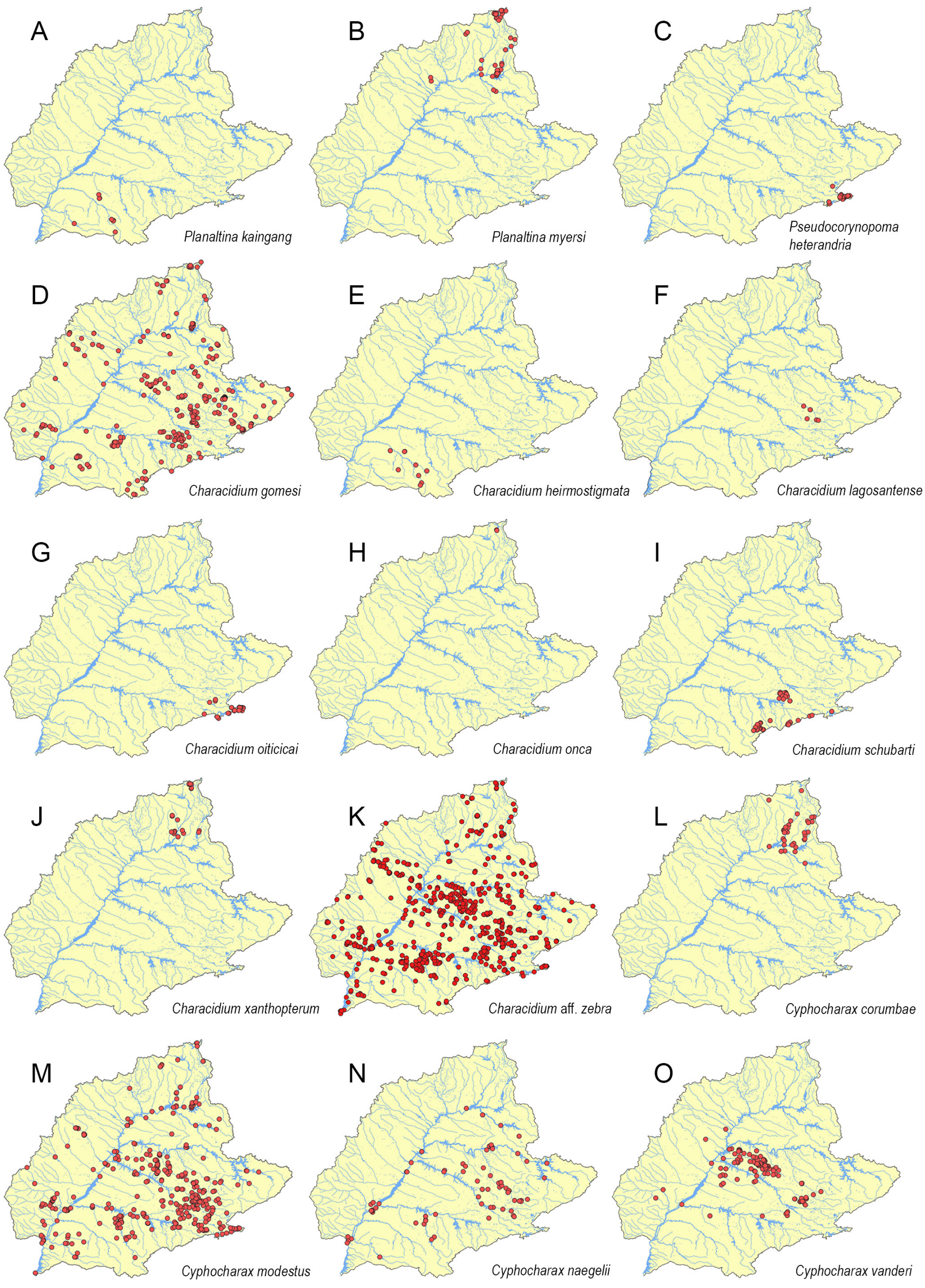



**FIGURE 11** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Planaltina kaingang*; **B.** *Planaltina myersi*; **C.** *Pseudocorynopoma heterandria*; **D.** *Characidium gomesi*; **E.** *Characidium heirmostigmata*; **F.** *Characidium lagosantense*; **G.** *Characidium oiticicai*; **H.** *Characidium onca*; **I.** *Characidium schubarti*; **J.** *Characidium xanthopterum*; **K.** *Characidium* aff. *zebra*; **L.** *Cyphocharax corumbae*; **M.** *Cyphocharax modestus*; **N.** *Cyphocharax naegelii*; **O.** *Cyphocharax vanderi*.

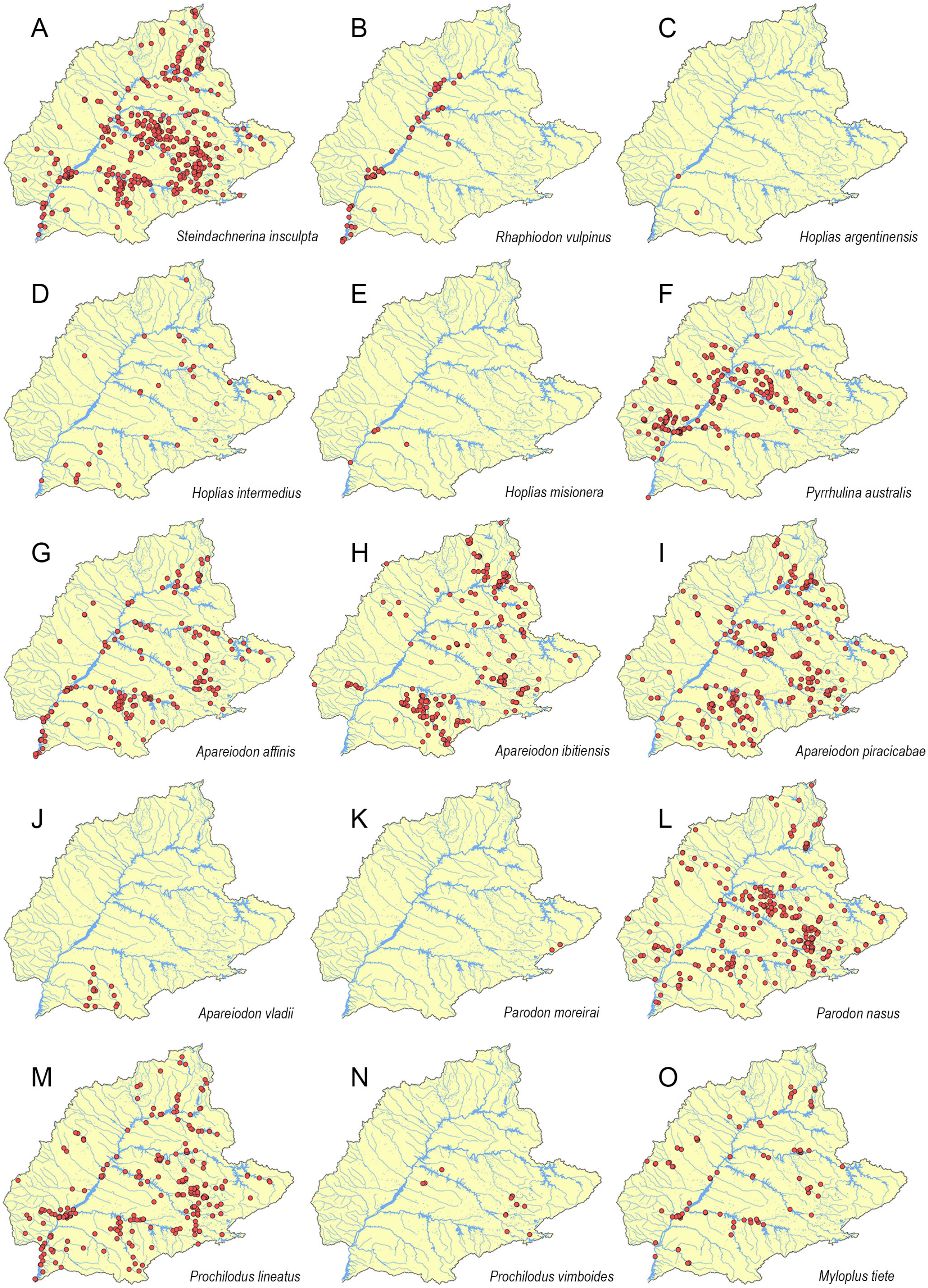



**FIGURE 12** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Steindachnerina insculpta*; **B.** *Rhaphiodon vulpinus*; **C.** *Hoplias argentinensis*; **D.** *Hoplias intermedius*; **E.** *Hoplias misionera*; **F.** *Pyrrhulina australis*; **G.** *Apareiodon affinis*; **H.** *Apareiodon ibitiensis*; **I.** *Apareiodon piracicabae*; **J.** *Apareiodon vladii*; **K.** *Parodon moreirai*; **L.** *Parodon nasus*; **M.** *Prochilodus lineatus*; **N.** *Prochilodus vimboides*; **O.** *Myloplus tiete*.

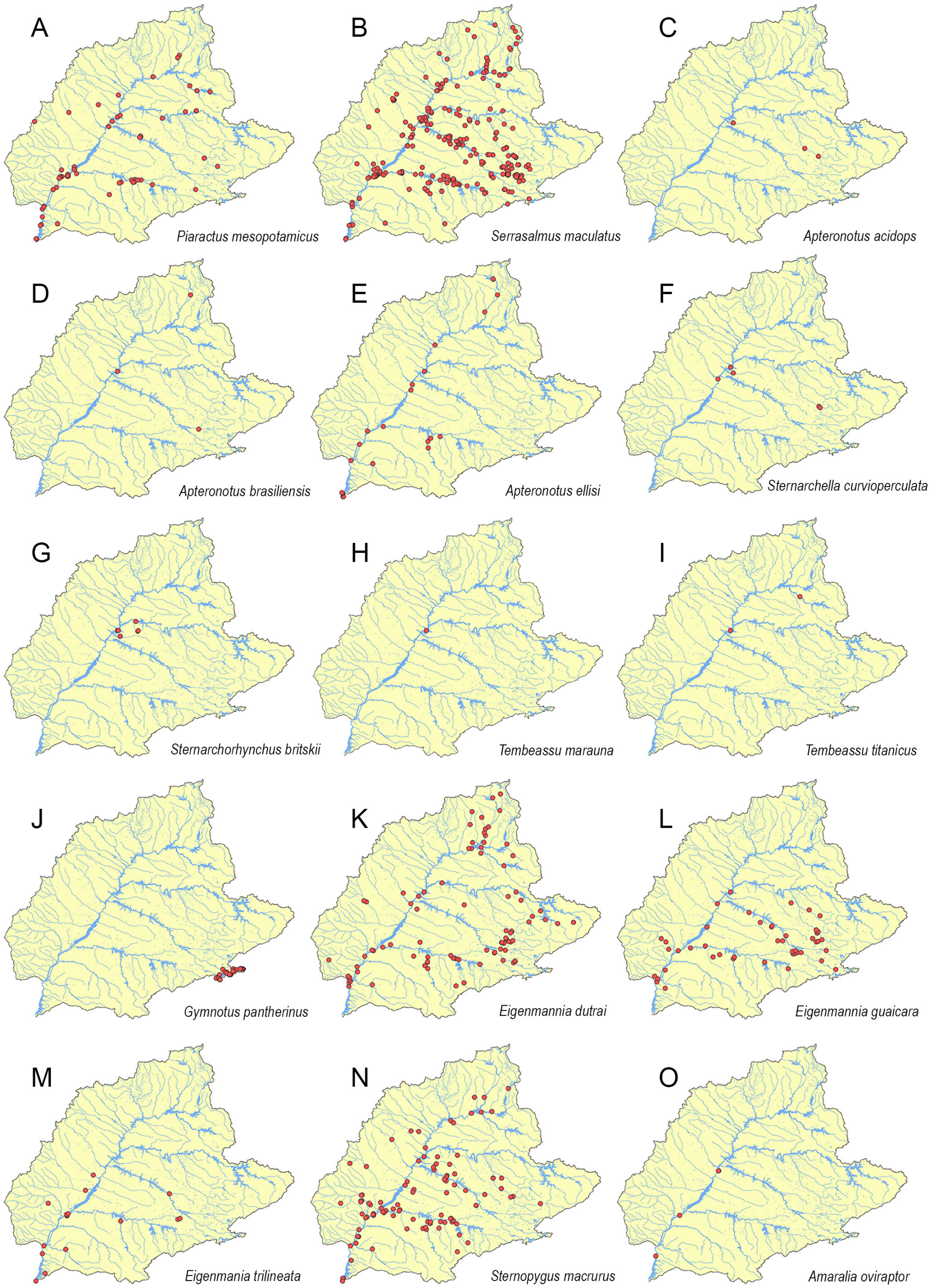



**FIGURE 13** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Piaractus mesopotamicus*; **B.** *Serrasalmus maculatus*; **C.** *Apteronotus acidops*; **D.** *Apteronotus brasiliensis*; **E.** *Apteronotus ellisi*; **F.** *Sternarchella curvioperculata*; **G.** *Sternarchorhynchus britskii*; **H.** *Tembeassu marauna*; **I.** *Tembeassu titanicus*; **J.** *Gymnotus pantherinus*; **K.** *Eigenmannia dutrai*; **L.** *Eigenmannia guairaca*; **M.** *Eigenmannia trilineata*; **N.** *Sternopygus macrurus*; **O.** *Amaralia oviraptor*.

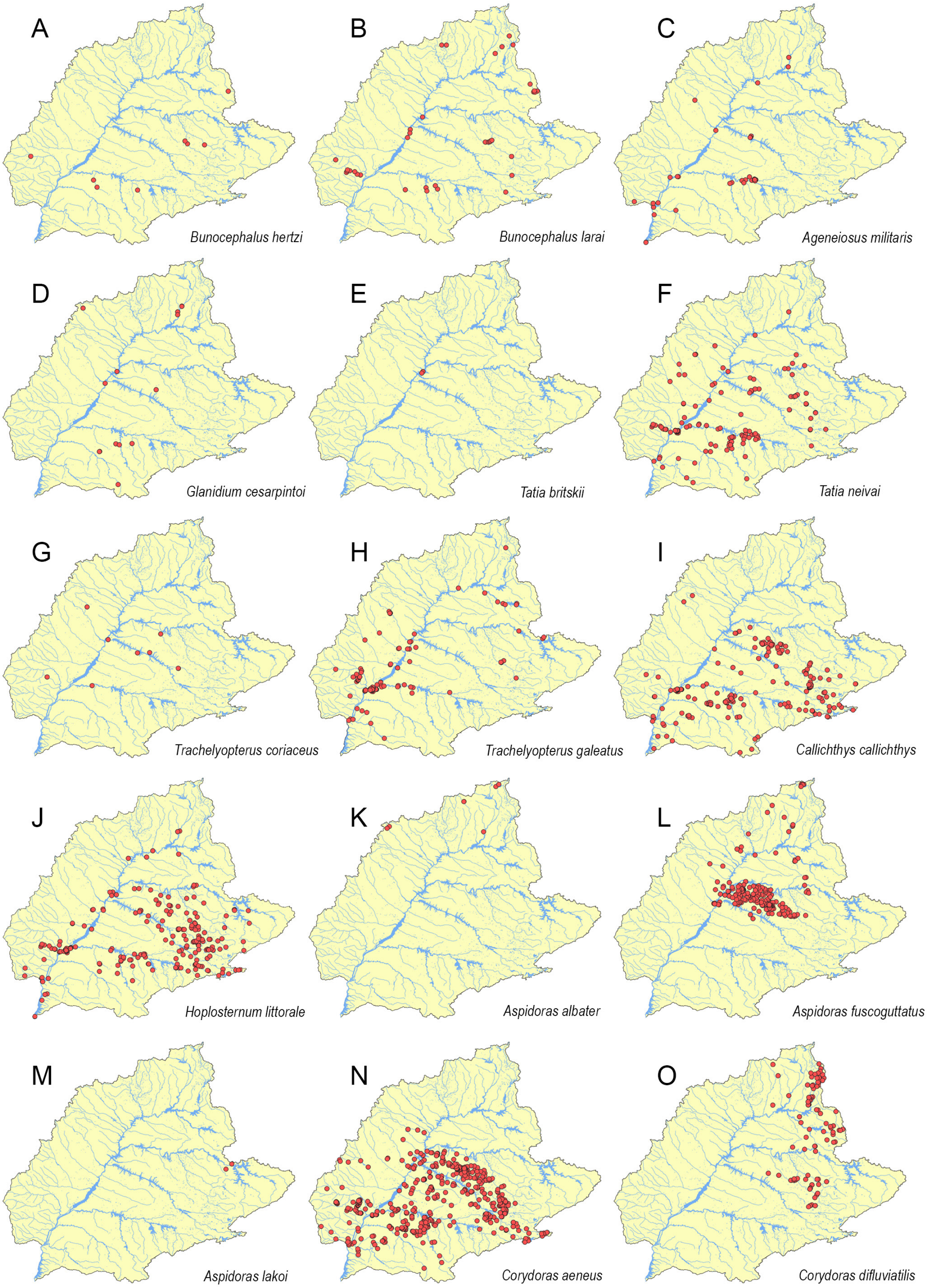



**FIGURE 14** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Bunocephalus hertzi*; **B.** *Bunocephalus larai*; **C.** *Ageneiosus militaris*; **D.** *Glanidium cesarpintoi*; **E.** *Tatia britskii*; **F.** *Tatia neivai*; **G.** *Trachelyopterus coriaceus*; **H.** *Trachelyopterus galeatus*; **I.** *Callichthys callichthys*; **J.** *Hoplosternum littorale*; **K.** *Aspidoras albater*; **L.** *Aspidoras fuscoguttatus*; **M.** *Aspidoras lakoi*; **N.** *Corydoras aeneus*; **O.** *Corydoras difluviatilis*.

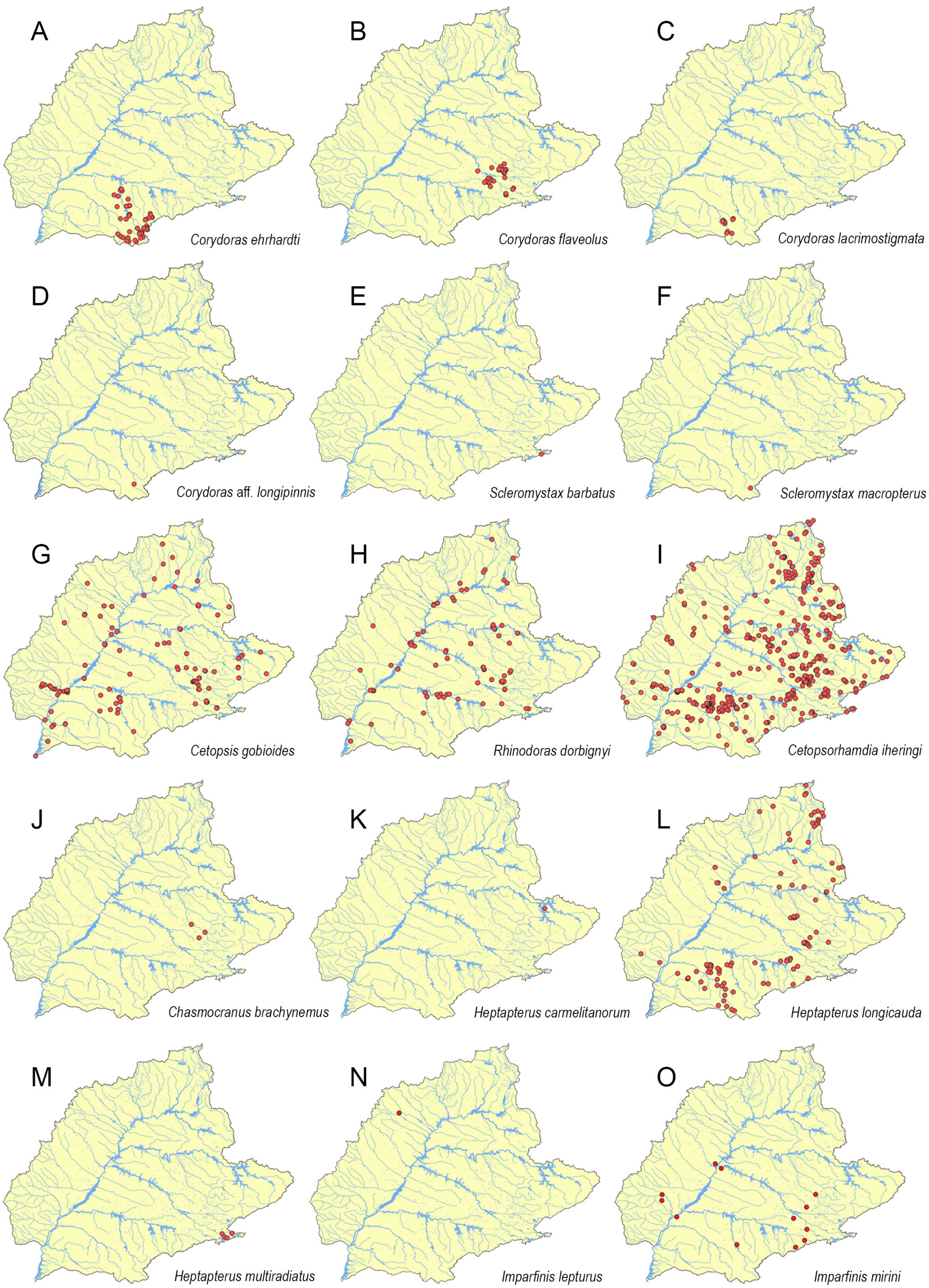



**FIGURE 15 |** Distribution maps of native fishes occurring in the upper Paraná. **A.** *Corydoras ehrhardti*; **B.** *Corydoras flaveolus*; **C.** *Corydoras lacrimostigmata*; **D.** *Corydoras* aff. *longipinnis*; **E.** *Scleromystax barbatus*; **F.** *Scleromystax macropterus*; **G.** *Cetopsis gobioides*; **H.** *Rhinodoras dorbignyi*; **I.** *Cetopsorhamdia iheringi*; **J.** *Chasmocranus brachynemus*; **K.** *Heptapterus carmelitanorum*; **L.** *Heptapterus longicauda*; **M.** *Heptapterus multiradiatus*; **N.** *Imparfinis lepturus*; **O.** *Imparfinis mirini*.

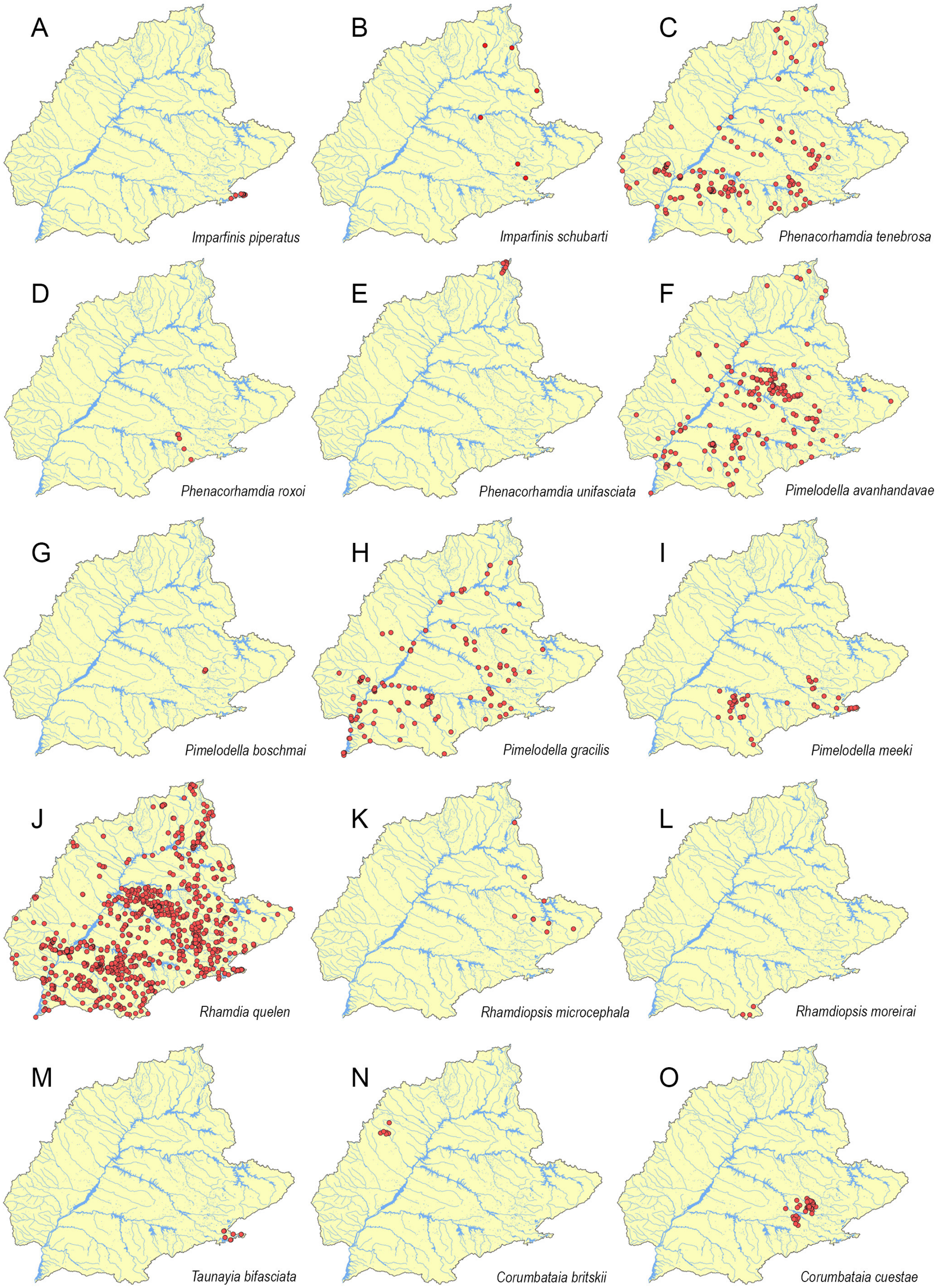



**FIGURE 16** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Imparfinis piperatus*; **B.** *Imparfinis schubarti*; **C.** *Phenacorhamdia tenebrosa*; **D.** *Phenacorhamdia roxoi*; **E.** *Phenacorhamdia unifasciata*; **F.** *Pimelodella avanhandavae*; **G.** *Pimelodella boschmai*; **H.** *Pimelodella gracilis*; **I.** *Pimelodella meeki*; **J.** *Rhamdia quelen*; **K.** *Rhamdiopsis microcephala*; **L.** *Rhamdiopsis moreirai*; **M.** *Taunayia bifasciata*; **N.** *Corumbataia britskii*; **O.** *Corumbataia cuestae*.

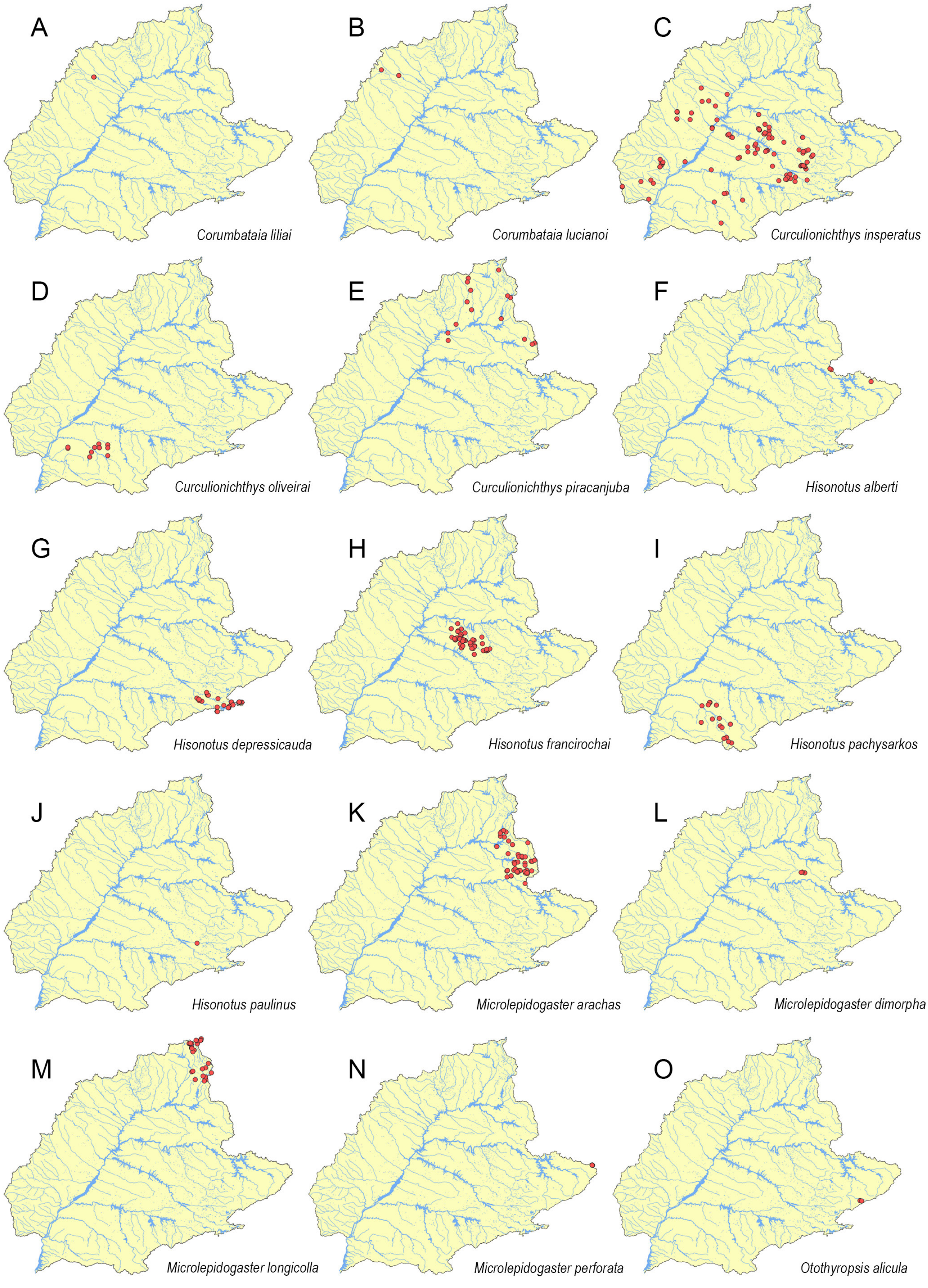



**FIGURE 17** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Corumbataia liliai*; **B.** *Corumbataia lucianoi*; **C.** *Curculionichthys insperatus*; **D.** *Curculionichthys oliveirai*; **E.** *Curculionichthys piracanjuba*; **F.** *Hisonotus alberti*; **G.** *Hisonotus depressicauda*; **H.** *Hisonotus francirochai*; **I.** *Hisonotus pachysarkos*; **J.** *Hisonotus paulinus*; **K.** *Microlepidogaster arachas*; **L.** *Microlepidogaster dimorpha*; **M.** *Microlepidogaster longicolla*; **N.** *Microlepidogaster perforata*; **O.** *Otothyropsis alicula*.

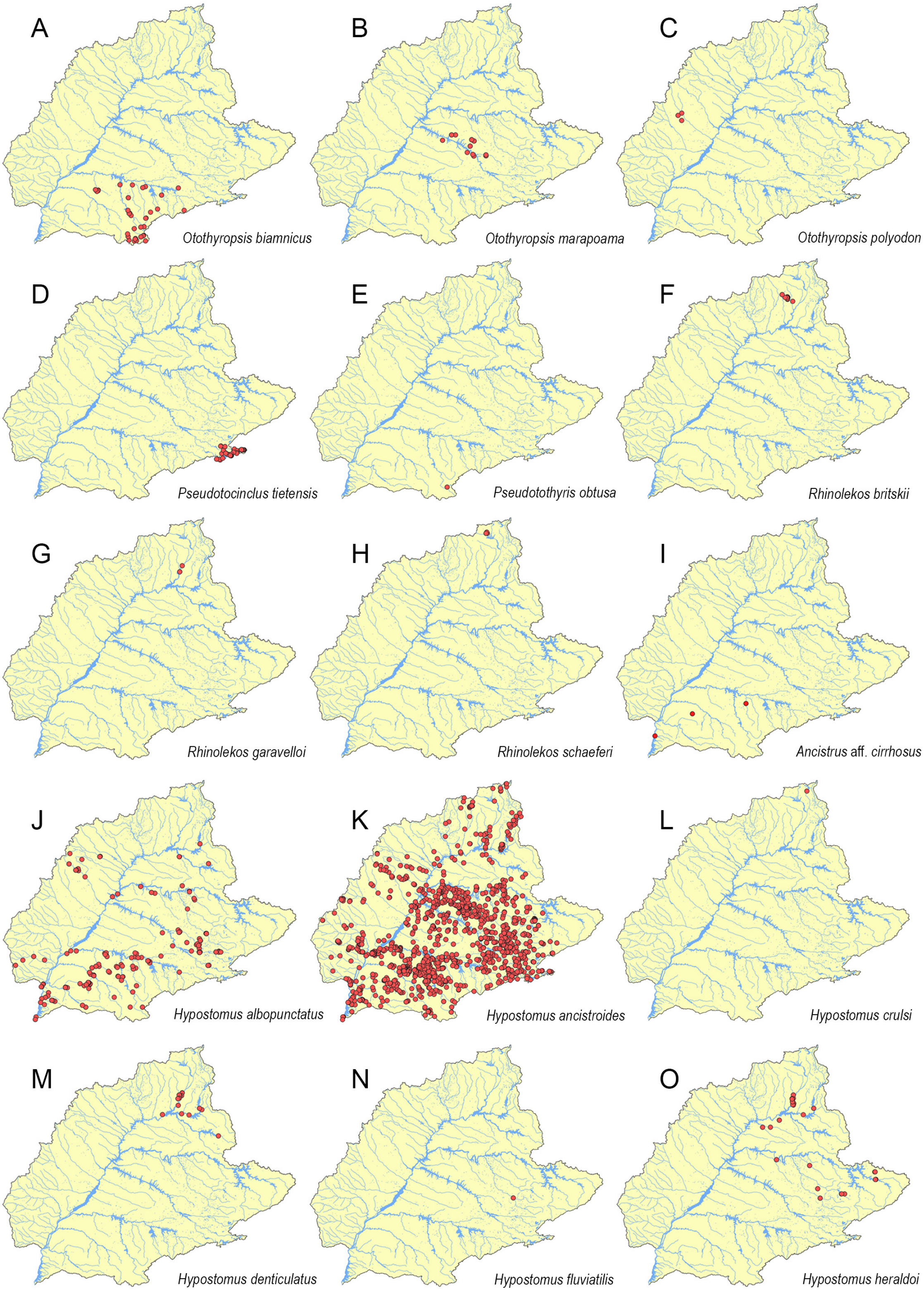



**FIGURE 18** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Otothyropsis biamnicus*; **B.** *Otothyropsis marapoama*; **C.** *Otothyropsis polyodon*; **D.** *Pseudotocinclus tietensis*; **E.** *Pseudotothyris obtusa*; **F.** *Rhinolekos britskii*; **G.** *Rhinolekos garavelloi*; **H.** *Rhinolekos schaeferi*; **I.** *Ancistrus* aff. *cirrhosus*; **J.** *Hypostomus albopunctatus*; **K.** *Hypostomus ancistroides*; **L.** *Hypostomus crulsi*; **M.** *Hypostomus denticulatus*; **N.** *Hypostomus fluviatilis*; **O.** *Hypostomus heraldoi*.

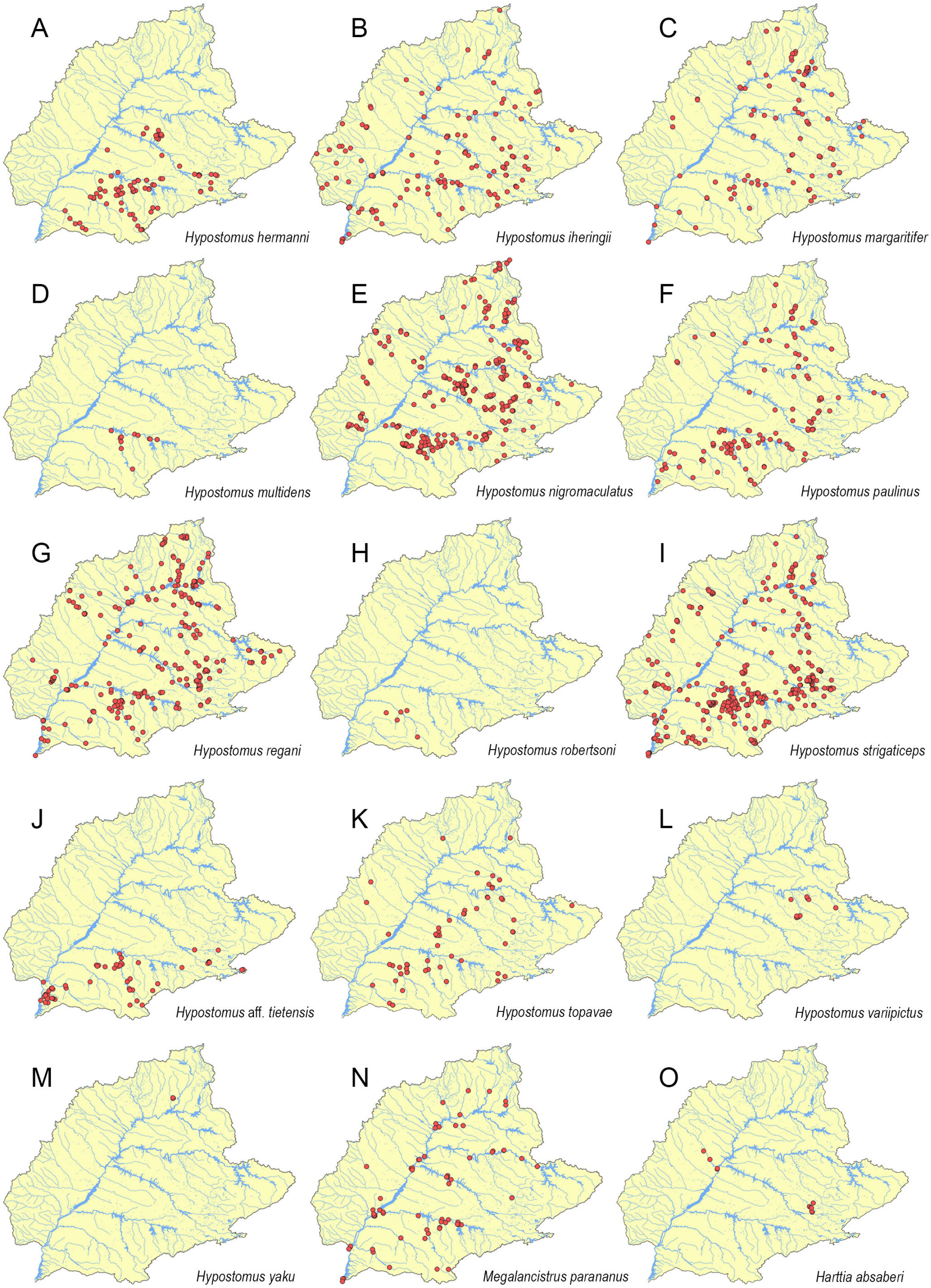



**FIGURE 19** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Hypostomus hermanni*; **B.** *Hypostomus iheringii*; **C.** *Hypostomus margaritifer*; **D.** *Hypostomus multidens*; **E.** *Hypostomus nigromaculatus*; **F.** *Hypostomus paulinus*; **G.** *Hypostomus regani*; **H.** *Hypostomus robertsoni*; **I.** *Hypostomus strigaticeps*; **J.** *Hypostomus* aff. *tietensis*; **K.** *Hypostomus topavae*; **L.** *Hypostomus variipictus*; **M.** *Hypostomus yaku*; **N.** *Megalancistrus parananus*; **O.** *Harttia absaberi*.

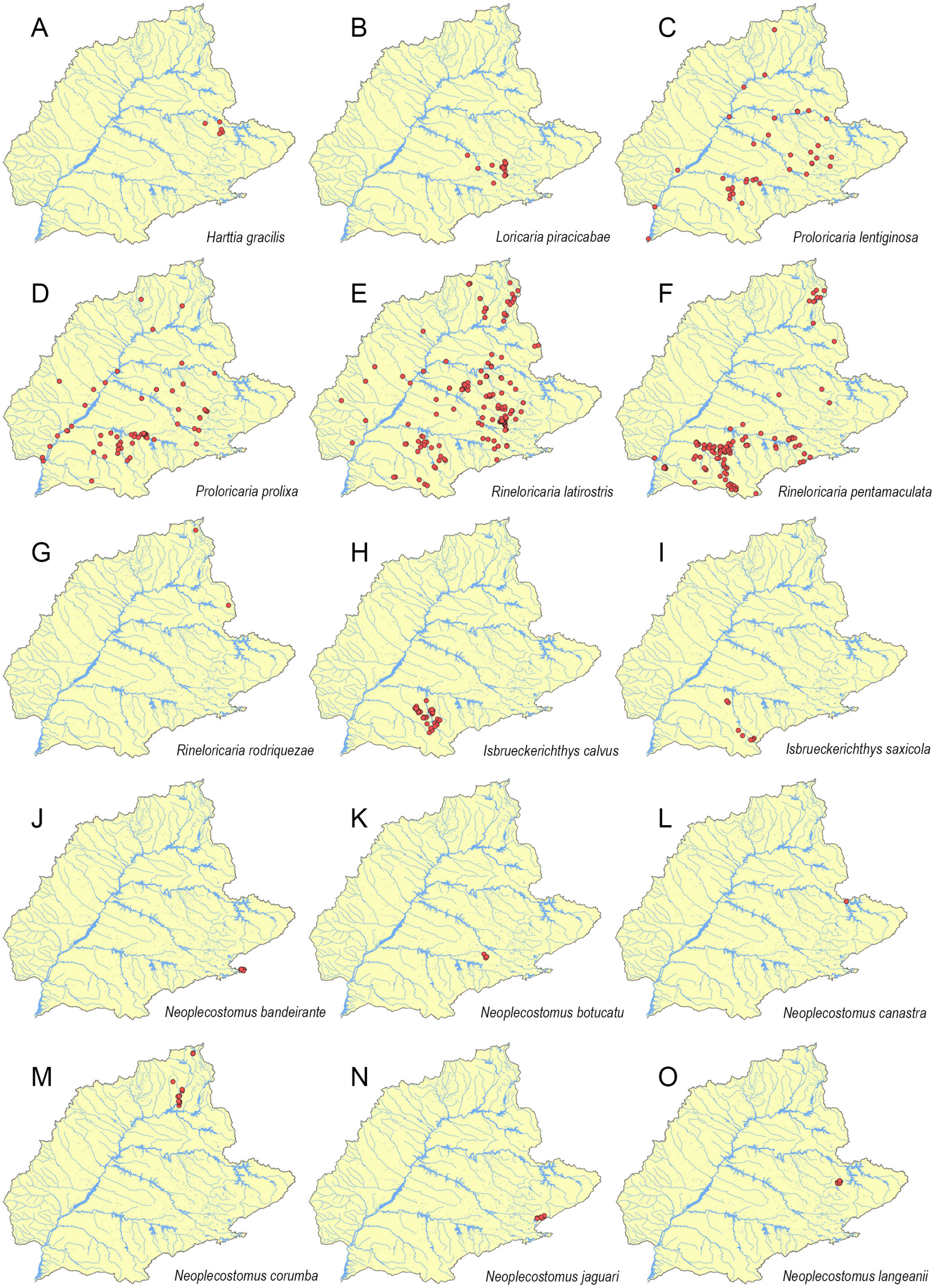



**FIGURE 20** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Harttia gracilis*; **B.** *Loricaria piracicabae*; **C.** *Proloricaria lentiginosa*; **D.** *Proloricaria prolixa*; **E.** *Rineloricaria latirostris*; **F.** *Rineloricaria pentamaculata*; **G.** *Rineloricaria rodriquezae*; **H.** *Isbrueckerichthys calvus*; **I.** *Isbrueckerichthys saxicola*; **J.** *Neoplecostomus bandeirante*; **K.** *Neoplecostomus botucatu*; **L.** *Neoplecostomus canastra*; **M.** *Neoplecostomus corumba*; **N.** *Neoplecostomus jaguari*; **O.** *Neoplecostomus langeanii*.

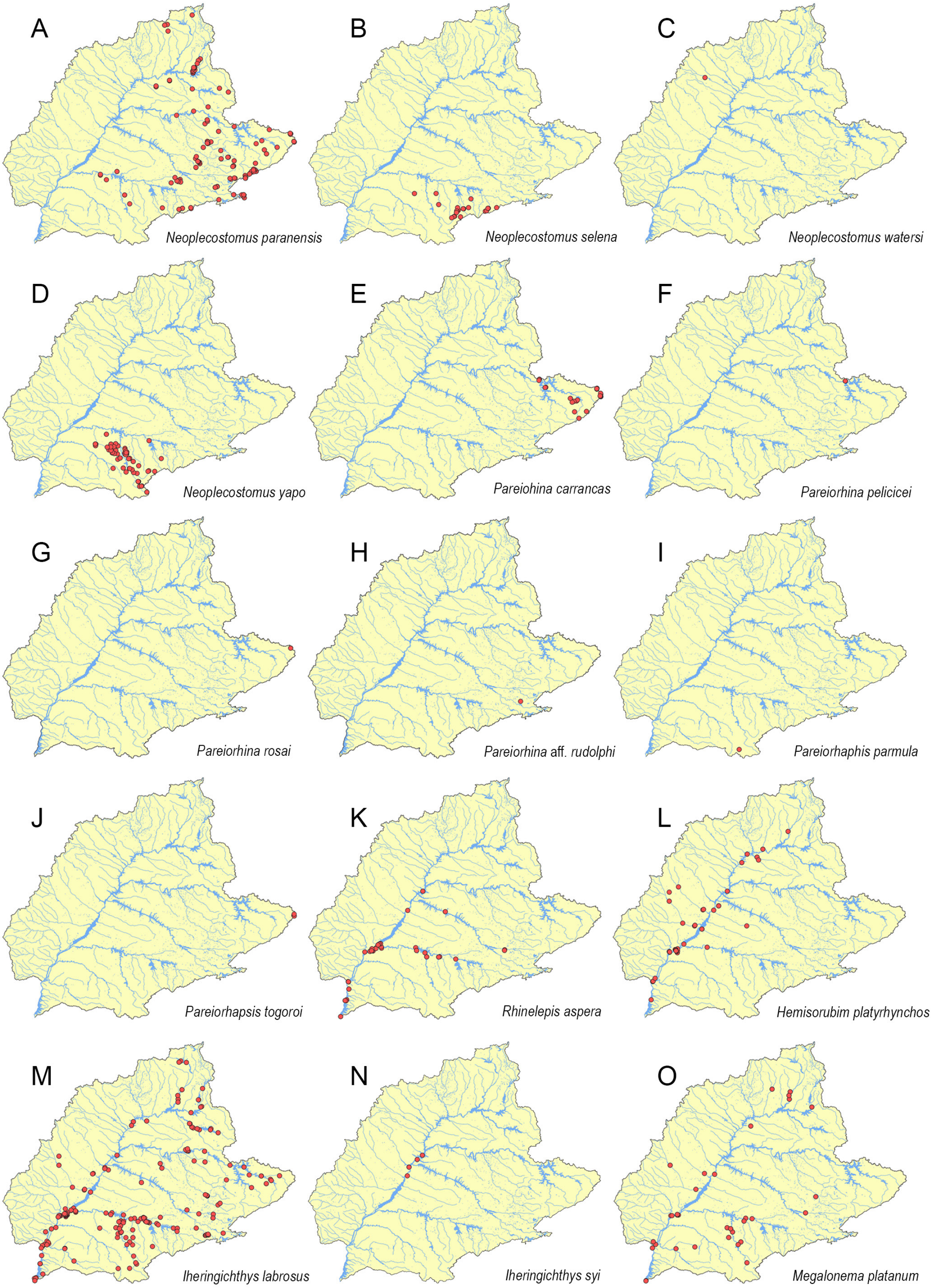



**FIGURE 21** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Neoplecostomus paranensis*; **B.** *Neoplecostomus selena*; **C.** *Neoplecostomus watersi*; **D.** *Neoplecostomus yapo*; **E.** *Pareiorhina carrancas*; **F.** *Pareiorhina pelicicei*; **G.** *Pareiorhina rosai*; **H.** *Pareiorhina* aff. *rudolphi*; **I.** *Pareiorhaphis parmula*; **J.** *Pareiorhaphis togoroi*; **K.** *Rhinelepis aspera*; **L.** *Hemisorubim platyrhynchos*; **M.** *Iheringichthys labrosus*; **N.** *Iheringichthys syi*; **O.** *Megalonema platanum*.

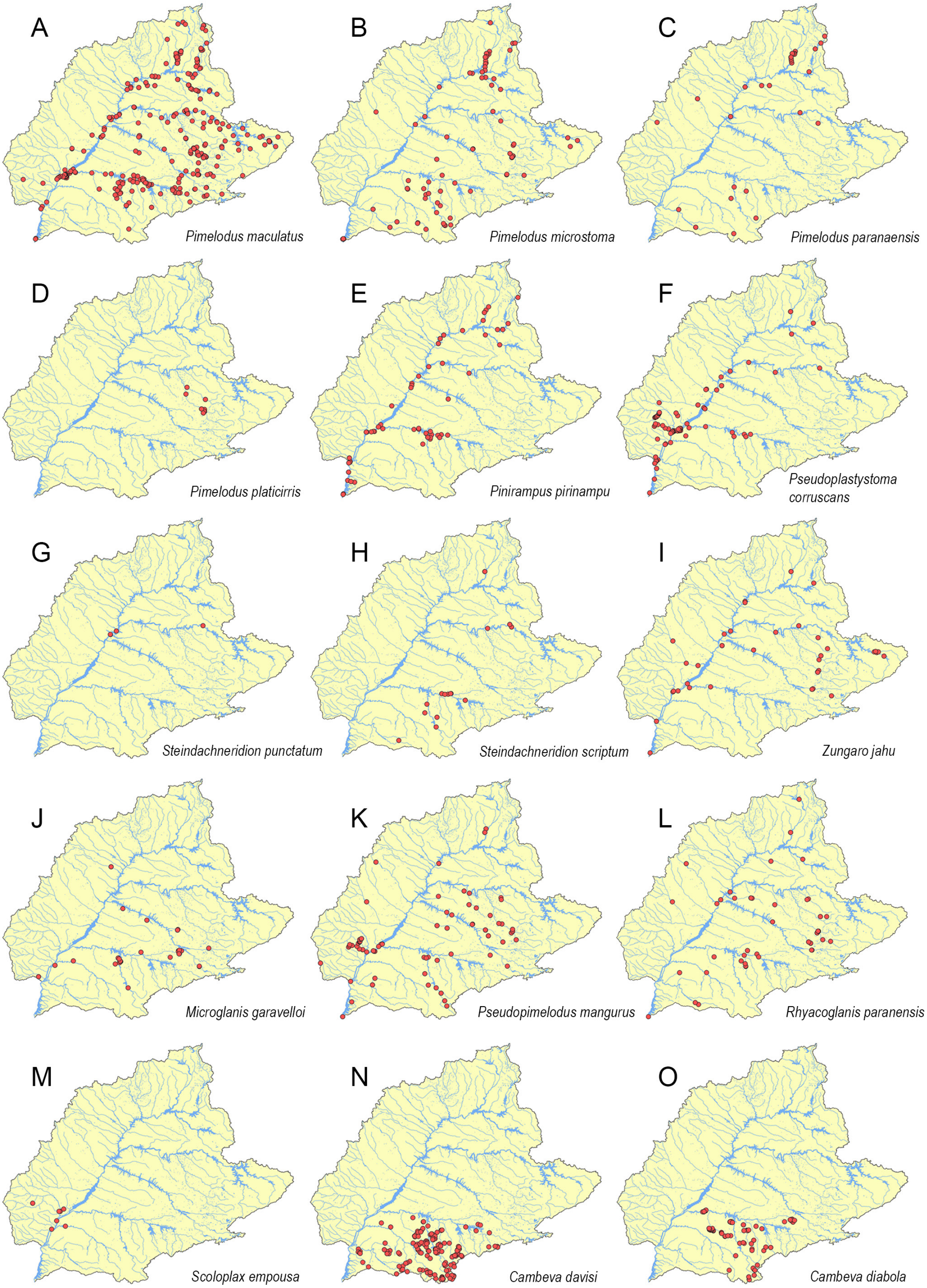



**FIGURE 22 |** Distribution maps of native fishes occurring in the upper Paraná. **A.** *Pimelodus maculatus*; **B.** *Pimelodus microstoma*; **C.** *Pimelodus paranaensis*; **D.** *Pimelodus platicirris*; **E.** *Pinirampus pirinampu*; **F.** *Pseudoplatystoma corruscans*; **G.** *Steindachneridion punctatum*; **H.** *Steindachneridion scriptum*; **I.** *Zungaro jahu*; **J.** *Microglanis garavelloi*; **K.** *Pseudopimelodus mangurus*; **L.** *Rhyacoglanis paranensis*; **M.** *Scoloplax empousa*; **N.** *Cambeva davisi*; **O.** *Cambeva diabola*.

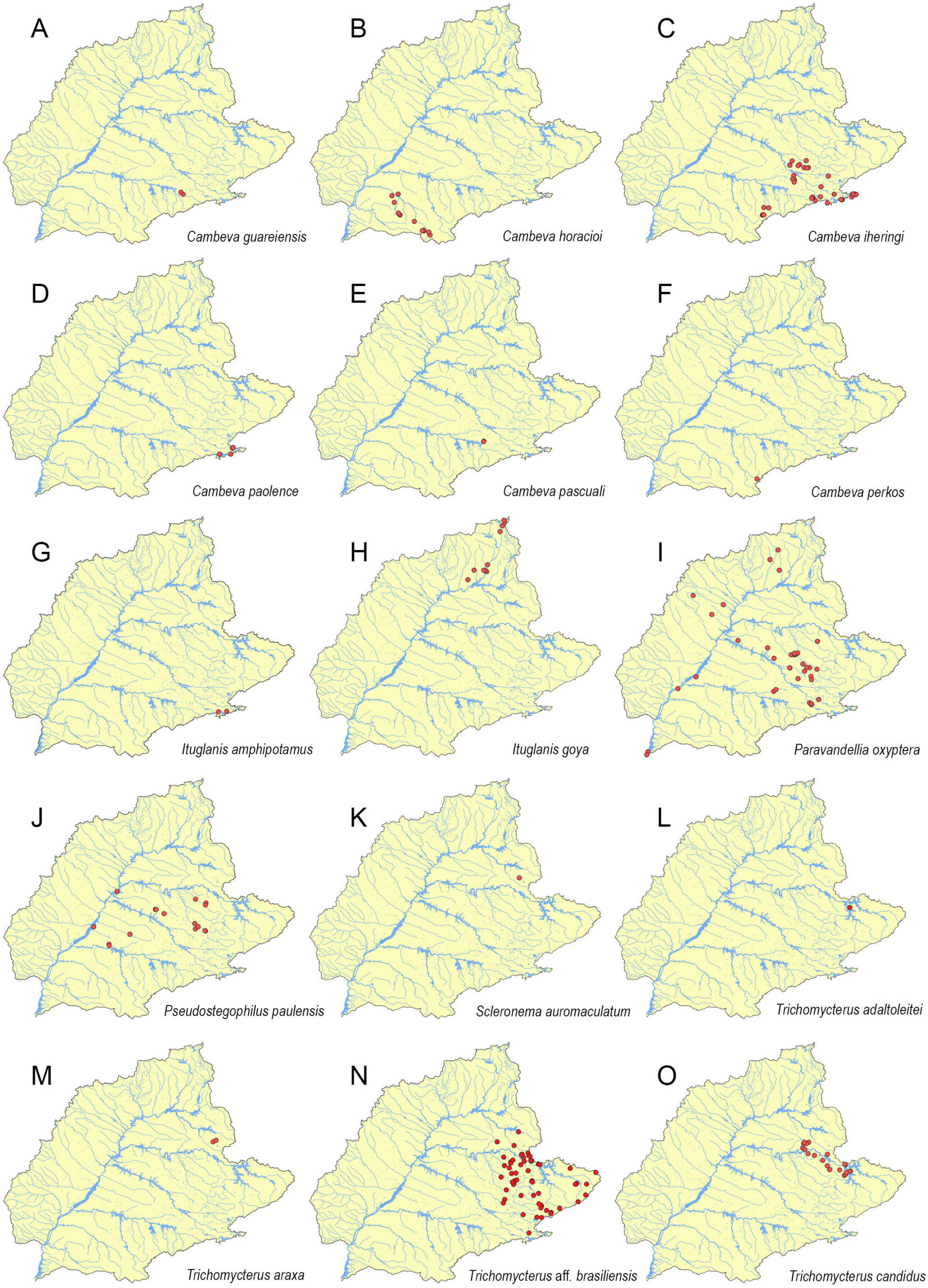



**FIGURE 23** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Cambeva guareiensis*; **B.** *Cambeva horacioi*; **C.** *Cambeva iheringi*; **D.** *Cambeva paolence*; **E.** *Cambeva pascuali*; **F.** *Cambeva perkos*; **G.** *Ituglanis amphipotamus*; **H.** *Ituglanis goya*; **I.** *Paravandellia oxyptera*; **J.** *Pseudostegophilus paulensis*; **K.** *Scleronema auromaculatum*; **L.** *Trichomycterus adaltoleitei*; **M.** *Trichomycterus araxa*; **N.** *Trichomycterus* aff. *brasiliensis*; **O.** *Trichomycterus candidus*.

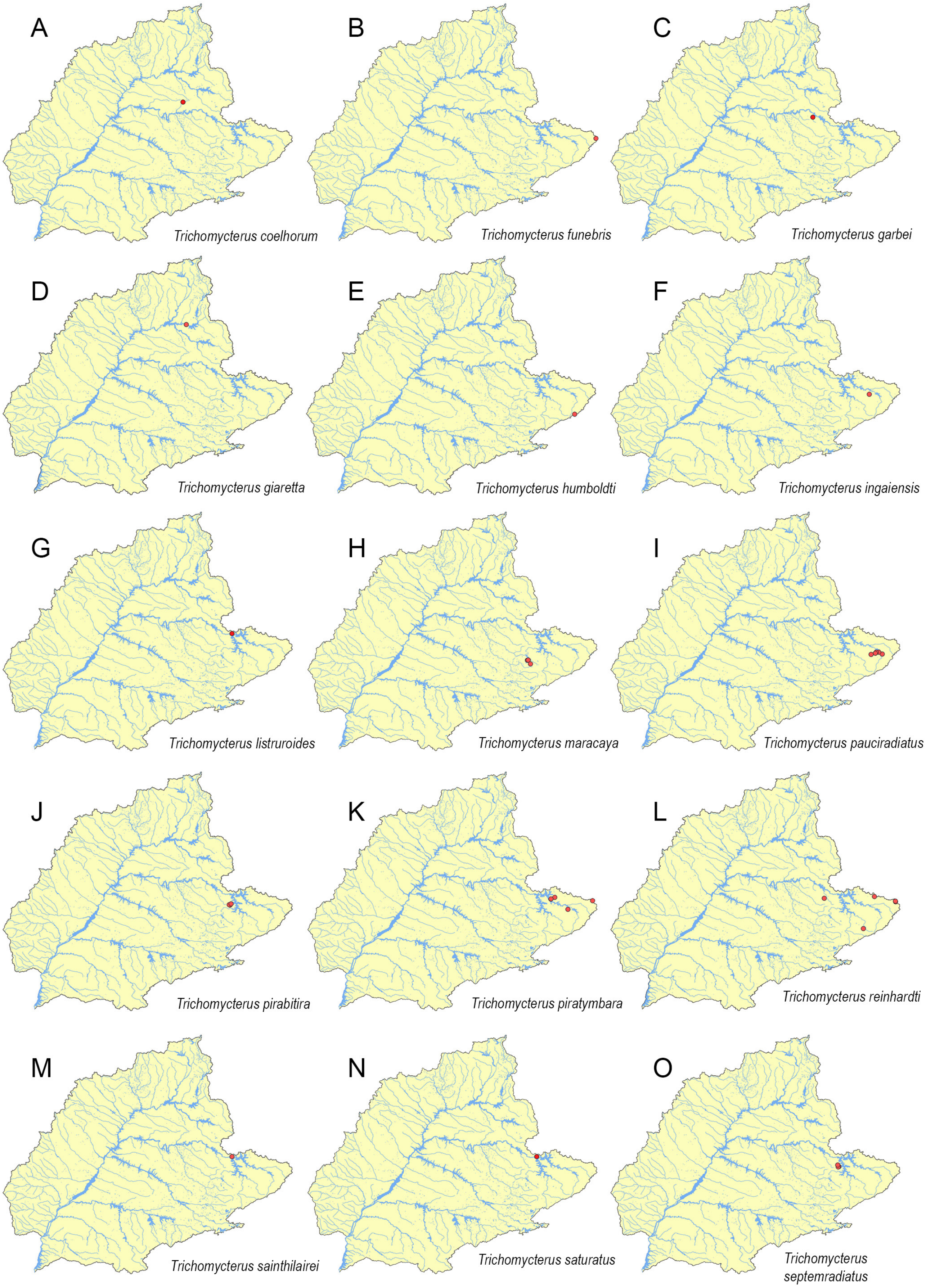



**FIGURE 24** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Trichomycterus coelhorum*; **B.** *Trichomycterus funebris*; **C.** *Trichomycterus garbei*; **D.** *Trichomycterus giaretta*; **E.** *Trichomycterus humboldti*; **F.** *Trichomycterus ingaiensis*; **G.** *Trichomycterus listruroides*; **H.** *Trichomycterus maracaya*; **I.** *Trichomycterus pauciradiatus*; **J.** *Trichomycterus pirabitira*; **K.** *Trichomycterus piratymbara*; **L.** *Trichomycterus reinhardti*; **M.** *Trichomycterus sainthilairei*; **N.** *Trichomycterus saturatus*; **O.** *Trichomycterus septemradiatus*.

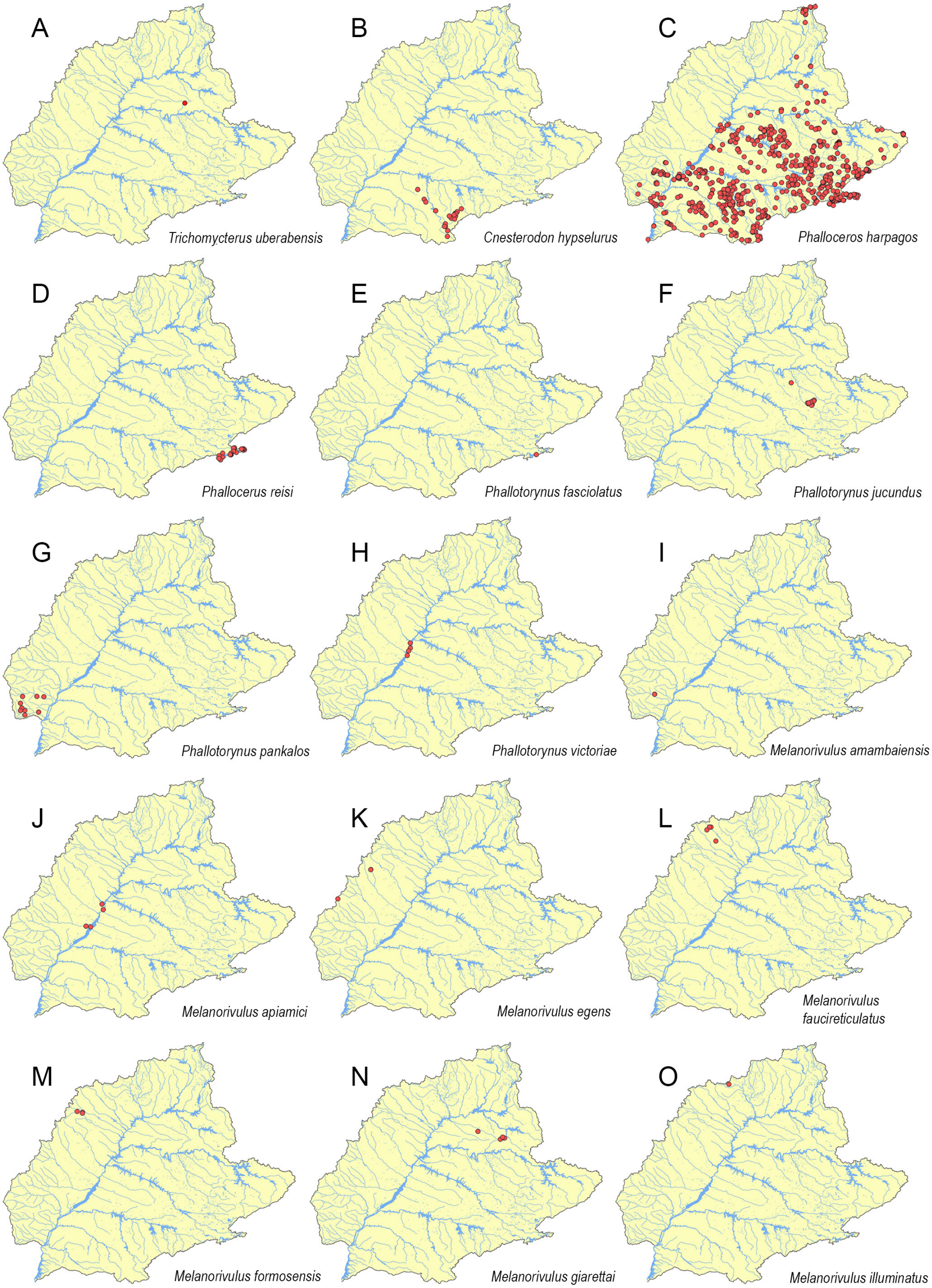



**FIGURE 25** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Trichomycterus uberabensis*; **B.** *Cnesterodon hypselurus*; **C.** *Phalloceros harpagos*; **D.** *Phalloceros reisi*; **E.** *Phallotorynus fasciolatus*; **F.** *Phallotorynus jucundus*; **G.** *Phallotorynus pankalos*; **H.** *Phallotorynus victoriae*; **I.** *Melanorivulus amambaiensis*; **J.** *Melanorivulus apiamici*; **K.** *Melanorivulus egens*; **L.** *Melanorivulus faucireticulatus*; **M.** *Melanorivulus formosensis*; **N.** *Melanorivulus giarettai*; **O.** *Melanorivulus illuminatus*.

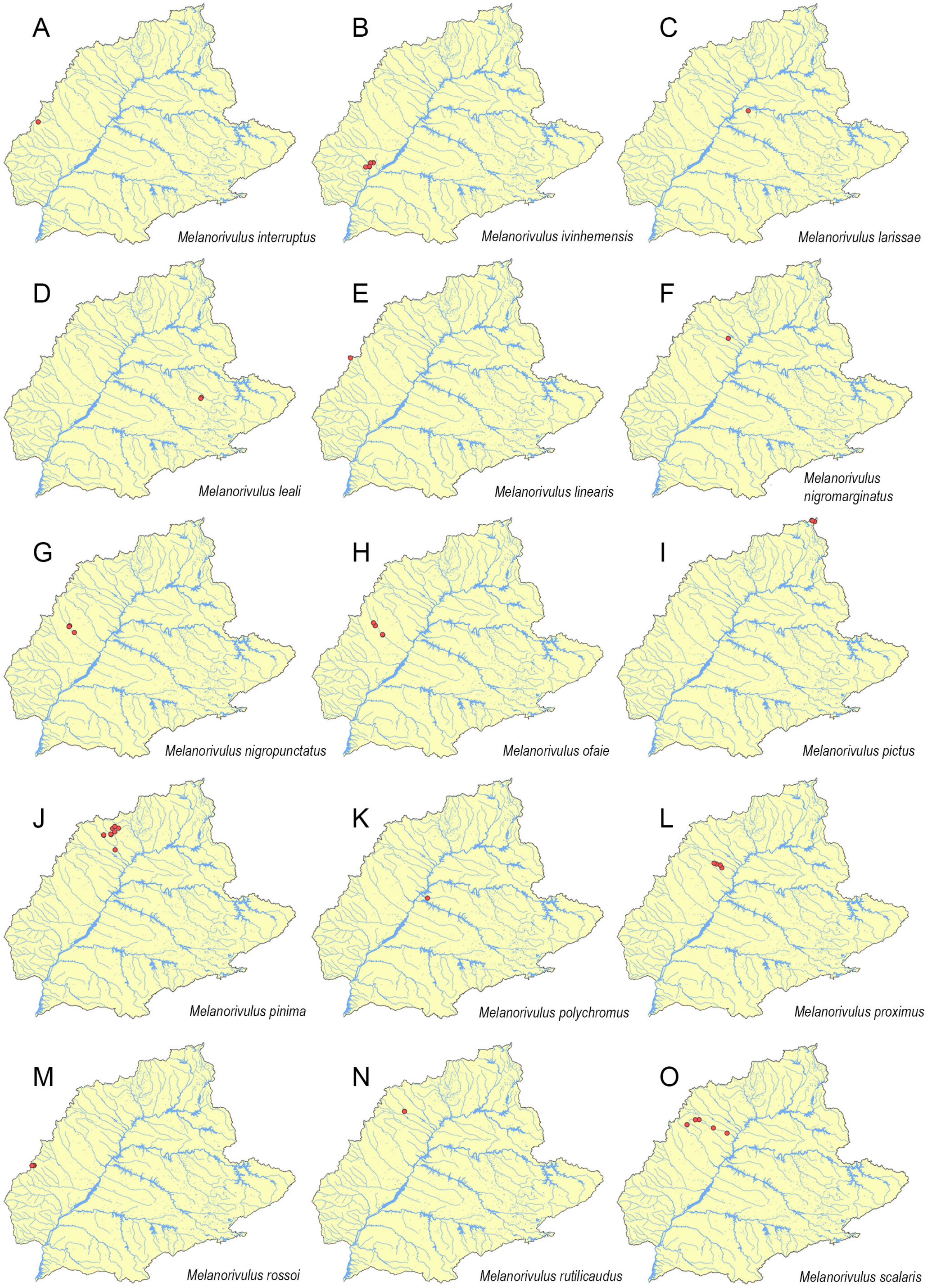



**FIGURE 26** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Melanorivulus interruptus*; **B.** *Melanorivulus ivinhemensis*; **C.** *Melanorivulus larissae*; **D.** *Melanorivulus leali*; **E.** *Melanorivulus linearis*; **F.** *Melanorivulus nigromarginatus*; **G.** *Melanorivulus nigropunctatus*; **H.** *Melanorivulus ofaie*; **I.** *Melanorivulus pictus*; **J.** *Melanorivulus pinima*; **K.** *Melanorivulus polychromus*; **L.** *Melanorivulus proximus*; **M.** *Melanorivulus rossoi*; **N.** *Melanorivulus rutilicaudus*; **O.** *Melanorivulus scalaris*.

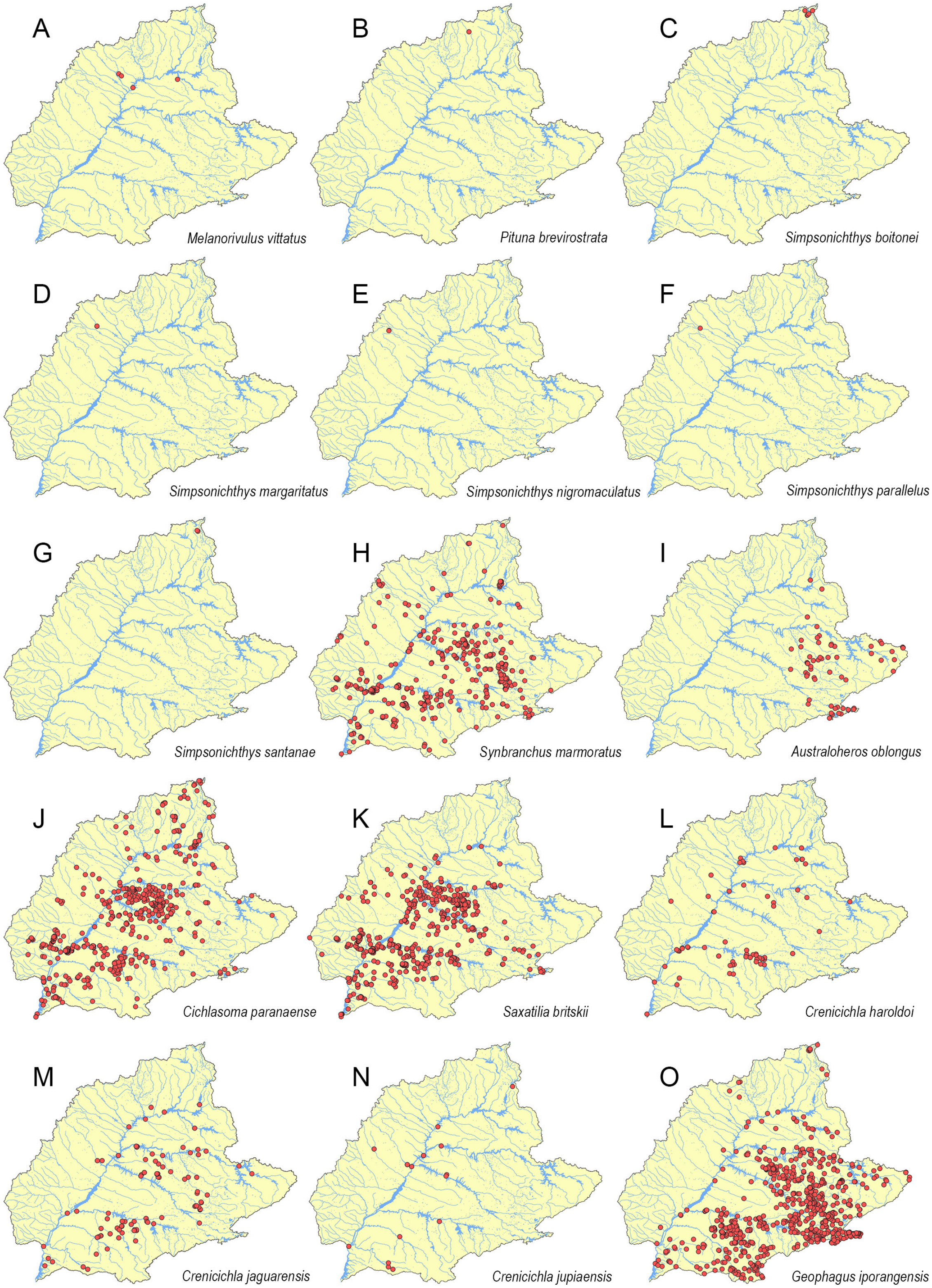



**FIGURE 27** | Distribution maps of native fishes occurring in the upper Paraná. **A.** *Melanorivulus vittatus*; **B.** *Pituna brevirostrata*; **C.** *Simpsonichthys boitonei*; **D.** *Simpsonichthys margaritatus*; **E.** *Simpsonichthys nigromaculatus*; **F.** *Simpsonichthys parallelus*; **G.** *Simpsonichthys santanae*; **H.** *Synbranchus marmoratus*; **I.** *Australoheros oblongus*; **J.** *Cichlasoma paranaense*; **K.** *Saxatilia britskii*; **L.** *Crenicichla haroldoi*; **M.** *Crenicichla jaguarensis*; **N.** *Crenicichla jupiaensis*; **O.** *Geophagus iporangensis*.

**Distribution patterns.** The visual examination of species maps allowed the recognition of distribution patterns geographically congruent in the upper rio Paraná. Five of those are described and discussed in more detail below.

**i. Species from higher portions of the upper rio Paraná.** The dichotomy of highlands and lowlands is a relative and fractal pattern. The pattern can be observed at a continental level (Eigenmann, 1909; Albert *et al*., 2011; Lima, Ribeiro, 2011) for the South American region, at the basin level Dagosta, de Pinna (2017, 2019), or even in streams. In watercourses there is a differentiation of the altitudinal gradient, with consequences for the fish assemblages. In any stream, it is possible to observe the differentiation of the fish fauna along the gradient from the headwaters to the mouth. Ultimately, it is exactly the same pattern that occurs at the continental level: some species are restricted to higher portions due to biogeographic barriers and/or ecological requirements, while others are more typical of lower elevation regions. This is no different for the upper rio Paraná basin, even though it is located in a relatively highland area of the South American continent, which is the Brazilian crystalline shield. Even in the Brazilian shield, some species may be more associated with higher lands while others are with lower lands.

Within the upper rio Paraná there are regions which are far higher than others, and this difference significantly affects the ichthyofaunistic composition. Some examples of species restricted to highlands in the basin are *Bryconamericus turiuba*, *Bunocephalus hertzi*, *Heptapterus longicauda*, *Psalidodon paranae*, the genera *Corumbataia*, *Neoplecostomus* (Fig. 28). This pattern can be less pronounced in some species (*e.g*., *Pimelodus paranaensis* and *Rhyacoglanis paranensis*).

Probably the most emblematic example to depicting the upland/lowland duality in the upper rio Paraná are the species of *Brycon* occurring in the basin (Fig. 29). Only two native species are known: *B. nattereri* and *B. orbignyanus*. Despite belonging to the same genus and inhabiting the same river basin, their geographical distribution is entirely different and shows virtually no overlap. The former is a typical dweller of large rivers with well-developed floodplains while the second is known exclusively from smaller rivers from headwater areas (Lima, 2017). The same pattern occurs to a lesser extent with at least two other species pairs, namely *Oligosarcus pintoi*/*O. paranaensis*, and *Salminus brasiliensis*/*S. hilarii*.

**ii. Species from lower portions of the upper rio Paraná.** The volume of water in a watercourse is directly related to its relative altitude. Lower parts of a hydrographic basin tend to concentrate more water, which flows down by gravitational force from higher lands. Therefore, species confined to lower lands are always associated with larger watercourses. In these lower regions, the hydrological regime has a pronounced drought/flood cycle. It is the main drive in the ecological processes and biological diversity patterns, with influence on feeding, reproduction, and distribution of species (Wootton, 1990; Message *et al*., 2016; Ota *et al*., 2018). Presently, such high/low water cycles are severely disrupted by the hydroelectric dams and reservoirs in the upper rio Paraná. Examples of species inhabiting exclusively the main water courses of the basin, *i.e*., the lowlands, are: *Cyphocharax naegelii*, *Piaractus mesopotamicus*, *Pinirampus pirinampu*, *Rhaphiodon vulpinus*, and *Rhinelepis aspera* (Fig. 30).

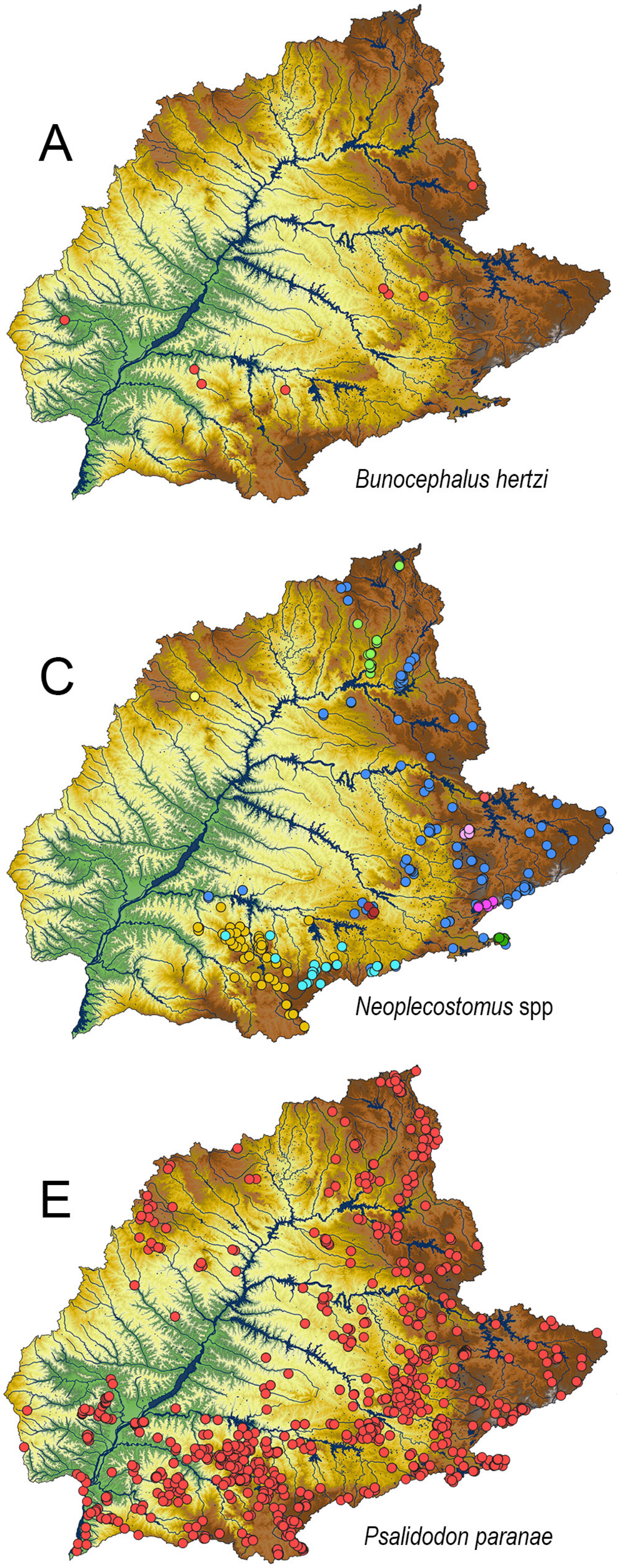



**FIGURE 28** | Examples of species that inhabit the upper portions of the upper rio Paraná basin. **A.** *Bunocephalus hertzi*; **B.** *Corumbataia* spp.; **C.** *Neoplecostumus* spp.; **D.** *Pimelodus paranaensis*; **E.** *Psalidodon paranae*; **F.** *Rhyacoglanis paranensis*.

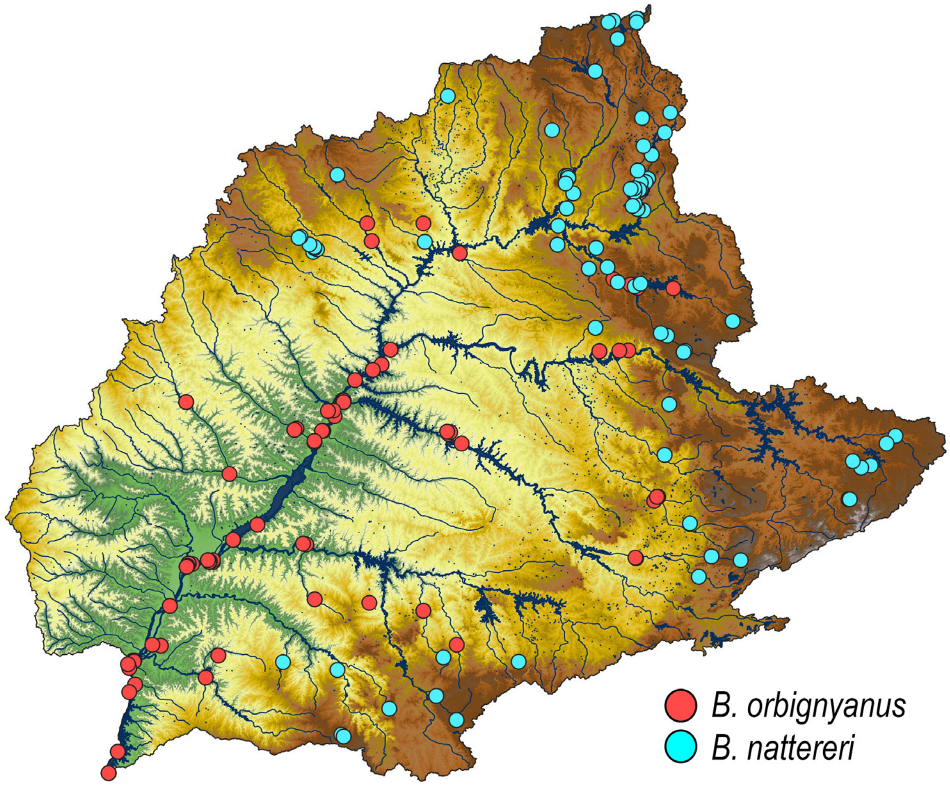



**FIGURE 29** | Species of *Brycon* inhabiting of the upper rio Paraná basin. Red dot: *Brycon orbignyanus*; Blue dot: *Brycon nattereri*.

**iii. Species with peripheral distribution.** Some species are present only in the periphery of the basin, in regions near adjacent drainages, occurring also in the latter. In such cases, those species only occur in those sectors of the upper rio Paraná and are interpreted as a result of geomorphological activity which resulted in faunistic exchanges with neighboring basins. In some cases, species have a broader distribution outside of the upper rio Paraná basin, such as *Astyanax lineatus*, *Gymnotus pantherinus*, *Hollandichthys multifasciatus*, *Hyphessobrycon boulengeri*, *Hyphessobrycon griemi*, *Ituglanis amphipotamus*, *Jupiaba acanthogaster*, *Mimagoniates microlepis*, *Pseudocorynopoma heterandria*, *Rhamdiopsis moreirai*, *Scleromystax barbatus*, and *Scleromystax macropterus* (Fig. 31). However, there are many examples where species have restricted distribution also in adjacent basins (*e.g.*, *Coptobrycon bilineatus*, *Glandulocauda melanopleura*, *Hyphessobrycon duragenys*, *Phalloceros reisi*, *Pseudotocinclus tietensis*, and *Taunayia bifasciata*).

Such processes are so common that some species seem to have invaded the upper rio Paraná in more than one catchment area, as seems to be the case with *Astyanax lineatus*, *Hyphessobrycon boulengeri*, *Jupiaba acanthogaster*, and *Mimagoniates microlepis.* Their current distributions have no connectivity in the upper rio Paraná and seem to be the result of independent events in different times. The Fig. 31 shows regions where such events may have taken place with different basins adjacent to the upper rio Paraná, as with the basins of the rios Iguaçu, Ribeira de Iguape, Paraíba do Sul, São Francisco, Tocantins, and Paraguai.

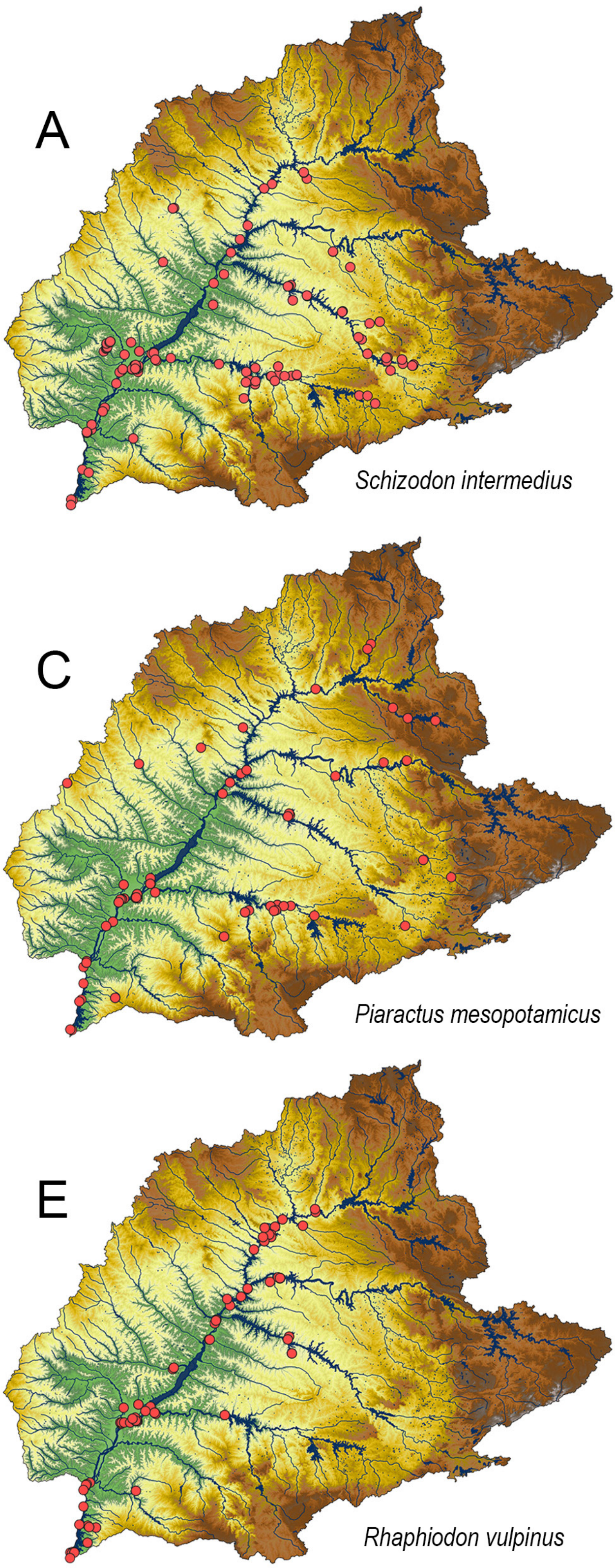



**FIGURE 30 |** Examples of species that inhabit the lower portions of the upper Paraná basin. **A.** *Schizodon intermedius*; **B.** *Cyphocharax naegelii*; **C.** *Piaractus mesopotamicus*; **D.** *Pinirampus pirinampu*; **E.** *Rhaphiodon vulpinus*; **F.** *Rhinelepis aspera*.

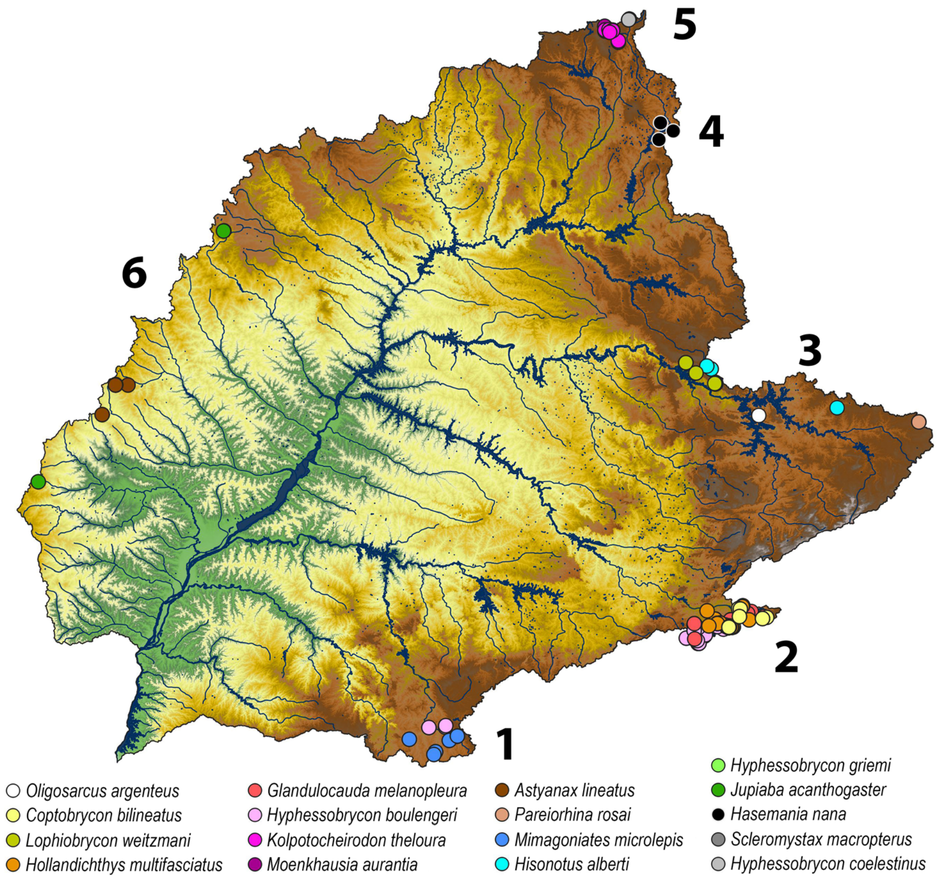



**FIGURE 31** | Examples of species that occur in the upper rio Paraná only in the peripheries of the basin and are shared with neighboring drainages. Numbers indicate zones of faunal exchange with adjacent basins: 1) rio Iguaçu and rio Ribeira de Iguape; 2) rio Paraíba do Sul and rio Ribeira de Iguape; 3) rio Doce and upper rio São Francisco; 4) rio Paracatu (rio São Francisco basin); 5) upper rio Tocantins and rio São Francisco; 6) rio Paraguai.

**iv. Eastern highlands.** In this case, lineages are concentrated in the highest portions of the eastern part of the basin, forming a nearly vertical line of occurrence points. Examples of fishes with such distribution includes: *Australoheros oblongus*, *Corydoras difluviatilis*, *Hypostomus heraldoi*, *Imparfinis schubarti*, *Rhamdiopsis microcephala*, *Microlepidogaster* spp. (Fig. 32) and *Trichomycterus* spp. Perhaps not coincidentally, five of those lineages are also present in the rio São Francisco basin (not exclusively in case of *Australoheros oblongus*, *Microlepidogaster* spp., and *Trichomycterus* spp.). It is premature at this point to determine whether such a pattern of distribution has any relationship with the biogeographic history of the rio São Francisco. Describing the pattern is a first step towards more studies on its possible causations. Two of the taxa presenting this pattern, *Hypostomus heraldoi* and *Imparfinis schubarti* were not recorded yet for the rio São Francisco basin.

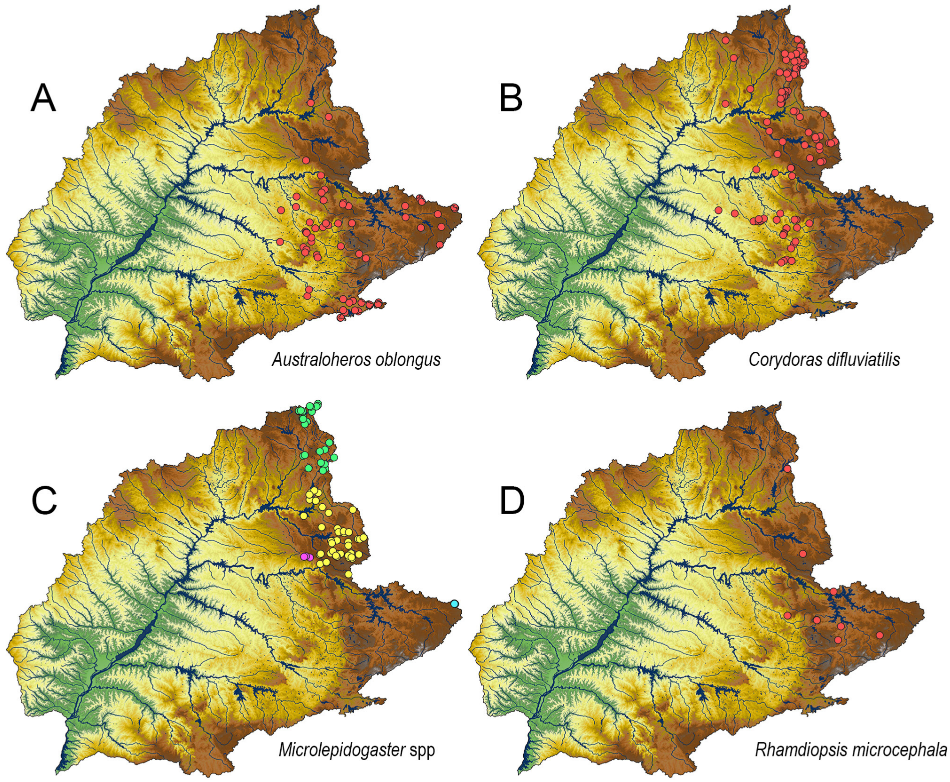



**FIGURE 32** | Examples of species that inhabit the Eastern highlands portions of the upper Paraná basin. **A.** *Australoheros oblongus*; **B.** *Corydoras difluviatilis*; **C.** *Microlepidogaster* spp.; **D.** *Rhamdiopsis microcephala*.

**v. Absence patterns.** One of the most intriguing distributional phenomena in biogeography is the absence of certain taxa in areas where they are expected to be found, based on the distribution of their close relatives and higher taxonomic groups (Dagosta, de Pinna, 2019). One conspicuous absence pattern in the upper rio Paraná is observed near the mouth of the rio Tietê into the rio Paraná channel. Some fishes are only found upstream to that region such as *Aspidoras fuscoguttatus* (Fig. 33A) *Curculionichthys piracanjuba*, *Hypostomus heraldoi* (Fig. 33B), and *Leporinus microphthalmus*. Conversely, some species have their distribution in the upper rio Paraná basin limited downstream to the region, as the case of *Aphyocharax dentatus* (Fig. 33A), *Callichthys callichthys*, *Eigenmannia guairaca*, *Leporinus lacustris*, *Psalidodon anisitsi*, *Psalidodon schubarti*, *Schizodon altoparanae* (Fig. 33B). Although some of these examples have records upstream this region, these can be the result of an increased distribution after the removal of barriers due to the construction of hydroelectric dams. The distribution of these species could potentially be associated with biogeographic barriers that no longer exist, such as the Urubupungá Falls, which were a series of waterfalls situated in this region. The construction of the Engenheiro Souza Dias Hydroelectric Power Plant (Jupiá Dam) in 1974 led to the submersion of these falls, eliminating potential biogeographic barriers for numerous fish species. After the construction, it is possible that several species have expanded their natural distribution above and below these barriers, thereby obscuring biogeographic signals that once existed there. Due to the construction occurred many

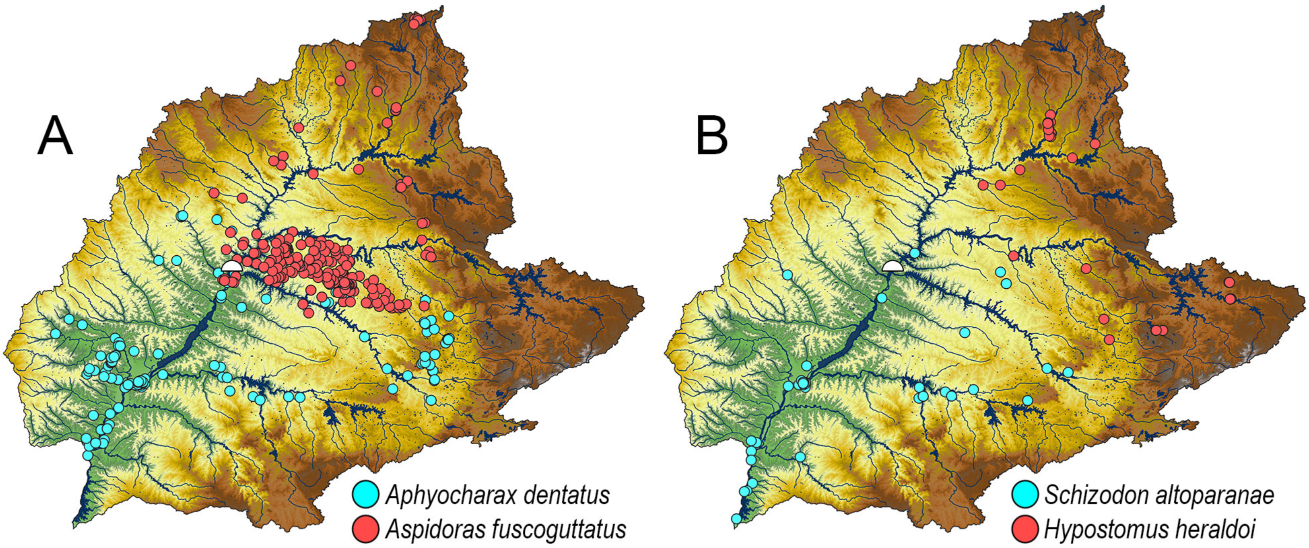



**FIGURE 33** | Examples of species with distribution probably restricted by the presence of an ancient geographical barrier. White semicircle represents the location of the former Urubupungá Falls, which was submerged with the construction of UHE Jupiá in 1974. **A.** Blue dot: *Aphyocharax dentatus*; red dot: *Aspidoras fuscoguttatus*; **B.** Blue dot: *Schizodon altoparanae*; red dot: *Hypostomus heraldoi*.

decades ago, even before the establishment of major ichthyological collections in the basin, it will be quite challenging, if not impossible, to understand the true role of many barriers in shaping the biogeographic history of the basin. At present, it is only possible to infer that the distributional limit of several species in the upper Paraná basin is, for unknown reasons, approximately at this region.

Another remarkable case is observed in the right bank tributaries of the rio Paraná, which lack widely distributed groups of the upper rio Paraná and other Brazilian shield basins, such as representatives of the Trichomycterinae lineages (*Cambeva* + *Trichomycterus*), *Geophagus*, *Neoplecostomus*, and *Phalloceros* (Fig. 34). Records of *Phalloceros* are found only in the lower areas of this region, near the channel of the rio Paraná, mainly in rio Ivinhema basin (Fig. 34C). In contrast, an unidentified species of *Cambeva* is recorded only in the headwaters of the rio Ivinhema, at the divide with the rio Paraguai basin (Fig. 34A), pending further taxonomic studies. Although the right bank is drained by tributaries that have been less sampled compared to those on the left bank of the upper rio Paraná, it is unlikely that these absences can be attributed to a collection artifact, as the absent species are conspicuous, easily identifiable components of the ichthyofaunistical assemblages wherever they are found. These absence patterns seem to indicate that the ichthyofauna inhabiting tributaries draining the right and left banks of the upper rio Paraná may have experienced considerably different biogeographic histories.

**Where is the richest fish diversity in the upper rio Paraná?** Results of the analysis of Species Richness and of Phylogenetic Diversity were practically identical. This means that the richest diversity of species and clades in the upper rio Paraná is located in the central portion of the basin, while the high-elevation regions have comparatively fewer species and phylogenetic lineages (Figs. 35–36). The region of greatest diversity

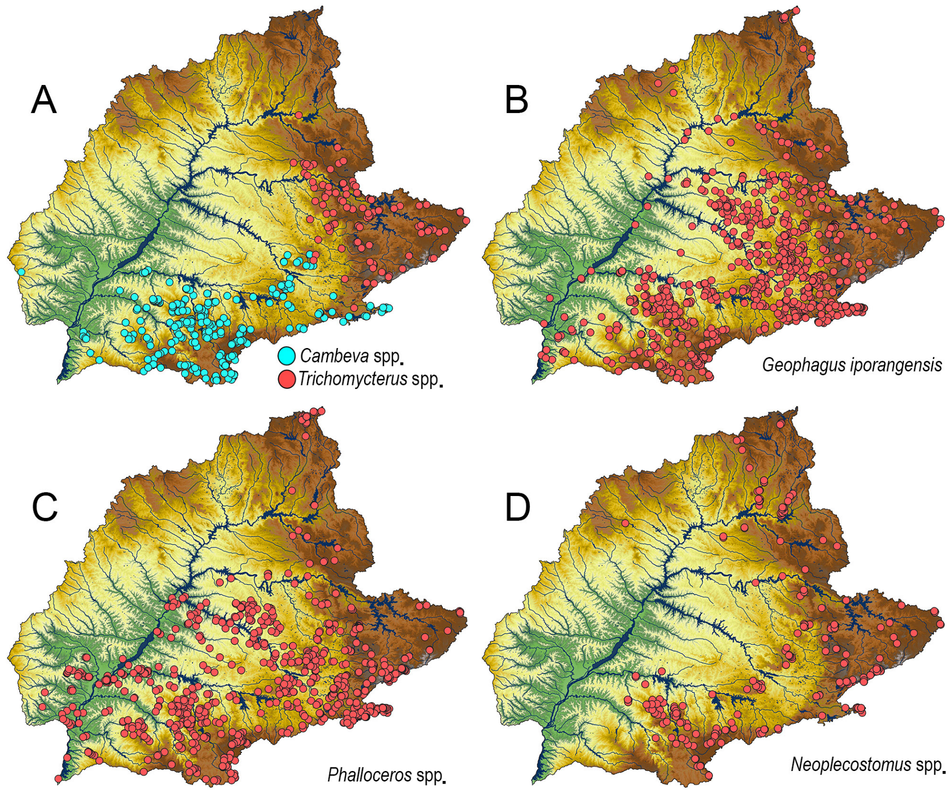



**FIGURE 34** | Examples of lineages absent in the right margin of the rio Paraná (downstream the confluence of rio Paranaíba and rio Grande). **A.** Red dot: *Cambeva* spp.; blue dot: *Trichomycterus* spp.; **B.** *Geophagus iporangensis*; **C.** *Phalloceros* spp.; **D.** *Neoplecostomus* spp.

is largely coincident with the lowland portion of the drainage, following a pattern detected in other South American river basins. According to several authors (*e.g*., Lima, Ribeiro, 2011; Dagosta, de Pinna, 2019; Albert *et al*., 2020) lowland regions tend to harbor greater diversity, more cases of sympatric species and fewer endemic species, which in fact corresponds to the pattern observed in the upper rio Paraná.

The greatest concentration of species and lineages is observed in the eastern part of the basin, in left-margin tributaries of the rio Paraná. This may be related with the longer course of those rivers when compared with those of the right margin. Besides historical and ecological factors, large areas have the potential to harbor greater species diversity than small areas (Williamson, 1988). It is also possible that, at least in part, such a pattern is a result of sampling bias. Left- and right-margin tributaries have not been equally sampled. Right-margin tributaries are mostly located in the State of Mato Grosso do Sul, where collections have been relatively sparse and where research institutions are ichthyologically underdeveloped, when compared to states drained by left-margin tributaries. Most of the samples of the basin are from the left margin, a region where most of the ichthyological research centers are located; *e.g*., Museu de Zoologia da Universidade de São Paulo (MZUSP); Departamento de Ciências Biológicas, Universidade Estadual Paulista "Júlio de Mesquita Filho", Instituto de Biociências, Letras e Ciências Exatas, São José do Rio Preto, São Paulo, Brazil (DZSJRP); Laboratório de

Ictiologia de Ribeirão Preto (LIRP); Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia) in Maringá; and Museu de Zoologia da Universidade Estadual de Londrina (MZUEL).

A similar situation was described as "botanical effect" by Moerman *et al*. (2006), showing that the greatest richness of plants is recorded in municipalities with universities. The mere presence of more numerous researchers in an area may explain the presence of more species of plants (or, in this case, fishes).

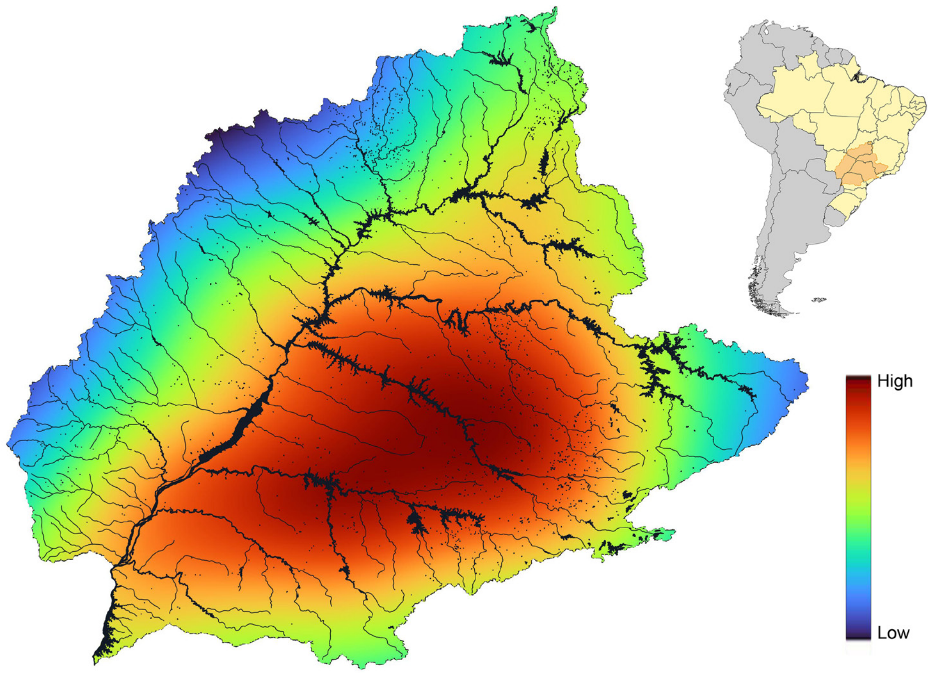



**FIGURE 35 |** Species richness fishes in the upper rio Paraná basin estimated by interpolation. Warmer colors indicate regions with greater species diversity, while cooler colors indicate regions with lower diversity.

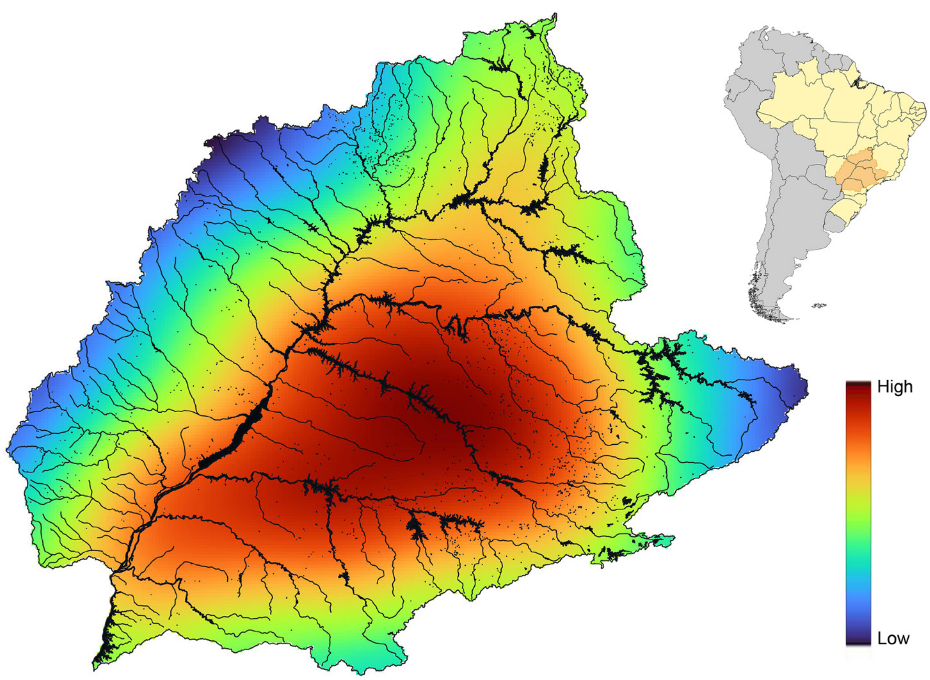



**FIGURE 36 |** Phylogenetic diversity of fishes in the upper rio Paraná basin estimated by interpolation. Warmer colors indicate regions with greater diversity of species lineages, while cooler colors indicate regions with lower diversity.

**Regions with the most distinctive fish faunas in the upper rio Paraná basin.** Weigth Endemism Index (WEI) analysis is able to detect areas with lower diversity yet with higher levels of endemism. Results show greater indices of endemism along the fringes of the upper Paraná, especially in headwaters of large left-margin tributaries such as the rio Grande and rio Tietê, and in headwaters of right-margin tributaries of the rio Paranaíba. The pattern is inverted in the central part of the basin, with great diversity and low endemism (Fig. 37). Such a figure shows a direct relationship between altitude and the presence of endemics. The outline of regions with higher WEI values corresponds to relatively higher areas in the basin.

**Changes in species composition along the basin.** Non-Metric Multidimensional Scaling (NMDS) analysis converts a matrix of Beta diversity into three spatial vectors (red, blue and green), allowing to detect spatial changes in fish assemblages. The geographic turnover in species composition found along the three axes represents the biotas of the rio Paranaíba headwaters (red), the left-bank tributaries of the upper rio Paraná (blue), and the right-bank tributaries of the upper rio Paraná (green). The central area along the channel of the rio Paraná, which delimits the lowlands of the basin (Fig. 38), is a mixture of the three axes. Not surprisingly, it is the area with the most diverse ichthyofauna of the upper rio Paraná (Figs. 35–36).

The upland fauna of the left-bank tributaries exhibits higher Beta diversity (*i.e.*, taxonomic turnover) across its distinct drainages. At least three regions can be identified (Fig. 38): Ponta Grossa Arch, Mata Atlântica and rio Grande headwaters. All three

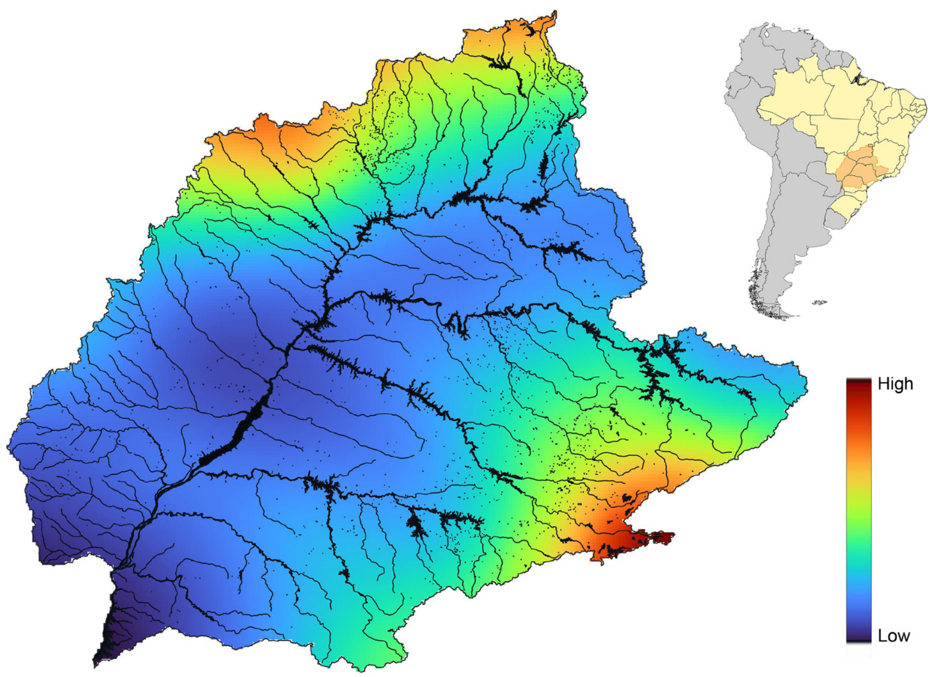



**FIGURE 37** | Weight Endemism Index map. Areas with warmer colors indicate regions with a high concentration of species with restricted distribution and few species with widespread distribution. The opposite is indicated by regions with cooler colors.

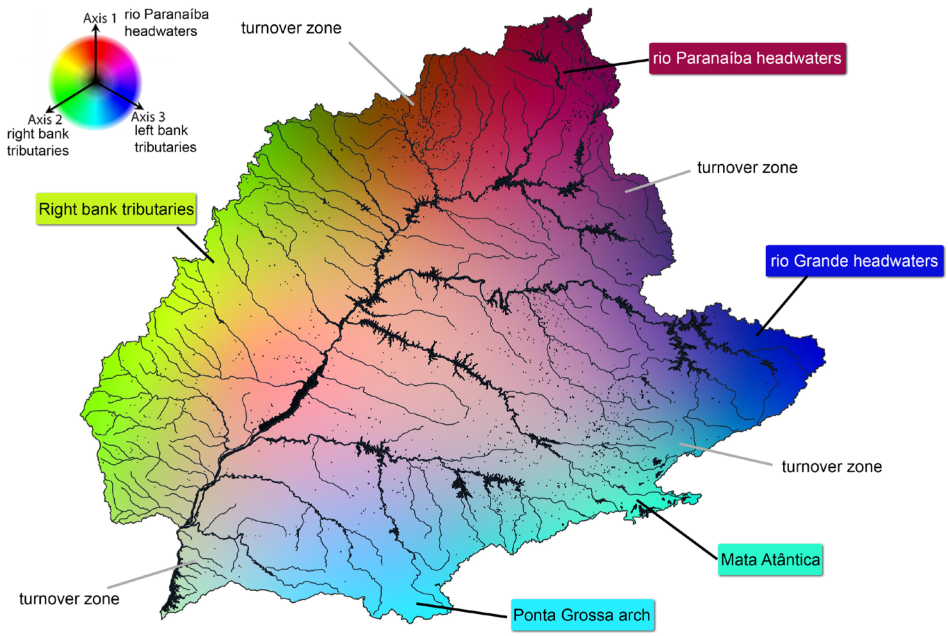



**FIGURE 38 |** NMDS analysis with spatial changes in fish assemblages in the upper rio Paraná.

correspond to bioregions found in Infomap Bioregions analysis (Fig. 39). The light-blue area herein named Ponta Grossa arch corresponds to areas "Ivaí and upper rio Piquiri" and "Ponta Grossa Arch I and II" in the bioregionalization. The turquoise-green area corresponds to the upper rio Tietê, while the dark blue region has its equivalent in the area "upper rio das Mortes".

Axis 2 (green) corresponds to right-bank tributaries of the rio Paraná, mostly draining the area of the State of Mato Grosso do Sul and with their headwaters in the Serra de Maracaju. That axis corresponds to areas 16–18 of the Infomap Bioregions analysis (Fig. 39) and shows minimal variation of faunistic composition between adjacent basins. As the maps show, whichever difference there is among those basins is due to some species of *Melanorivulus*. Such inter-basin differences are several orders of magnitude smaller than the turnover seen in the left bank, where basins have entirely different biogeographic histories and even genera which are not found in neighboring drainages.

Finally, axis 3 (red) corresponds to the headwaters of the rio Paranaíba, which borders the drainages of Araguaia, Tocantins, and São Francisco. That axis coincides with the area "Águas Emendadas" of the Infomap Bioregions analysis (Fig. 39). This is the axis with the smallest area, showing that the ichthyofaunistic composition of the region is concentrated in a more restricted area. The axis comprises left-bank rivers of the rio Paranaíba, while those of the right bank are within a turnover zone, having an ichthyofauna influenced by other right-bank tributaries of the rio Paraná.

**Bioregionalization within the upper rio Paraná.** Partitioning into biogeographic regions implemented by the software Infomap Bioregions (Fig. 39) is an approach relevant for understanding fish distribution because it segregates regions based on distributions of taxa, generating regionalizations that can serve as foundation for studies on ecology, biogeography, evolution and conservation (Vilhena, Antonelli, 2015). Of

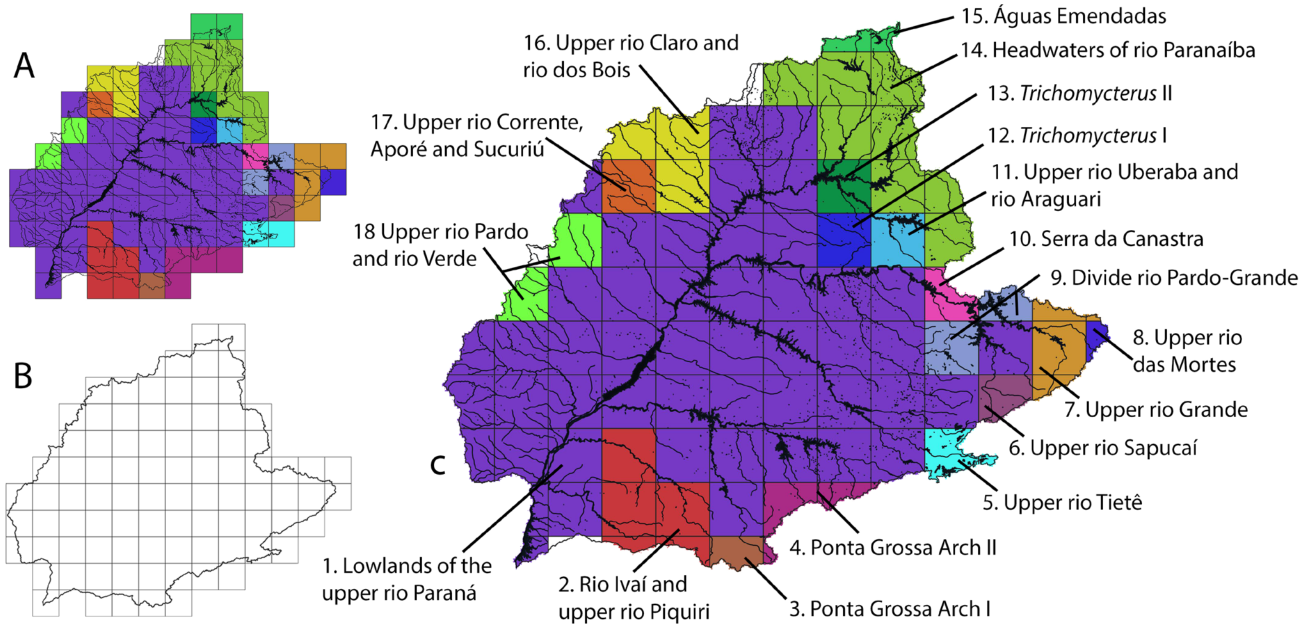



**FIGURE 39** | **A.** Bioregionalization of the upper rio rio Paraná ichthyofauna using bipartite networks and clustering algorithms from the Infomap Bioregions software. **B.** Upper rio Paraná basin outline and 1º quadricles present in the basin. **C.** Croped result using the upper rio Paraná basin outline.

18 bioregions defined, 17 are located in the periphery of the basin, in regions bordering other biomes and basins (Fig. 39). Such a pattern is related with the presence of taxa shared among adjacent regions and linked to the hypothesis that restricted-range species are found in high-elevation regions. All defined regions include endemic species (*e.g.*, *Creagrutus varii*, *Trichomycterus uberabensis*, *Melanorivulus nigropunctatus*) or species with restricted distribution in the upper rio Paraná, *i.e.*, species that occur in other basins, but restricted to peripheral bioregions within the upper rio Paraná (*e.g.*, *Characidium xanthopterum*, *Hisonotus alberti*, *Phalloceros reisi*).

Regardless of the variation of employed parameters, biogeographic regions in right-bank tributaries are spatially restricted, supported by the presence of Rivulidae, a group with high levels of endemism and mostly having narrow ranges (Abilhoa *et al.*, 2010). The bioregions along the southeastern border, spanning from the “rio Ivaí and upper rio Piquiri” to the “upper rio Tietê” áreas, exhibit consistent stability across various parameters. The same is true for bioregions in the northern borders of the basin, *e.g.*, the “Águas Emendadas” and “Serra da Canastra” bioregions. Contrastingly, the regions of the headwaters of the rio Grande (“Serra da Canastra”, “Divide rio Pardo-Grande”, “upper rio Sapucaí”, “upper rio das Mortes”) and “Right-bank tributaries of the upper rio Paraná” have a complex and relatively inconsistent bioregionalization, with the delimitations of areas sensitive to alterations in the database or employed parameters.

**1. Lowlands of the upper rio Paraná.** This is the largest bioregion found in this study and corresponds to Pattern “Lowland species” discussed above. Approximately $^{2}/_{3}$ of the area of the basin is composed of this region, located in its central area where there is the main channel of the rio Paraná and extends at least up to the middle course of its tributaries. This region concentrates most of the biodiversity of the basin (Figs. 35–36). Several of the species showing this pattern are typically found in the main channels of large rivers, with some found also in several other neotropical basins, such as *Hemisorubim platyrhynchos*, *Pinirampus pirinampu*, *Pseudoplatystoma corruscans*, and *Rhapiodon vulpinus*, while others are endemic to the basin, such as *Cyphocharax naegelii*, *Schizodon intermedius*, etc. This region also includes endemic species with somewhat more limited distributions and associated with smaller tributaries (*e.g.*, *Planaltina britskii*).

**2. Rio Ivaí and upper rio Piquiri.** This bioregion comprises mostly the rio Ivaí basin, with a sector of the rio Piquiri basin. According to Frota *et al*. (2016), the rio Ivaí basin has approximately 100 species, 13 of which are endemic. The same authors propose that the high degree of endemism is related to the numerous waterfalls that isolate those species in the upper reaches of the drainage. Some species, including *Cambeva horacioi*, *Characidium heirmostigmata*, *Corydoras lacrimostigmata*, and *Hisonotus pachysarkos* are responsible for the delimitation of the region. Other species also occurring in adjacent basins were also relevant for the recognition of the region, *Apareiodon vladii*, *Bryconamericus coeruleus*, *Curculionichthys oliveirai*, *Hypostomus robertsoni*, and *Planaltina kaingang*. The region has elements shared exclusively with the rio Iguaçu drainage, as *Cambeva davisi* (Morais-Silva *et al*., 2018; Reis *et al*., 2020) and *Psalidodon bifasciatus* (Neves *et al*., 2020; Reis *et al*., 2020), which suggest a historical relationship between those regions.

The most remarkable biogeographic fact of this region is, as earlier pointed by Deprá *et al*. (2018), the absence of several species otherwise widespread in the upper rio Paraná. Their list can be expanded to include *Leporinus lacustris*, *Megaleporinus piavussu*, *Myloplus tiete*, among others. Literature records and databases of scientific collections make this absence pattern still more striking. The rio Ivaí basin lacks not only elements typical of the upper rio Paraná, but also elements otherwise present in most of cis-Andean South America, as the cases of Sternopygidae (*Eigenmannia* spp. and *Sternopygus macrurus* are the representatives present elsewhere in the upper rio Paraná), Doradidae (*Rhinodoras dorbignyi*) and Lebiasinidae (*Pyrrhulina australis*). Other species widely distributed in the La Plata basin, but absent in the rio Ivaí basin are: *Leporinus striatus*, *Moenkhausia* aff. *sanctaefilomenae*, *Paravandellia oxyptera*, *Pimelodus maculatus*, *Rhaphiodon vulpinus*, *Pinirampus pirinampus*, and *Zungaro jahu*. These absences, added to the endemic elements and those shared with the rio Iguaçu, indicate a high degree of historical differentiation of the rio Ivaí drainage and, as a consequence, of this entire region relative to the rest of the upper rio Paraná.

**3–4. Ponta Grossa Arch I and II.** These two regions are discussed together because they share similar biogeographic histories and faunas. Both areas comprise the headwaters of the left-bank tributaries of the middle and upper rio Paranapanema. Some species are found exclusively in the area delimited by the two regions, such as *Cnesterodon hypselurus*, *Otothyropsis biamnicus*, and *Neoplecostomus selenae*.

The main river basin of the region is the rio Tibagi, which has few examples of endemic species. Among species previously considered endemic to the rio Tibagi, only *Isbrueckerichthys saxicola* is still restricted to the basin. Ponta Grossa Arch I and II are part of one of the regions of the upper Rio Paraná with deep historical relationships with neighboring basins. They include several taxa which, in the upper rio Paraná, are only found there, although also present in neighboring basins. Those taxa occur only marginally in the upper rio Paraná but have broader distributions in other basins such as the rio Iguaçu and rio Ribeira de Iguape. Some examples are: *Cambeva davisi*, and *Corydoras ehrhardti* (rio Iguaçu and rio Ribeira de Iguape), *Characidium schubarti* (Ribeira de Iguape), *Hyphessobrycon griemi* (Coastal drainages, rio Iguaçu and rio Ribeira de Iguape), *Otothyropsis polyodon*, *Pareiorhaphis parmula*, and *Rhamdiopsis moreirai* (rio Iguaçu), and *Pseudotothyris obtusa* (Coastal drainages and rio Ribeira de Iguape).

The numerous examples are not simply a coincidence but represent a biogeographic history shared by these two basins. The headwaters of the rio Paranapanema in those regions are associated with the Ponta Grossa Arch, as are the headwaters of rio Iguaçu and rio Ribeira de Iguape. That geological formation includes a complex system of fault lineaments and rifted blocks which has imparted a highly dynamic tectonics (Ribeiro, 2006). Vertical movements among faulted blocks and erosive evolution of rivers along such rifts promote ichthyofaunistic mixing between adjacent drainages (Ribeiro, 2006).

**5. Upper rio Tietê.** This bioregion is composed of the headwaters of the rio Tietê draining the western slope of the Serra do Mar escarpment. The Tietê headwaters are relatively poor in fish diversity, with *ca*. of 60 spp. (*cf*. Marceniuk *et al*., 2011). However, their ichthyofaunistic composition is quite peculiar and distinct from that in the rest of the upper rio Paraná (Langeani, 1989; Marceniuk *et al*., 2011), and it is probably the most singular region in the entire basin. The fish fauna is characterized by the presence of some endemic species such as *Neoplecostomus bandeirante* and *Piabina anhembi*, but the headwaters of the rio Tietê have many elements shared with neighboring Coastal Atlantic drainages (Langeani, 1989; Ribeiro, 2006; Ribeiro *et al*., 2006; Menezes *et al*., 2008). Some examples are: *Coptobrycon bilineatus*, *Glandulocauda melanopleura*, *Gymnotus pantherinus*, *Hollandichthys multifasciatus*, *Hyphessobrycon bifasciatus*, *Hyphessobrycon boulengeri*, *Hyphessobrycon duragenys*, *Ituglanis amphipotamus*, *Mimagoniates microlepis*, *Phalloceros reisi*, *Pseudocorynopoma heterandria*, *Pseudotocinclus tietensis*, and *Taunayia bifasciata*.

Southeastern Brazil is a tectonically active area and prone to deformations which presumably had consequences for the aquatic biota (Cobbold *et al*., 2001; Ribeiro, 2006). Geomorphological mechanisms responsible for faunistic sharing listed above are associated with reactivation and deformations of the Continental Rift of Southeastern Brazil (CRSB) and are discussed by Ribeiro (2006).

**6. Upper rio Sapucaí.** The rio Sapucaí is a tributary of the rio Grande and its headwaters drain the Serra da Mantiqueira, which at that region is the divide between the upper rio Paraná and the rio Paraíba do Sul (along with the states of Rio de Janeiro and São Paulo). According to Ingenito, Buckup (2007), the Serra da Mantiqueira is an efficient geographic barrier for the faunal separation of the two basins since they share no species at that region. Data herein compiled corroborate that conclusion and Fig. 39 shows that the region of the Serra da Mantiqueira has no elements shared between the upper Paraná and neighboring basins. The region of the upper rio Sapucaí was defined in this analysis exclusively on the basis of endemic elements, as *Parodon moreirai* and *Otothyropsis alicula*. Another lineage endemic to the region is a yet undescribed species, currently unassigned to any trichomycterine subgroup (DZSJRP 13957) reported by Thereza, Langeani (2019).

**7. Upper rio Grande.** This region comprises the tributaries forming the rio Grande, including the part of the rio das Mortes, rio Capivari, rio Ingaí among others, all with their headwaters in the Serra da Mantiqueira. The region is delimited by the analysis on the basis of several siluriforms taxa, most of which of *Trichomycterus*: *T. humboldti*, *T. ingaiensis*, *T. pauciradiatus*, and *T. piratymbara*. Other catfishes endemic to the region are *Microlepidogaster perforata* and *Pareiorhina carrancas*.

**8. Upper rio das Mortes.** At the southeastern State of Minas Gerais, the Serra da Mantiqueira and the Espinhaço range complex separate four major hydrographic systems in Brazil: rio São Francisco, upper rio Paraná, rio Doce and rio Paraíba do Sul (Oliveira, Oyakawa, 2019). One of the basins originating in that region is that of rio das Mortes, one of the tributaries of the rio Grande. This region was delimited by the analysis on the basis of the congruent distribution of three siluriforms: *Pareiorhaphis togoroi*, *Pareiorhina rosai*, and *Trichomycterus funebris*. The first two species require further comments.

Oliveira, Oyakawa (2019) described *Pareiorhaphis togoroi* from the headwaters of the rio das Mortes, a highly significant record as it was the first species of the genus to be recorded in the upper Paraná basin. The presence of that lineage in the headwaters of the rio das Mortes was considered as probably relictual and it should explain the past distribution of the group (Oliveira, Oyakawa, 2019). Another species which underscores the historical specificity of this region is the presence of *Pareiorhina rosai*, previously only known from headwater streams of the rio Paraopeba and rio das Velhas (rio São Francisco basin) (FL and collaborators, working in progress). The occurrence of this species suggests a putative hydrogeological complexity of the region.

**9. Divide rio Pardo-Grande.** This region includes the headwaters of the rio Pardo, tributary of the middle rio Grande plus part of drainages of the Furnas dam, formed by the damming of the rio Grande. Five endemic species are known to this region, all siluriforms. Only *Trichomycterus maracaya* is endemic to the upper rio Pardo, with remaining ones (*Neoplecostomus langeanii*, *Trichomycterus adaltoleitei*, *T. pirabitira*, *T. septemradiatus*) endemic of tributaries draining directly into the rio Grande. In the region there is also the only record of *Oligosarcus argenteus* in the upper rio Paraná basin, a species more widely distributed in the rio Doce and upper rio São Francisco basins.

**10. Serra da Canastra.** The Serra da Canastra is located at southwestern portion of the State of Minas Gerais. The region possesses a high-elevation, rugged topography, with many steep elevations and deep valleys. The Serra da Canastra is the divide between the basins of rio São Francisco and upper rio Paraná, with the latter represented by the headwaters of the rio Grande, to the south, and the rio Paranaíba, to the northwest, which receives influx from the headwaters of the rio Araguari.

The region has a dense and complex network of tributaries which is reflected in the fish fauna of the region which, though poor, shows many endemic elements. Some of those endemics are: *Aspidoras lakoi*, *Hisonotus alberti*, *Lophiobrycon weitzmani*, *Neoplecostomus canastra*, *Pareiorhina pelicicei*, *Trichomycterus listruroides*, *T. sainthilairei*, and *T. saturatus.* All those species are recorded exclusively in the Serra da Canastra versant of the upper Paraná. Other endemic species are present in the portion drained by the rio São Francisco, showing that the present limits of those drainages represent an important biogeographic barrier for aquatic biotas, lacking shared elements present in some other water divides of the upper rio Paraná basin.

**11. Upper rio Uberaba and rio Araguari.** The region "Upper rio Uberaba and rio Araguari" comprises the headwaters of the rio Uberaba basin, one of the largest right-bank tributaries of the rio Grande, plus part of the rio Araguari drainage, one of the largest left-bank tributaries of the rio Paranaíba. The region is located in the Triângulo Mineiro region, Minas Gerais State, Brazil.

Several elements corroborate this region as a biogeographically relevant area and distinctive from the rest of the upper Paraná. There are exclusive elements to the rio Uberaba basin, as *Hasemania uberaba*, *Hyphessobrycon uaiso*, and *Microlepidogaster dimorpha*, and others to the rio Araguari, as *Scleronema auromaculatum*, and *Trichomycterus araxa*. Although in the proximity of a large urban center, the city of Uberaba, the region harbors some undescribed taxa, such as a species of *Glandulocauda* (MZUSP 114314, see Fagundes *et al*., 2015 as Glandulocaudinae sp.) from the rio Araguari basin and a new genus and species of Crenuchidae (see Ribeiro *et al*., 2019) from the rio Uberaba basin.

Costa *et al*. (2022) discuss the disjunct distribution of *Scleronema*, with a single record in the region herein delimited and all other species in the South American subtropical region of southern Brazil, Paraguay, Uruguay, and northeastern Argentina. Those authors argue that such distribution results from extinction of intermediate populations caused either by past events (*e.g*., Cenozoic climatic changes) or more recent factors (anthropic environmental changes), or still are result of a sampling gap. In addition, *Glandulocauda* has congeners in the rio Iguaçu basin, upper rio Tietê and adjoining coastal rivers. The explanation for those two lineages in the region seems to be the same offered by Ribeiro (2006) as "Pattern B". Interestingly, the adjacent region, Serra da Canastra, was employed by the latter to illustrate a pattern of sister-group relationships between the endemic ichthyofauna of the Brazilian coastal drainages and the adjacent shield. One of the examples cited is *Lophiobrycon* at the Serra da Canastra, sister group to remaining glandulocaudines. As *Scleronema auromaculatum* is considered by Costa *et al*. (2022) as sister group to all congeners, a relictual pattern seems to be a more likely explanation for these similar biogeographical patterns.

**12–13. *Trichomycterus* I and II.** These two regions are discussed together because both bioregions were defined solely on the presence of recently described species of *Trichomycterus* known only from their respective type localities. The *Trichomycterus* I bioregion is defined by the species *T. coelhorum* and *T. uberabensis*, known only from the rio Uberaba basin. The *Trichomycterus* II bioregion is delimited only by the presence of *Trichomycterus giarettai*, endemic from a tributary of the rio Paranaíba. Both regions are relatively poorly sampled, and future inventories may provide a more reliable picture of their ichthyofaunal composition. In addition, more information regarding the distributions of these species has the potential to blur the evidence of these areas as distinct biogeographic regions, which is rather tenuous in comparison with other regions of the upper rio Paraná basin defined herein.

**14. Headwaters of rio Paranaíba.** The rio Paranaíba has its headwaters in the extreme northeast of the upper Paraná basin, where it forms an intricate divide with the São Francisco basin. The divide is an assemblage of small elevated formations with various local names (*e.g*., Serra da Tiririca, east of Paracatu, MG; Chapada da Ponte Firme, north of Patos de Minas, MG; Chapadão dos Pilões, west of Guarda-Mor, MG; and others). Pavanelli, Britski (1999) were the first authors to acknowledge that the region possessed a fish assemblage distinct from the upper rio Paraná, with endemic elements. One of the species defining the region, *Hasemania nana*, is shared exclusively with the São Francisco basin and considered herein as evidence of past events of ichthyofaunistic interchange between adjacent basins. Other species endemic to the upper rio Paranaíba in the region delimited by the analysis are: *Creagrutus varii*, *Hypostomus yaku*, *Microlepidogaster arachas*, *Pituna brevirostrata*, *Rhinolekos britskii*, *R. garavelloi*, *Rineloricaria rodriquezae*, and *Simpsonichthys santanae*.

**15. Águas Emendadas.** This region contains one of the most distinctive ichthyofauna of the entire upper rio Paraná. The situation is similar to that of the upper rio Tietê, whose composition includes endemic elements along with species shared with neighboring basins. The headwaters of the rio São Marcos, right-bank tributary of the rio Paranaíba, share species with the rio Tocantins headwaters (*Moenkhausia aurantia*) and rio São Francisco (*Kolpotocheirodon theloura* and *Planaltina myersi*) (Aquino *et al*., 2009; Aquino, 2013). An emblematic case of the faunistic mixture in the region is that of *Hyphessobrycon coelestinus*, present in the headwaters of the three basins (Aquino, Carvalho, 2014). Fittingly, the headwaters of the three basins are physically very close in the region of the Planalto Central, between the State of Goiás and the Distrito Federal.

Besides a considerable faunal sharing with adjacent basins, the region also contains rich endemism, among which *Characidium onca*, *Hyphessobrycon balbus*, *Hasemania crenuchoides*, *Hypostomus crulsi*, *Phenacorhamdia unifasciata*, and *Simpsonichthys boitonei*.

**16–18. Right-bank tributaries of the upper Paraná.** The analysis delimited three distinct regions in the headwaters of right-bank tributaries of the upper rio Paraná. Those regions are discussed together here, not having particularly distinct biogeographic histories as per current knowledge. Right-margin tributaries of the upper rio Paraná are shorter in length than those on the left bank. Except for rivulid species, they have few endemic elements, except for the headwaters of some tributaries of the rio Paranaíba. They do not have any taxa shared exclusively with the rio Araguaia basin, and only three elements shared with the rio Paraguai drainage: *Astyanax lineatus*, *Hyphessobrycon herbertaxelrodi*, and *Jupiaba acanthogaster*. The first species is broadly distributed in the Paraguai basin, occurring also in some tributaries of the rio Madeira, such as the Guaporé and Mamoré (Dagosta, de Pinna, 2019). In the upper rio Paraná it was recorded in the headwaters of rivers Anhanduí and Pardo (Fig. 8).

*Jupiaba acanthogaster* is widespread in the upper rios Paraguai, Tapajós, Xingu and Araguaia-Tocantins drainages (Ribeiro *et al*., 2013). In the upper Paraná it was recorded only in the upper reaches of rio Sucuriú and rio Ivinhema (Lopes *et al*., 2020). As discussed by Ribeiro *et al*. (2013), the presence of the species in the Paraguai basin is associated with a capture event from the rio Tapajós. The same explanation accounts for the presence of this rheophilic species in the fringes of the upper rio Paraná, probably originating from the rio Paraguai.

In the upper rio Paraná, *Hyphessobrycon herbertaxelrodi* is known exclusively from the rio Aporé (FRC, pers. obs.). Nonetheless, the species occurs in the middle and lower sectors of the Aporé basin, and is not rheophilic. The species is also very popular in the aquarium trade, and maybe its presence is due to human dispersal, rather than indicative of a common biogeographic history between the upper rio Paraná and rio Paraguai. Additional collecting in the region of Serra de Maracaju, the hydrographic divide between those basins, may offer new data to better understand this case, and also provide additional examples of exclusive taxon sharing in the drainages.

Remaining areas of right-bank tributaries recognized in the analysis owe their delimitation due mainly to species of Rivulidae. Region 16 comprises sectors of the upper rio Claro and rio dos Bois, both in the State of Goiás, and is delimited by the presence of four endemic species of *Melanorivulus*: *M. faucireticulatus* (rio Claro), *M. nigromarginatus* (middle rio Corrente), *M. pinima* (rio Claro and rio dos Bois), and *M. illuminatus* (rio dos Bois).

Region 17, on the other hand, comprises the headwaters of rios Corrente, Aporé and Sucuriú, and is delimited by four endemic siluriforms (*Corumbataia liliai*, *C. lucianoi*, *Imparfinis lepturus*, and *Neoplecostomus watersi*), plus five endemic rivulids (*Melanorivulus formosensis*, *M. rutilicaudus*, *Simpsonichthys margaritatus*, *S. nigromaculatus*, and *S. parallelus*). Finally, region 18 includes the headwaters of the rio Pardo and is defined by the occurrence of *Astyanax lineatus*, *Melanorivulus egens*, *M. interruptus*, and *M. rossoi*.

## DISCUSSION

**A distinct ichthyofauna.** The fish families with greatest diversity in the upper rio Paraná are somewhat as distinct as in other neotropical basins, for example, the Amazon basin. Amazonian rivers are strongly dominated by Characidae (Dagosta, de Pinna, 2019), which alone represent ¼ of the entire fish diversity, while in the upper rio Paraná basin the predominant family is Loricariidae. Such distinction does not seem to be a result of taxonomic bias. The predominance of loricariids may be related to the fact that the upper rio Paraná basin drains mostly highlands, favoring thus the diversification of rheophilic lineages.

Another important difference is the extremely reduced number of Cichlidae in the upper Paraná, with only eight native species. In the Amazon basin, cichlids represent the third most diverse family, with almost 10% of all its fish species in the basin, while in the upper Paraná cichlids are less than 3% of the total. Other taxa with limited representation in the upper rio Paraná basin, yet exhibiting substantial diversity within the lowland Amazonian regions, are doradids, auchenipterids, hemiodontids, and gymnotiforms.

The most species-rich genus in the upper Paraná is *Melanorivulus*, with 23 valid species. This is a surprising high number, representing over one-third of the known diversity of a genus broadly distributed in South America, including most of Brazil, in addition to Argentina, Bolivia, and Paraguay. The Amazon basin, for example, has 27 *Melanorivulus* species recorded so far (Dagosta, de Pinna, 2019). The next most diverse genera in the upper Paraná are *Hypostomus* (21 spp.), *Trichomycterus* (20 spp.), and *Neoplecostomus* (10 spp.), all representing rheophilic lineages. The former two genera are particularly striking when compared to their numbers in the Amazon, with 30 species of *Hypostomus* and 17 species of *Trichomycterus*. In the case of *Trichomycterus*, such a difference is probably due to biogeographic reasons. As noted by Dagosta, de Pinna (2019), that genus is typical of South American highlands and is present only in peripheral areas of the Amazon basin.

In the case of *Hypostomus*, the situation may be related to the poor taxonomic knowledge about the genus, which probably underestimates the number of species in both basins. However, it is intriguing to note that although there is a low number of *Hypostomus* species in the Amazon basin, there is a substantial diversity of species from other Loricariidae genera, particularly within the Ancistrinae. Conversely, in the upper rio Paraná basin, the situation is entirely opposite: there are very few species and other genera of Loricariidae (especially within Ancistrinae), but a significant abundance of *Hypostomus* species. This pattern suggests that *Hypostomus* has undergone diversification in the upper rio Paraná, occupying ecological niches that are typically filled by ancistrins in the Amazon. Lujan *et al*. (2011) demonstrated distinct loricariid lineages that partitioned guilds as consumers of woody debris. A similar process might be associated with the diversification of *Hypostomus* in the upper rio Paraná. Another comparable situation applies to *Pimelodus*, which exhibits its highest diversity within the rio La Plata basin, but only a few other lineages of pimelodids inhabit the region compared to the Amazon basin.

The number of different lineages in the upper rio Paraná is also noteworthy. Most of its species are concentrated in small genera, with almost half of them with a single species in the basin. In total, there are 125 genera for 341 species, making an average of 2.7 species/genus. The equivalent average in the Amazon basin is twice that and most species are concentrated in a few mega-diverse genera, like *Corydoras*, *Apistogramma*, *Hyphessobrycon*, and *Moenkhausia*, etc. In the upper Paraná, only four genera (*Melanorivulus*, *Trichomycterus*, *Hypostomus*, and *Neoplecostomus*) contain ten or more species. Such pattern demonstrates a low frequency of sympatry among related lineages, a common phenomenon in South American highlands (Lima, Ribeiro, 2011; Albert *et al*., 2020).

Another metric that reveals the limited number of lineages in the upper rio Paraná is the presence of only six orders. None of the orders of fishes in the Peripheral Division of Myers (1938) is present, not even those which are present in the middle-lower Paraná, immediately downstream from the ancient Sete Quedas falls, such as Atheriniformes, Beloniformes, Clupeiformes, Myliobatiformes, Acanthuriformes, and Carangiformes. Such lineages colonized South America via marine invasions, and their diversification took place between the Eocene and Middle Miocene (~45–13 Ma) (Bloom, Lovejoy, 2017). Additional remarkable absences in the upper Paraná are the families Hypopomidae and Rhamphichthyidae, typical components of South American lowlands which have an older biogeographical history in the continent, unrelated to marine invasion events. Such absences may translate into a long period of separation between the upper Paraná and the lowland regions of South America heavily populated with those lineages.

Finally, it is curious that the upper rio Paraná virtually lacks any native species of *"Hemigrammus"* or *"Hyphessobrycon"* in its main channel, with the latter present only in the periphery of the basin, resulting from faunistic the former, having as its only possible representative a species from the *Moenkhausia bonita* / *Hemigrammus marginatus* clade (see further details in Tab. 1) and the latte exchanges with neighboring basins. Those genera are among the most highly diverse in Characidae and largely responsible for the predominance of that family in the Amazonian region. Their absence in the main channel of the upper Paraná may explain, in part, the reduced number of characids in that basin when compared to many other South American drainages.

**Probably non-native species.** Compiling a list of native species from the upper rio Paraná region can prove to be a rather challenging task. Given the extensive urbanization of the area and the long-standing alterations in its biota, it can be difficult to understand the nature and origin of some of its species. In such cases, historical records from literature and scientific collections have been decisive in solving these issues. Below are presented some species that require a more in-depth discussion about their origin in the upper rio Paraná basin.

***Bujurquina vittata*** **(Heckel, 1840) and** ***Hypostomus*** **cf.** ***latirostris*** **(Regan, 1904).** These species were recorded in the upper rio Paraná only in the Lago do Amor, a body of water located within the campus of the Universidade Federal de Mato Grosso do Sul, Campo Grande, the capital of the State of Mato Grosso do Sul. Carvalho, Eduardo (2022) argue that these records are natural, as the region is close to the headwaters of the rio Paraguai. Although headwaters of the upper rio Paraná and rio Paraguai basins are close to each other, they are separated by the Serra de Maracaju, which act as an effective barrier for fish fauna, as few reliable examples of shared species between the basins in this region exist (*e.g.*, *Jupiaba acanthogaster*, see Lopes *et al*., 2020). It is also noteworthy that the species in question are not rheophilic, the latter being generally more prone to the consequences of headwater capture due to their distribution restricted to upstream regions. The area around Campo Grande is well sampled, but additional records of these species have not been found. It is important to remember that urban ecosystems are hotspots for biological invasions, as they are a focus of species release (Gaertner *et al*., 2017), which seems to be the case with the Lago do Amor. In this study, these species are tentatively considered non-native until further studies can be conducted.

***Corydoras nattereri*** **Steindachner, 1876.** The species was described from the Rio de Janeiro and its records in the upper Paraná are from Langeani *et al*. (2007) and Marceniuk *et al*. (2011). The first collection records of the species in that basin date back to the late 1990s, from a stream in the Taiaçupeba reservoir tributary, which is part of the upper rio Tietê. Luiz Wada (pers. comm. to FCTL, 2014) mentioned that the species was intentionally introduced in the upper rio Tietê by an aquarium fish dealer. It is noteworthy that Langeani (1989), a comprehensible survey of the ichthyofauna of the upper rio Tietê, did not record the species, which may suggest that the species was introduced and established after that time, or else that the distribution of the species in the basin is now very restricted at the moment. In this study, the species is tentatively considered non-native pending further investigation.

***Hemigrammus parana*** **Marinho, Carvalho, Langeani & Tatsumi, 2008.** Originally described by Marinho *et al.* (2008) from the upper Paraná, this species was only first recorded in the basin early 2000s. Since then, it has been frequently and abundantly recorded, with some of lots used to described the species containing hundreds of specimens. The species has been reported in the rio Araguaia-Tocantins basin and there are very similar morphotypes in the rio Teles Pires and in the upper rio Xingu basins. Considering that the species is quite common where it occurs, it is striking that it was not sampled in the upper rio Paraná during many years of ichthyological inventories. In the basin, its distribution is restricted to stretches above the confluence of the rio Tietê with the rio Paraná, which is a typical distributional pattern of some invasive species in the upper Paraná that likely originate from the Araguaia-Tocantins basin. Thus, we consider that this species is very likely an introduction from the Araguaia-Tocantins with an undetectable origin. Ironically, the species is named after the basin (*Hemigrammus parana*), where it is probably invasive. More information on species with a similar history of introduction is presented in the "Discussion - The threat of non-native species" section.

***Hyphessobrycon eques*** **(Steindachner, 1882).** Ota *et al*. (2018) conducted the first study that questioned whether the species is native to the upper rio Paraná. Although some lots documented its presence in the basin in the 1970s, before the construction of Itaipu (MZUSP 28629: collected in 1974; MNRJ 26275: collected in 1975; ZUEC 4628: collected in 1975), all these records refer to the same location in the city of Botucatu, São Paulo state. *Hyphessobrycon eques* did not appear in the CETESB surveys in the reservoir region neither in any ichthyological study in the basin before the construction of Itaipu. Since the species is quite common in the aquarium trade, at least these old records in Botucatu - SP likely relate to such activity. The species seems to possess a great adaptive capacity, as it has successfully established itself in other basins such as the rio Paraíba do Sul, rio Doce, and rio São Francisco. Molecular studies at the population level may indicate the most likely scenario that explains the presence of the species in the upper Paraná. Currently, we tentatively consider the species to have been introduced.

***Gymnogeophagus*** **cf.** ***setequedas*** **Reis, Malabarba & Pavanelli, 1992.** Paratypes of *G. setequedas* (MZUSP 42715) were collected at Missal, PR, located upstream from the Itaipu dam, but downstream from the Sete Quedas falls. Therefore, in Langeani *et al*. (2007), the record of this species in the upper Paraná is no longer valid, as it has not been collected in the basin ever since. More recently, *Gymnogeophagus taroba* Casciotta, Almirón, Piálek & Říčan, 2017 was described from the rio Iguaçu, which also flows downstream from the Sete Quedas falls. Specimens of *Gymnogeophagus* in the Itaipu surroundings have been identified as *G. taroba*. Lot MCP 45929 is a juvenile, very similar to G. *setequedas*, and represents the first record of the genus in the upper Paraná, above Sete Quedas falls. The species is tentatively considered as non-native here, as the Itaipu region is very well sampled and, until now, no records have been made except for the MCP 45929.

***Poecillia hollandi*** **(Henn, 1916).** The species was described from the rio São Francisco, with occurrences also in the rio Parnaíba basin (Figueiredo, 1997). In the upper Paraná, there are records from Casatti *et al*. (2006), Langeani *et al*. (2007), Ota *et al*. (2018), and Reis *et al*. (2020). In collections, the oldest records date back to the mid-2000s. It is important to note that *Pamphorichthys* was reviewed by Figueiredo (1997), who did not present any record in the upper rio Paraná. The known distribution of the species in the basin is associated with the main channel of the rio Paraná, with some records in the lower rio Grande and rio Tietê. Such a restricted distribution pattern to the channel is typical of some invasive species, discussed in more detail in the section "Discussion - The threat of non-native species". Species identification is also uncertain, given the difficulty in separating it from *Poecillia araguaiensis* (Costa, 1991), which further complicates understanding of the species' origin. Given so many uncertainties about the taxon, the species is provisionally considered non-native until further studies elucidate these issues.

***Moenkhausia* cf. *gracilima* Eigenmann, 1908.** This species was described from "Serpa, rio Amazonas", and is widely distributed in the rio Amazonas lowlands, rio Madeira, rio Tapajós and rio Trombetas basins. Despite this range of distribution, there are records of populations very similar to *M. gracilima* in the upper rio Paraná. Some of them were misidentified as *Hemigrammus marginatus* Ellis, 1911 (*i.e*., upper rio Paraná floodplain) (Ota *et al*., 2018), a species currently restricted to the rio São Francisco basin and rivers of Northeastern Brazil (Ota *et al*., 2015). Marinho, Langeani (2016) speculated the possibility that these populations belong to a new species, but emphasized the need for more investigation, as some characters overlap those from the populations from the rio Amazonas basin. Therefore, the species is identified as *M*. cf. *gracilima*, and provisionally considered herein non-native until new studies provide more information to solve this question.

***Poecilia vivipara* Bloch & Schneider, 1801.** This species was described from Suriname, with wide distribution in South America, extending from Venezuela all along the coast to the río de La Plata, in Argentina (Lucinda, 2003). In the upper rio Paraná, there are some records in the upper rio Tietê from the 1960s–70s, but it was introduced in various Brazilian regions as a mosquito control policy (*cf*. Azevedo-Santos *et al*., 2016), which led several authors to consider the species as non-native in the basin (*e.g*., Langeani *et al*., 2007). Molecular studies may help to understand if any of the populations in the upper rio Paraná are native. Thus, the species is considered here as provisionally non-native.

***Triportheus nematurus* (Kner, 1858).** Originally it was described from the rio Cuiabá, rio Paraguai basin. Besides this basin, it also occurs naturally in the lower rio Paraná basin (Portugal, 1990). There are two records of the species, theoretically, upstream from the Sete Quedas falls before the construction of Itaipu. Based on these records, the species could be considered native to the upper rio Paraná basin. However, there is strong evidence of mistakes in the locality of these collections, and they should be considered doubtful. Both collections were made by CETESB (Companhia Ambiental do Estado de São Paulo) during an ichthyofaunal survey in the region of influence of the Itaipu construction. The lot MZUSP 19854 was collected in "rio Paraná, Porto Verde, Paraná, Brazil" under the field number CET77070005. Only this species was collected in this field number, but other species were collected in the Porto Verde - Paraná under different field numbers. It is noteworthy that among the collected species, there are fishes that do not naturally occur in the upper rio Paraná basin, such as *Mylossoma duriventre* (Cuvier, 1818) (MZUSP 20375), *Potamotrygon amandae* Loboda & Carvalho, 2013

(MZUSP 13361), *Hypophthalmus edentatus* Spix & Agassiz, 1829 (MZUSP 13360), and *Pseudohemiodon laticeps* (Regan, 1904) (MZUSP 25350). The same pattern occurs with lot MZUSP 21086, which has the locality "rio Paraná, acima de Sete Quedas. Período da coleta: 1977 a 1980, Guaíra, Paraná, Brasil" and the field number CET77000001. Several other species were sampled under the same field number, among which *Plagioscion squamosissimus* (Heckel, 1840) (MZUSP 21654), *Diapoma guarani* (Mahnert & Géry, 1987) (MZUSP 21075), and *Potamorhina squamoralevis* (Braga & Azpelicueta, 1983) (MZUSP 21092) can be highlighted as not native to the upper Rio Paraná. In other words, both lots MZUSP 19854 and MZUSP 21086 appear to have been sampled below Sete Quedas and are not reliable records of *Triportheus nematurus* in the upper rio Paraná River before the submersion of Sete Quedas. It should be noted that the lot MZUSP 21092 of *Potamorhina squamoralevis* was examined in the revision of the genus by Vari (1984), and the author considered it to be below Sete Quedas. Portugal (1990) examined the aforementioned lots of *Triportheus nematurus* and still considered the species not naturally occurring in the upper Paraná. It is also worth considering the extensive history of ichthyological studies in the upper Paraná without any record of the species before the construction of Itaipu. Currently, the species has dozens of records in the basin after this event, which also suggests that the most likely scenario is that the locality of lots MZUSP 19854 and MZUSP 21086 must be incorrect. Therefore, in the present study, the species is provisionally considered non-native.

**Conservation.** Despite its major economic and biodiversity relevance, the fish fauna of the upper Paraná basin is undergoing a fast-growing collapse in the last decades, caused by intense anthropic deterioration of the landscape and loss of natural habitats, two of the main threats to freshwater organisms (Agostinho *et al*., 2007b). The main factors in that destruction are fast and uncontrolled urban expansion, deforestation, obstruction of natural water courses by dams, and water pollution by pesticides, industrial residues, and domestic sewage.

Practical and financial limitations make it impossible to preserve all populations of all species everywhere. Therefore, it is necessary to have priority of certain regions over others for conservation purposes. Accurate determination of priorities requires: (1) good knowledge about biodiversity and its geographical distribution; (2) using biogeography as a tool to understand patterns of distribution of organisms and to build strategies that minimize threats and maximize conservation of both biodiversity and habitats (Margules, Pressey, 2000; Roberge, Angelstam, 2004).

Biodiversity loss in freshwaters is greater than in terrestrial or marine ecosystems (Nogueira *et al*., 2010). Given that, plus their great diversity, the preservation of freshwater habitats should be a priority in environmental conservation, especially in a megadiverse country like Brazil (Strayer, Dudgeon, 2010). Unfortunately, that is not the case at all. Historically, aquatic organisms have not been considered in the delimitation of preservation areas, in large part due to insufficient data on their taxonomy and geographic distribution (Heilpern, 2015; Dagosta *et al*., 2021).

**Priority areas for conservation.** Results of the present biogeographic analyses, when compared with existing areas of environmental protection (Fig. 40) and those of threatened species (Fig. 41), show that the diversity of fishes in the upper rio Paraná is alarmingly vulnerable. Existing protected areas are ineffective in preserving the fish assemblages with the highest endemism rates in the basin. This happens because areas for protection are delimited according to biodiversity patterns of terrestrial organisms, which do not necessarily overlap with those of the aquatic fauna. Most of the area under protection in the basin is concentrated in a single biogeographical region ("Lowlands of the upper rio Paraná"), leaving most of the rich and heterogeneous diversity of fishes of the upper rio Paraná largely unprotected.

As shown in Fig. 35, the majority of the species in the basin is concentrated in lowland regions, near the main channel of the rio Paraná and in large left-bank tributaries. However, solely the Federal Reservation "Área de Proteção Ambiental das Ilhas e Várzeas do rio Paraná" and the "Parque Estadual das Várzeas do rio Ivinhema", both in the extreme south of the basin, have significant coverage and association with lowlands and to the major water courses of the basin (Fig. 40). It is clear that the bulk of the biodiversity of fishes in the upper rio Paraná has inadequate protection.

Although there are some federal and local-state preserves in the periphery of the basin, where endemic elements are concentrated, their dimensions and position are insufficient to warrant protection to those lineages exclusive to the drainage. A single biogeographic region, area "13. Águas Emendadas", is located completely inside a complex of protected areas called "Floresta Nacional de Brasília" and "Área de Proteção Ambiental da bacia do rio São Bartolomeu". Other four bioregions have part of their

**FIGURE 40** | Protection areas in the upper rio Paraná basin. Light pink (federal reserves), green (state reserves), black (municipal reserves).

area protected, such as "6. upper rio Sapucaí" and "7. upper rio Grande", which have their headwaters within the "Área de Proteção Ambiental da Serra da Mantiqueira"; "10. Serra da Canastra", with its right-bank margin on the rio Grande within "Parque Nacional da Serra da Canastra"; and "15. upper rio Corrente, Aporé e Verde", where the origin of the rio Corrente is located in the "Parque Nacional das Emas".

Tiny portions of biogeographic area "5. upper rio Tietê" are covered by the "Parque Estadual da Serra do Mar" and by the "Parque Estadual de Itapetinga"; and of area "4. Ponta Grossa Arch II" is in the "Parque Estadual Nascentes do Paranapanema". Remaining regions with endemic fish faunas are completely outside of any protected area. Again, it is very clear that current areas of environmental protection are insufficient to warrant the preservation of the complex fish fauna of the upper Paraná system.

**Threatened species.** The upper rio Paraná has 33 species under some form of threat (Tab. 1). This corresponds to 10% of all species in the basin, an extremely high proportion when compared to other Brazilian drainages. The rio Paraguai basin, for example, has only 1% of its fauna threatened (FRC, pers. obs.). Most of the threatened species belong to the Siluriformes and Cyprinodontiformes, with 11 species each, followed by the Characiformes with seven, Gymnotiformes with three and Cichliformes with one. The single family with most threatened species is Rivulidae, especially the genera *Melanorivulus* with five species and *Simpsonichthys* with four.

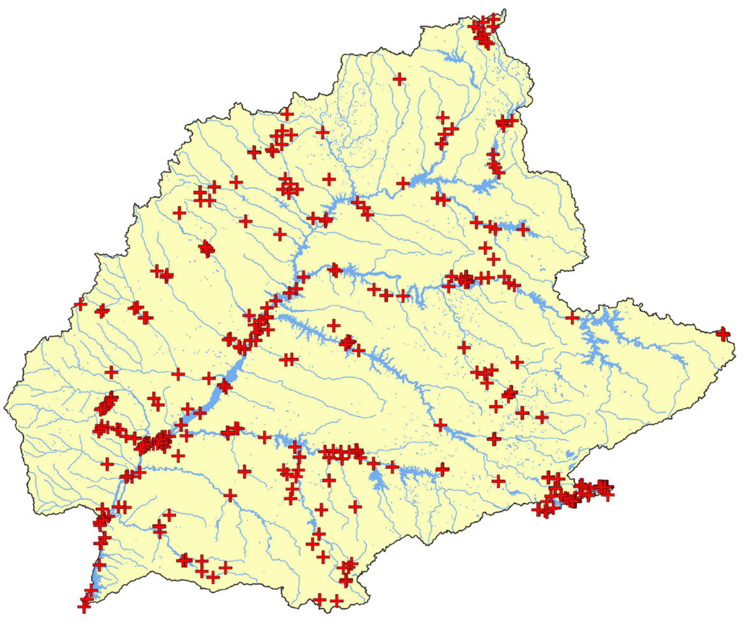


**FIGURE 41** | Records of threatened species in the upper rio Paraná basin.

The concept of biome is not particularly enlightening for freshwater fish because their evolutionary and biogeographic history is more closely related to the history of hydrographic basins than to terrestrial environments. Still, it is possible to identify some biome-related patterns with conservation outcomes (Fig. 42). Comparing the outlines of the biomes Cerrado e Mata Atlântica in the upper Paraná against the occurrence of threatened species, ten species occupy both terrains, 12 exclusively the Cerrado and 11 only the Mata Atlântica. Species present in both biomes are typically broadly-distributed inhabitants of large rivers. The Cerrado contains all threatened rivulids of the upper rio Paraná, plus two species of *Hasemania* and one of *Cambeva*. The biome Mata Atlântica is far more diversified in its threatened fauna, with species belonging to eleven different genera, mainly characids and loricariids.

Some general patterns emerge when the distribution of threatened species is plotted on a map of the upper Paraná basin (Fig. 41). There is a pronounced concentration of records of threatened species in some regions, but some of those need to be interpreted with reservation because they are accumulations of points representing few species with broad distributions. In such cases, the concentration of records of endangered is less significant, since those species occur in other regions. Greater conservation attention should be directed towards threatened species that are not found anywhere else.

There are a cluster of records immediately upstream from Sete Quedas falls to the mouth of rio Ivinhema. They are nearly all records of *Brycon orbygnianus*, *Myloplus tiete* and *Pseudoplatystoma corruscans*. Another cluster of records of threatened species also associated with the main channel of the rio Paraná exists in the area of influence of the reservoirs of Jupiá and Ilha Solteira, both of which predominantly of *Brycon orbygnianus*. In the same region there are several records of *Crenicichla jupiaensis* and of two species of

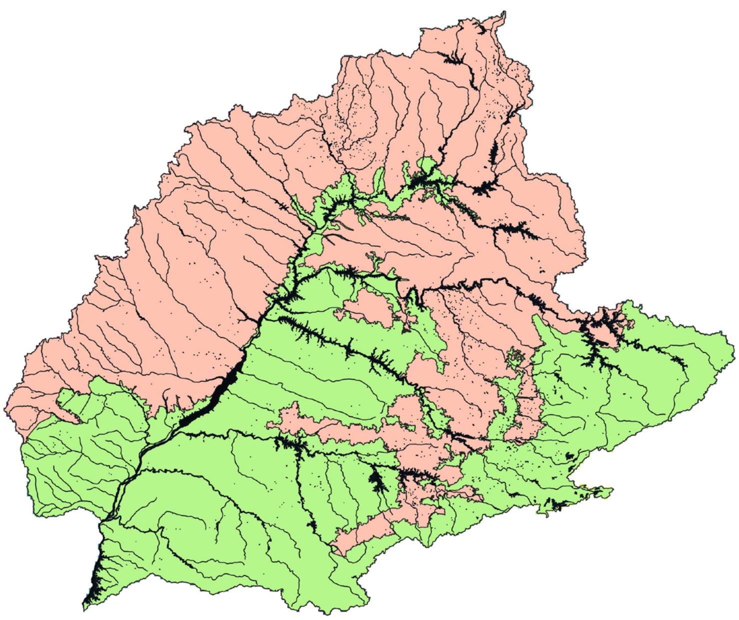


**FIGURE 42** | Biomes of the upper rio Paraná: Cerrado (light orange) and Mata Atlântica (light green).

Gymnotiformes threatened in the basin, with *Sternarchorhynchus britskii* and *Tembeassu marauna* also known exclusively from that region. Other concentration of records is associated with the Salto Grande reservoir in the rio Paranapanema, with many points of *Myloplus tiete*, *Pseudoplatystoma corruscans* and *Steindachneridion scriptum*; and in the area of influence of UHE Volta Grande in the Rio Grande, with records of *Brycon orbygnianus*, *Myloplus tiete*, and *Steindachneridion scriptum*. Two clusters of records with a more restricted distribution are the upper Tietê with, *Cambeva paolence*, *Heptapterus multiradiatus*, *Hyphessobrycon duragenys*, *Pseudotocinclus tietensis*, *Phallotorynus fasciolatus*, and *Spintherobolus papilliferus*; and the region of Águas Emendadas, with *Hasemania crenuchoides*, *Simpsonichthys boitonei*, and *S. santanae*.

In order to better understand where the threatened species of the upper Paraná are concentrated, an analysis of species richness was conducted exclusively with threatened species. Results indicate that four regions concentrate most of the threatened species: main channel of the rio Paraná near Sete Quedas; sector of the rio Paraná near Jupiá and Ilha Solteira; headwaters of rio Tietê; and Águas Emendadas (Fig. 43). As discussed previously, the two former regions concentrate mostly those species with broader distributions within the basin, and the two latter ones those species with narrow distributions. The region near Sete Quedas is broadly covered by the Federal Reservation "Área de Proteção Ambiental das Ilhas e Várzeas do rio Paraná" and "Parque Estadual das Várzeas do rio Ivinhema". A similar situation is that of Águas Emendadas, covered by the "Floresta Nacional de Brasília" and the "Área de Proteção Ambiental da bacia do rio São Bartolomeu". No protected areas exist for the remaining two regions which concentrate the occurrence of many threatened species.

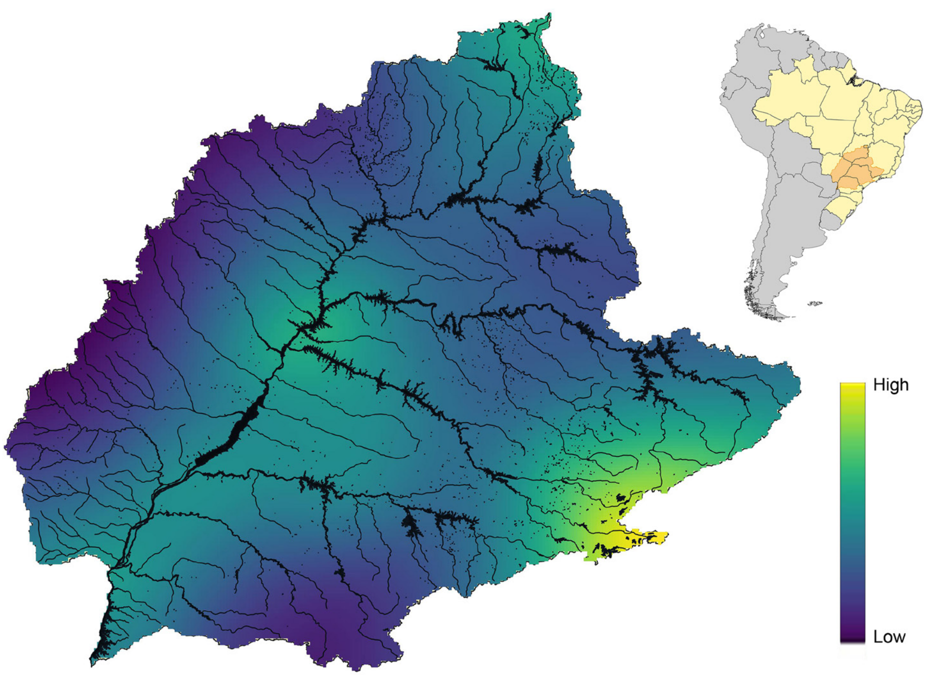



**FIGURE 43** | Concentration and distribution of threatened species in the upper rio Paraná basin. Yellowish colors indicate a greater concentration of endangered species, whereas bluish shades of colors indicate a lesser concentration of endangered species.

We recommend herein a higher level of protection to the region of the upper rio Tietê, which is both a biogeographic region distinct from the rest of the upper Paraná (Fig. 39), and also holds a large amount of threatened species with very narrow distributions. The Fig. 40 clearly shows that the protected areas "Parque Estadual da Serra do Mar" and "Parque Estadual de Itapetinga" cover a negligible portion of that bioregion. Another recommendation is that an area of protection be established for the region of influence of the Jupiá and Ilha Solteira reservoirs, which concentrate many records of threatened species typical of the main channel of the rio Paraná, some of which exclusive and lacking any form of protection.

**The threat of non-native species.** According to Vitule *et al*. (2009), introductions of non-native fish species have multiple negative effects on native faunas, like predation, competition, pathogen and parasite transmission and the possibility of hybridization. Translocation of fish to locations outside of their native areas may promote biotic homogenization, decreases functional diversity, and threaten native diversity by changes in ecosystemic processes (Vitule, Pozenato, 2012; Santos *et al*., 2023). One of their most deleterious effects is the replacement of endemic elements with common and generalist species. This is exactly the effect observed in many areas of the upper Paraná, a phenomenon particularly well-documented in the basin (*cf*. Orsi, Agostinho, 1999; Júlio Júnior, 2009; Cavaretto *et al*., 2020) and one of the great challenges for the conservation of its fishes.

According to Gubiani *et al.* (2018), the upper rio Paraná is the basin in neotropical region with the highest number of non-native species. Herein, we reinforce this trend by significantly increasing the number to 128 documented non-native species (includind three hybrids), which significantly surpasses the figures reported in previous publications. The basin hosts non-native species from 14 distinct orders, which is more than twice the six native orders of the basin. As a comparison, the entire rio Parnaíba basin, one of the largest drainage in the Brazilian northeast, has a total of 139 native species (Ramos *et al*., 2014). A comparison with the non-native fishes in the Amazon basin is more striking still. Doria *et al*. (2021) estimated 41 non-native Amazonian species, across a territory, which covers Brazil, Peru, Bolivia, Ecuador, Venezuela, and Colombia. This shows the alarming situation of the upper rio Paraná, which has probably the largest number of non-native species of any Neotropical basin. Such numbers are second only to the 160 non-native species of the Mississipi and Great Lake regions in the USA (Ricciardi, 2001; Rasmussen, 2002).

The numbers above are expected to further aggravate in the future, due to two reasons. First and most obviously, because a list of non-native species potentially never stabilizes, with the established ones becoming permanent and additional ones introduced at any moment. A second reason is ecological and relates to the "invasional meltdown" model proposed by Simberloff, Von Holle (1999), according to which ecosystems become increasingly more prone to invasions, as the cumulative number of invaders also increases and generate facilitating interactions that potentialize their impact. As the number of invaders increases, so does the vulnerability of the ecosystem to other threats such as disease, climatic change, and further invasions, all leading to the reduction or extinction of native species.

Factors responsible for the introduction of species in the upper Paraná are multiple, diffuse, and are associated with specific taxa in Tab. 2. At least two main routes of allochthonous species can be recognized (Fig. 44): a southern route resulting from the building of the Itaipu reservoir; and a northern route from the Araguaia-Tocantins basin. In general, species which colonized the upper Paraná via Itaipu have a denser concentration of records in the southern portion of the basin (Figs. 45E–H), while the opposite happens with species invading from the north (Figs. 45A–D). Also importantly, allochthonous species colonize foremost the main channels of large rivers, less so than peripheral areas and smaller tributaries (Fig. 45).

The construction of the Itaipu dam is responsible for most invasions in the upper Paraná, including multiple and widely disjunct lineages of neotropical fishes, such as Myliobatiformes, Clupeiformes, Characiformes, Siluriformes, Beloniformes, Cichliformes, and Carangiformes. Invading species are also broadly variable in body sizes, including large forms such as *Pterodoras granulosus* and *Pseudoplatystoma reticulatum*

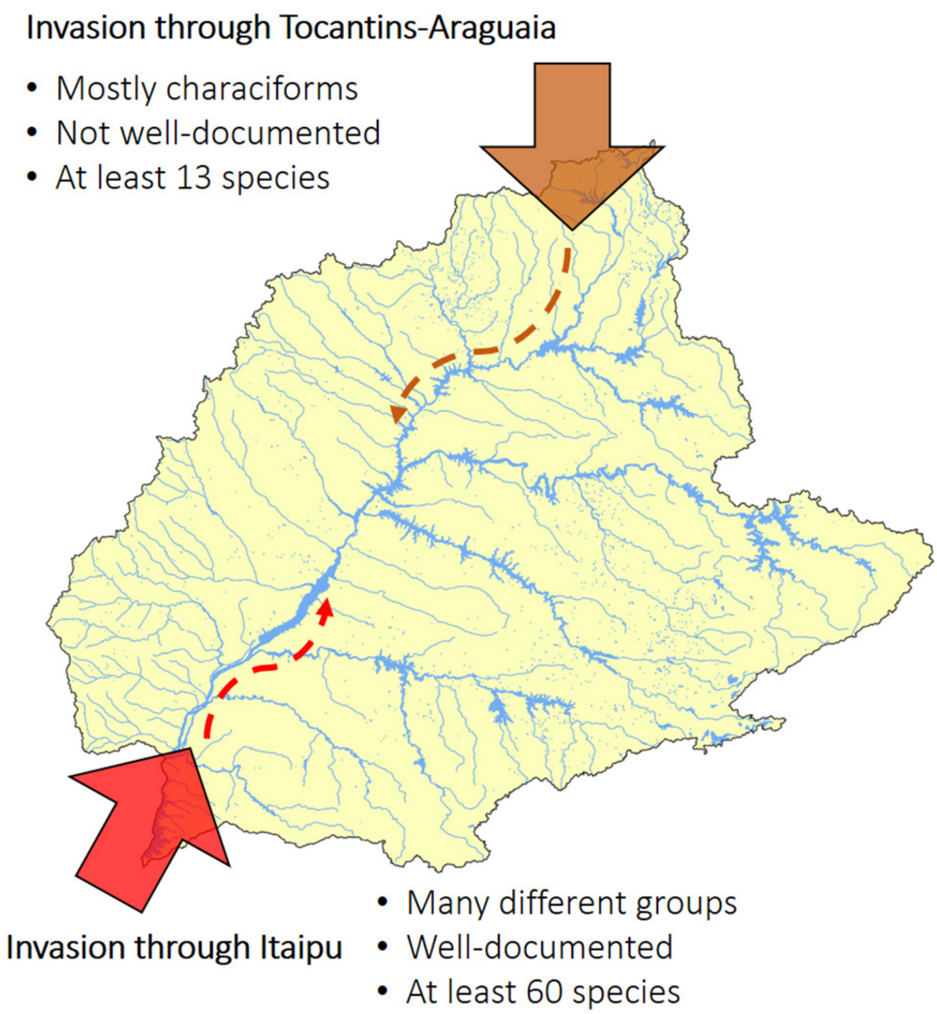



**FIGURE 44** | The Main pathways for the entry of invasive species in the upper Paraná through neighboring basins: the southern (red arrow) and northern (brown arrow) routes.

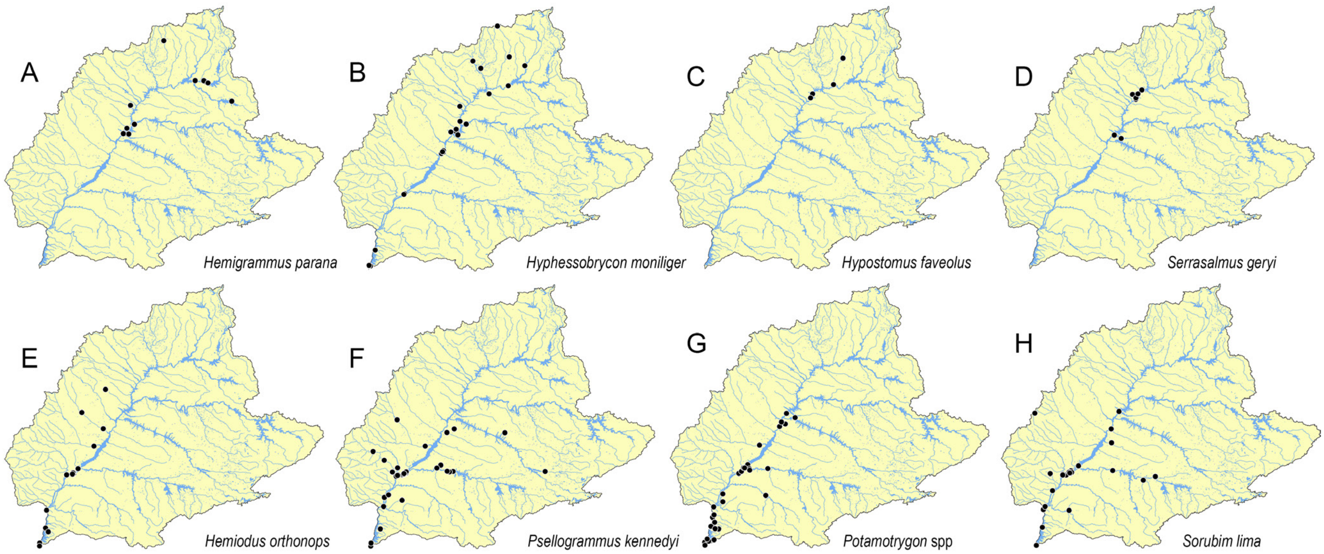



**FIGURE 45** | Examples of invasive species that have potentially colonized the upper rio Paraná via the northern route (**A–D**) and by the southern route (**E–H**). **A.** *Hemigrammus parana*; **B.** *Hyphessobrycon moniliger*; **C.** *Hypostomus faveolus*; **D.** *Serrasalmus geryi*; **E.** *Hemiodus orthonops*; **F.** *Psellogrammus kennedyi*; **G.** *Potamotrygon* spp.; **H.** *Sorubim lima*.

along with small ones as *Aphyocharax anisitsi* or *Psellogrammus kennedyi*. Besides, invading lineages cover a wide array of reproductive strategies and preferred habitats. Some invaders, such as *Sorubim lima* are migratory, while others like the cichlid *Crenicichla niederleinii* are sedentary. These examples demonstrate that the suppression of the old biogeographic barrier allowed a generalized invasion of species in the upper Paraná from the middle-lower Paraná, apparently largely unrestricted. Despite this, the upper Paraná region still lacks many of typical fish fauna elements that are found immediately downstream from Itaipu. The invasions in the region may also have been facilitated by the opening of the "Canal da Piracema" in 2002, which is a transposition system for the spawning of migratory species (Makrakis *et al*., 2007).

The expansion of the distribution of an assemblage of species by the suppression of a previous biogeographic barrier is called Biotic Dispersal (Platnick, Nelson, 1978), also known as mass coherent dispersal or concerted dispersal (Morrone, 2009). As pointed out by Dagosta, de Pinna (2017) the main consequence of biotic dispersal is the mixing of faunas and the ensuing historical reticulation of areas. This is precisely the case with Itaipu, which artificially allowed the geographic expansion of several different lineages that succeeded in trespassing the area of the ancient barrier, causing an historic admixture of biotas. The building of the Itaipu dam is a classic example of human-caused biotic dispersal.

Another wave of invasion is happening, or happened, in the northern portion of the upper rio Paraná. A large number of fish species from the Tocantins-Araguaia basin is recorded, starting in the 2000's, and have gradually increased since then. Curiously, in this case, most of the species belong to the Characiformes (Anostomidae, Characidae, Serrasalmidae) and Cichliformes (Cichlidae). The first record of an invasive rio Araguaia species in the upper rio Paraná basin were made by Pavanelli *et al*. (2007) with *Leporinus trigrinus*. Later, Zawadzki *et al*. (2008b) reported the occurrence of *Hypostomus faveolus* and *Hyphessobrycon moniliger* in the rio Meia Ponte, a tributary of the Paranaíba. These authors consider the occurrence as non-natural, attributable to the practice of releasing fishes from the rio Araguaia basin into the rio Meia Ponte basin by recreational fishermen and ranchers from the Goiânia city area (capital of Goiás State). In fact, there is no additional information which explains the presence of so many species of those basins in the upper Paraná. Some species of Cichlidae, like *Geophagus sveni* and *Satanoperca setepele* have spread so quickly and ubiquitously in reservoirs of the main channel of the upper Paraná that they received their own popular name (respectively "Porquinho" and "Zoiúdo"). More recently, employing *Leporinus tigrinus* as a model, Cavaretto *et al*. (2020) illustrate that this pattern of downstream invasion originating from the northern reaches of the basin indeed appears to be occuring. However, according to the authors, the underlying cause driving this southward dispersion of species along the course of the rio Paraná remains unsolved.

Another cause of invasion in the upper Paraná is aquaculture. In this case, there are introduced species which are not established, and are not recorded to breed naturally in the basin, as evidenced by the absence of juvenile specimens. This seems to be the case at least with the cyprinids *Ctenopharyngodon idella* and *Hypophthalmichthys nobilis*, and with the characiforms *Brycon hilarii* and *Colossoma macropomum*. The status of the remaining species is uncertain in some cases, while in others is very clear that the species are established in the basin. Some of them, like sciaenids, tilapias, and *Cichla*, have expanded their presence in the reservoirs of the upper Paraná to a degree where they are often the only abundant species in those places. Species introduced by aquaculture are usually well-known taxonomically and often originating from other continents, so that their allochthonous status is evident. On the other hand, they are selected for cultivation and thus particularly adaptable and fertile, quickly spreading throughout different environments and competing heavily with the local fauna.

Aquarium activities are also an important source of fish invasions in the upper Paraná. Again, species from other continents are readily identifiable as favorites in the aquarium trade, but some cases are not as obvious. For example, *Hyphessobrycon eques*, *Hyphessobrycon flammeus*, and *Gymnocorymbus ternetzi* could only be identified as invasive based on historic museum records. Those cases provide confirmation of the importance of long-term biological collections in the knowledge and preservation of the biota. In the case of *Hyphessobrycon eques* and *Gymnocorymbus ternetzi*, those two species have spread in such a way that they can be found in practically every tributary of the upper rio Paraná.

The presence of some invading species (*Aequidens plagiozonatus*, *Brachyhypopomus gauderio*, *Erythrinus erythrinus*, *Gymnotus pantanal*, and *Hoplerythrinus unitaeniatus*) may be associated with the discard of live baits in amateur and sports fishing (Orsi, Britton, 2014; Garcia *et al*., 2015). Those species are commonly sold in stores as live bait for predatory target-fish. Other species possibly in that category include *Prochilodus lineatus*, *Synbranchus* aff. *marmoratus* and other Gymnotiformes that are native to the upper Paraná but which are also found in other basins like the lower Paraná and Paraguai. Specimens from those populations, if released into the upper Paraná, may potentially interbreed with local populations and change the genetic makeup, masking biogeographic signals.

Finally, a final source of invaders in the upper Paraná is via mosquito-erradication programs. *Aedes aegypti* (Linnaeus, 1762), from Africa, is a vector of zika, chikungunya,

**TABLE 2 |** List of non-native fish species occurring in the upper rio Paraná basin. Asterisk represent probably non-native species which are discussed in further detail in "Probably non-native species" section of Discussion.

| Taxon | Record in the upper rio Paraná basin | Remarks | Origin |
|---|---|---|---|
| **MYLIOBATIFORMES** | | | |
| Potamotrygonidae | | | |
| *Potamotrygon amandae* Loboda & Carvalho, 2013 | Ota *et al.* (2018) *Potamotrygon motoro* (Müller & Henle, 1841) in Langeani *et al.* (2007) | | Itaipu |
| *Potamotrygon falkneri* Castex & Maciel, 1963 | Langeani *et al.* (2007) | | Itaipu |
| **OSTEOGLOSSIFORMES** | | | |
| Arapaimidae | | | |
| *Arapaima gigas* (Schinz, 1822) | Carvalho *et al.* (2015) | | Aquaculture |
| **CLUPEIFORMES** | | | |
| Dorosomatidae | | | |
| *Platanichthys platana* (Regan, 1917) | Langeani *et al.* (2007) | At least part of its distribution in the upper rio Paraná is due to migration upstream after Itaipu. There is another population in the upper rio Tietê whose origin is unknown | Itaipu / Piracema Channel |
| **CYPRINIFORMES** | | | |
| Cobitidae | | | |
| *Misgurnus anguillicaudatus* (Cantor, 1842) | Nobile *et al.* (2017) | Stray (introduced but not established) | Aquarism |
| Cyprinidae | | | |
| *Carassius auratus* (Linnaeus, 1758) | Meschiatti, Arcifa (2009) | Stray (introduced but not established) | Aquaculture |
| *Ctenopharyngodon idella* (Valenciennes, 1844) | Langeani *et al.* (2007) | Stray (introduced but not established) | Aquaculture |
| *Cyprinus carpio* Linnaeus, 1758 | Langeani *et al.* (2007) | | Aquaculture / Fish stocking CESP |
| *Hypophthalmichthys nobilis* (Richardson, 1845) | Langeani *et al.* (2007) MZUEL 15861 | Stray (introduced but not established) | Aquaculture |
| **CHARACIFORMES** | | | |
| Acestrorhynchidae | | | |
| *Acestrorhynchus pantaneiro* Menezes, 1992 | Ota *et al.* (2018) | | Piracema Channel |
| Anostomidae | | | |
| *Leporinus tigrinus* Borodin, 1929 | Ota *et al.* (2018) | | Probably from the rio Tocantins-Araguaia basin |
| *Leporinus unitaeniatus* Garavello & Santos, 2009 | Okubo (2022) | | Probably from the rio Tocantins-Araguaia basin |
| *Megaleporinus macrocephalus* (Garavello & Britski, 1988) | *Leporinus macrocephalus* in Langeani *et al.* (2007) | | Aquaculture and Piracema Channel |
| *Schizodon borellii* (Boulenger, 1900) | Ota *et al.* (2018) Autochthonous in Langeani *et al.* (2007) | According to Okubo (2022) the species need to be taxonomically confirmed in the upper rio Paraná | N/A |
| Bryconidae | | | |
| *Brycon amazonicus* (Agassiz, 1829) | Lima *et al.* (2017) | Stray (introduced but not established) | Aquaculture |
| *Brycon hilarii* (Valenciennes, 1903) | Langeani *et al.* (2007) | Stray (introduced but probably not established) | Aquaculture and Piracema Channel |

**TABLE 2** | (Continued)

| Taxon | Record in the upper rio Paraná basin | Remarks | Origin |
|---|---|---|---|
| Characidae | | | |
| Aphyocharacinae | | | |
| *Aphyocharax anisitsi* Eigenmann & Kennedy, 1903 | Autochthonous in Ota *et al.* (2018), but allochthonous in Langeani *et al.* (2007) | Recently, it has become increasingly common in the upper rio Paraná. Oldest lot of the species dating back to 1982 | Itaipu |
| Characinae | | | |
| *Charax leticiae* Lucena, 1987 | Menezes, Lucena (2014) | | Probably from the rio Tocantins-Araguaia basin |
| *Cynopotamus kincaidi* (Schultz, 1950) | Langeani *et al.* (2007) | | Itaipu |
| *Roeboides descalvadensis* Fowler, 1932 | Langeani *et al.* (2007) | | Itaipu / Piracema Channel |
| Cheirodontinae | | | |
| *Odontostilbe pequira* (Steindachner, 1882) | New record NUP 14338 | | Itaipu |
| *Serrapinnus calliurus* (Boulenger, 1900) | Ota *et al.* (2018) | | ? |
| *Serrapinnus kriegi* (Schindler, 1937) | Vicentim *et al.* (2019) | | ? |
| Stethaprioninae | | | |
| *Hemigrammus ora* Zarske, Le Bail & Géry, 2006 | Ota *et al.* (2018) | | Probably from the rio Tocantins-Araguaia basin |
| *Hemigrammus parana* Marinho, Carvalho, Langeani & Tatsumi, 2008* | Marinho *et al.* (2008) | | Probably from the rio Tocantins-Araguaia basin |
| *Hyphessobrycon eques* (Steindachner, 1882)* | Reis *et al.* (2020) | Tentatively considered as non-native. Further information can be found in the "Questionable native or non-native species" section. | Aquarism / Itaipu |
| *Hyphessobrycon flammeus* Myers, 1924 | Carvalho *et al.* (2014) | There are reports that ornamental fish breeders introducing the species in the upper rio Tietê for subsequent capture and sale | Aquarism |
| *Hyphessobrycon moniliger* Moreira, Lima & Costa, 2002 | Zawadzki *et al.* (2008b) | | Probably from the rio Tocantins-Araguaia basin |
| *Gymnocorymbus ternetzi* (Boulenger, 1895) | Langeani *et al.* (2007) | | Aquarism |
| *Moenkhausia australis* Eigenmann, 1908 | Ota *et al.* (2018) | | Itaipu |
| *Moenkhausia costae* (Steindachner, 1907) | Langeani, Rego (2014) | | Aquarism? |
| *Moenkhausia* cf. *gracilima* Eigenmann, 1908 | Ota *et al.* (2018) | | Probably from the rio Tocantins-Araguaia basin |
| *Moenkhausia forestii* Benine, Mariguela & Oliveira, 2009 | Ota *et al.* (2018) | | Itaipu |
| *Psellogrammus kennedyi* (Eigenmann, 1903) | Ota *et al.* (2018) | | Piracema Channel |
| Stevardiinae | | | |
| *Bryconamericus exodon* Eigenmann, 1907 | Langeani *et al.* (2007) | | Itaipu / Piracema Channel |
| *Diapoma guarani* (Mahnert & Géry, 1987) | Ota *et al.* (2018) | | Itaipu / Piracema Channel |
| *Knodus* aff. *moenkhausii* (Eigenmann & Kennedy, 1903) | Langeani *et al.* (2007) | | ? |
| Iguanodectidae | | | |
| *Bryconops melanurus* (Bloch, 1794) | New record (CITL 464) | | ? |
| Serrasalmidae | | | |
| *Colossoma macropomum* (Cuvier, 1818) | Langeani *et al.* (2007) | Stray (introduced but not established) | Aquaculture |
| *Colossoma macropomum* vs. *Piaractus mesopotamicus* | Casimiro *et al.* (2018) | Stray (introduced but not established) | Aquaculture |

**TABLE 2** | (Continued)

| Taxon | Record in the upper rio Paraná basin | Remarks | Origin |
|---|---|---|---|
| *Metynnis lippincottianus* (Cope, 1870) | Ota *et al.* (2018). *Metynnis maculatus* (Kner, 1858) and *M. mola* Eigenmann & Kennedy, 1903 in Langeani *et al.* (2007) | | Aquaculture |
| *Mylossoma duriventre* (Cuvier, 1818) | Autochthonous in Langeani *et al.* (2007) | | ? |
| *Pygocentrus piraya* (Cuvier, 1819) | New record (LIRP 7144) | | ? |
| *Serrasalmus geryi* Jégu & Santos, 1988 | Deprá *et al.* (2021) | | Probably from the rio Tocantins-Araguaia basin |
| *Serrasalmus marginatus* Valenciennes, 1837 | Ota *et al.* (2018). Autochthonous in Langeani *et al.* (2007) | | Itaipu / Piracema Channel |
| Triportheidae | | | |
| *Triportheus nematurus* (Kner, 1858)* | Langeani *et al.* (2007) | Further information can be found in the “Questionable native or non-native species” section. | Itaipu / Piracema Channel |
| *Triportheus signatus* (Garman, 1890) | Portugal (1990) | | Fish stocking CESP |
| Curimatidae | | | |
| *Curimatopsis myersi* Vari, 1982 | Vicentim *et al.* (2019) | | ? |
| *Cyphocharax gillii* (Eigenmann & Kennedy, 1903) | Langeani *et al.* (2007) | | Itaipu |
| *Steindachnerina brevipinna* (Eigenmann & Eigenmann, 1889) | Langeani *et al.* (2007) | | Piracema Channel |
| Erythrinidae | | | |
| *Erythrinus erythrinus* (Bloch & Schneider, 1801) | Langeani *et al.* (2007) | | Fishing bait ou Itaipu |
| *Hoplerythrinus unitaeniatus* (Agassiz, 1829) | Langeani *et al.* (2007) | | Fishing bait ou Itaipu |
| *Hoplias mbigua* Azpelicueta, Benítez, Aichino & Mendez, 2015 | Ota *et al.* (2018) | | Itaipu |
| Hemiodontidae | | | |
| *Hemiodus orthonops* Eigenmann & Kennedy, 1903 | Langeani *et al.* (2007) | | Piracema Channel |
| **GYMNOTIFORMES** | | | |
| Apteronotidae | | | |
| *Apteronotus albifrons* (Linnaeus, 1766) | Langeani *et al.* (2007) | | Itaipu / Piracema Channel |
| *Apteronotus caudimaculosus* Santana, 2003 | Langeani *et al.* (2007) | | Itaipu / Piracema Channel |
| Gymnotidae | | | |
| *Gymnotus paraguensis* Albert & Crampton, 2003 | Langeani *et al.* (2007) | | Itaipu / Piracema Channel |
| *Gymnotus pantanal* Fernandes, Albert, Daniel-Silva, Lopes, Crampton & Almeida-Toledo, 2005* | Júlio Júnior *et al.* (2009), but autochthonous in Langeani *et al.* (2007) | | Fishing bait / Piracema Channel |
| Hypopomidae | | | |
| *Brachyhypopomus gauderio* Giora & Malabarba, 2009 | *Brachyhypopomus pinnicaudatus* (Hopkins, Comfort, Bastian & Bass, 1990) in Langeani *et al.* (2007) | | Fishing bait or Itaipu |
| Rhamphichthyidae | | | |
| *Gymnorhamphichthys britskii* Carvalho, Ramos & Albert, 2011 | Reis *et al.* (2020) | | Itaipu |
| *Rhamphichthys hahni* (Meinken, 1937) | Langeani *et al.* (2007) | | Itaipu |

**TABLE 2** | (Continued)

| Taxon | Record in the upper rio Paraná basin | Remarks | Origin |
|---|---|---|---|
| **SILURIFORMES** | | | |
| Auchenipteridae | | | |
| *Ageneiosus inermis* (Linnaeus, 1766) | Langeani *et al*. (2007) | | Itaipu |
| *Ageneiosus ucayalensis* Castelnau, 1855 | Ota *et al*. (2018), but autochthonous in Langeani *et al*. (2007) | | Itaipu |
| *Auchenipterus osteomystax* (Miranda Ribeiro, 1918) | Ota *et al*. (2018) | | Itaipu |
| *Trachycorystes porosus* Eigenmann, 1888 | New record (DZSJRP 18277) | | ? |
| Callichthyidae | | | |
| *Corydoras nattereri* Steindachner, 1876* | Autochthonous in Langeani *et al*. (2007) | Tentatively considered as non-native. Further information can be found in the “Questionable native or non-native species” section | Aquarism |
| *Lepthoplosternum pectorale* (Boulenger, 1895) | Ota *et al*. (2018), but autochthonous in Langeani *et al*. (2007) | | Itaipu |
| *Megalechis picta* (Müller & Troschel, 1849) | New record (NUP 8787) | | ? |
| *Megalechis thoracata* (Valenciennes, 1840) | *Megalechis personata* (Ranzani, 1841) in Langeani *et al*. (2007) | | ? |
| Clariidae | | | |
| *Clarias gariepinus* (Burchell, 1822) | Langeani *et al*. (2007) | | Aquaculture |
| Doradidae | | | |
| *Platydoras armatulus* (Valenciennes, 1840) | Langeani *et al*. (2007) | | Itaipu |
| *Pterodoras granulosus* (Valenciennes, 1821) | Langeani *et al*. (2007) | | Itaipu |
| *Ossancora eigenmanni* (Boulenger, 1895) | *Oxydoras eigenmanni* in Langeani *et al*. (2007) | | Itaipu |
| *Trachydoras paraguayensis* (Eigenmann & Ward, 1907) | Langeani *et al*. (2007) | | Itaipu |
| Heptapteridae | | | |
| *Heptapterus mustelinus* (Valenciennes, 1835) | Langeani *et al*. (2007) | | Itaipu |
| *Pimelodella taenioptera* Miranda Ribeiro, 1914 | Langeani *et al*. (2007) NUP 3991 | Junior synonym of *P. gracilis* in Slobodian (2017) | Itaipu / Piracema Channel |
| Ictaluridae | | | |
| *Ictalurus punctatus* (Rafinesque, 1818) | Reis *et al*. (2020) | | Aquaculture |
| Loricariidae | | | |
| Hypostominae | | | |
| *Hypostomus cochliodon* Kner, 1854 | Langeani *et al*. (2007) | | Itaipu |
| *Hypostomus commersonii* Valenciennes, 1836 | Langeani *et al*. (2007) | | Itaipu |
| *Hypostomus dlouhyi* Weber, 1985 | Langeani *et al*. (2007) | | ? |
| *Hypostomus faveolus* Zawadzki, Birindelli & Lima, 2008 | Zawadzki *et al*. (2008b) | | Probably from the rio Tocantins-Araguaia basin |
| *Hypostomus* cf. *latirostris* (Regan, 1904)* | Carvalho, Eduardo (2022) | Tentatively considered as non-native. Further information can be found in the “Questionable native or non-native species” section | ? |
| *Hypostomus microstomus* Weber, 1987 | Ota *et al*. (2018) | | Itaipu |
| *Hypostomus ternetzi* (Boulenger, 1895) | Langeani *et al*. (2007) | | Itaipu |
| *Pterygoplichthys ambrosettii* (Holmberg, 1893) | Ota *et al*. (2018), but autochthonous in Langeani *et al*. (2007) | | Aquaculture |

**TABLE 2** | (Continued)

| Taxon | Record in the upper rio Paraná basin | Remarks | Origin |
|---|---|---|---|
| *Pterygoplichthys joselimaianus* (Weber, 1991) | Zawadzki *et al.* (2008b) | | Probably from the rio Tocantins-Araguaia basin |
| Loricariinae | | | |
| *Farlowella hahni* Meinken, 1937 | Langeani *et al.* (2007) | | Itaipu |
| *Loricaria simillima* Regan, 1904 | Langeani *et al.* (2007) | | Itaipu |
| *Loricariichthys platymetopon* Isbrücker & Nijssen, 1979 | Langeani *et al.* (2007) | | Itaipu / Piracema Channel |
| *Loricariichthys rostratus* Reis & Pereira, 2000 | Langeani *et al.* (2007) | | Itaipu / Piracema Channel |
| *Pyxiloricaria menezesi* Isbrücker & Nijssen, 1984 | Vicentim *et al.* (2019) | | ? |
| Pimelodidae | | | |
| *Hypophthalmus oremaculatus* Nani & Fuster de Plaza, 1947 | *Hypophthalmus edentatus* Spix & Agassiz, 1829 in Langeani *et al.* (2007) | | Itaipu |
| *Leiarius marmoratus* (Gill, 1870) | Casimiro *et al.* (2018) | Stray (introduced but not established) | Aquaculture |
| *Leiarius marmoratus vs. Pseudoplatystoma reticulatum* | Casimiro *et al.* (2018) | Stray (introduced but not established) | Aquaculture |
| *Phractocephalus hemioliopterus* (Bloch & Schneider, 1801) | Casimiro *et al.* (2018) | Stray (introduced but not established) | Aquaculture |
| *Pimelodus mysteriosus* Azpelicueta, 1998 | Ota *et al.* (2018) | | Itaipu |
| *Pimelodus ornatus* Kner, 1858 | Langeani *et al.* (2007) | | Itaipu |
| *Pseudoplatystoma reticulatum* Eigenmann & Eigenmann, 1889 | Ota *et al.* (2018). *P. fasciatum* in Langeani *et al.* (2007) | | Itaipu |
| *Pseudoplatystoma reticulatum vs. P. corruscans* | Vaini *et al.* (2014) | Probably stray. According to Baggio *et al.* (2016) hybrid specimens were likely to escape from aquaculture even if hybrids between species are fertile (Prado *et al.*, 2012). In the rio Uruguay, lower Paraná and rio Paraguay basins, the species are sympatric, but with a low level of natural hybridization (Carvalho *et al.*, 2013) | Aquaculture |
| *Sorubim lima* (Bloch & Schneider, 1801) | Langeani *et al.* (2007) | | Itaipu / Fish stocking CESP |
| **SALMONIFORMES** | | | |
| Salmonidae | | | |
| *Oncorhynchus mykiss* (Walbaum, 1792) | Magalhães *et al.* (2002) | Stray (introduced but not established) | Aquaculture |
| **CYPRINODONTIFORMES** | | | |
| Poeciliidae | | | |
| *Poecillia hollandi* (Henn, 1916)* | Autochthonous in Langeani *et al.* (2007) | Tentatively considered as non-native. Further information can be found in the “Questionable native or non-native species” section | ? |
| *Poecillia reticulata* Peters, 1859 | Langeani *et al.* (2007) | | Mosquito control |
| *Poecillia vivipara* Bloch & Schneider, 1801* | Langeani *et al.* (2007) | Tentatively considered as non-native. Further information can be found in the "Questionable native or non-native species" section | Mosquito control |
| *Xiphophorus helleri* Heckel, 1848 | Langeani *et al.* (2007) | | Aquarism |
| *Xiphophorus maculatus* (Günther, 1866) | Langeani *et al.* (2007) | | Aquarism |
| **BELONIFORMES** | | | |
| Belonidae | | | |
| *Potamorrhaphis eigenmanni* Miranda Ribeiro, 1915 | New record (NUP 3041) | | Piracema Channel |

**TABLE 2** | (Continued)

| Taxon | Record in the upper rio Paraná basin | Remarks | Origin |
|---|---|---|---|
| **CENTRARCHIFORMES** | | | |
| Centrarchidae | | | |
| *Lepomis macrochirus* Rafinesque, 1819 | Shibatta, Dias (2006) | | Aquarism |
| *Micropterus salmoides* (Lacepède, 1802) | Langeani *et al.* (2007) | | Fish stocking |
| **CICHLIFORMES** | | | |
| Cichlidae | | | |
| *Aequidens plagiozonatus* Kullander, 1984 | Ota *et al.* (2018) | | Fishing bait ou Aquarism |
| *Apistogramma commbrae* (Regan, 1906) | Ota *et al.* (2018) | | Piracema Channel / Aquarism |
| *Astronotus crassipinnis* Heckel, 1840 | Langeani *et al.* (2007) | | Aquarism / Fish stocking CESP |
| *Bujurquina vittata* (Heckel, 1840)* | Carvalho, Eduardo (2022) | Tentatively considered as non-native. Further information can be found in the "Questionable native or non-native species" section | ? |
| *Chaetobranchopsis australis* Eigenmann & Ward, 1907 | Ota *et al.* (2018) | | ? |
| *Cichla kelberi* Kullander & Ferreira, 2006 | Langeani *et al.* (2007) | | Fish stocking |
| *Cichla piquiti* Kullander & Ferreira, 2006 | Langeani *et al.* (2007) | | Fish stocking |
| *Coptodon rendalli* (Boulenger, 1897) | *Tilapia rendalli* in Langeani *et al.* (2007) | | Aquaculture |
| *Crenicichla semifasciata* (Heckel, 1840) | Roa-Fuentes *et al.* (2015) | | ? |
| *Crenicichla niederleinii* (Holmberg, 1891) | Langeani *et al.* (2007) | | Piracema Channel |
| *Geophagus sveni* Lucinda, Lucena & Assis, 2010 | *Geophagus proximus* (Castelnau, 1855) in Langeani *et al.* (2007) | | Probably from the rio Tocantins-Araguaia basin |
| *Gymnogeophagus* cf. *setequedas* Reis, Malabarba & Pavanelli, 1992* | New record (MCP 45929) | | Itaipu |
| *Heros notatus* (Jardine, 1843) | New record (CITL 465) | | Aquarism |
| *Heterotilapia buettikoferi* (Hubrecht, 1881) | New record (DZSJRP 21359) | | Aquaculture |
| *Laetacara araguaiae* Ottoni & Costa, 2009 | Ota *et al.* (2018) | | Probably from the rio Tocantins-Araguaia basin |
| *Oreochromis niloticus* (Linnaeus, 1758) | Langeani *et al.* (2007) | | Aquaculture |
| *Satanoperca setepele* Ota, Deprá, Kullander, Graça & Pavanelli, 2022 | Ota *et al.* (2022) | | Probably from the rio Tocantins-Araguaia basin |
| **ACANTHURIFORMES** | | | |
| Sciaenidae | | | |
| *Plagioscion squamosissimus* (Heckel, 1840) | Langeani *et al.* (2007) | | Fish stocking |
| **CARANGIFORMES** | | | |
| Achiridae | | | |
| *Catathyridium jenynsii* (Günther, 1862) | Langeani *et al.* (2007) | | Itaipu |

and dengue fever to humans. In Brazil, many regions have promoted the introduction of non-native "mosquito fish" (*Poecilia reticulata* and *P. vivipara*) as biological control of mosquito larvae (Lucinda, 2003; Langeani *et al*., 2007; Azevedo-Santos *et al*., 2016). Those events seem to account, at least partially, for the presence of the two species of *Poecilia* in the upper rio Paraná. *Poecilia reticulata* is also widely common in the aquarium trade and has an extensive distribution throughout the basin. *Poecilia vivipara* has a more restricted distribution in the basin and is less frequently found. Further details concerning the latter species can be found in the topic "Probably Non-Native Species" of the discussion section.

Another concern with non-native species is the presence of hybrids. The continental Brazilian fish farms cultivate fish in ponds located along the banks of natural water bodies or in open net-cages placed in dam reservoirs. In the upper rio Paraná, there are documented occurrences of hybridization, such as *Pseudoplatystoma corruscans vs*. *P. reticulatum*, *Piracturus mesopotamicus vs. Colossoma macropomum*, and *Leiarius marmoratus* (Gill, 1870) *vs*. *Pseudoplatystoma reticulatum* (Vaini *et al*., 2014; Casimiro *et al*., 2018; Yabu *et al*., 2018). Such occurrences result from escapes in farming operations during river floods or periods of heavy rainfall (Casimiro *et al*., 2018). In the rio Ivinhema basin, the situation has become quite problematic, as the hybrid *Pseudoplatystoma corruscans vs*. *P. reticulatum* has become more abundant than the pure parental species, leading to genetic erosion in the native population of *P. corruscans* (Vaini *et al*., 2014). In the rio Mogi-Guaçu basin, there are also reports of Post-F1 hybrids with detected introgression genetics of hybrids into the pure parental species (Freitas-Souza *et al*., 2022).

**The threat of hydroelectric dams.** In addition to promoting the invasion of non-native species in the upper rio Paraná, the construction of dams produces numerous negative environmental consequences for the basin and its fish fauna. Hydroelectric dams transform rivers into reservoirs, leading to the extirpation of rheophilic species and collapse of migratory fish populations (Winemiller *et al*., 2016; Hrbek *et al*., 2018; Tagliacollo *et al*., 2021). The consequently loss and fragmentation of habitats are two of the main threats to aquatic ecosystems (Agostinho *et al*., 2007a,b, 2016; Pelicice *et al*., 2015a). Nevertheless, most of the world's major rivers have been dammed (Nilsson *et al*., 2005) and, in Brazil, hydroelectric power generation accounts for over 65% of the energy produced in the country (EPE, 2021).

The upper rio Paraná basin is severely regulated by 65 operating hydroelectric power plants (UHEs), as well as Small Hydroelectric Power Plants (PCHs) and Hydroelectric Power Generating Centers (CGHs) (ANA, 2023; Fig. 46). As a result, the main course of its major left-bank tributaries (*i.e*., rios Paranaíba, Grande, Tietê, Paranapanema) is regulated by cascades of reservoirs (Agostinho *et al*., 2016). Only in the rio Paranapanema there are 11 hydroelectric power plants (Pelicice *et al*., 2018), which have profoundly changed its biotic characteristics (Nogueira *et al*., 2006; Orsi *et al*., 2016).

The damming of a river creates a new ecosystem upstream of the dam, as the lotic ecosystem is suddenly transformed into a lentic or semi-lentic environment (Baxter, 1977). As a result, reservoirs of the upper rio Paraná were primarily filled by small-sized, sedentary, opportunistic, and generalist fishes adapted to such habitat. The most abundant species include *Astyanax lacustris*, *Moenkhausia* aff. *intermedia*, *M. bonita*, *Steindachnerina insculpta* (Orsi, Britton, 2014; Pelicice *et al*., 2018; Ferraz *et al*., 2022).

Consequently, these become abundant prey and resources for native and non-native piscivorous lineages, which thrive after damming, such as the natives *Hoplias* aff. *malabaricus* and *Serrasalmus maculatus* (Hahn, Fugi, 2007; Pereira *et al*., 2016).

Furthermore, damming also facilitates the dispersal and establishment of non-native species (Rocha *et al*., 2023). The lacustrine zone of a reservoir, being deeper, becomes a hostile environment for most species. Under such conditions, *Plagioscion squamosissimus* has become one of the most abundant species in reservoirs of the upper rio Paraná (Agostinho *et al*., 2007a). Cichlids such as *Geophagus sveni* and *Satanoperca setepele* (previously identified in the literature of the upper rio Paraná as *G. proximus* and *S. pappaterra*, respectively; see Ota *et al*., 2018) are native species from the rio Araguaia-Tocantins basin, with sedentary habits, parental care, and higher population densities in lacustrine and flooded regions. After being introduced in the upper rio Paraná, both species benefited from the ecological conditions of reservoirs (*i.e*., lentic and oligotrophic environment), with high abundances of *G. sveni* being observed at the UHE Três Irmãos (Moretto *et al*., 2008) and at the UHE Itaipu (Gois *et al*., 2015).

Downstream impacts of dams are related to changes in water flow dynamics due to flow control. These effects are more evident when reservoirs are built in cascade and directly affect rheophilic species (Agostinho *et al*., 2008; Ganassin *et al*., 2021). One example is *Crenicichla jupiaensis*, a species described from the Urubupungá Falls, which suffered an abrupt population decline after the type locality was flooded by the Jupiá Reservoir (Graça *et al*., 2009). Additionally, the construction of other dams in the upper rio Paraná has negatively influenced its distribution, as the species inhabits riffle environments (Lima *et al*., 2008; Oyakawa *et al*., 2009). Currently, *C. jupiaensis* is categorized as “Endangered” (MMA, 2022) and occurs mainly in the rio Piquiri. However, recent records of the species in the rio Cinzas (Jarduli *et al*., 2020) emphasize the importance of tributaries free of dams for its maintenance (Marques *et al*., 2018).

There is also the retention of sediments and nutrients downstream to the dams, which affects primary productivity and increases water transparency. Thus, non-native species of visual-oriented predators, such as *Cichla kelberi* and *C. piquiti*, are favored. These species, introduced from the rio Araguaia-Tocantins basin, have disrupted native species assemblages, causing a decline in population density or local extinction of prey, especially small characids (Pelicice, Agostinho, 2009; Pelicice *et al*., 2015b; Pelicice *et al*., 2018) and young individuals of migratory species, such as *Pinirampus pirinampu* (Luiz *et al*., 2011).

Downstream areas are also vulnerable to the demands of electrical power generation which, by creating variable flow regimes, may intensify erosive processes (Souza Filho *et al*., 2004). During periods of high energy demand, the discharge of a large volume of water can induce the reversal of flow in downstream tributaries free of dams (Souza Filho, 2009), thereby conveying low-quality water from the reservoir to the tributaries. Thus, the homogenization of limnological variables in tributaries favors the spread of species adapted to the reservoir environment (opportunistic and/or non-native), potentially promoting biotic homogenization in these areas (Petsch, 2016; Ferreira *et al*., 2018; Brito *et al*., 2020).

Migratory species play essential ecosystem roles, cycling nutrients, controlling community structure, and often serving as top predators. Due to their size and musculature, they have historically been prized for both human consumption and recreational fishing, generating income for fishing communities (Agostinho *et al*., 2007b; Baily *et al*., 2021). However, migratory fish are among the first to decline or disappear in dammed areas of the upper rio Paraná (Agostinho *et al*., 2008), as they require extensive free-flowing river stretches for reproduction. These species undertake seasonal upstream migrations (in the main channel and its tributaries) to reach spawning sites (Agostinho *et al*., 2004b; Pompeu *et al*., 2012; Azevedo-Santos *et al*., 2021). Additionally, nursery areas are necessary for eggs and larvae to be transported downstream (Agostinho *et al*., 2004b; Pompeu *et al*., 2012; Pelicice *et al*., 2015a), while marginal lagoons are used as refuge and feeding sites for juveniles (Kipper *et al*., 2011; Ferraz *et al*., 2022). However, these areas also tend to be suppressed by landscape modification due to dam construction (Zhang, Gu, 2023). Dams function as physical barriers and reservoirs as ecological barriers, generating unfavorable gradients of hydrological and limnological conditions (Okada *et al*., 2005; Nobile *et al*., 2019). As a result, the abundance of adult migratory fish declines within reservoirs due to decreased water velocity and increased water transparency. Eggs and larvae of these species also decline just below the dam as a direct response to reduced water flow during drift movements (Pelicice *et al*., 2015a; Picapedra *et al*., 2023). In rivers with cascades of reservoirs (*e.g*., rios Grande, Tietê, Paranapanema) there are also records of population imprisonment, leading to local extinctions (Agostinho *et al*., 2008).

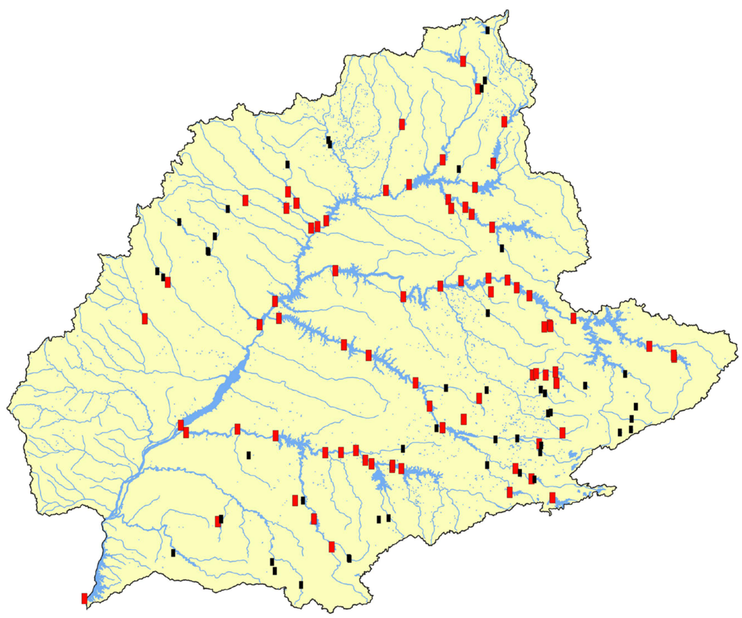


**FIGURE 46** | Hydroelectric power plants (red squares) and small hydroelectric power plants (black squares) in the upper rio Paraná basin.

**A not-so-promising future, to say the least.** The upper rio Paraná basin combines a considerable diversity of species, a high endemism rate, and a complex biogeographic history. However, the intense anthropization in the region has significantly altered and severely threatened it. This not only affects the landscapes and biodiversity but also the region's history. The most pernicious aspect of environmental alterations is the disconnection from the reality of the past, a process known as shifting baseline syndrome. With ongoing environmental degradation, the accepted thresholds for environmental conditions are continually being lowered with each generation (Soga, Gaston, 2018). Due to the absence of information regarding past environmental conditions, individuals from each new generation tend to perceive the circumstances in which they were raised as natural.

In the case of the upper rio Paraná basin, the situation may be so severe and profound that even researchers are unable to come to conclusive findings on certain issues, such as whether some species are native or not, or how and when some invasive species arrived. The role of various waterfalls, which are now submerged by hydroelectric reservoirs (Fig. 47), to the biogeography of upper rio Paraná basin fishes may never be adequately understood. For example, the presence of *Pseudoplatystoma corruscans* and *Rhinelepis aspera* in the rio Mogi-Guaçu basin, a tributary of the rio Grande, could go unnoticed as non-native species if historical records did not indicate their absence in the region prior to their introduction (Schubart, 1964a,b; Meschiatti, Arcifa, 2009). In these cases, it is possible that the Marimbondo Falls complex (Andorinhas, Patos Paulista, and Ferrador) in the rio Grande may have acted as a biogeographic barrier for these species. This hypothesis is currently challenging to test, serving as an example of how a significant part of the biogeographic history of the basin has been lost due to human modifications. Ultimately, current recognized patterns of species distribution are only a fraction of the natural structure and complexity that the basin once had.

Future conservation efforts must focus on biogeographic regions and priority taxa to avert the loss of unique elements of fish fauna and more fragments of this basin's history. The upper rio Paraná basin serves as a future snapshot of many Brazilian rivers if they do not have appropriate preservation policies to balance biodiversity and development.

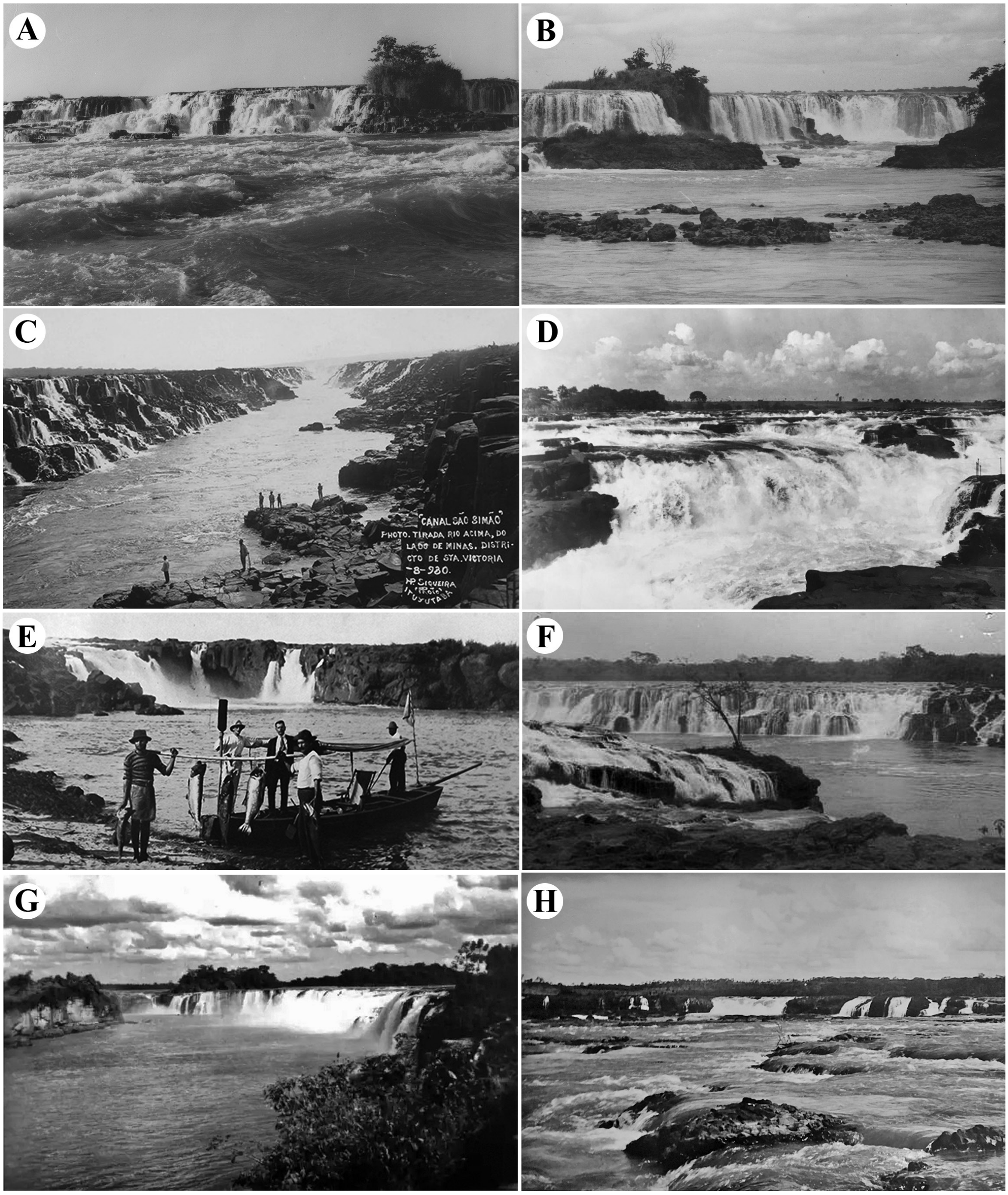



**FIGURE 47 |** The role of these ancient potential geographic barriers in structuring the biodiversity of the basin will never be fully understood. **A.** Onça Waterfall, rio Grande, Municipality of Santa Fé do Sul, SP. Submerged with the construction of the UHE Ilha Solteira; **B.** Marimbondo Waterfall, rio Grande, Municipality of Icém, SP. Site where the construction of the UHE Marimbondo took place; **C.** São Simão channel, rio Paranaíba, Municipality of São Simão, GO, 1930. Site where the construction of the UHE São Simão took place; **D.** Avanhandava Falls, rio Tietê, Municipality of José Bonifácio, SP. Submerged with the construction of the UHE Nova Avanhandava took place; **E.** Urubupungá Falls, rio Paraná River, Municipality of Três Lagoas, MS. Site where the construction of the UHE Jupiá took place; **F.** Itapura Falls, rio Tietê, Municipality of Itapura, SP, 1940. Submerged with the construction of the UHE Jupiá. **G.** Dourada Waterfall, rio Paranaíba, divide between Goiás and Minas Gerais states, municipalities of Cachoeira Dourada GO/MG. Submerged with the construction of the UHE de Cachoeira Dourada. **H.** Dos Índios Waterfall, rio Grande, divide between São Paulo and Minas Gerais states, municipalities of Oureste, SP and Iturama, MG. Submerged with the construction of the UHE de Água Vermelha.

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## REFERENCES

- **Abell R, Thieme ML, Revenga C, Bryer M, Kottelat M, Bogutskaya N *et al*.** Freshwater ecoregions of the world: A new map of biogeographic units for freshwater biodiversity conservation. BioScience. 2008; 58(5):403–14. https://doi.org/10.1641/B580507
- **Abilhoa V, Vitule JRS, Bornatowski H.** Feeding ecology of *Rivulus luelingi* (Aplocheiloidei: Rivulidae) in a Coastal Atlantic Rainforest stream, southern Brazil. Neotrop Ichthyol. 2010; 8(4):813–18. http://dx.doi.org/10.1590/S1679-62252010005000012
- **Agência Nacional de Águas e Saneamento Básico (ANA)** [Internet]. Brasília; 2023. Available from: https://www.gov.br/ana/pt-br
- **Agência Nacional de Energia Elétrica (ANEEL).** Sistema de Informações Geográficas do Setor Elétrico - SIGEL [Internet]. Brasília; 2021. Available from: https://sigel.aneel.gov.br/Down/
- **Agostinho AA, Thomaz SM, Minte-Vera CV, Winemiller KO.** Biodiversity in the high Paraná River floodplain. In: Gopal B, Junk WJ, Davis JA, editors. Biodiversity in wetlands: assessment, function and conservation. Leiden: Backhuys Publishers; 2000. p.89–118.
- **Agostinho AA, Thomaz SM, Gomes LC.** Threats for biodiversity in the floodplain of the upper Paraná River: effects of hydrological regulation by dams. Ecohydrol Hydrobiol. 2004a; 4(3):255–68. Available from: http://repositorio.uem.br:8080/jspui/bitstream/1/5287/1/242.pdf
- **Agostinho AA, Gomes LC, Veríssimo S, Okada EK.** Flood regime, dam regulation and fish in the upper Paraná River: effects on assemblage attributes, reproduction and recruitment. Rev Fish Biol Fish. 2004b; 14(1):11–19. https://doi.org/10.1007/s11160-004-3551-y

- **Agostinho AA, Gomes LC, Pelicice FM, editors.** Ecologia e manejo de recursos pesqueiros em reservatórios do Brasil. Maringá: Eduem; 2007a.
- **Agostinho AA, Pelicice FM, Petry AC, Gomes LC, Júlio Júnior HF.** Fish diversity in the upper Paraná River basin: habitats, fisheries, management and conservation. Aquat Ecosyst Health Manag. 2007b; 10(2):174–86. https://doi.org/10.1080/14634980701341719
- **Agostinho AA, Pelicice FM, Gomes LC.** Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. Braz J Biol. 2008; 68(S4):1119–32. https://doi.org/10.1590/S1519-69842008000500019
- **Agostinho AA, Bonecker CC, Gomes LC.** Effects of water quantity on connectivity: the case of the upper Paraná River floodplain. Ecohydrol Hidrobiol. 2009; 9(1):99–113. https://doi.org/10.2478/v10104-009-0040-x
- **Agostinho AA, Gomes LC, Santos NCL, Ortega JCG, Pelicice FM.** Fish assemblages in Neotropical reservoirs: colonization patterns, impacts and management. Fish Res. 2016; 173(Pt1):26–36. http://dx.doi.org/10.1016/j.fishres.2015.04.006
- **Albert JS, Fernandes-Matioli MC, Almeida-Toledo LF.** New species of *Gymnotus* (Gymnotiformes, Teleostei) from southeastern Brazil: toward the deconstruction of *Gymnotus carapo*. Copeia. 1999; 1999(2):410–21. https://doi.org/10.2307/1447486
- **Albert JS, Petry P, Reis RE.** Major biogeographic and phylogenetic patterns. In: Albert JS, Reis RE, editors. Historical biogeography of Neotropical freshwater fishes. Berkeley, CA: University of California; 2011. p.21–57.
- **Albert JS, Tagliacollo VA, Dagosta FCP.** Diversification of Neotropical freshwater fishes. Annu Rev Ecol Evol Syst. 2020; 51:27–53. https://doi.org/10.1146/annurev-ecolsys-011620-031032
- **Alkmin FF.** Geological background: a tectonic panorama of Brazil. In: Vieira BC, Salgado AAR, Santos LJC, editors. Landscapes and landforms of Brazil. Dordrecht: Springer; 2015. p.9–17. https://doi.org/10.1007/978-94-017-8023-0-2
- **Almeida FFM.** O planalto basáltico da bacia do Paraná. Bol Paul Geogr. 1956; 24:3–34.
- **Almeida FFM, Carneiro CDR.** Origem e evolução da Serra do Mar. Rev Bras Geociênc. 1998; 28:135–50.
- **Alves RM, Oliveira IHR, Pasa R, Kavalco KF.** A new species of genus *Psalidodon* Eigenmann, 1911 related to the *P. paranae* complex (Characiformes Characidae) from Upper Paranaíba river basin, Brazil, supported by genetic and morphometric data. Biodivers J. 2020; 11(4):807–14. https://doi.org/10.31396/Biodiv.Jour.2020.11.4.807.814
- **Amaral Campos A.** Primeira contribuição ao conhecimento da fauna ictiológica de Monte Alegre (Estado de São Paulo). Pap Avulsos Zool. 1944; 4(11):169–76.
- **Amaral Campos A.** Sôbre os caracídios do rio Mogi-Guaçu (Estado de São Paulo). Arq Zool. 1945; 4(11):431–65.
- **Andrade BN, Langeani F.** A new species of *Neoplecostomus* Eigenmann & Eigenmann, 1888 (Siluriformes: Loricariidae: Neoplecostominae) from the upper rio Paraná basin. Neotrop Ichthyol. 2014; 12(4):675–81. https://doi.org/10.1590/1982-0224-20130195
- **Assine ML, Merino ER, Pupim FN, Warren LV, Guerreiro RL, McGlue MM.** Geology and geomorphology of the Pantanal basin. In: Bergier I, Assine ML, editors. Dynamics of the Pantanal wetland in South America. Cham: Springer; 2015. p.23–50. https://doi.org/10.1007/698_2015_349
- **Aquino PPU.** Peixes de riacho do Brasil central: Biogeografia, ecologia e conservação. [PhD Thesis]. Brasília: Universidade de Brasília; 2013. Available from: https://repositorio.unb.br/handle/10482/15532
- **Aquino PPU, Carvalho FR.** Peixe da vez: *Hyphessobrycon coelestinus* Myers, 1929. Bol Soc Bras Ictiol. 2014; (109):30.
- **Aquino PPU, Schneider MS, Maria JM, Fonseca CP, Arakawa HB, Cavalcanti DR.** Ictiofauna dos córregos do Parque Nacional de Brasília, bacia do alto rio Paraná, Distrito Federal, Brasil Central. Biota Neotrop. 2009; 9(1):217–30. http://dx.doi.org/10.1590/S1676-06032009000100021
- **Azevedo-Santos VM, Roxo FF.** A new species of the genus *Pareiorhina* (Teleostei: Siluriformes: Loricariidae) from the upper rio Paraná basin, southeastern Brazil. Zootaxa. 2015; 3937(2):377–85. https://doi.org/10.11646/zootaxa.3937.2.8

- **Azevedo-Santos VM, Vitule JRS, Garcia-Berthou E, Pelicice FM, Simberloff D.** Misguided strategy for mosquito control. Science. 2016; 351(6274):675. https://doi.org/10.1126/science.351.6274.675
- **Azevedo-Santos VM, Britski HA, Oliveira C, Benine RC.** 2019. Ichthyofauna of streams of the Rio Sapucaí basin, upper Rio Paraná system, Minas Gerais, Brazil. Biota Neotrop. 2019; 19(1):e20180617. http://dx.doi.org/10.1590/1676-0611-bn-2018-0617
- **Azevedo-Santos VM, Daga VS, Pelicice FM, Henry R.** Drifting in a free-flowing river: Distribution of fish eggs and larvae in a small tributary of a Neotropical reservoir. Biota Neotrop. 2021; 21(4):e20211227. https://doi.org/10.1590/1676-0611-BN-2021-1227
- **Azevedo-Santos VM, Katz AM, Zawadzki CH, Deprá GC.** Notes on some type specimens of the Natural History Museum of Pirassununga, São Paulo, Brazil. Zootaxa. 2023; 5284(3):540–52. https://doi.org/10.11646/zootaxa.5284.3.5
- **Azpelicueta MM, Britski HA.** *Iheringichthys syi* (Siluriformes: Pimelodidae), a new pimelodid species from upper Paraná basin, Brazil. Neotrop Ichthyol. 2012; 10(1):45–52. https://doi.org/10.1590/S1679-62252012000100004
- **Baggio RA, Moretti CB, Bialetzki A, Boeger WA.** Hybrids between *Pseudoplatystoma corruscans* and *P. reticulatum* (Siluriformes: Pimelodidae) previously reported in the Upper Paraná River are likely escapes from aquaculture farms: evidence from microsatellite markers. Zoologia. 2016; 33(1):e20150200. https://doi.org/10.1590/S1984-4689zool-20150200
- **Baily D, Batista-Silva VF, Cassemiro FAS, Lemes P, Graça WJ, Oliveira AG *et al*.** The conservation of migratory fishes in the second largest river basin of South America depends on the creation of new protected áreas. Aquatic Conserv. 2021; 31:2515–32. https://doi.org/10.1002/aqc.3594
- **Barbosa MA, Azevedo-Santos VM.** A new species of the catfish genus *Trichomycterus* (Teleostei: Siluriformes: Trichomycteridae) from the rio Paraná basin, southeastern Brazil. Vertebr Zool. 2012; 62(3):357–62.
- **Barbosa MA, Katz AM.** A new species of the catfish genus *Trichomycterus* (Teleostei: Siluriformes: Trichomycteridae) from the Paranaíba basin, Central Brazil. Vertebr Zool. 2016; 66(3):261–65. Available from: https://www.senckenberg.de/wp-content/uploads/2019/08/03_vertebrate_zoology_66-3_barbosa_261-265.pdf
- **Baxter RM.** Environmental effects of dams and impoundments. Annu Rev Ecol Syst. 1977; 8:255–83.
- **Bini LM, Diniz-Filho JAF, Rangel T, Bastos R, Pinto MP.** Challenging Wallacean and Linnean shortfalls: knowledge gradients and conservation planning in a biodiversity hotspot. Diversity Distrib. 2006; 12(5):475–82. https://doi.org/10.1111/j.1366-9516.2006.00286.x
- **Bloom DD, Lovejoy NR.** On the origins of marine-derived freshwater fishes in South America. J Biogeogr. 2017; 44(9):1927–38. https://doi.org/10.1111/jbi.12954
- **Böhlke JE, Weitzman SH, Menezes NA.** Estado atual da sistemática dos peixes de água doce da América do Sul. Acta Amazon. 1978; 8(4):657–77.
- **Bonetto AA.** The Paraná River system. In: Davies BR, Walkers KF, editors. The ecology river systems. Dordrecht: Dr. W. Junk Publishers; 1986. p.541–55.
- **Brito MFG, Daga VS, Vitule JRS.** Fisheries and biotic homogenization of freshwater fish in the Brazilian semiarid region. Hydrobiologia. 2020; 847:3877–95. https://doi.org/10.1007/s10750-020-04236-8
- **Britski HA.** Sobre uma nova espécie de *Curimata* da bacia do Paraná, no estado de São Paulo (Pisces, Curimatidae). Pap Avulsos Zool. 1980; 33(23):327–33.
- **Britski HA, Garavello JC.** Sobre *Leporinus octofasciatus* Steindachner da bacia do Paraná (Anostomidae). Pap Avulsos Zool. 1978; 31(16):237–50.
- **Britski HA, Langeani F.** *Pimelodus paranaensis*, sp. n., um novo Pimelodidae (Pisces, Siluriformes) do Alto Paraná, Brasil. Rev Bras Zool. 1988; 5(3):409–17. https://doi.org/10.1590/S0101-81751988000300006
- **Britski HA, Luengo JA.** Sobre *Crenicichla jupiaiensis*, sp.n., espécie aberrante, do rio Paraná (Pisces, Cichlidae). Pap Avulsos Zool. 1968; 21(18):169–82.

- **Calegari BB, Lehmann PA, Reis RE.** Two new species of cascudinhos of the genus *Otothyropsis* (Siluriformes: Hypoptopomatinae) from the rio Paraná basin, Brazil. Zootaxa. 2013; 3619(2):130–44. http://dx.doi.org/10.11646/zootaxa.3619.2.2
- **Calegari BB, Morlis WG, Reis RE.** A new species of *Otothyropsis* (Siluriformes: Loricariidae) from the upper Río Paraná basin, Paraguay, with a discussion of the limits between *Otothyropsis* and *Hisonotus*. Zootaxa. 2017; 4244(2):231–45. https://doi.org/10.11646/zootaxa.4244.2.5
- **Calegari BB, Reis RE.** A new species of *Microlepidogaster* (Siluriformes: Loricariidae: Hypoptopomatinae) from the upper rio Paraná basin, Brazil. Neotrop Ichthyol. 2010; 8(3):625–30. https://doi.org/10.1590/S1679-62252010000300007
- **Carvalho FR, Eduardo WNM.** Peixes. In: Carvalho FR, Mangia S, Garcia MEC, Laps RR, Ferreira VL, Santana DJ *et al*., editors. Guia de identificação dos vertebrados do Lago do Amor: peixes, anfíbios, répteis, aves e mamíferos. Campo Grande: Editora UFMS; 2022. p.10–22.
- **Carvalho FR, Langeani F.** *Hyphessobrycon uaiso*: new characid fish from the rio Grande, upper rio Paraná basin, Minas Gerais State (Ostariophysi: Characidae), with a brief comment about some types of *Hyphessobrycon*. Neotrop Ichthyol. 2013; 11(3):525–36, http://dx.doi.org/10.1590/S1679-62252013000300006.
- **Carvalho FR, Jesus GC, Langeani F.** Redescription of *Hyphessobrycon flammeus* Myers, 1924 (Ostariophysi: Characidae), a threatened species from Brazil. Neotrop Ichthyol. 2014; 12(2):247–56. https://doi.org/10.1590/1982-0224-20130197
- **Carvalho FR, Casatti L, Manzotti AR, Ravazzi DW.** First record of *Arapaima gigas* (Schinz, 1822) (Teleostei: Osteoglossomorpha), the "pirarucu", in the upper Paraná River basin, Southeast Brazil. Check List. 2015; 11(5):1729. http://dx.doi.org/10.15560/11.5.1729
- **Casatti L, Carvalho FR, Veronezi JL, Lacerda DR.** Reproductive biology of the neotropical superfetaceous *Pamphorichthys hollandi* (Cyprinodontiformes: Poeciliidae). Ichthyol Explor Freshw. 2006; 17(1):59–64.
- **Casimiro ACR, Garcia DAZ, Vidotto-Magnoni AP, Britton JR, Agostinho AA, Almeida FS *et al*.** Escapes of non-native fish from flooded aquaculture facilities: the case of Paranapanema River, southern Brazil. Zoologia. 2018; 35:e14638. https://doi.org/10.3897/zoologia.35.e14638
- **Cassemiro FA, Albert JS, Antonelli A, Menegotto A, Wüest RO, Cerezer F *et al*.** Landscape dynamics and diversification of the megadiverse South American freshwater fish fauna. Proc Natl Acad Sci USA. 2023; 120(2):e2211974120. https://doi.org/10.1073/pnas.2211974120
- **Castro RMC.** Evolução da ictiofauna de riachos sul-americanos: padrões gerais e possíveis processos. In: Caramaschi EPR, Mazzoni R, Peresneto PR, editors. Ecologia de peixes de riachos. Rio de Janeiro: PPGE-UFRJ; 1999. p.139–55.
- **Castro RMC, Casatti L, Hertz FS, Vari RP, Melo ALA, Martins LSF *et al*.** Structure and composition of the stream ichthyofauna of four tributary rivers of the upper Rio Paraná basin, Brazil. Ichthyol Explor Freshw. 2005; 16(3):193–214.
- **Castro RMC, Casatti L, Santos HF, Ferreira KM, Ribeiro AC, Benine RC *et al*.** Estrutura e composição da ictiofauna de riachos do rio Paranapanema, Sudeste e Sul do Brasil. Biota Neotrop. 2003; 3(1):1–31. https://doi.org/10.1590/S1676-06032003000100007
- **Castro RMC, Casatti L, Santos HF, Melo ALA, Martins LSF, Ferreira KM *et al*.** Estrutura e composição da ictiofauna de riachos da bacia do Rio Grande no estado de São Paulo, sudeste do Brasil. Biota Neotrop. 2004; 4(1):1–39. https://doi.org/10.1590/S1676-06032004000100006
- **Cavalli D, Frota A, Lira AD, Gubiani EA, Margarido VP, Graça WJ.** Update on the ichthyofauna of the Piquiri River basin, Paraná, Brazil: a conservation priority area. Biota Neotrop. 2018; 18(2):e20170350. https://doi.org/10.1590/1676-0611-BN-2017-0350
- **Cavaretto RC, Souza-Shibatta L, Celestino LF, Silva PS, Shibatta OA, Sofia SH *et al*.** Evidence for the unexpected dispersal of *Leporinus tigrinus* Borodin, 1929 through hydroelectric dams in the most regulated Neotropical river basin. Aquat Invasions. 2020; 15(3):497–513. https://doi.org/10.3391/ai.2020.15.3.09

- **Cetra M, Barrella W, Neto FL, Abílio GM, Bruno J, Mello, Rodrigo SA.** Fish fauna of headwater streams that cross the Atlantic Forest of south São Paulo state. Check List. 2012; 8(3):421–25. https://doi.org/10.15560/8.3.421
- **Chuctaya J, Bührnheim CM, Malabarba LR.** Two new species of *Odontostilbe* historically hidden under *O. microcephala* (Characiformes: Cheirodontinae). Neotrop Ichthyol. 2018; 16(1):e170047. https://doi.org/10.1590/1982-0224-20170047
- **Cobbold PR, Meisling KE, Mount VS.** Reactivation of an obliquely rifted margin, Campos and Santos basins, southeastern Brazil. AAPG Bull. 2001; 85(11):1925–44.
- **Costa WJEM.** Seven new species of the killifish genus *Rivulus* (Cyprinodontiformes: Rivulidae) from the Paraná, Paraguay and upper Araguaia river basins, central Brazil. Neotrop Ichthyol. 2005; 3(1):69–82. https://doi.org/10.1590/S1679-62252005000100003
- **Costa WJEM.** *Rivulus illuminatus*, a new killifish from the serra dos Caiapós, upper rio Paraná basin, Brazil (Teleostei: Cyprinodontiformes: Rivulidae). Ichthyol Explor Freshw. 2007; 18(3):193–98.
- **Costa WJEM.** A new species of *Rivulus* from the Claro River drainage, upper Paraná River basin, central Brazil, with redescription of *R. pinima* and *R. vittatus* (Cyprinodontiformes: Rivulidae). Ichthyol Explor Freshw. 2008a; 18(4):313–23.
- **Costa WJEM.** *Rivulus formosensis*, a new aplocheiloid killifish from the upper Corrente River drainage, upper Paraná River basin, central Brazil (Cyprinodontiformes: Rivulidae). Ichthyol Explor Freshw. 2008b; 19(1):85–90.
- **Costa WJEM.** *Rivulus giarettai*, a new killifish from the Araguari River drainage, upper Paraná River basin, Brazil. Ichthyol Explor Freshw. 2008c; 19(1):91–95.
- **Costa WJEM.** *Simpsonichthys margaritatus*, a new seasonal miniature killifish from the upper Paraná River basin, central Brazilian Cerrado (Cyprinodontiformes: Rivulidae). Ichthyol Explor Freshw. 2012; 22(4):313–18.
- **Costa WJEM.** A new killifish of the genus *Melanorivulus* from the upper Paraná River basin, Brazil (Cyprinodontiformes: Rivulidae). Vertebr Zool. 2013; 63(3):277–81. https://doi.org/10.3897/vz.63.e31444
- **Costa WJEM.** Three new species of the killifish genus *Melanorivulus* from the Rio Paraná Basin, central Brazilian Cerrado (Cyprinodontiformes, Aplocheilidae). Zoosyst Evol. 2018; 94(1):17–27. https://doi.org/10.3897/zse.94.21321
- **Costa WJEM, Katz AM.** Integrative taxonomy supports high species diversity of south-eastern Brazilian mountain catfishes of the *T. reinhardti* group (Siluriformes: Trichomycteridae). Syst Biodivers. 2021; 19(6):601–21. https://doi.org/10.1080/14772000.2021.1900947
- **Costa WJEM, Azevedo-Santos VM, Mattos JLO, Katz AM.** Molecular phylogeny, taxonomy and distribution patterns of trichomycterine catfishes in the middle Rio Grande drainage, south-eastern Brazil (Siluriformes: Trichomycteridae). Fishes. 2023; 8(4):206. https://doi.org/10.3390/fishes8040206
- **Costa WJEM, Sampaio WMS, Giongo P, Almeida FP, Azevedo-Santos VM, Katz AM.** An enigmatic interstitial trichomycterine catfish from south-eastern Brazil found at about 1000 km away from its sister group (Siluriformes: Trichomycteridae). Zool Anz. 2022; 297:85–96. https://doi.org/10.1016/j.jcz.2022.02.007
- **Costa-Silva GJ, Oliveira C, Silva GSC.** New species of *Rineloricaria* (Siluriformes: Loricariidae) from the Paranaíba River basin, Brazil. Zootaxa. 2021; 5072(6):531–40. https://doi.org/10.11646/zootaxa.5072.6.2
- **Craig JM, Malabarba LR, Crampton WGR, Albert JS.** Revision of banded knifefishes of the *Gymnotus carapo* and *G. tigre* clades (Gymnotidae Gymnotiformes) from the Southern Neotropics. Zootaxa. 2018; 4379(1):47–73. https://doi.org/10.11646/ZOOTAXA.4379.1.3
- **Dagosta FCP, de Pinna M.** Biogeography of Amazonian fishes: Deconstructing river basins as biogeographic units. Neotrop Ichthyol. 2017; (15):e170034. http://dx.doi.org/10.1590/1982-0224-20170034.
- **Dagosta FCP, de Pinna M.** The fishes of the Amazon: distribution and biogeographical patterns, with a comprehensive list of species. Bull Am Mus Nat Hist. 2019; (431):1–163.
- **Dagosta FCP, de Pinna M, Peres CA, Tagliacollo VA.** Existing protected areas provide a poor safetynet for threatened Amazonian fish species. Aquatic Conserv. 2021; 31(5):1167–89. https://doi.org/10.1002/aqc.3461

- **Daru BH, Farooq H, Antonelli A, Faurby S.** Endemism patterns are scale dependent. Nat Commun. 2020; 11(2115):1–11. https://doi.org/10.1038/s41467-020-15921-6
- **Datovo A, Aquino PPU, Langeani F.** A new species of *Ituglanis* (Siluriformes: Trichomycteridae) from the Tocantins and Paranaíba river basins, central Brazil, with remarks on the systematics of the genus. Zootaxa. 2016; 4171(3):439–58. https://doi.org/10.11646/zootaxa.4171.3.2
- **Datovo A, Carvalho M, Ferrer J.** A new species of the catfish genus *Trichomycterus* from the La Plata River basin, southern Brazil, with comments on its putative phylogenetic position (Siluriformes: Trichomycteridae). Zootaxa. 2012; 3327:33–44. https://doi.org/10.11646/zootaxa.3327.1.3
- **Deprá GC, Aguilera G, Faustino-Fuster DR, Katz AM, Azevedo-Santos VM.** Redefinition of *Heptapterus* (Heptapteridae) and description of *Heptapterus carmelitanorum*, a new species from the upper Paraná River basin in Brazil. Zoosyst Evol. 2022; 98(2):327–43. https://doi.org/10.3897/zse.98.89413
- **Deprá GC, Graça WJ, Pavanelli CS, Avelino GS, Oliveira C.** Molecular phylogeny of *Planaltina* Böhlke (Characidae: Stevardiinae) and comments on the definition and geographic distribution of the genus, with description of a new species. PLoS ONE. 2018; 13(5):e0196291. https://doi.org/10.1371/journal.pone.0196291
- **Dias AM, Tejerina-Garro FL.** Changes in the structure of fish assemblages in streams along an undisturbed-impacted gradient, upper Paraná River basin, Central Brazil. Neotrop Ichthyol. 2010; 8(3):587–98. https://doi.org/10.1590/S1679-62252010000300003.
- **Dias AC, Zawadzki CH.** *Hypostomus hermanni* redescription and a new species of *Hypostomus* (Siluriformes: Loricariidae) from Upper Paraná River basin, Brazil. Neotrop Ichthyol. 2021; 19(2):e200093. https://doi.org/10.1590/1982-0224-2020-0093
- **Dopazo M, Dutra GM, Pastana M, Presti P, Trevisan JP, Soares KDA.** Antônia Amaral Campos: Alipianas. Bol Soc Bras Ictiol. 2021; 136:70–78.
- **Doria CRC, Agudelo E, Akama A, Barros B, Bonfim M, Carneiro L *et al*.** The silent threat of non-native fish in the Amazon: ANNF database and review. Front Ecol Evol. 2021; 9:646702. https://doi.org/10.3389/fevo.2021.646702
- **Dubois A.** 'Retraction' of taxonomic papers: the meaning of the word 'issued' and related ones in zoological nomenclature. Zoosystema. 2020; 42(26):519–23. https://doi.org/10.5252/zoosystema2020v42a26
- **Edler D, Guedes T, Zizka A, Rosvall M, Antonelli A.** Infomap bioregions: Interactive mapping of biogeographical regions from species distributions. Syst Biol. 2017; 66(2):197–204. https://doi.org/10.1093/sysbio/syw087
- **Eigenmann CH.** The Archiplata-Archhelenis theory. In: Hatcher JB, editor. Reports of the Princeton University Expeditions to Patagonia, 1896–1899. Princeton: Princeton University; 1909. p.293–374.
- **Eigenmann CH, Norris AA.** Sobre alguns peixes de S. Paulo, Brazil. Rev Mus Paul. 1900; 4:349–362.
- **Eigenmann CH.** The Cheirodontinae, a subfamily of minute characid fishes of South America. Mem Carnegie Mus. 1915; 7(1):1–99.
- **Eigenmann CH.** *Pimelodella* and *Typhlobagrus*. Mem Carnegie Mus. 1917; 7(4):229–58.
- **Eigenmann CH.** The Pygidiidae, a family of South American catfishes. Mem Carnegie Mus. 1918; 7(5):259–398.
- **Eigenmann CH.** The American Characidae. Mem Mus Comp Zool. 1921; 43(3):209–310.
- **Ellis MD.** On the species of *Hasemania, Hyphessobrycon*, and *Hemigrammus* collected by J. D. Haseman for the Carnegie Museum. Ann Carnegie Mus. 1911; 8:148–63.
- **Empresa de Energia Energética (EPE).** Balanço energético Nacional: ano base 2020. Rio de Janeiro: EPE; 2021.
- **Esguícero ALH, Arcifa M.** The fish fauna of the Jacaré-Guaçu River basin, upper Paraná River basin. Biota Neotrop. 2011; 11(1):103–13. http://dx.doi.org/10.1590/S1676-06032011000100010

- **Esguícero ALH, Castro RMC, Pereira TNA.** *Bunocephalus hertzi*, a new banjo catfish from the upper Rio Paraná basin, Brazil (Siluriformes: Aspredinidae), with the redescription of *Bunocephalus larai* Ihering, 1930. Zootaxa. 2020; 4742(1):105–16. https://doi.org/10.11646/zootaxa.4742.1.6
- **Fagundes DC, Leal CG, Carvalho DR, Junqueira NT, Langeani F, Pompeu PS.** The stream fish fauna from three regions of the upper Paraná River basin. Biota Neotrop. 2015; 15(2):e20140187. https://doi.org/10.1590/1676-06032015018714
- **Faith DP.** Conservation evaluation and phylogenetic diversity. Biol Conserv. 1992; 61(1):1–10. https://doi.org/10.1016/0006-3207(92)91201-3
- **Ferraris Jr. C, Santana CD, Vari RP.** Checklist of Gymnotiformes (Osteichthyes: Ostariophysi) and catalogue of primary types. Neotrop Ichthyol. 2017; 15(1):e160067. https://doi.org/10.1590/1982-0224-20160067
- **Ferraz JD, Geller IV, Garcia DAZ, Pereira AD, Pine MB, Jarduli LR *et al.*** Early life stages and interanual variations of fish from Canoas reservoirs, lower Paranapanema River, Brazil. Actapesca News. 2022; 10(2):74–86. https://doi.org/10.46732/actafish.2022.10.2.74-86
- **Ferreira KM, Ribeiro AC.** *Corumbataia britskii* (Siluriformes: Loricariidae: Hypoptopomatinae) a new species from the upper Rio Paraná basin, Mato Grosso do Sul, Central Brazil. Zootaxa. 2007; 1386(1):59–68. https://doi.org/10.11646/zootaxa.1386.1.7
- **Ferreira K, Lopes TM, Affonso IP, Agostinho AA, Gomes LC.** Dam reverse flow events influence limnological variables and fish assemblages of a downstream tributary in a Neotropical floodplain. 2018; 36(2):305–13. https://doi.org/10.1002/rra.3584
- **Fialho AP, Oliveira LG, Tejerina-Garro FL, Gomes LC.** Fish assemblage structure in tributaries of the Meia Ponte River, Goiás, Brazil. Neotrop Ichthyol. 2007; 5(1):53–60. https://doi.org/10.1590/S1679-62252007000100007
- **Figueiredo CA.** Revisão taxonômica de *Pamphorichthys* Regan, 1913 (Cyprinodontiformes, Poeciliidae). [Master Dissertation]. Rio de Janeiro: Universidade Federal do Rio de Janeiro; 1997.
- **Freitas-Souza D, Nobile AB, Prado FD, Serrano EA, Lima FP, Foresti F *et al*.** Genetic markers indicate that hybrids of *Pseudoplatystoma* (Siluriformes, Pimelodidae) are reproducing in natural environments in southeastern Brazil. Biol Invasions. 2022; 24:1049–58. http://dx.doi.org/10.1007/s10530-021-02701-6
- **Froehlich O, Vilela MJA, Cavallaro MR, Cordeiro LM.** Inventário da ictiofauna do Complexo Aporé-Sucuriú. In: Pagotto TCS, Souza PR, organizers. Biodiversidade do Complexo Aporé-Sucuriú: Subsídios à conservação e manejo do bioma Cerrado. Campo Grande: EDUFMS; 2006. p.89–102.
- **Froehlich O, Cavallaro M, Sabino J, Súarez YR, Vilela MJA.** Checklist da ictiofauna do Estado de Mato Grosso do Sul, Brasil. Iheringia, Sér Zool. 2017; 107:e2017151. https://doi.org/10.1590/1678-4766e2017151
- **Frota A, Deprá GC, Petenucci LM, Graça WJ.** Inventory of the fish fauna from Ivaí River basin, Paraná State, Brazil. Biota Neotrop. 2016; 16(3):e20150151. https://doi.org/10.1590/1676-0611-BN-2015-0151
- **Frota A, Ota RR, Deprá GC, Ganassin MJM, Graça WJ.** A new inventory for fishes of headwater streams from the rio das Cinzas and rio Itararé basins, rio Paranapanema system, Paraná, Brazil. Biota Neotrop. 2020; 20(1):e20190833. https://doi.org/10.1590/1676-0611-bn-2019-0833
- **Gaertner M, Wilson JRU, Cadotte MW, MacIvor JS, Zenni RD, Richardson DM.** Non-native species in urban environments: patterns, processes, impacts and challenges. Biol Invasions. 2017; 19:3461–69. https://doi.org/10.1007/s10530-017-1598-7
- **Galves W, Shibatta OA, Jerep FC.** Estudos sobre diversidade de peixes da bacia do alto rio Paraná: uma revisão histórica. Semina Cienc Biol Saúde. 2009; 30(2):141–54. https://doi.org/10.5433/1679-0367.2009v30n2p141
- **Ganassin MJM, Muñoz-Mas R, Oliveira FJM, Muniz CM, Santos NCL, García-Berthou E *et al*.** Effects of reservoir cascades on diversity, distribution, and abundance of fish assemblages in three Neotropical basins. Sci Total Environ. 2021; 78:146246. https://doi.org/10.1016/j.scitotenv.2021.146246

- **Garcia DAZ, Hernandes MC, Silva-Souza AT, Orsi ML.** Establishment of non-native predator (Pisces, Erythrinidae) in a tributary of the Upper Paraná River basin, south Brazil. Neotrop Biol Conserv. 2015; 10(3):177–81. https://doi.org/10.4013/nbc.2015.103.08
- **Godoy MP.** Nova espécie de "*Sternarchella*" Eigenmann (Pisces, Gymnoti, Sternarchidae). Rev Bras Biol. 1968; 28(4):351–55.
- **Godoy MP.** Nova espécie de "*Plecostomus*" Gronovius, 1763 (Pisces, Loricariidae, Nematognathi). Rev Bras Biol. 1969; 29(2):175–80.
- **Gois KS, Pelicice FM, Gomes LC, Agostinho AA.** Invasion of an Amazonian cichlid in the upper Paraná River: facilitation by dams and decline of a phylogenetically related species. Hydrobiologia. 2015; 746:401–13. https://doi.org/10.1007/s10750-014-2061-8
- **Gomes AL.** Descrição de uma nova espécie de "Luciopimelodinae" do rio Mogi Guaçu, estado de São Paulo (Pisces, Nematognathi, Pimelodidae). Rev Bras Biol. 1956; 16(4):403–13.
- **Gomes AL, Azevedo P.** Os peixes de Monte Alegre do Sul, estado de São Paulo. Pap Avulsos Zool. 1960; 14(16):133–51.
- **Gomes AL, Schubart O.** Descrição de "*Chasmocranus brachynema*" sp.n., novo "Luciopimelodinae" da bacia do rio Mogi Guaçu, estado de São Paulo. Rev Bras Biol. 1958; 18(4):413–16.
- **Gosline WA.** Contributions to the classification of the loricariid catfishes. Arq Mus Nac. 1947; 41:79–134.
- **Graça WJ, Pavanelli CS, Lorscheider C, Margarido WP.** Threatened fishes of the world: *Crenicichla jupiaensis* Britski & Luengo, 1968 (Cichlidae). Environ Biol Fish. 2009; 84:53–54. https://doi.org/10.1007/s10641-008-9385-z
- **Gubiani EA, Ruaro R, Ribeiro VR, Eichelberger ACA, Bogoni RF, Lira AD *et al*.** Non-native fish species in Neotropical freshwaters: how did they arrive, and where did they come from? Hydrobiologia. 2018; 817:57–69. https://doi.org/10.1007/s10750-018-3617-9
- **Hahn NS, Fugi R.** Alimentação de peixes em reservatórios brasileiros: alterações e consequências nos estágios iniciais do represamento. Oecol Bras. 2007; 11(4):469–80. https://doi.org/10.4257/oeco.2007.1104.01
- **Haseman JD.** An annotated catalog of the cichlid fishes collected by the expedition of the Carnegie Museum to central South America, 1907–1910. Ann Carnegie Mus. 1911; 7(3–4):329–73.
- **Haseman JD, Eigenmann CH.** A brief report upon the expedition of the Carnegie Museum to Central South America. Together with a list of localities at which Mr. Haseman collected. Ann Carnegie Mus. 1911; 7(3–4):287–314. Available from: https://www.biodiversitylibrary.org/page/9956938
- **Heilpern S.** Biodiversity: Include freshwater species. Nature. 2015; 518:67. https://doi.org/10.1038/518167d
- **Henry R.** The connectivity of the Paranapanema River with two lateral lakes in its mouth zone into the Jurumirim Reservoir. Acta Limnol Bras. 2005; 17(1):57–69. Available from: https://www.actalb.org/article/627b113b782aad05cd1891e5/pdf/alb-17-1-57.pdf
- **Hiruma ST, Riccomini C, Modenesi-Gautieri MC, Hackspacher PC, Hadler Neto JC, Franco-Magalhães AOB.** Denudation history of the Bocaina plateau, Serra do Mar, southeastern Brazil: relationships to Gondwana breakup and passive margin development. Gondwana Res. 2010; 18(4):674–87. https://doi.org/10.1016/j.gr.2010.03.001
- **Hrbek T, Meliciano NV, Zuanon J, Farias IP.** Remarkable geographic structuring of rheophilic fishes of the lower Araguaia River. Front Genet. 2018; 9:295. https://doi.org/10.3389/fgene.2018.00295
- **Hueck K, Seibert P.** Vegetationskarte von Südamerika. Band IIa. Sttutgart: Fischer; 1981.
- **Instituto Brasileiro de Geografia e Estatística (IBGE).** Censo Demográfico 2022: População e domicílios. Rio de Janeiro: IBGE, 2023.
- **von Ihering R.** Descriptions of four new loricariid fishes of the genus *Plecostomus* from Brazil. Ann Mag Nat Hist. 1905; 15:558–61.
- **von Ihering R.** Diversas especies novas de peixes nematognathas do Brasil. Notas preliminares. Rev Mus Paul. 1907; (1):13–39.
- **von Ihering R.** Algumas especies novas de peixes d'agua doce (Nematognatha) (*Corydoras*, *Plecostomus*, *Hemipslichthys*). Rev Mus Paul. 1911; 8:380–404.

- **von Ihering R.** Da vida dos peixes: ensaios e scenas de pescarias. São Paulo: Companhia Melhoramentos; 1929.
- **von Ihering R.** Notas ecológicas referentes a peixes d'agua doce do estado de S. Paulo e descripção de 4 especies novas. Arch Inst Biol. 1930: 3:93–104.
- **Ingenito LFS, Buckup PA.** The Serra da Mantiqueira, south-eastern Brazil, as a biogeographical barrier for fishes. J Biogeogr. 2007; 34(7):1173–82. https://doi.org/10.1111/j.1365-2699.2007.01686.x
- **Instituto Chico Mendes de Conservação da Biodiversidade (ICMBIO).** Livro vermelho da fauna brasileira ameaçada de extinção – Vol I. Brasília, DF: ICMBio/MMA; 2018. Available from: https://www.gov.br/icmbio/pt-br/centrais-de-conteudo/publicacoes/publicacoes-diversas/livro_vermelho_2018_vol1.pdf
- **Jarduli LR, Garcia DAZ, Vidotto-Magnoni AP, Casimiro ACR, Vianna NC, Aleira FS *et al.*** Fish fauna from the Paranapanema River basin, Brazil. Biota Neotrop. 2020; 20(1):e20180707. http://dx.doi.org/10.1590/1676-0611-BN-2018-0707
- **Jerep FC, Shibatta OA.** A new species of *Bryconamericus* (Characidae: Stevardiinae: Diapomini) from the upper rio Paraná basin, Brazil. Neotrop Ichthyol. 2017; 15(3):e170028. http://dx.doi.org/10.1590/1982-0224-20170028
- **Jerep FC, Shibatta OA, Zawadzki CH.** A new species of *Hypostomus* Lacépède, 1803 (Siluriformes: Loricariidae) from the upper rio Paraná basin, Southern Brazil. Neotrop Ichthyol. 2007; 5(4):435–42. https://doi.org/10.1590/S1679-62252007000400002
- **Júlio Júnior HF, Dei Tos C, Agostinho AA, Pavanelli CS.** A massive invasion of fish species after eliminating a natural barrier in the upper rio Paraná basin. Neotrop Ichthyol. 2009; 7(4):709–18. https://doi.org/10.1590/S1679-62252009000400021
- **Katz AM, Barbosa MASV, Costa WJEM.** Two new species of the catfish genus *Trichomycterus* from the Paraná river basin, southeastern Brazil (Teleostei: Trichomycteridae). Ichthyol Explor Freshw. 2013; 23(4):359–66.
- **Katz AM, Costa WJEM.** A new species of the catfish genus *Cambeva* from the Paranapanema river drainage, southeastern Brazil (Siluriformes: Trichomycteridae). Trop Zool. 2020; 33(1):2–13. https://doi.org/10.4081/tz.2020.63
- **Kier G, Barthlott W.** Measuring and mapping endemism and species richness: A new methodological approach and its application on the flora of Africa. Biodivers Conserv. 2001; 10:1513–29. https://doi.org/10.1023/A:1011812528849
- **Kipper D, Bialetzki A, Santin M.** Composição taxonômica da assembleia de larvas de peixes no reservatório de Rosana, Rio Paranapanema, Brasil. Biota Neotrop. 2011; 11(1):421–26. https://doi.org/10.1590/S1676-06032011000100039
- **Kner R.** Zur Familie der Characinen. III. Folge der Ichthyologische Beiträge. Denkschriften der Kaiserlichen Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Klasse. 1859; 17:137–82.
- **Kner R.** Zur Familie der Characinen. III. Folge der Ichthyologische Beiträge. Denkschriften der Kaiserlichen Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Klasse. 1860; 18:9–62.
- **Langeani F.** Ictiofauna do Alto Curso do rio Tietê (SP): taxonomia. [Master Dissertation]. São Paulo: Universidade de São Paulo; 1989.
- **Langeani F, Castro RMC, Oyakawa OT, Shibatta OA, Pavanelli CS, Casatti L.** Diversidade da ictiofauna do alto rio Paraná: composição atual e perspectivas futuras. Biota Neotrop. 2007; 7(3):181–97. https://doi.org/10.1590/S1676-06032007000300020
- **Langeani F, Rego ACL.** Guia ilustrado dos peixes da bacia do rio Araguari. Uberlândia: Grupo de Mídia Central (GMBC); 2014.
- **Lima AF, Makrakis MC, Silva PS, Azevedo AV, Makrakis S, Assumpção L *et al.*** Padrões de distribuição e ocorrência espaço-temporal de ovos e larvas de peixes nos rios Pardo e Anhanduí, bacia do alto rio Paraná, Brasil. Rev Bras Biocien. 2013; 11(1):7–13.
- **Lima FCT.** *Crenicichla jupiaensis* Britski & Luengo, 1968. In: Machado ABM, Drummond GM, Paglia AP, editors. Livro Vermelho da Fauna Brasileira Ameaçada de Extinção. Brasília, DF, Minas Gerais: Ministério do Meio Ambiente, Fundação Biodiversitas; 2008. p.183–84.
- **Lima FCT.** A revision of the cis-andean species of the genus *Brycon* Müller & Troschel (Characiformes: Characidae). Zootaxa. 2017; 4222(1):1–189. https://doi.org/10.11646/zootaxa.4222.1.1

- **Lima F, Ribeiro A.** Continental-scale tectonic controls of biogeography and ecology. In: Alberts J, Reis R, editors. Historical biogeography of neotropical freshwater fishes. Berkeley: University of California Press; 2011. p.145–64.
- **Lippert BG, Calegari BB, Reis RE.** A new species of *Otothyropsis* (Siluriformes: Hypoptopomatinae) from eastern Brazil. Copeia. 2014; 2014(2):238–44. https://doi.org/10.1643/CI-13-057
- **Lomolino MV.** Conservation biogeography. In: Lomolino MV, Heaney LR, editors. Frontiers of biogeography: new directions in the geography of nature. Sunderland: Sinauer Associates; 2004. p.293–96.
- **Lopes D, Taveira TTM, Severo-Neto F, Carvalho FR.** First record of *Jupiaba acanthogaster* (Eigenmann, 1911) (Ostariophysi, Characidae) in the upper Paraná River basin, Brazil. Check List. 2020; 16(4):889–93. https://doi.org/10.15560/16.4.889
- **Lucinda PHF.** Family Poeciliidae. In: Reis RE, Kullander SO, Ferraris Jr. C, editors. Check list of the freshwater fishes of South and Central America. Porto Alegre: Edipucrs; 2003; p.555–81.
- **Luiz TF, Velludo MR, Peret AC, Rodrigues Filho JL, Peret AM.** Diet, reproduction and population structure of the introduced Amazonian fish *Cichla piquiti* (Perciformes: Cichlidae) in the Cachoeira Dourada reservoir (Paranaíba River, central Brazil). Rev Biol Trop. 2011; 59(2):727–41. Available from: https://www.scielo.sa.cr/pdf/rbt/v59n2/a15v59n2.pdf
- **Lujan NK, German DP, Winemiller KO.** Do wood-grazing fishes partition their niche?: morphological and isotopic evidence for trophic segregation in Neotropical Loricariidae. Funct Ecol. 2011; 25(6):1327–38. https://doi.org/10.1111/j.1365-2435.2011.01883.x
- **Magalhães ALB, Andrade RF, Ratton TF, Brito MFG.** Ocorrência da truta arco-íris *Oncorhynchus mykiss* (Walbaum, 1792) (Pisces: Salmonidae) no alto rio Aiuruóca e tributários, bacia do rio Grande, Minas Gerais, Brasil. Bol Mus Biol Mello Leitão. 2002; 14:35–42.
- **Makrakis S, Gomes LC, Makrakis MC, Fernandez DR, Pavanelli CS.** The canal da piracema at Itaipu dam as a fish pass system. Neotrop Ichthyol. 2007; 5(2):185–95. https://doi.org/10.1590/S1679-62252007000200013
- **Marceniuk AP, Hilsdorf AWS, Langeani F.** A ictiofauna de cabeceiras do rio Tietê, São Paulo, Brasil. Biota Neotrop. 2011; 11(3):217–35. https://doi.org/10.1590/S1676-06032011000300020
- **Margules CR, Pressey RL.** Systematic conservation planning. Nature. 2000; 405:243–53. https://doi.org/10.1038/35012251
- **Marinho MMF, Carvalho FR, Langeani F, Tatsumi FL.** A new *Hemigrammus* Gill from upper Paraná system, southeastern Brazil (Characiformes: Characidae). Zootaxa. 2008; 1724(1):52–60. https://doi.org/10.11646/zootaxa.1724.1.2
- **Marinho MMF, Langeani F.** Reconciling more than 150 years of taxonomic confusion: the true identity of *Moenkhausia lepidura*, with a key to the species of the *M. lepidura* group (Characiformes: Characidae). Zootaxa. 2016; 4107(3):338–52. https://doi.org/10.11646/zootaxa.4126.4.10
- **Marques H, Dias JHP, Perbiche-Neves G, Kashiwaqui EAL, Ramos IP.** Importance of dam-free tributaries for conserving fish biodiversity in Neotropical reservoirs. Biol Conserv. 2018; 224:347–54. https://doi.org/10.1016/j.biocon.2018.05.027
- **Martinelli LA, Silva AM, Camargo PB, Moretti LR, Tomazelli AC, Silva DML *et al*.** Levantamento das cargas orgânicas lançadas nos rios do estado de São Paulo. Biota Neotrop. 2002; 2(2):1–18. https://doi.org/10.1590/S1676-06032002000200006
- **Martins FO, Calegari BB, Langeani F.** *Microlepidogaster arachas*, a new species of hypoptopomatine catfish (Siluriformes: Loricariidae) from the upper rio Paraná basin, Brazil. Zootaxa. 2013; 3608(5):379–88. https://doi.org/10.11646/zootaxa.3608.5.6
- **Martins FO, Langeani F.** *Rhinolekos*, a new genus with three new species of Hypoptopomatinae (Siluriformes: Loricariidae) from upper Rio Paraná. Neotrop Ichthyol. 2011a; 9(1):65–78. https://doi.org/10.1590/S1679-62252011000100004
- **Martins FO, Langeani F.** *Microlepidogaster dimorpha*, a new species of Hypoptopomatinae (Siluriformes: Loricariidae) from the upper Rio Paraná system. Neotrop Ichthyol. 2011b; 9(1):79–86. https://doi.org/10.1590/S1679-62252011000100005

- **Martins FO, Langeani F.** *Hisonotus piracanjuba*, a new species of Hypoptopomatinae (Siluriformes: Loricariidae) from the rio Paranaíba, upper rio Paraná system, central Brazil. Ichthyol Explor Freshw. 2012; 23(1):29–36.
- **Martins FO, Langeani F, Zawadzki CH.** A new spiny species of *Hypostomus* Lacépède (Loricariidae: Hypostominae) from thermal waters, upper rio Paraná basin, central Brazil. Neotrop Ichthyol. 2014; 12(4):729–36. https://doi.org/10.1590/1982-0224-20140035
- **Melo MRS, Brito Ribeiro MCL, Lima FCT.** A new, narrowly distributed, and critically endangered species of *Characidium* (Characiformes: Crenuchidae) from the Distrito Federal, Central Brazil. Neotrop Ichthyol. 2021; 19(1):e200061. https://doi.org/10.1590/1982-0224-2020-0061
- **Menezes NA, Figueiredo JL, Britski HA.** Ichthyological collection building at the Museu de Zoologia da Universidade de São Paulo, Brazil. In: Pietsch TW, Anderson Jr. WD, editors. Collection building in ichthyology and herpetology. Lawrence: American Society of Ichthyologists and Herpetologists; 1997. p.561–65.
- **Menezes NA, Lucena CAS.** A taxonomic review of the species of *Charax* Scopoli, 1777 (Teleostei: Characidae: Characinae) with description of a new species from the rio Negro bearing superficial neuromasts on body scales, Amazon basin, Brazil. Neotrop Ichthyol. 2014; 12(2):193–228. https://doi.org/10.1590/1982-0224-20130175
- **Menezes NA, Ribeiro AC, Weitzman SH, Torres RA.** Biogeography of Glandulocaudinae (Teleostei: Characiformes: Characidae) revisited: phylogenetic patterns, historical geology and genetic connectivity. Zootaxa. 2008; 1726:33–48. http://dx.doi.org/10.11646/zootaxa.1726.1.3
- **Menezes NA, Weitzman SHE, Burns JR.** A systematic review of *Planaltina* (Teleostei: Characiformes: Characidae: Glandulocaudinae: Diapomini) with a description of two new species from the upper rio Paraná, Brazil. Proc Biol Soc Wash. 2003; 116(3):557–600.
- **Meschiatti AJ, Arcifa MS.** A review on the fishfauna of Mogi-Guaçu River basin: a century of studies. Acta Limnol Brasil. 2009; 21(1):135–59. Available from: https://app.periodikos.com.br/article/627da19e782aad07b35c1a3f/pdf/alb-21-1-135.pdf
- **Message H, Santos D, Baumgartner M, Affonso I.** Planícies de Inundação: a biodiversidade do rio Paraná ameaçada. Ciênc Hoje. 2016; 56(334):36–39.
- **Milani EJ.** Comentários sobre a origem e a evolução tectônica da bacia do Paraná. In: Montesso-Neto V, Bartorelli A, Carneiro CDR, Brito-Neves BB, editors. Geologia do continente Sul-Americano: evolução da obra de Fernando Flávio Marques de Almeida. Editora Becca; 2004. p.265–79.
- **Milani EJ, Thomaz Filho A.** Sedimentary basins of South America. In: Cordani UG, Milani EJ, Thomaz Filho A, Campos DA, editores. Tectonic evolution of South America. Rio de Janeiro: 31th International Geological Congress; 2000. p.389–449.
- **Ministério do Meio Ambiente (MMA).** Portaria Nº 300, de 13 de dezembro de 2022. Available from: https://www.in.gov.br/en/web/dou/-/portaria-gm/mma-n-300-de-13-de-dezembro-de-2022-450425464
- **Ministério do Meio Ambiente (MMA).** Portaria Nº 354, de 23 de Janeiro de 2023. Available from: https://www.in.gov.br/en/web/dou/-/portaria-mma-n-354-de-27-de-janeiro-de-2023-460770327
- **Miranda Ribeiro A.** Tres generos e dezesete especies novas de peixes brasileiros determinados nas collecções do Museu Paulista. Rev Mus Paul. 1918; 10:631–46.
- **Moerman DE, Estabrook GF.** The botanist effect: counties with maximal species richness tend to be home to universities and botanists. J Biogeogr. 2006; 33(11):1969–74. https://doi.org/10.1111/j.1365-2699.2006.01549.x
- **Mota TFM, Fabrin TMC, Deprá GC, Gasques LS, Oliveira AVD, Pavanelli CS, Prioli SMAP, PRIOLI AJ.** Molecular characterization of *Moenkhausia* (Pisces: Characiformes) populations with different lateral line developmental levels. An Acad Bras Ciênc. 2018; 90(3):2815–25. https://doi.org/10.1590/0001-3765201820170493
- **Moraes FR.** Uma coleção de história em um museu de ciências naturais: o Museu Paulista de Hermann von Ihering. An Mus Paul. 2008; 16(1):203–33. https://doi.org/10.1590/S0101-47142008000100006
- **Morais-Silva JP, Oliveira AV, Fabrin TMC, Diamante NA, Prioli SMAP, Frota A *et al.*** Geomorphology influencing the diversification of fish in small-order rivers of neighboring basins. Zebrafish. 2018; 15(4):389–97. https://doi.org/10.1089/zeb.2017.1551

- **Moretto EM, Marciano FT, Velludo MR, Fenerich-Verani N, Espíndola ELG, Rocha O.** The recent occurrence, establishment and potential impact of *Geophagus proximus* (Cichlidae: Perciformes) in the Tietê River reservoirs: an Amazonian fish species introduced in the Paraná basin (Brazil). Biodivers Conserv. 2008; 17:3013–25. https://doi.org/10.1007/s10531-008-9413-5
- **Morrone JJ.** Evolutionary biogeography: an integrative approach with case studies. New York: Columbia University Press; 2009.
- **Myers G.** Fresh-water fishes and West Indian zoogeography. Annu Rep Board Regents Smithson Inst. 1938; 3465:339–64.
- **Neves MP, Silva PC, Delariva RL, Fialho CB, Netto-Ferreira AL.** First record of *Astyanax bifasciatus* Garavello & Sampaio, 2010 (Teleostei, Ostariophysi, Characidae) in the Piquiri river basin, upper Paraná river basin. Check List. 2020; 16(1):93–101. https://doi.org/10.15560/16.1.93116
- **Nielsen DTB, Neves PABA, Ywamoto EV, Passos MA.** *Melanorivulus polychromus*, a new species of killifish from the rio São José dos Dourados drainage, middle rio Paraná basin, southwestern Brazil, with a redescription of *Melanorivulus apiamici* (Cyprinodontiformes: Rivulidae). Aqua. 2016; 22(2):79–88.
- **Nilsson C, Reidy C, Dynesius M, Revenga C.** Fragmentation and flow regulation of the world's large river systems. Science. 2005; 308(5720):405–08. https://doi.org/10.1126/science.1107887
- **Nobile AB, Freitas-Souza D, Lima FP, Perez ILB, Britto SGC, Ramos IP.** Occurrence of *Misgurnus anguillicaudatus* (Cantor, 1842) (Cobitidae) in the Taquari River, Upper Paraná Basin, Brazil. J Appl Ichthyol. 2017; 33(3):527–29. https://doi.org/10.1111/jai.13279
- **Nobile AB, Freitas-Souza D, Lima FP, Queiroz J, Bayona-Perez IL, Carvalho ED *et al*.** Damming and seasonality as modulators of fish community structure in a small tributary. Ecol Freshw Fish. 2019; 28:563–72. https://doi.org/10.1111/eff.12475
- **Nogueira C, Buckup PA, Menezes NA, Oyakawa OT, Kasecker TP, Ramos Neto MM *et al*.** Restricted-range fishes and the conservation of Brazilian freshwaters. PLoS ONE. 2010; 5(6):e11390. https://doi.org/10.1371/journal.pone.0011390
- **Nogueira MG, Jorcin A, Vianna NC, Britto YCT.** Reservatórios em cascata e os efeitos na limnologia e organização das comunidades bióticas (Fitoplâncton, Zooplâncton e Zoobentos): um estudo de caso no Rio Paranapanema (SP/PR). In: Nogueira MG, Henry R, Jorcin A, editors. Ecologia de Reservatórios: Impactos potenciais, ações de manejo e sistemas em cascata. São Carlos: Rima; 2006. p.83–126.
- **Northcote TG, Arcifa MS, Froehlich O.** Effects of impoundment and drawdown on the fish community of a South American river. SIL Proceedings. 1985; 22(4):2704–11. https://doi.org/10.1080/03680770.1983.11897757
- **Ochoa LE, Silva GSC, Costa e Silva GJ, Oliveira C, Datovo A.** New species of *Trichomycterus* (Siluriformes: Trichomycteridae) lacking pelvic fins from Paranapanema basin, southeastern Brazil. Zootaxa. 2017; 4319(3):550–60. https://doi.org/10.11646/zootaxa.4319.3.7
- **Okada EK, Agostinho AA, Gomes LC.** Spatial and temporal gradients in artisanal fisheries of a large Neotropical reservoir, the Itaipu Reservoir, Brazil. Can J Fish Aquat Sci. 2005; 62:714–24. https://doi.org/10.1139/f05-015
- **Okubo VKN.** Os Anostomidae da bacia do Alto rio Paraná. [Undergraduate monography]. São José do Rio Preto: Universidade Estadual Paulista "Júlio de Mesquita Filho"; 2022. Available from: https://repositorio.unesp.br/handle/11449/217430
- **Oliveira AK, Garavello JC, Cesario VV, Cardoso RT.** Fish fauna from Sapucaí-Mirim River, tributary of Grande River, upper Paraná River basin, Southeastern Brazil. Biota Neotrop. 2016; 16(1):e20140192. https://doi.org/10.1590/1676-0611-BN-2014-0192
- **Oliveira JC, Oyakawa OT.** New loricariid fishes from headwaters on Serra da Mantiqueira and Complexo do Espinhaço, Minas Gerais State, Brazil (Teleostei: Siluriformes: Loricariidae). Zootaxa. 2019; 4586(3):401–24. https://doi.org/10.11646/zootaxa.4586.3.1
- **Oliveira U, Soares-Filho B, Leitão RFM, Rodrigues HO.** BioDinamica: a toolkit for analyses of biodiversity and biogeography on the Dinamica-EGO modelling platform. PeerJ. 2019; 7:e7213. https://doi.org/10.7717/peerj.7213

- **Oliveira U, Vasconcelos MF, Santos AJ.** Biogeography of amazon birds: Rivers limit species composition, but not areas of endemism. Sci Rep. 2017; 7:2992. https://doi.org/10.1038/s41598-017-03098-w
- **Orsi ML, Agostinho AA.** Introdução de espécies de peixes por escapes acidentais de tanques de cultivo em rios da Bacia do Rio Paraná, Brasil. Rev Bras Zool. 1999; 16(2):557–60. https://doi.org/10.1590/S0101-81751999000200020
- **Orsi ML, Almeida FS, Swarça AC, Garcia AC, Garcia DAZ, Vianna NC *et al*.** Ovos, larvas e juvenis dos peixes da bacia do rio Paranapanema: uma avaliação para a conservação. Assis: Triunfal; 2016.
- **Orsi ML, Britton JR.** Long-term changes in the fish assemblage of a neotropical hydroelectric reservoir. J Fish Biol. 2014; 84(6):1964–70. https://doi.org/10.1111/jfb.12392
- **Ota RR, Deprá GC, Graça WJ, Pavanelli CS.** Peixes da planície de inundação do alto rio Paraná e áreas adjacentes: revised, annotated and updated. Neotrop Ichthyol. 2018; 16(2):e170094. http://dx.doi.org/10.1590/1982-0224-20170094
- **Ota RR, Deprá GC, Kullander S, Graça WJ, Pavanelli CS.** A new species of *Satanoperca* (Teleostei: Cichlidae) from the Rio Tocantins basin, Brazil. Neotrop Ichthyol. 2022; 19(4):e210116. https://doi.org/10.1590/1982-0224-2021-0116
- **Ota RP, Lima FCT, Pavanelli CS.** A new species of *Hemigrammus* Gill, 1858 (Characiformes: Characidae) from the central and western Amazon and rio Paraná-Paraguai basins. Zootaxa. 2015; 3948(2):218–32. https://doi.org/10.11646/zootaxa.3948.2.4
- **Oyakawa OT, Fichberg I, Langeani F.** *Harttia absaberi*, a new species of loricariid catfish (Siluriformes: Loricariidae: Loricariinae) from the upper rio Paraná basin, Brazil. Neotrop Ichthyol. 2013; 11(4):779–86. https://doi.org/10.1590/S1679-62252013000400005
- **Oyakawa OT, Menezes NA, Shibatta OA, Lima FCT, Langeani F, Pavanelli CS *et al*.** Peixes de água doce. In: Bressan PM, Kierulff MCM, Sugieda AM, editors. Fauna ameaçada de extinção no Estado de São Paulo: Vertebrados. São Paulo: Fundação Parque Zoológico de São Paulo, Secretaria do Meio Ambiente; 2009. p.350–424.
- **Pavanelli CS, Britski HA.** Description of a new species of *Steindachnerina* (Teleostei: Characiformes: Curimatidae) from the upper Paraná River basin, Brazil. Ichthyol Explor Freshw. 1999; 10(3):211–16.
- **Pavanelli CS, Graça WJ, Zawadzki CH, Britski HA, Vidotti AP, Avelino GS *et al*.** Fishes from the Corumbá Reservoir, Paranaíba River drainage, upper Paraná River basin, State of Goiás, Brazil. Check List. 2007; 3(1):58–64. https://doi.org/10.15560/3.1.58
- **Peixoto LAW, Campos-da-Paz R, Menezes NA, Santana CD, Triques M, Datovo A.** Systematics of Neotropical electric knifefish *Tembeassu* (Gymnotiformes, Apteronotidae). Syst Biodivers. 2022; 20(1):1–19. https://doi.org/10.1080/14772000.2022.2032460
- **Peixoto LAW, Pastana MNL, Ballen GA.** New species of glass knifefish genus *Eigenmannia* (Gymnotiformes: Sternopygidae) with comments on the morphology and function of the enlarged cephalic lateral-line canals of Sternopygidae. J Fish Biol. 2021; 98(1):142–53. https://doi.org/10.1111/jfb.14564
- **Pelicice FM, Agostinho AA.** Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir. Biol Invasions. 2009; 11:1789–801. http://dx.doi.org/10.1007/s10530-008-9358-3
- **Pelicice FM, Azevedo-Santos VM, Esguícero ALH, Agostinho AA, Arcifa MS.** Fish diversity in the cascade of reservoirs along the Paranapanema River, Southeast Brazil. Neotrop Ichthyol. 2018; 16(2):e170150. https://doi.org/10.1590/1982-0224-20170150
- **Pelicice FM, Azevedo-Santos VM, Vitule JRS, Orsi ML, Lima Junior DP, Magalhães ALB *et al*.** Neotropical freshwater fishes imperilled by unsustainable policies. Fish Fish. 2017; 18(6):1119–33. https://doi.org/10.1111/faf.12228
- **Pelicice FM, Bialetzki A, Camelier P, Carvalho FR, García-Berthou E, Pompeu PS *et al*.** Human impacts and the loss of Neotropical freshwater fish diversity. Neotrop Ichthyol. 2021; 19(3):e210134. https://doi.org/10.1590/1982-0224-2021-0134
- **Pelicice FM, Latini JD, Agostinho AA.** Fish fauna disassembly after the introduction of a voracious predator: main drivers and the role of the invader's demography. Hydrobiologia. 2015b; 746:271–83. https://doi.org/10.1007/s10750-014-1911-8

- **Pelicice FM, Pompeu PS, Agostinho AA.** Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish. Fish Fish. 2015a; 16(4):697–715. https://doi.org/10.1111/faf.12089
- **Pereira ES, Mauad JRC, Takemoto RM, Lima-Júnior SE.** Fish parasite diversity in the Amambai river, State Mato Grosso do Sul, Brazil. Acta Sci Biol Sci. 2018; 40(1):e36330. http://dx.doi.org/10.4025/actascibiolsci.v40i1.36330
- **Pereira LS, Agostinho AA, Delariva R.** Effects of river damming in Neotropical piscivorous and omnivorous fish: feeding, body condition and abundances. Neotrop Ichthyol. 2016; 14(1):e150044. https://doi.org/10.1590/1982-0224-20150044.
- **Petsch DK.** Causes and consequences of biotic homogenization in freshwater ecosystems. Int Rev Hydrobiol. 2016; 101(34):113–22. https://doi.org/10.1002/iroh.201601850
- **Picapedra PHS, Kashiwaqui EAL, Piana PA, Sanches PV.** A long-term study on the larval distribution of the migratory fish *Salminus brasiliensis* (Characiformes: Bryconidae) in a dam-free section of the Paraná River, Brazil. Environ Biol Fish. 2023; 106:641–56. https://doi.org/10.1007/s10641-023-01403-3
- **Pimentel MM, Fuck RA, Jost H, Ferreira Filho CF, Araújo SM.** The basement of the Brasília fold belt and the Goiás magmatic arc. In: Cordani UG, Milani EJ, Thomaz Filho A, Campos DA, editors. Tectonic evolution of South America. 31th International Geological Congress: Rio de Janeiro: 2000. p.195–229.
- **Pinto OMO.** Cinquenta anos de investigação ornitológica: História das origens e do desenvolvimento da coleção ornitológica do Museu Paulista e de seu subsequente progresso no Departamento de Zoologia da Secretaria da Agricultura. Arq Zool. 1945; 4(8):261–340.
- **Platnick NI, Nelson G.** A method of analysis for historical biogeography. Syst Zool. 1978; 27(1):1–16. https://doi.org/10.2307/2412808
- **Pompeu PS, Agostinho AA, Pelicice FM.** Existing and future challenges: the concept of successful fish passage in South America. River Res Appl. 2012; 28(4):504–12. https://doi.org/10.1002/rra.1557
- **Portugal LP.** Revisão sistemática do gênero *Triportheus* Cope (Teleostei, Characiformes, Characidae). [Master Dissertation]. São Paulo: Universidade de São Paulo; 1990.
- **Prado FD, Nunes TL, Senhorini JA, Bortolozzi J, Foresti F, Porto-Foresti F.** Cytogenetic characterization of F1, F2 and backcross hybrids of the Neotropical catfish species *Pseudoplatystoma corruscans* and *Pseudoplatystoma reticulatum* (Pimelodidae, Siluriformes). Genet Mol Biol. 2012; 35(1):57–64. https://doi.org/10.1590/S1415-47572012005000010
- **R Development CoreTeam.** R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. 2017. Available from: https://www.r-project.org/
- **Ramirez JLM.** Filogenia molecular dos anostomidae e filogeografia das espécies com cromossomos sexuais ZZ/ZW do gênero *Leporinus*. [PhD Thesis]. São Carlos: Universidade Federal de São Carlos; 2015.
- **Ramos TPA, Ramos RTC, Ramos SAQA.** Ichthyofauna of the Parnaíba River basin, northeastern Brazil. Biota Neotrop. 2014; 14(1):e20130039. https://doi.org/10.1590/S1676-06020140039
- **Rasmussen JL.** The Cal-Sag and Chicago Sanitary and Ship Canal: a perspective on the spread and control of selected aquatic nuisance fish species. Rock Island: US Fish and Wildlife Service; 2002. Available from: http://micrarivers.org/wp-content/uploads/2018/04/ConnectingChannelsPaperFinal.pdf
- **Reia L, Gabriel SCS, James RG, Vicensotto AMPF, Ricardo CB.** Ichthyofauna of the ribeirão Sucuri, a tributary of the rio Tietê, upper rio Paraná basin, southeastern Brazil Check List. 2020; 16(3):711–28. https://doi.org/10.15560/16.3.711
- **Reis RB.** Taxonomical revision of *Cambeva stawiarski* (Miranda Ribeiro, 1968) (Siluriformes, Trichomycteridae) with the description of a new species from the Rio Iguaçu basin, Paraná State, Brazil. [Master Dissertation]. Maringá: Universidade Estadual de Maringá; 2021. Available from: http://repositorio.uem.br:8080/jspui/handle/1/6562
- **Reis RB, Frota A, Deprá GC, Ota RR, Graça WJ.** Freshwater fishes from Paraná State, Brazil: an annotated list, with comments on biogeographic patterns, threats, and future perspectives. Zootaxa. 2020; (4):451–94. https://doi.org/10.11646/zootaxa.4868.4.1

- **Ribeiro AC.** Tectonic history and the biogeography of the freshwater fishes from the coastal drainages of eastern Brazil: an example of faunal evolution associated with a divergent continental margin. Neotrop Ichthyol. 2006; 4(2):225–46. https://doi.org/10.1590/S1679-62252006000200009
- **Ribeiro AC, Jacob RM, Silva RRSR, Lima FCT, Ferreira DC, Ferreira KM *et al*.** Distributions and phylogeographic data of rheophilic freshwater fishes provide evidences on the geographic extension of a central-brazilian amazonian palaeoplateau in the area of the present day Pantanal Wetland. Neotrop Ichthyol. 2013; 11(2):319–26. https://doi.org/10.1590/S1679-62252013000200010
- **Ribeiro AC, Lima FCT, Riccomini C, Menezes NA.** Fishes of the Atlantic Rainforest of Boracéia: testimonies of the Quaternary fault reactivation within a Neoproterozoic tectonic province in Southeastern Brazil. Ichthyol Explor Freshw. 2006; 17(2):157–64.
- **Ribeiro DC, Chagas JMA, Thereza MR, Langeani F.** Checklist and key for the identification of fish fauna of the Uberaba River, upper Paraná River system, Brazil. ZooKeys. 2019; 875:129–55. https://doi.org/10.3897/zookeys.875.31977
- **Ricciardi A.** Facilitative interactions among aquatic invaders: is an “invasional meltdown” occurring in the Great Lakes? Can J Fish Aquat Sci. 2001; 58(12):2513–25. https://doi.org/10.1139/f01-178
- **Ringuelet RA.** Zoogeografía y ecología de los peces de aguas continentales de la Argentina y consideraciones sobre las áreas ictiológicas de América del Sur. Ecosur 2. 1975; 2(3):1–122. Available from: http://sedici.unlp.edu.ar/handle/10915/48003
- **Roa-Fuentes CA, Zeni J, Varella H, Langeani F, Molina M.** First record of *Crenicichla semifasciata* (Heckel, 1840) (Teleostei: Cichlidae) in the upper rio Paraná basin, Brazil. Check List. 2015; 11(2):1–05. https://doi.org/10.15560/11.2.1610
- **Roberge JM, Angelstam P.** Usefulness of the umbrella species concept as a conservation tool. Conser Biol. 2004; 18(1):76–85. https://doi.org/10.1111/j.1523-1739.2004.00450.x
- **Robertson MP, Visser V, Hui C.** Biogeo: An R package for assessing and improving data quality of occurrence record datasets. Ecography. 2016; 39(4):394–401. https://doi.org/10.1111/ecog.02118
- **Rocha B, García-Berthou E, Cianciaruso MV.** Non-native fishes in Brazilian freshwaters: identifying biases and gaps in ecological research. Biol Invasions. 2023; 25:1643–58. https://doi.org/10.1007/s10530-023-03002-w
- **Rosa FR, Longo JM, Santos JCC, Casseb AA, Militão JSLT, Oliveira MS *et al*.** Status da diversidade de peixes durante a instalação de reservatórios hidrelétricos no médio Rio Verde (Mato Grosso do Sul - Brasil). Braz J Dev. 2020; 6(11):91775–92. https://doi.org/10.34117/bjdv6n11-548
- **Roxo FF, Oliveira C, Zawadzki CH.** Three new species of the loricariid genus *Neoplecostomus* (Teleostei: Siluriformes) from Upper Rio Paraná basin, southeastern Brazil. Zootaxa. 2012; 3233:1–21.
- **Roxo FF, Silva GSC, Waltz BT, Melo JEG.** A new species of *Hisonotus* (Siluriformes: Otothyrinae) from the upper rio Paraná and rio São Francisco basins, Brazil. Zootaxa. 2016; 4109(2):227–38. https://doi.org/10.11646/zootaxa.4109.2.7
- **Roxo FF, Silva GSC, Zawadzki CH.** *Neoplecostomus canastra*, a new catfish (Teleostei: Siluriformes) species from upper Rio Paraná basin. Zootaxa. 2017; 4294(2):226–40. https://doi.org/10.11646/zootaxa.4294.2.6
- **Roxo FF, Zawadzki CH, Troy WP.** Description of two new species of *Hisonotus* Eigenmann & Eigenmann, 1889 (Ostariophysi, Loricariidae) from the rio Paraná-Paraguay basin, Brazil. ZooKeys. 2014; 395:57–78. http://dx.doi.org/10.3897/zookeys.395.6910
- **Salgado FLK.** Description of *Astyanax argentum* new species Salgado, 2021 (Ostariophysi: Characiformes: Characidae) from the drainage of the Mogi-Guaçu river, upper Paraná basin. Núcleo do Conhecimento. 2021; 10:133–61.
- **Sallun Filho W, Karmann I.** Geomorphological map of the Serra da Bodoquena karst, west-central Brazil. J Maps. 2007; 3(1):282–95. https://doi.org/10.1080/jom.2007.9710845
- **Santos AC.** Sistemática de *Piabina* Reinhardt, 1867 (Ostariophysi: Characidae). [Master Dissertation]. São José do Rio Preto: Universidade Estadual Paulista “Júlio de Mesquita Filho”; 2014. Available from: https://repositorio.unesp.br/handle/11449/136484

- **Santos AC, Gonçalves CC, Carvalho FR.** Ichthyofauna of the "Cachoeira de São Roberto" and fishes of lower Preto River, upper Paraná River basin, Brazil. Biota Neotrop. 2017; 17(1):e20160196. https://doi.org/10.1590/1676-0611-BN-2016-0196
- **Santos BRB, Teresa FB, Borges PP, Casatti L, Tejerina-Garro FL, Pompeu PS *et al*.** Tropical headwater streams and the role of non-native species on fish assemblage's diversity. Biol Invasions. 2023; 25:3103–18. https://doi.org/10.1007/s10530-023-03093-5
- **Santos GB.** A ictiofauna da bacia do Alto Paraná (Rio Grande e Rio Paranaíba). MG Biota. 2010; 2(6):5–25.
- **Sarmento-Soares LM, Birindelli JLO.** A new species of the catfish genus *Centromochlus* (Siluriformes: Auchenipteridae: Centromochlinae) from the upper rio Panańa basin, Brazil. Neotrop Ichthyol. 2015; 13(1):77–86. https://doi.org/10.1590/1982-0224-20140042
- **Schubart O.** Lista dos peixes da bacia do rio Mogi Guaçu. Atas da Sociedade Biológica do Rio de Janeiro. 1962; 6(3):26–32.
- **Schubart O.** Duas novas espécies de peixe da família Pimelodidae do Rio Mogi Guaçu (Pisces, Nematognathi). Bol Mus Nac. 1964a; 244:1–22.
- **Schubart O.** Sobre algumas Loricariidae da bacia do rio Mogi Guaçu (Pisces, Nematognatha). Bol Mus Nac. 1964b; 251:1–19.
- **Schubart O, Gomes AL.** Descrição de *Cetopsorhamdia iheringi* sp.n. (Pisces, Nematognathi, Pimelodidae, Luciopimelodinae). Rev Bras Biol. 1959; 19:1–07.
- **Shibatta OA, Dias J.** 40 peixes do Brasil: CESP 40 anos. Rio de Janeiro: Doiis; 2006.
- **Serra JP, Campos FFS, Castro ALS.** Composição e estrutura da comunidade de peixes de um afluente do rio Tietê, bacia do alto Paraná. Rev Agrogeoambiental. 2015; 7(1):87–96. https://doi.org/10.18406/2316-1817v7n12015678
- **Serra JP, Langeani F.** A new *Hasemania* Ellis from the upper rio Paraná basin, with the redescription of *Hasemania crenuchoides* Zarske & Géry (Characiformes: Characidae). Neotrop Ichthyol. 2015; 13(3):479–86. https://doi.org/10.1590/1982-0224-20140107
- **Silva FSD, Deus JRM, Hilsdorf WS.** The upper reached ichthyofauna of the Tietê River, São Paulo, Brazil: aspects of their diversity and conservation. Biodivers Conserv. 2006; 15(11):3569–77. https://doi.org/10.1007/s10531-004-1460-y
- **Silva GSC.** A new species of *Phenacorhamdia* Dahl 1961 (Siluriformes: Heptapteridae) from the Paranapanema River basin, southeastern Brazil. Zootaxa. 2020; 4890(2):275–82. https://doi.org/10.11646/zootaxa.4890.2.8
- **Silva GSC, Reia L, Morimoto CK, Benine RC, Oliveira C.** Integrative taxonomy of *Imparfinis* (Siluriformes, Heptapteridae) from the upper Paraná River basin, Brazil, with description of a new species. Zootaxa. 2023; 5249(3):357–77. https://doi.org/10.11646/zootaxa.5249.3.3
- **Silva GSC, Roxo FF, Souza CS, Oliveira C.** Two new species of *Corumbataia* (Hypoptopomatinae: Loricariidae) from Rio Corrente, upper Rio Paraná basin, Brazil. Zootaxa. 2018; 4483(2):317–30. https://doi.org/10.11646/zootaxa.4483.2.5
- **Silva JC, Rosa RR, Galdioli EM, Soares CM, Domingues WM, Veríssimo S *et al*.** Importance of dam-free stretches for fish reproduction: the last remnant in the Upper Paraná River. Acta Limnol Bras. 2017; 29:e106. https://doi.org/10.1590/s2179-975x10216
- **Silveira LGG.** Revisão taxonômica de *Characidium lagosantense* Travassos, 1947 (Crenuchidae: Characiformes: Ostariophysi), com descrição de uma nova espécie para o Alto Rio Paraná. [Master Dissertation]. São José do Rio Preto: Universidade Estadual Paulista "Júlio de Mesquita Filho"; 2008. Available from: https://repositorio.unesp.br/handle/11449/87575
- **Silveira LGG, Langeani F, Graça WJ, Pavanelli CS, Buckup PA.** Characidium xanthopterum (Ostariophysi: Characiformes: Crenuchidae): a new species from the central Brazilian Plateau. Neotrop Ichthyol. 2008; 6(2):169–74.
- **Simberloff D, Von Holle B.** Positive interactions of nonindigenous species: Invasional meltdown? Biol Invasions. 1999; 1:21–32. https://doi.org/10.1023/A:1010086329619

- **Slobodian V.** Taxonomic revision of *Pimelodella* Eigenmann & Eigenmann, 1888 (Siluriformes: Heptapteridae): an integrative proposal to delimit species using a multidisciplinary strategy. [PhD Thesis]. São Paulo: Universidade de São Paulo; 2017. Available from: https://teses.usp.br/teses/disponiveis/38/38131/tde-19022018-142608/pt-br.php
- **Smith WS, Stefani MS, Espíndola ELG, Rocha O.** Changes in fish species composition in the middle and lower Tietê River (São Paulo, Brazil) throughout the centuries, emphasizing rheophilic and introduced species. Acta Limnol Bras. 2018; 30:e310. https://doi.org/10.1590/S2179-975X0118
- **Soares YFF, Aquino PPU, Bagley JC, Langeani F, Colli GR.** Two new species of *Hypostomus* suckermouth armored catfishes (Teleostei: Loricariidae) from Central Brazil. J Fish Biol. 2021; 99(3):905–20. https://doi.org/10.1111/jfb.14777
- **Soga M, Gaston KJ.** Shifting baseline syndrome: causes, consequences, and implications. Front Ecol Environ. 2018; 16(4):222–30. https://doi.org/10.1002/fee.1794
- **Souza MRF.** Variação da nadadeira adiposa e nova ocorrência de *Hasemania nana* (Lütken, 1875) (Characiformes, Characidae) no alto rio Paraná. [Master Dissertation]. Campo Grande: Universidade Federal de Mato Grosso do Sul; 2021. Available from: https://repositorio.ufms.br/handle/123456789/4877
- **Souza Filho EE.** Evaluation of the Upper Paraná River discharge controlled by reservoirs. Braz J Biol. 2009; 69(S2):707–16. https://doi.org/10.1590/S1519-69842009000300024
- **Souza Filho EE, Rocha PC, Comunello E, Stevaux JC.** Effects of the Porto Primavera Dam on physical environment of the downstream floodplain. In: Thomaz SM, Agostinho AA, Hahn NS, editors. The Upper Paraná River and its floodplain: physical aspects, ecology and conservation. Leiden: Backhuys Publishers; 2004. p.55–74.
- **Souza Filho EE, Stevaux JC.** Geologia e geomorfologia do complexo rio Baía, Curutuba, Ivinheima. In: Vazzoler AEAM, Agostinho AA, Hahn NS, editors. A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e socioeconômicos. Maringá: EDUEM, 1997; p.3–46.
- **Stevaux JC.** Upper Paraná River (Brazil) geomorphology and paleoclimatology. Quat Int. 1994; 21:143–61. https://doi.org/10.1016/1040-6182(94)90028-0
- **Stevaux JC.** Climatic events during the Late Pleistocene and Holocene in the upper Paraná River: Correlation with NE Argentina and South-Central Brazil. Quat Int. 2000; (72):73–85. https://doi.org/10.1016/S1040-6182(00)00023-9
- **Strayer DL, Dudgeon D.** Freshwater biodiversity conservation: recent progress and future challenges. Freshw Sci. 2010; 29(1):344–58. https://doi.org/10.1899/08-171.1
- **Súarez YR.** Spatial and temporal variation in fish species diversity and composition in streams of Ivinhema River Basin, upper Paraná River. Biota Neotrop. 2008a; 8(3):197–204. http://dx.doi.org/10.1590/S1676-06032008000300018
- **Súarez YR.** Fish, lower Ivinhema River basin streams, state of Mato Grosso do Sul, Brazil. Check List. 2008b; 4(3):226–31. https://doi.org/10.15560/4.3.226
- **Súarez YR, Lima-Junior SE.** Spatial and temporal variation in stream fish assemblages of Guiraí River basin, upper Paraná basin. Biota Neotrop. 2009; 9(1):102–11. https://doi.org/10.1590/S1676-06032009000100012
- **Súarez YR, Petrere Júnior M.** Associações de espécies de peixes em ambientes lóticos da bacia do rio Iguatemi, Estado do Mato Grosso do Sul. Acta Sci Biol Sci. 2003; 25(2):364–67. http://dx.doi.org/10.4025/actascibiolsci.v25i2.2024
- **Súarez YR, Petrere Júnior M.** Gradientes de diversidade nas comunidades de peixes da bacia do rio Iguatemi, Mato Grosso do Sul, Brasil. Iheringia, Sér Zool. 2006; 96(2):197–204. http://dx.doi.org/10.1590/S0073-47212006000200009
- **Súarez YR, Souza MM, Ferreira FS, Pereira MJ, Silva EA, Ximenes LQL *et al*.** Patterns of species richness and composition of fish assemblages in streams of the Ivinhema River Basin, upper Paraná River. Acta Limnol Bras. 2011; 23(2):177–88. http://dx.doi.org/10.1590/S2179-975X2011000200008
- **Súarez YR, Valério SB, Tondato KK, Ximenes LQL, Felipe TRA.** Determinantes ambientais da ocorrência de espécies de peixes em riachos de cabeceira da bacia do rio Ivinhema, alto rio Paraná. Acta Sci Bio Sci. 2007; 29(2):145–50. https://doi.org/10.4025/actascibiolsci.v29i2.520

- **Tagliacollo VA, Dagosta FCP, de Pinna M, Reis RE, Albert JS.** Assessing extinction risk from geographic distribution data in Neotropical freshwater fishes. Neotrop Ichthyol. 2021; 19(3):e210079. https://doi.org/10.1590/1982-0224-2021-0079
- **Teixeira W, Sabaté P, Barbosa J, Noce CM, Carneiro MA.** Archean and Paleoproterozoic tectonic evolution of the São Francisco craton, Brazil. In: Cordani UG, Milani EJ, Thomaz Filho A, Campos DA, editors. Tectonic evolution of South America. Rio de Janeiro: 31th International Geological Congress; 2000. p.101–37.
- **Tencatt LFC, Britto MR, Isbrücker IJH, Pavanelli CS.** Taxonomy of the armored catfish genus *Aspidoras* (Siluriformes: Callichthyidae) revisited, with the description of a new species. Neotrop Ichthyol. 2022; 20(3):1–159. https://doi.org/10.1590/1982-0224-2022-0040
- **Tencatt LFC, Britto MR, Pavanelli CS.** A new species of *Corydoras* Lacépède, 1803 (Siluriformes: Callichthyidae) from the upper rio Paraná basin, Brazil. Neotrop Ichthyol. 2014; 12(1):89–96. https://doi.org/10.1590/S1679-62252014000100009
- **Thereza MR, Langeani F.** Bagres e cascudos do Rio Grande, Alto Rio Paraná. Curitiba: Editora CRV; 2019.
- **Thomaz SM, Bini LM, Bozelli RL.** Floods increase similarity among aquatic habitats in river-floodplain systems. Hydrobiologia. 2007; 579:1–13. https://doi.org/10.1007/s10750-006-0285-y
- **Tonella LH, Ruaro R, Daga VS, Garcia DAZ, Júnior OBV, Lobato-de Magalhães T *et al*.** Neotropical freshwater fishes: A dataset of occurrence and abundance of freshwater fishes in the Neotropics. Ecology. 2023; 104(4):e3713. https://doi.org/10.1002/ecy.3713
- **Travassos H.** Ictiofauna de Pirassununga. I. Subfamília Parodontinae. Eigenmann, 1910 (Actinopterygii, Cypriniformes). Bol Mus Nac Zool. 1955; 129:1–31.
- **Travassos H.** Ictiofauna de Pirassununga. II. Sôbre Characidiinae H. Travassos, 1952 (Cypriniformes – Characoidei). Bol Mus Nac Zool. 1956; 135:1–14.
- **Travasos H.** Ictiofauna de Pirassununga. IV. Subordem Gymnotoidei Berg 1940 (Actinopterygii - Cypriniformes). Bol Mus Nac Zool. 1960; 217:1–34.
- **Travassos H, Pinto SY.** Ictiofauna de Pirassununga. III. Família Cichlidae (Perciformes, Actinopterygii). Bol Mus Nac Zool. 1957; 169:3–20.
- **Uieda VS, Barreto MG.** Composição da ictiofauna de quatro trechos de diferentes ordens do Rio Capivara, Bacia do Tietê, Botucatu, São Paulo. Rev Bras Zoociênc. 1999; 1(1–2):55–67. Available from: https://periodicos.ufjf.br/index.php/zoociencias/article/view/24299
- **Vaini JO, Grisolia AB, Prado FD, Porto-Foresti F.** Genetic identification of interspecific hybrid of Neotropical catfish species (*Pseudoplatystoma corruscans* vs. *Pseudoplatystoma reticulatum*) in rivers of Mato Grosso do Sul State, Brazil. Neotrop Ichthyol. 2014; 12(3):635–41. https://doi.org/10.1590/1982-0224-20130169
- **Van der Laan R, Fricke R.** Eschmeyer's catalog of fishes: Family-group names. [Internet]. San Francisco: California Academy of Science; 2023. Available from: http://www.calacademy.org/scientists/catalog-of-fishes-family-group-names
- **Vanegas-Rios J, Britzke R, Mirande JM.** Geographic variation of *Moenkhausia bonita* (Characiformes: Characidae) in the rio de la Plata basin, with distributional comments on *M. intermedia*. Neotrop Ichthyol. 2019; 17(1):e170123. https://doi.org/10.1590/1982-0224-20170123
- **Vanzolini PE.** As viagens de Johann Natterer no Brasil, 1817–1835. Pap Avulsos Zool. 1993: 38(3):17–60.
- **Vanzolini PE.** A contribuição Zoológica dos primeiros naturalistas viajantes no Brasil. Revista USP. 1996; (30):190–238. https://doi.org/10.11606/issn.2316-9036.v0i30p190-238
- **Vari RP.** Systematics of the neotropical characiform genus *Potamorhina* (Pisces: Characiformes). Smithson Contrib Zool. 1984; 400:1–36.
- **Vari RP.** The Curimatidae, a lowland Neotropical fish family (Pisces: Characiformes): distribution, endemism, and phylogenetic biogeography. In: Vanzolini PE, Heyer WR, editors. Rio de Janeiro: Proceedings of a workshop on Neotropical distribution patterns, Academia Brasileira de Ciências; 1988. p.343–77.
- **Vicentin W, Ferreira FS, Súarez YR.** Ichthyofauna of lotic environments in the Ivinhema river basin, upper Paraná River, Mato Grosso do Sul state, Brazil. Biota Neotrop. 2019; 19(4):e20190735. https://doi.org/10.1590/1676-0611-bn-2019-0735

- **Vieira TB, Tejerina-Garro FL.** Assessment of fish assemblages in streams of different orders in the Upper Paraná River basin, Central Brazil. Iheringia, Sér Zool. 2014; 104(2):175–83. https://doi.org/10.1590/1678-476620141042175183
- **Vilhena D, Antonelli A.** A network approach for identifying and delimiting biogeographical regions. Nat Commun. 2015; 6:6848. https://doi.org/10.1038/ncomms7848
- **Vitule JRS, Freire CA, Simberloff D.** Introduction of non-native freshwater fish can certainly be bad. Fish Fish. 2009; 10(1):98–108. https://doi.org/10.1111/j.1467-2979.2008.00312.x
- **Vitule JRS, Pozenato LP.** Homogeneização biótica: Misturando organismos em um mundo pequeno e globalizado. Estud Biol. 2012; 34:239–45. Available from: https://periodicos.pucpr.br/estudosdebiologia/article/view/22925/22024
- **Vitule JRS, Skóra F, Abilhoa V.** Homogenization of freshwater fish faunas after the elimination of a natural barrier by a dam in Neotropics. Divers Distrib. 2012; 18:111–20. https://doi.org/10.1111/j.1472-4642.2011.00821.x
- **Volcan MV, Klotzel B, Lanés LEK.** Two new species of *Melanorivulus* (Cyprinodontiformes: Cynolebiidae) from Rio Verde drainage, upper Rio Paraná basin, Brazil. Zootaxa. 2017; 4236(1):82–94. https://doi.org/10.11646/zootaxa.4236.1.4
- **Volcan MV, Severo-Neto F, Lanés LEK.** Unrecognized biodiversity in a world's hotspot: three new species of *Melanorivulus* (Cyprinodontiformes: Rivulidae) from tributaries of the right bank of the Rio Paraná basin, Brazilian Cerrado. Zoosyst Evol. 2018; 94(2):263–80. http://dx.doi.org/10.3897/zse.94.24406
- **Weber C.** Subfamily Hypostominae (Armored catfishes). In: Reis RE, Kullander SO, Ferraris Jr. C, editors. Check list of the freshwater fishes of South and Central America. Porto Alegre: Edipucrs; 2003. p.351–72.
- **Williams PH, Humphries CJ.** Biodiversity, taxonomic relatedness, and endemism in conservation. Oxford: Oxford University Press; 1994.
- **Williamson M.** Relationship of species number to area, distance and other variables. In: Myers AA, Giller PS, editors. Analytical biogeography: an integrated approach to the study of animal and plant distributions. London: Chapman & Hall; 1988. p.91–115.
- **Wootton RJ.** Ecology of teleost fishes. London; New York: Chapman and Hall; 1990.
- **Winemiller KO, McIntyre PB, Castello L, Fluet-Chouinard E, Giarrizzo T, Nam S *et al*.** Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. Science. 2016; 351(6269):128–29. https://doi.org/10.1126/science.aac7082
- **Yabu MHS, Vidotto-Magnoni AP, Casimiro ACR, Garcia DAZ, Costa ADA, Prado FD *et al*.** First record of non-native hybrid catfish *Pseudoplatystoma reticulatum* × *Leiarius marmoratus* in the Upper Paraná River basin, Brazil. J Fish Biol. 2018; 92:261–67.
- **Ywamoto EV, Nielsen DTB, Oliveira C.** Description of a new species of the *Melanorivulus* pictus species-group (Cyprinodontiformes: Rivulidae) from the Rio Paraná basin in Brazil. Zootaxa. 2020; 4852(1):125–32. https://doi.org/10.11646/zootaxa.4852.1.6
- **Zawadzki CH, Birindelli JLO, Lima FCT.** A new pale-spotted species of *Hypostomus* Lacépède (Siluriformes: Loricariidae) from the rio Tocantins and rio Xingu basins in central Brazil. Neotrop Ichthyol. 2008b; 6(3):395–402. https://doi.org/10.1590/S1679-62252008000300012
- **Zawadzki CH, Roxo FF, Graça WJ.** *Hisonotus pachysarkos*, a new species of cascudinho from the rio Ivaí basin, upper rio Paraná system, Brazil (Loricariidae: Otothyrinae). Ichthyol Explor Freshw. 2016; 26(4):373–83.
- **Zawadzki CH, Weber C, Pavanelli CS.** Two new species of *Hypostomus* Lacèpéde (Teleostei: Loricariidae) from the upper rio Paraná basin, central Brazil. Neotrop Ichthyol. 2008a; 6(3):403–12. https://doi.org/10.1590/S1679-62252008000300013
- **Zhang AT, Gu VX.** Global dam tracker: A database of more than 35,000 dams with location, catchment, and attribute information. Sci Data. 2023; 10:111. https://doi.org/10.1038/s41597-023-02008-2
- **Ziesler R, Ardizzone GD.** The inland waters of Latin America. COPESCAL, Technical Paper. 1979; (1):1–171.

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