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Original article

Fish diversity in the cascade of reservoirs along the Paranapanema River, southeast Brazil

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The Paranapanema River is a major tributary of the upper Paraná river basin. Eleven hydropower dams regulate its main course, but no study has investigated fish diversity in these impoundments at the basin-scale. The present study investigated spatial patterns of richness, composition, and abundance of native (non-migratory and migratory) and non-native fishes in the cascade of reservoirs along the Paranapanema River. The study is based on data collected from 34 independent studies conducted in nine reservoirs (47 samples). The compilation recorded 161 species, being 111 native (14 migratory) and 50 non-native. Total richness ranged between 56 and 112 species/reservoir, with a mean of 72 (49.9 non-migratory, 8.1 migratory and 14 non-native). The number of non-migratory species showed no spatial trend along the cascade system, but migratory and non-native richness increased toward downstream reaches. We also observed spatial variation in species composition along the cascade system, but some non-native fishes were widely distributed. Migratory fishes showed low relative abundance (usually < 10%), while non-native species were common and more abundant, especially in reservoirs downstream. Our results revealed a high diversity of fishes in the cascade of impoundments, but indicated that migratory fishes are rare, while non-native species are common or dominant.

Keywords: Dam, Fish fauna, Longitudinal, Migratory fish, Non-native.

O rio Paranapanema é um dos principais afluentes da bacia do alto rio Paraná. Onze hidrelétricas regulam o seu canal principal, contudo, não existe estudo, em escala de bacia, que tenha investigado a diversidade de peixes nos represamentos. O presente estudo investigou padrões espaciais de riqueza, composição e abundância de peixes nativos (não-migradores e migradores) e não-nativos na cascata de reservatórios do rio Paranapanema. O estudo se baseou em dados coletados por 34 estudos independentes conduzidos em nove reservatórios (47 amostras). Registramos 161 espécies, sendo 111 nativas (14 migradoras) e 50 não-nativas. A riqueza total variou entre 56 e 112 espécies/reservatório, com média de 72 (49,9 nativas, 8,1 migradoras e 14 não-nativas). O número de espécies não-migradoras não apresentou padrão de variação ao longo do sistema em cascata, mas a riqueza de migradores e peixes não-nativos aumentou em direção aos trechos de jusante. A composição de espécies variou ao longo do gradiente longitudinal, porém algumas espécies não-nativas apresentaram ampla distribuição. Espécies migradoras apresentaram baixa abundância relativa (usualmente < 10%), enquanto que as não-nativas foram comuns e abundantes, especialmente em reservatórios de jusante. Os resultados revelaram alta diversidade de peixes na cascata de reservatórios, mas indicaram que peixes migradores são raros, enquanto que espécies não-nativas são comuns ou dominantes.

Palavras-chave: Barragem, Ictiofauna, Longitudinal, Não-nativo, Peixes migradores.

Introduction

Hydropower dams affect the functioning of main rivers in South America (Agostinho *et al.*, 2016), resulting in a number of negative impacts on biodiversity, especially fishes (Pringle *et al.*, 2000; Agostinho *et al.*, 2007a). Dams block migratory routes, preventing the completion of life cycles (Godinho, Kynard, 2008; Pelicice, Agostinho, 2008); they also cause profound changes in river hydrology and physical/chemical processes that are key to the functioning of fluvial ecosystems (Poff *et al.*, 1997). As a result, the structure of fish assemblages in impounded areas experience strong shifts. The diversity of

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migratory and rheophilic fishes decline (Petrere Jr., 1996; Hoeinghaus *et al.*, 2009; Petesse, Petrere Jr., 2012; Santos *et al.*, 2017), while opportunistic (lentic-adapted) and non-native species, benefited by the impoundment, spread and dominate assemblages (Pelicice, Agostinho, 2009; Espínola *et al.*, 2010; Britton, Orsi, 2012; Vitule *et al.*, 2012).

The upper Paraná river basin is a special case. This basin is severely regulated by hundreds of large and small dams, which cover almost half of the impounded area in Brazil (Agostinho *et al.*, 2007a). In addition, the main course of all major tributaries (*i.e.*, Paranaíba, Grande, Tietê, Paranapanema) is regulated by cascades of large dams (Agostinho *et al.*, 2016). For example, eleven hydropower dams regulate the main course of the Paranapanema River, creating a cascade of impoundments along the entire river system. Studies that investigated fish diversity in these reservoirs (*e.g.*, Barrella, Petrere Jr., 2003; Hoffmann *et al.*, 2005; Duke Energy, 2008; Orsi, Britton, 2014; Santos *et al.*, 2017; Garcia *et al.*, 2018) indicated that assemblages are composed primarily of small-sized sedentary species, in addition to several non-native fishes. These studies, however, focused on specific impoundments; no study has investigated the whole cascade system, in order to provide a more complete picture about taxonomic diversity and abundance patterns. It is poorly known, for example, whether assemblage structure is homogenized among reservoirs (*e.g.*, Petesse, Petrere Jr., 2012) or contingent to each impoundment. This information is important to guide management and conservation plans, since the Paranapanema basin is severely disturbed by different human activities (*e.g.*, dams, agriculture, urbanization, aquaculture), demanding specific actions to preserve fish diversity and fishing stocks.

In this sense, this study gathered the available information to provide a comprehensive overview of fish diversity in the cascade of reservoirs along the Paranapanema River. Our main objective was to reveal the structure of fish assemblages in these impoundments, investigating spatial patterns of species richness, composition and abundance of native (non-migratory and migratory) and non-native fishes. In particular, we predict that non-migratory and non-native fishes dominate impoundments in terms of species richness and abundance, as evidenced by previous studies (*e.g.*, Barrella, Petrere Jr., 2003; Petesse, Petrere Jr., 2012; Agostinho *et al.*, 2016). We also expected a trend of increasing species richness, together with changes in composition, along the cascade – a common pattern in large river systems (*e.g.*, Oberdorff *et al.*, 1993; Araújo *et al.*, 2009). Finally, we predict that migratory species are rare (abundance and richness) in impoundments, especially in segments where dams are close to each other (middle/upper reaches) and critical habitats are limited or lacking.

Material and Methods

Study area. The Paranapanema River is a main tributary of the upper Paraná river basin. Its sources are located in São Paulo State, and the river runs west *ca*. 900 km, mostly along the border between São Paulo and Paraná States, to join the Paraná River downstream. Dozens of hydropower dams were built in the basin during the 20th century. Eleven large dams regulate the main channel (Fig. 1), affecting the upper, middle and lower reaches of the basin. The first large impoundment date back to 1932, but most dams were constructed after 1970 (Tab. 1). There are marked variations in the size of reservoirs; the largest are located in upper and lower reaches (Tab. 1). Fish passages (ladders) were installed in five dams, namely Canoas I, Canoas II, Ourinhos, Paranapanema and Piraju (Arcifa, Esguícero, 2012; Britto, Carvalho, 2013).

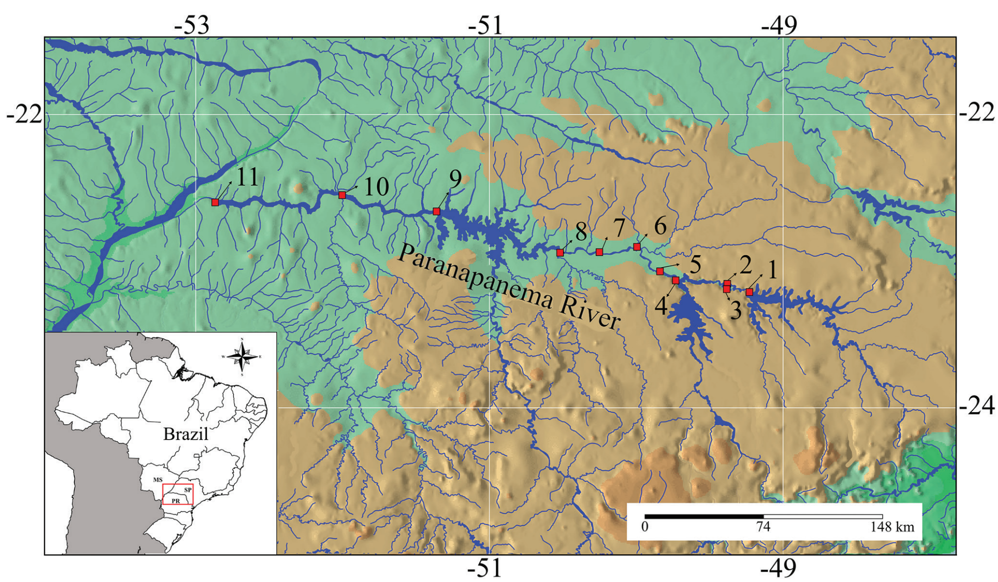

Fig. 1. The cascade of dams (red squares) along the Paranapanema River. Dams: 1 = Jurumirim; 2 = Piraju; 3 = Paranapanema; 4 = Chavantes; 5 = Ourinhos; 6 = Salto Grande; 7 = Canoas II; 8 = Canoas I; 9 = Capivara; 10 = Taquaruçu; 11 = Rosana. States: MS = Mato Grosso do Sul; PR = Paraná; SP = São Paulo.

Tab. 1. Hydroelectric dams along the Paranapanema River. Information about dams: date of construction, power installed (MW), dam height (m), distance from the mouth (km), presence of fishway. Information about reservoirs: area (km^2), volume (x 10^6 m^3), residence time (average days), maximum depth (m) and length (km). Source: Agostinho *et al.* (2007a); Duke Energy (2008); Pelicice *et al.* (2015a); websites of hydropower companies. "-" = unavailable information. Basin subdivision in upper, middle and lower reaches followed the Sistema Integrado de Gerenciamento de Recursos Hídricos do Estado de São Paulo (Governo do Estado de São Paulo, 2018).

Reservoir	Sequence	Reach	Dam					Reservoir				
			Date	Power	Height	Distance	Fishway	Area	Volume	Residence	Depth	Length
Jurumirim	1	Upper	1962	98	35	527		546	7900	334	40	90
Piraju	2	Upper	2002	80	38	496	ladder	12.8	105	-	-	22
Paranapanema	3	Upper	1932	31	16	487	ladder	1.5	-	-	-	9
Chavantes	4	Upper	1970	414	89	439		400	8795	353	78	40
Ourinhos	5	Middle	2005	33	-	422	ladder	5	20.8	1	9	6
Salto Grande	6	Middle	1958	74	25	388		12	44.2	1.4	9.2	15
Canoas II	7	Middle	1998	72	25	354	ladder	22.5	140	4.4	16.5	30
Canoas I	8	Middle	1998	81	29	320	ladder	30.8	207	6	26	30
Capivara	9	Middle	1975	619	59	212		576	10540	126.8	52.5	110
Taquaruçu	10	Lower	1992	526	61	134		105.5	672.5	7.9	26.5	60
Rosana	11	Lower	1986	353	30	25		220	1920	18.6	26	90

Data collection. We gathered data on fish diversity (species richness, composition and abundance) from studies conducted in the basin (Tab. 2). We selected only studies conducted in the impounded area (*i.e.*, lentic and semi-lentic habitats) and adjacent environments directly affected by the impoundment (*i.e.*, upstream stretches, tributaries, lateral lakes, and fish passage facilities). We excluded studies or data collected in environments not affect by the impoundment (*i.e.*, free-flowing streams and rivers), in addition to sites downstream from the dam. We searched for studies in different databases (Web of Science, Scopus, SciELO and Google), private libraries, and performed cross-reference searches. We performed exhaustive searches, and used different keywords in databases (*e.g.*, fish, ichthyofauna, diversity, Paranapanema, Paraná). The survey collected published references (scientific journals and book chapters, 78%) and unpublished material (theses, reports and databases, 22%) (Tab. 2).

In total, we gathered 34 independent studies that investigated fish diversity in nine reservoirs, between 1991 and 2012 (Tab. 2). Some studies investigated more than one reservoir, so our sample size totaled 47 samples. Sampling effort was distributed heterogeneously: Jurumirim, Salto Grande, Capivara, and Rosana received more effort, while Ourinhos and Taquaruçu were less investigated. We found no study conducted in Piraju and Paranapanema reservoirs. Fish sampling employed different gears, but gill nets and seines prevailed (Tab. 2). Most samples (77%) were collected at least 10 years after the construction of the impoundment. It means that fish assemblages have responded to reservoir conditions and community structure have shifted to another regime and stability (Agostinho *et al.*, 2007a). Our study, therefore, focus on reservoir fish assemblages.

We obtained species lists from each sample, which were organized to build a "sample x species" matrix. Each sample was considered an independent unit (Tab. 2), and we only considered taxa identified to the species level; those reported as "sp." or "spp." were discarded. Species names and taxonomic classification were carefully checked and, when necessary, updated and corrected following Froese, Pauly (2016), Eschmeyer *et al*. (2017), Eschmeyer, Fong (2017) and recent literature; updates are shown on Tab. **S1** (Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni). We then assigned species as native (non-migratory or long distance migratory) and non-native. We used pertinent literature to assign species as long distance migratory, *i.e.*, those that migrate more than 100 km (*sensu* Agostinho *et al.*, 2003). Equally, we followed scientific literature to assign species as non-native, *i.e.*, species introduced to the Paranapanema river basin (*sensu* Reis *et al.*, 2003; Graça, Pavanelli, 2007; Julio Jr. *et al.*, 2009; Britton, Orsi, 2012; Garavello *et al.*, 2012; Orsi, Britton, 2014; Ortega *et al.*, 2015; Froese, Pauly, 2016; Garcia *et al.*, 2018). Abundance data was recorded whenever available (Tab. 2), and used to calculate species relative abundances (%).

Data analysis. Analyses focused on three groups: (i) native non-migratory species (NT); (ii) native long-distance migratory species (LDM); and (iii) non-native species (NNS). All analyses considered these three groups separately.

To investigate total taxonomic richness in the impoundments, we calculated species accumulation curves based on sampling effort (n = 47). Sample order in the original matrix (sample x species) was randomized 500 times, building expected curves for native (NT + LDM) and non-native species (NNS). We also calculated three non-parametric estimators to estimate total richness: Chao-1, ICE (Incidence-based Coverage Estimator), and Jackknife. These analyses were conducted in the software EstiMateS 5.0 (Colwell, 2006).

Tab. 2. Samples collected from 34 studies that investigated fish diversity in the cascade of reservoirs along the Paranapanema River. For each sample we provide the sampling period, reservoir age, target environment (FL = fish ladder; LG = lateral lagoon; RS = reservoir; RV = river; TB = tributary), sampling gears (CN = cast net; FS = artisanal fishery; GN = gill nets; PL = plankton net; OB = observation; SN = seine; SV = sieve; TP = trap), abundance data (x = available), and data source.

Samples	Reservoir	Period	Age	Environment	Gear	Abundance	Source
1	Jurumirim	1994-1995	32-33	RS	GN	X	Barrella, Petrere Jr. (2003)
2	Jurumirim	1995-1996	33-34	LG, RS	GN, SV	X	Carvalho *et al.* (1998)
3	Jurumirim	1996-1997	34-35	LG, RS, TB	GN		Carvalho, Silva (1999)
4	Jurumirim	1998-1999	36-37	LG	SN, SV	X	Carvalho *et al.* (2005)
5	Jurumirim	2005-2006	43-44	LG, RS, TB	FS		Novaes, Carvalho (2009)
6	Jurumirim	2005-2006	43-44	LG, RS, TB	FS		Novaes, Carvalho (2013)
7	Jurumirim	1991	29	RS, TB	GN		Carvalho *et al.* (1991) apud Kurchevski, Carvalho (2014)
8	Jurumirim	2003	41	LG, RS, RV	GN, SN, SV		Carvalho *et al.* (2003) apud Kurchevski, Carvalho (2014)
9	Jurumirim	2007	45	RS	GN		Zanatta (2007) apud Kurchevski, Carvalho (2014)
10	Jurumirim	2012	50	LG, RS, RV	GN, SN, SV	X	Kurchevski (2012) apud Kurchevski, Carvalho (2014)
11	Chavantes	2001	30	RS	GN	X	Unpublished data
12	Chavantes	2005-2006	35-36	RS	GN, SN, SV	X	Magnoni (2009)
13	Chavantes	2010-2011	40-41	RS	GN	X	Caetano *et al.* (2011)
14	Ourinhos	2006-2009	1-4	LG, RS, TB	CN, GN, SN, SV	X	CBA (2009)
15	Salto Grande	2001	43	RS	GN	X	Unpublished data
16	Salto Grande	1992-1993	34-35	RS, RV	GN		Dias, Garavello (1998)
17	Salto Grande	1993-1995	35-37	RS, RV	GN		Dias (2003)
18	Salto Grande	2005-2006	47-48	LG, RS	GN, SN, SV	X	Brandão *et al.* (2009)
19	Salto Grande	2005-2006	47-48	LG	GN		Vianna (2008)
20	Canoas II	2001	3	RS	GN	X	Unpublished data
21	Canoas II	2000-2001	2-3	RS, LG, FL	SN		Britto, Sirol (2007)
22	Canoas II	2000-2006	2-8	RS, LG, FL	SN, SV	X	Britto (2009)
23	Canoas II	2001-2002	2-3	RS, LG, FL	SN	X	Britto, Carvalho (2013)
24	Canoas I	2001	3	RS	GN	X	Unpublished data
25	Canoas I	2000-2001	2-3	RS, LG, FL	SN		Britto, Sirol (2007)
26	Canoas I	2000-2006	2-8	RS, LG, FL	SN, SV	X	Britto (2009)
27	Canoas I	2001-2002	2-3	RS, LG, FL	SN	X	Britto, Carvalho (2013)
28	Capivara	2001	26	RS	GN	X	Unpublished data
29	Capivara	1992-1993	17-18	TB	GN	X	Bennemann *et al.* (2000)
30	Capivara	2001-2002	26-27	TB, RS	GN	X	Bennemann *et al.* (2013)
31	Capivara	1993-1995	17-19	RS	GN		Dias (2003)
32	Capivara	1994-1995	18-19	RS	GN	X	Barrella, Petrere Jr. (2003)
33	Capivara	2001-2002	26-27	RS	CN, GN, SN, SV	X	Hoffmann *et al.* (2005)
34	Capivara	2001-2002	26-27	TB	CN, GN	X	Shibatta *et al.* (2007)
35	Capivara	2003-2004	28-29	TB	GN		Vianna, Nogueira (2008)
36	Capivara	1990-1994	15-19	RS	GN		Orsi, Britton (2014)
37	Capivara	2001-2010	26-35	RS	GN		Orsi, Britton (2014)
38	Taquaruçu	2001	9	RS	GN	X	Unpublished data
39	Taquaruçu	1993-2000	1-8	RS	GN	X	Britto, Carvalho (2006)
40	Rosana	2001	15	RS	GN	X	Unpublished data
41	Rosana	1994-1995	8-9	RS	GN	X	Barrella, Petrere Jr. (2003)
42	Rosana	1997-1998	11-12	TB	GN	X	Abilhôa, Bastos (2005)
43	Rosana	2000-2001	14-15	RS	SN, OB	X	Casatti *et al.* (2003)
44	Rosana	2002	16	RS, RV, TB	SN, PL	X	Kipper *et al.* (2011)
45	Rosana	2003	17	RS, TB	TP	X	Pelicice *et al.* (2005)
46	Rosana	2004-2005	18-19	LG	SN	X	Ferrareze, Nogueira (2011)
47	Rosana	2005-2007	19-21	RS	SN, TP	X	Pelicice, Agostinho (2009); Pelicice *et al.* (2015b)

To investigate spatial variation in species richness and composition, we pooled the 47 samples within each reservoir to build a "reservoir x species" matrix. We then calculated total richness per reservoir for each group (NT, LDM and NNS). To investigate spatial variations in species composition, we used Non-Metric Multidimensional Scaling (NMDS) based on Jaccard distance (presence/absence). We conducted three NMDS, one for each group. These analyses were carried out in the software Past 1.75b (Hammer *et al.*, 2001).

We also investigated trends in abundance. Twenty-two studies (Tab. 2) provided abundance data for all species in the assemblage (number, density or capture per effort); we used these data to calculate the relative abundance (%) of each species, generating an abundance-based "sample x species" matrix (32 samples). We used this matrix to investigate spatial variation in the relative abundance of LDM and NNS in assemblages, by plotting samples against reservoirs (scatterplot). We also calculated the range of relative abundance (minimum-maximum) for each species along the cascade system.

Results

We recorded 161 fish species in the cascade of reservoirs along the Paranapanema River, being 111 native and 50 non-native to the basin (Tab. 3). Most species belonged to the order Characiformes, followed by Siluriformes and Cichliformes.

Tab. 3. Fish species recorded in the cascade of reservoirs along the Paranapanema River. LDM = long distance migratory; NNS = non-native. Taxonomic classification followed Eschmeyer, Fong (2017).

Species	LDM	NNS
MYLIOBATIFORMES		
Potamotrygonidae		
Potamotrygon cf. *motoro* (Müller & Henle, 1841)		X
CYPRINIFORMES		
Cyprinidae		
Cyprinus carpio Linnaeus, 1758		X
CHARACIFORMES		
Crenuchidae		
Characidium fasciatum Reinhardt, 1867		
Characidium zebra Eigenmann, 1909		
Erythrinidae		
Hoplias intermedius (Günther, 1864)		*X*
Hoplias lacerdae Miranda Ribeiro, 1908		X
Hoplias malabaricus (Bloch, 1794)		
Parodontidae		
Apareiodon affinis (Steindachner, 1879)		
Apareiodon ibitiensis Amaral Campos, 1944		
Apareiodon piracicabae (Eigenmann, 1907)		
Parodon nasus Kner, 1859		
Cynodontidae		
Rhaphiodon vulpinus Spix & Agassiz, 1829	X	

Tab. 3. (continued).

Species	LDM	NNS
Serrasalmidae		
Metynnis lippincottianus Cope, 1870		X
Metynnis mola Eigenmann & Kennedy, 1903		
Myloplus levis (Eigenmann & McAtee, 1907)		
Myloplus tiete (Eigenmann & Norris, 1900)		
Piaractus mesopotamicus (Holmberg, 1887)	X	
Serrasalmus maculatus Kner, 1858		
Serrasalmus marginatus Valenciennes, 1837		X
Anostomidae		
Leporellus pictus (Kner, 1858)		
Leporellus vittatus (Valenciennes, 1850)		
Leporinus amblyrhynchus Garavello & Britski, 1987		
Leporinus friderici (Bloch, 1794)		
Leporinus lacustris Amaral Campos, 1945		
Leporinus octofasciatus Steindachner, 1915		
Leporinus paranensis Garavello & Britski, 1987		
Leporinus striatus Kner, 1858		
Megaleporinus elongatus (Valenciennes, 1850)	X	
Megaleporinus macrocephalus (Garavello & Britski, 1988)		X
Megaleporinus obtusidens (Valenciennes, 1837)	X	
Schizodon altoparanae Garavello & Britski, 1990		
Schizodon borellii (Boulenger, 1900)		X
Schizodon intermedius Garavello & Britski, 1990		
Schizodon nasutus Kner, 1858		
Curimatidae		
Cyphocharax modestus (Fernández-Yépez, 1948)		
Cyphocharax nagelii (Steindachner, 1881)		
Steindachnerina brevipinna (Eigenmann & Eigenmann, 1889)		X
Steindachnerina insculpta (Fernández-Yépez, 1948)		
Prochilodontidae		
Prochilodus lineatus (Valenciennes, 1837)	X	
Lebiasinidae		
Pyrrhulina australis Eigenmann & Kennedy, 1903		
Triportheidae		
Triportheus angulatus (Spix & Agassiz, 1829)		X
Triportheus nematurus (Kner, 1858)		X
Bryconidae		
Brycon nattereri Günther, 1864		
Brycon orbignyanus (Valenciennes, 1850)	X	
Salminus brasiliensis (Cuvier, 1816)	X	
Salminus hilarii Valenciennes, 1850	X	
Acestrorhynchidae		
Acestrorhynchus lacustris (Lütken, 1875)		
Characidae		
Aphyocharax anisitsi Eigenmann & Kennedy, 1903		
Aphyocharax dentatus Eigenmann & Kennedy, 1903		X
Astyanax bockmanni Vari & Castro, 2007		
Astyanax fasciatus (Cuvier, 1819)		
Astyanax lacustris (Lütken, 1875)		
Astyanax paranae Eigenmann, 1914		
Bryconamericus iheringii (Boulenger, 1887)		
'Cheirodon' stenodon Eigenmann, 1915		
Piabarchus stramineus (Eigenmann, 1908)		
Galeocharax gulo (Cope, 1870)		
Hemigrammus marginatus Ellis, 1911		

Tab. 3. (continued).

Species	LDM	NNS
Hyphessobrycon anisitsi (Eigenmann, 1907)		
Hyphessobrycon bifasciatus Ellis, 1911		
Hyphessobrycon eques (Steindachner, 1882)		X
Moenkhausia intermedia Eigenmann, 1908		
Odontostilbe weitzmani Chuctaya, Bührnheim & Malabarba, 2018		X
Oligosarcus paranensis Menezes & Géry, 1983		
Oligosarcus pintoi Amaral Campos, 1945		
Piabina argentea Reinhardt, 1867		
Roeboides descalvadensis Fowler, 1932		X
Planaltina britskii Menezes, Weitzman & Burns, 2003		
Serrapinnus heterodon (Eigenmann, 1915)		
Serrapinnus notomelas (Eigenmann, 1915)		
GYMNOTIFORMES		
Gymnotidae		
Gymnotus cf. *carapo* Linnaeus, 1758		
Gymnotus inaequilabiatus (Valenciennes, 1839)		X
Gymnotus sylvius Albert & Fernandes-Matioli, 1999		
Rhamphichthyidae		
Rhamphichthys hahni (Meinken, 1937)		X
Hypopomidae		
Brachyhypopomus gauderio Giora & Malabarba, 2009		X
Sternopygidae		
Eigenmannia cf. *trilineata* López & Castello, 1966		
Eigenmannia virescens (Valenciennes, 1836)		
Sternopygus macrurus (Bloch & Schneider, 1801)		
Apteronotidae		
Apteronotus cf. *caudimaculosus* de Santana, 2003		X
Apteronotus brasiliensis (Reinhardt, 1852)		
Apteronotus ellisi (Alonso de Arámburu, 1957)		
SILURIFORMES		
Cetopsidae		
Cetopsis gobioides Kner, 1858		
Auchenipteridae		
Ageneiosus militaris Valenciennes, 1836		
Auchenipterus osteomystax (Miranda Ribeiro, 1918)		X
Tatia intermedia (Steindachner, 1877)		X
Tatia neivai (Ihering, 1930)		
Trachelyopterus galeatus (Linnaeus, 1766)		X
Doradidae		
Ossancora eigenmanni (Boulenger, 1895)		X
Pterodoras granulosus (Valenciennes, 1821)	X	X
Rhinodoras dorbignyi (Kner, 1855)		
Trachydoras paraguayensis (Eigenmann & Ward, 1907)		X
Heptapteridae		
Imparfinis schubarti (Gomes, 1956)		
Phenacorhamdia tenebrosa (Schubart, 1964)		
Pimelodella avanhandavae Eigenmann, 1917		X
Pimelodella gracilis (Valenciennes, 1835)		
Pimelodella meeki Eigenmann, 1910		
Rhamdia cf. *quelen* (Quoy & Gaimard, 1824)		
Pimelodidae		
Hypophthalmus edentatus Spix & Agassiz, 1829		X
Iheringichthys labrosus (Lütken, 1874)		
Megalonema platanum (Günther, 1880)		
Pimelodus absconditus Azpelicueta, 1995		
Pimelodus maculatus Lacepède, 1803	X	
Pimelodus microstoma Steindachner, 1877		
Pimelodus ornatus Kner, 1858		X
Pimelodus paranaensis Britski & Langeani, 1988		
Pinirampus pirinampu (Spix & Agassiz, 1829)	X	
Pseudoplatystoma corruscans (Spix & Agassiz, 1829)	X	
Pseudoplatystoma fasciatum (Linnaeus, 1766)	X	X
Sorubim lima (Bloch & Schneider, 1801)	X	X
Steindachneridion scriptum (Miranda-Ribeiro, 1918)	X	
Zungaro jahu (Ihering, 1898)	X	
Pseudopimelodidae		
Pseudopimelodus mangurus (Valenciennes, 1835)		
Clariidae		
Clarias gariepinus (Burchell, 1822)		X
Trichomycteridae		
Trichomycterus diabolus Bockmann, Casatti & de Pinna, 2004		
Callichthyidae		
Callichthys callichthys (Linnaeus, 1758)		
Corydoras aeneus (Gill, 1858)		
Corydoras ehrhardti Steindachner, 1910		
Corydoras paleatus (Jenyns, 1842)		X
Hoplosternum littorale (Hancock, 1828)		
Loricariidae		
Hypostomus albopunctatus (Regan, 1908)		
Hypostomus ancistroides (Ihering, 1911)		
Hypostomus auroguttatus Kner, 1854		X
Hypostomus hermanni (Ihering, 1905)		
Hypostomus iheringi (Regan, 1908)		
Hypostomus margaritifer (Regan, 1908)		
Hypostomus multidens Jerep, Shibatta, Zawadzki, 2007		
Hypostomus myersi (Gosline, 1947)		X
Hypostomus nigromaculatus (Schubart, 1964)		
Hypostomus paulinus (Ihering, 1905)		
Hypostomus regani (Ihering, 1905)		
Hypostomus roseopunctatus Reis, Weber & Malabarba, 1990		X
Hypostomus strigaticeps (Regan, 1908)		
Hypostomus ternetzi (Boulenger, 1895)		X
Hypostomus tietensis (Ihering, 1905)		
Hypostomus topavae (Godoy, 1969)		
Hypostomus variostictus (Miranda Ribeiro, 1912)		X
Loricaria simillima Regan, 1904		
Loricariichthys labialis (Boulenger, 1895)		X
Loricariichthys platymetopon Isbrücker & Nijssen, 1979		X
Megalancistrus parananus (Peters, 1881)		
Paraloricaria vetula (Valenciennes, 1835)		X
Proloricaria prolixa (Isbrücker & Nijssen, 1978)		
Pterygoplichthys ambrosettii (Holmberg, 1893)		X
Rhinelepis aspera Spix & Agassiz 1829	X	
SYNBRANCHIFORMES		
Synbranchidae		
Synbranchus cf. *marmoratus* Bloch, 1795		
PLEURONECTIFORMES		
Achiridae		

Tab. 3. (continued).

Species	LDM	NNS
Catathyridium jenynsii (Günther, 1862)		X
CICHLIFORMES		
Cichlidae		
Astronotus crassipinnis Heckel, 1840		X
Cichla kelberi Kullander & Ferreira, 2006		X
Cichla piquiti Kullander & Ferreira, 2006		X
Cichlasoma paranaense Kullander, 1983		
Coptodon rendalli (*Boulenger*, *1897*)		X
Crenicichla britskii Kullander, 1982		
Crenicichla haroldoi Luengo & Britski, 1974		
Crenicichla jaguarensis Haseman, 1911		
Crenicichla cf. *niederleinii* (Holmberg, 1891)		
Geophagus brasiliensis (Quoy & Gaimard, 1824)		
Oreochromis niloticus (Linnaeus, 1758)		X
Satanoperca aff. *pappaterra* (Heckel, 1840)		X
CYPRINODONTIFORMES		
Poeciliidae		
Phalloceros harpagos Lucinda, 2008		
Poecilia reticulata Peters, 1859		X
PERCIFORMES		
Sciaenidae		
Plagioscion squamosissimus (Heckel, 1840)		X

Considering only native species (NT + LDM = 111 species), the accumulation curve tended to stabilize (Fig. 2), but non-parametric estimators indicated that total richness is underestimated (Chao-1 = 132.4 ±13.2 SD; ICE = 125.1 ± 0.01; Jackknife-1 = 129.6 ±7.6). Among native species, we recorded 14 long-distance migratory species (Tab. 3). Considering non-native species (NNS = 50), the accumulation curve also tended to stabilize (Fig. 2), and non-parametric estimators confirmed this trend (Chao-1 = 60.1 ±7.2; ICE = 60.5 ±0.01; Jackknife-1 = 63.7 ±3.7). We recorded three non-native migratory species (Tab. 3).

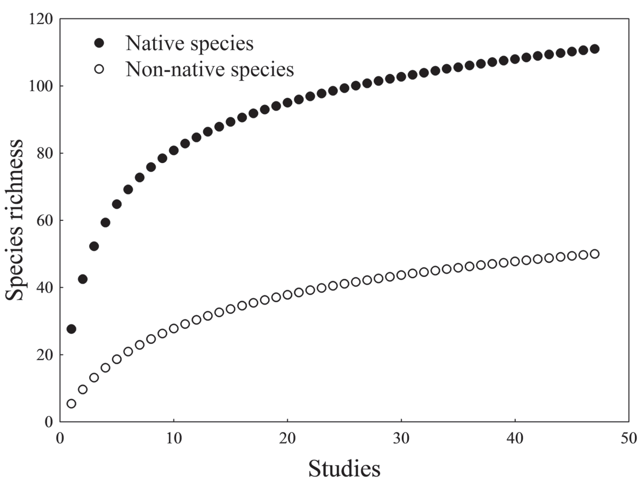

Fig. 2. Species accumulation curves controlled by sampling effort (47 samples). Curves were calculated separately for native and non-native species.

Reservoirs showed a mean species richness of 72 species (range: 56 to 112). Considering only NT, each reservoir had 49.9 species on average (range: 39 to 80), with no longitudinal trend along the cascade system (Fig. 3). Migratory species were recorded in all reservoirs, with a mean value of 8.1 species/reservoir (range: 3 to 12). However, LDM richness showed a clear longitudinal pattern, with higher values in reservoirs located below Salto Grande dam (Fig. 3). Non-native species were also recorded in all reservoirs, with a mean of 14 NNS per reservoir (range: 8 to 23). Reservoirs located in the lower reach, together with Salto Grande, contained more NNS (Fig. 3).

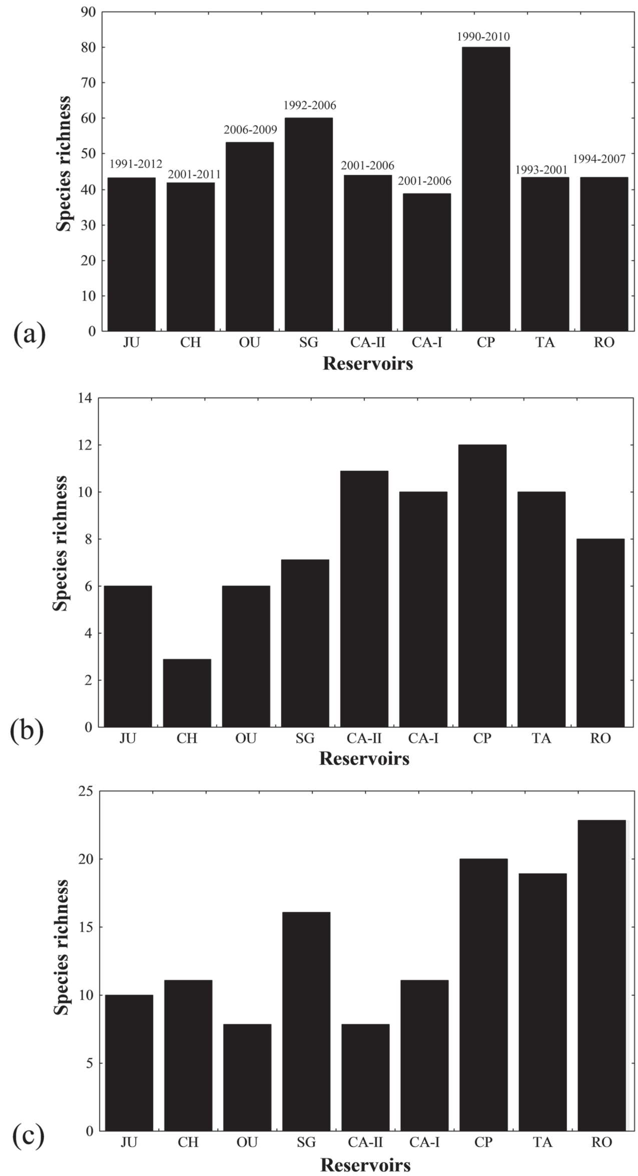

Fig. 3. Species richness in the cascade of reservoirs along the Paranapanema River, separated as native non-migratory (a), native long-distance migratory (b) and non-native species (c). The sampling period is shown above each bar. Reservoir codes: JU = Jurumirim; CH = Chavantes; OU = Ourinhos; SG = Salto Grande; CA-II = Canoas II; CA-I = Canoas I; CP = Capivara; TA = Taquaruçu; RO = Rosana.

Non-Metric Multidimensional Scaling (NMDS; stress = 0.14) showed a longitudinal gradient of species composition for NT (Fig. 4a). Jurumirim (first reservoir in the cascade) and Rosana (last in the cascade) were placed in opposing ends along axis 1 (Fig. 4a); some reservoirs located in middle and lower reaches overlapped, indicating similar composition. Many species seemed to be widely distributed in the cascade system, while some were restricted to specific impoundments (Tab. 4). Considering LDM, the NMDS (stress = 0.13) also revealed a longitudinal gradient, but formed two groups: upstream and downstream Salto Grande reservoir (Fig. 4b). The first group was composed of species with wide distribution in the cascade system, while the second group included large-sized species (Tab. 5). Regarding NNS, most reservoirs overlapped in the ordination; because the stress value was higher (= 0.22), the plot was not interpreted. Based on Tab. 6, some NNS were widely distributed in the cascade, but no species was present in all reservoirs. Other NNS were restricted to some reservoir or segment, creating a turnover pattern.

The most abundant species in the cascade system included small native characids (Tab. 4), such as *Astyanax lacustris*, *Schizodon nasutus*, *Serrasalmus maculatus*, *Steindachnerina insculpta* and *Apareiodon affinis*, and the catfish *Iheringichthys labrosus*. Migratory fishes, on the other hand, showed very low abundance in assemblages (Tab. 5), where *Pimelodus maculatus* was the most abundant and frequent. In almost all samples (88%), LDM summed less than 10% of total abundance (range: 0 to 35.8%), with higher values in Canoas I, Canoas II and Capivara reservoirs (Fig. 5a). Differently, NNS were more abundant and summed more than 10% of total abundance in most samples (range: 0 to 90%) (Fig. 5b). Higher values were recorded in reservoirs located downstream (Capivara, Taquaruçu and Rosana). The most abundant species in the cascade system were *Plagioscion squamosissimus* and *Hyphessobrycon eques*, in addition to others abundant in specific reservoirs or stretches, such as *Roeboides descalvadensis*, *Serrasalmus marginatus*, *Loricariichthys platymetopon* and *Hypophthalmus edentatus* (Tab. 6).

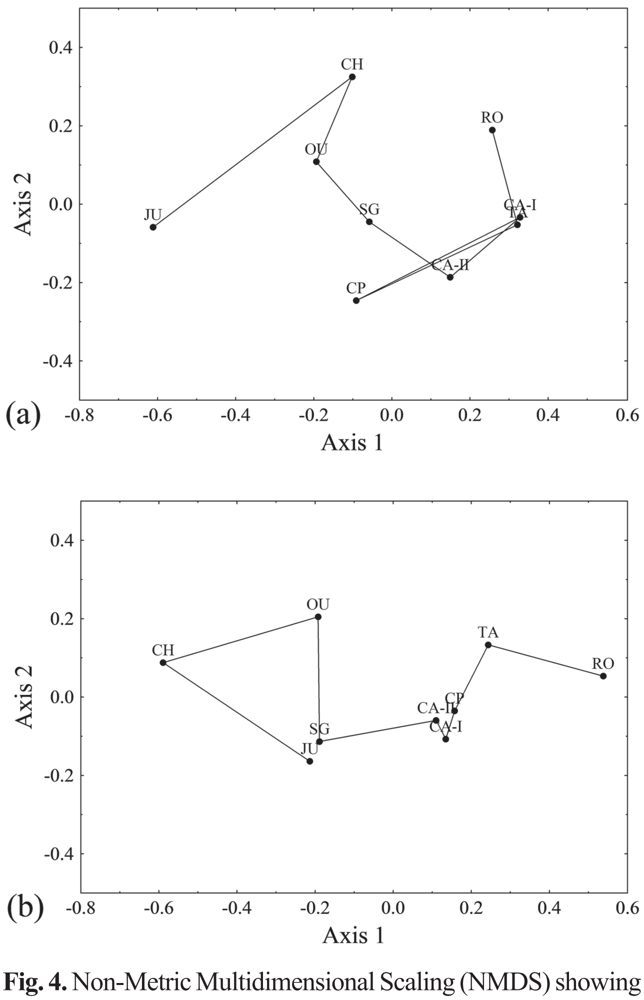

Fig. 4. Non-Metric Multidimensional Scaling (NMDS) showing variation in assemblage composition in the cascade of reservoirs along the Paranapanema River, considering native non-migratory species (a) and native long-distance migratory species (b). The line connecting reservoirs indicates the sequence in the cascade system. Reservoir names (codes) are shown in Fig. 3.

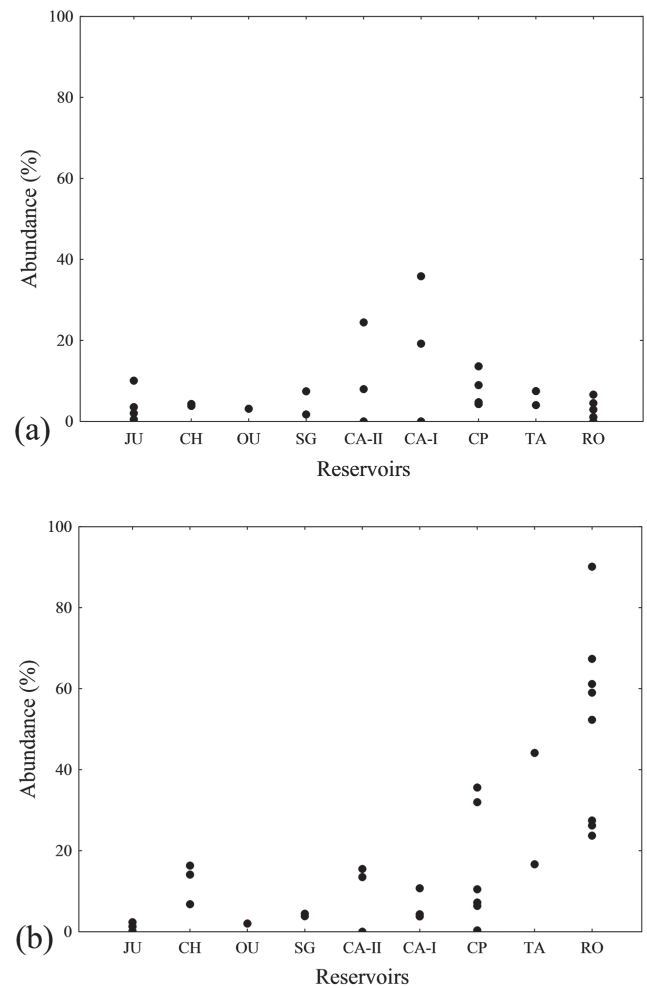

Fig. 5. Relative abundance (%) of long-distance migratory fishes (a) and non-native species (b) in the cascade of reservoirs along the Paranapanema River. Each dot is a sample (n = 32). Reservoir names (codes) are shown in Fig. 3.

Tab. 4. Distribution of non-migratory native species in the cascade of reservoirs along the Paranapanema River (gray = presence), based on all studies (47 samples). Numbers are the relative abundance range (percentage, min-max), based on studies that provided abundance data (32 samples); the most abundant species in the cascade are highlighted in bold. Reservoir names (codes) are shown in Fig. 3.

Species	JU	CH	OU	SG	CA-II	CA-I	CP	TA	RO
Leporinus amblyrhynchus	0 - 0.1	0 - 0.5	4.3	0 - 0.1	0	0 - 0.4	0 - 4.3	0 - 0.1	0 - 0.3
Leporinus friderici	0 - 1.3	0 - 0.8	0	1.1 0.2	0.3 - 2.5	0.2 - 5.1	0.2 - 1.8	0.2 - 1.7	0 - 1.2
Leporinus octofasciatus	0 - 0.2	0 - 0.3	0.2	0 - 0.1	0 - 1.3	0 - 2.3	0 - 1.1	0 - 0.6	0 - 0.1
Schizodon nasutus	**0.1 - 7.7**	**1.9 - 7.6**	**2.4**	**4.2 - 9.8**	**1.5 - 3.9**	**0.3 - 6.1**	**1.2 - 2.8**	**3.2 - 7.6**	**0 - 2.0**
Astyanax lacustris	**0 - 11.5**	**7.4 - 34.8**	**4.9**	**9.4 - 24.9**	**4.2 - 8.0**	**2.3 - 7.0**	**1.4 - 32.2**	**1.0 - 3.2**	**0 - 3.1**
Galeocharax gulo	0 - 1.8	1.4 - 7.6	2.0	1.3 - 1.7	0 - 3.1	0 - 1.9	0 - 0.7	0 - 0.3	0 - 0.1
Serrasalmus maculatus	**2.0 - 10.6**	**1.1 - 3.6**	**3.7**	**4.5 - 5.2**	**0.9 - 3.7**	**0.6 - 1.2**	**0 - 3.6**	**0.2 - 1.5**	**0 - 11.1**
Cyphocharax modestus	7.4 - 76.9	0 - 0.2	1.6	0 - 1.7	0 - 0.9	0 - 0.1	0 - 0.5	0 - 1.2	0 - 2.1
Steindachnerina insculpta	**1.9 - 9.4**	**0 - 13.6**	**17.1**	**0 - 19.2**	**0 - 0.4**	**0 - 0.2**	**0 - 8.1**	**0 - 8.3**	**0 - 7.7**
Hoplias malabaricus	0.5 - 2.8	0 - 1.1	1.2	0.3 - 1.6	0 - 0.9	0 - 0.8	0.1 - 1.4	0.2 - 1.3	0 - 8.4
Apareiodon affinis	**0 - 5.0**	**0 - 52.5**	**19.8**	**2.2 - 3.8**	**0 - 37.0**	**0 - 11.1**	**0 - 30.2**	**1.3 - 8.0**	**0 - 8.1**
Geophagus brasiliensis	0 - 0.6	0.4 - 1.7	1.8	0.5 - 4.1	0 - 0.2	0 - 0.6	0 - 1.2	0 - 0.2	0 - 3.8
Hypostomus ancistroides	0 - 2.6	0 - 0.1	1.2	0 - 0.5	0 - 0.4	0 - 0.6	0 - 1.8	0.7 - 0.8	0 - 0.6
Iheringichthys labrosus	**0 - 0.6**	**1.1 - 2.8**	**1.9**	**6.6 - 35.7**	**0 - 14.5**	**0 - 24.4**	**1.6 - 5.9**	**5.9 - 9.2**	**0 - 4.1**
Astyanax fasciatus	0.5 - 5.1	0 - 8.1	2.6	0.3 - 4.3	0 - 1.8	0 - 0.4	0 - 7.9	0 - 0.1	
Serrapinnus notomelas	**0 - 52.6**	**0 - 0.3**	**0**	**0**	**0 - 21.3**	**0 - 12.7**	**0 - 0.9**		**0 - 9.2**
Hypostomus strigaticeps	0 - 0.1	0 - 0.1	5.5	0 - 0.7	0 - 0.2		0 - 0.1		
Gymnotus cf. *carapo*	0 - 0.2	0 - 0.7	0	0 - 0.4		0 - 0.4	0 - 0.4	0 - 0.2	0 - 0.6
Eigenmannia cf. *trilineata*	0 - 0.1	0 - 0.4	0	0 - 1.7			0 - 0.1		0 - 2.7
Rhamdia cf. *quelen*	0 - 0.5	0 - 0.1	0.2	0.3 - 0.5			0 - 5.8		0 - 0.3
Piabina argentea	0 - 0.1	0 - 0.3	0	0			0 - 0.3		
Hoplosternum littorale	0 - 9.1	0 - 0.7	0.2	0 - 0.8			0 - 0.7		
Hypostomus regani	0 - 1.4	0 - 0.5	7.4	0-0.1	0 - 6.6	0 - 1.7	0 - 5.8	0 - 1.1	
Characidium zebra	0	0 - 0.1	0				0 - 0.6		0 - 0.2
Synbranchus cf. *marmoratus*	0 -0.1	0 - 0.1	0				0 - 0.4		0 - 0.1
'Cheirodon' stenodon	0 - 48.5	0 - 1.4		0			0 - 0.1		
Leporinus striatus	0 - 0.2		0	0	0	0	0 - 0.5	0 - 0.2	0 - 0.1
Piabarchus stramineus	0 - 0;6		0	0 - 0.5	0 - 1.3	0 - 4.0	0 - 0.7	0 - 47.9	0 - 50.0
Eigenmannia virescens	0 - 0.1		1.0	0	0	0 - 0.1	0 - 0.7	0 - 0.9	0 - 0.1
Astyanax bockmanni	0 - 0.2		0.1	0 - 0.2	0 - 0.2		0 - 5.5		
Oligosarcus paranensis	0 - 1.4		0.3	0			0 - 1.0		
Hypostomus paulinus	0 - 0.2		0.1	0					
Hemigrammus marginatus	**0 - 0.1**		**0**		**0 - 43.9**	**0 - 72.9**	**0 - 2.7**	**0 - 0.1**	**0 - 54.8**
Rhinodoras dorbignyi	0 - 1.4		0		0	0 - 0.4	0 - 0.9	0 - 0.3	0 - 5.6
Gymnotus sylvius	0 - 0.3		0				0 - 0.1		
Apareiodon piracicabae	0 - 1.1			0 - 4.1	0 - 0.9		0 - 3.9	0.2 - 0.3	0 - 0.3
Bryconamericus iheringhii	0 - 0.4			0			0 - 0.2		
Leporellus vitatus	0 - 0.1				0 - 0.4	0	0 - 0.9	0 - 0.3	
Schizodon intermedius	0 - 5.2				0 - 0.1	0 - 0.1	0 - 12.8	0 - 2.1	
Acestrorhynchus lacustris		**1.6 - 6.5**	**6.9**	**6.6 - 17.6**	**0 - 9.3**	**0 - 1.7**	**0 - 9.4**	**1.7-4.2**	**0.1 - 4.7**
Myloplus tiete		0 - 0.1	0	0 - 0.1	0	0 - 0.1	0 - 0.3	0 - 0.4	0 - 0.1
Crenicichla britskii		0 - 0.7	0.1	0 - 0.6	0 - 0.2	0 - 0.6	0 - 0.7	0 - 0.4	0 - 1.8
Crenicichla cf. *niederleinii*		0 - 2.8	0.1	0.1 - 0.2	0 - 1.1	0 - 2.1	0 - 1.3	0 - 0.3	0 - 0.1
Megalancistrus parananus		0 - 0.1	0.7	0	0 - 0.4	0 - 0.2	0 - 0.1	0.1 - 0.1	0 - 0.1
Hypostomus maragaritifer		0 - 0.1	2.0	0 - 0.1	0 - 8.2	0 - 1.6	0 - 0.4	0 - 1.4	
Proloricaria prolixa		0 - 0.1	0.3	0.8 - 2.0	0 - 1.8	0 - 7.9	0 - 0.5	0 - 0.4	
Sternopygus macrurus		0 - 0.3	0	0.2 - 0.6			0 - 0.3	0 - 0.2	0 - 0.4

Tab. 4. (continued).

Species	JU	CH	OU	SG	CA-II	CA-I	CP	TA	RO
Cichlasoma paranaense		0 - 0.1	0.2	0 - 0.1			0 - 0.2		0 - 0.9
Crenicichla haroldoi		0 - 2.9		0.2 - 0.2	0 - 0.2	0 - 1.3	0 - 1.2	0 - 1.2	0 - 0.2
Tatia neivai		0 - 0.5		0 - 0.3	0 - 1.3	0 - 0.6	0 - 0.4	0 - 0.1	0 - 0.1
Hypostomus iheringii		0		0 - 0.3			0 - 3.2		
Crenicichla jaguarensis		0 - 0.3		0 - 0.1					
Astyanax paranae		0 - 0.1					0 - 20.8		
Leporinus paranensis			0.1	0 - 0.1	0	0	0	0 - 0.1	
Hypostomus hermanni			0	0	0		0		
Hypostomus nigromaculatus			0	0	0 - 0.2		0 - 0.1		
Pimelodella gracilis			0	0					0 - 0.1
Hypostomus albopunctatus			0.2			0	0 - 1.9		
Parodon nasus			0				0 - 1.5		
Moenkhausia intermedia				0 - 0.2	0 - 1.8	0 - 1.6	0 - 32.2	0.2 - 2.1	0 - 1.0
Cyphocharax nagelli				0	0 - 0.1		0 - 0.1	0 - 0.2	
Pyrrhulina australis				0	0 - 0.3		0		
Schizodon altoparanae				0		0	0 - 0.1	0 - 0.1	0 - 0.1
Leporinus lacustris				0			0 - 0.5	0 - 0.1	0 - 7.7
Apteronotus ellisi				0			0 - 0.5	0 - 0.1	
Ageneiosus militaris				0 - 0.1			0 - 0.2		0 - 0.6
Hypostomus tietensis				0			0 - 0.3		
Callichthys callichthys	0 - 0.5						0		
Pimelodella meeki	0 - 0.1						0		
Leporellus pictus	0								
Hyphessobrycon anisitsi	0 - 6.9								
Characidium fasciatum	0 - 0.4								
Serrapinnus heterodon		0 - 0.1							
Hypostomus multidens		0 - 0.1							
Oligosarcus pintoi			0						0 - 5.6
Hyphessobrycon bifasciatus			0						
Metynnis mola			0						
Phalloceros harpagos			0						
Phenacorhamdia tenebrosa			0						
Planaltina bristkii				0					
Corydoras aeneus				0					
Hypostomus topavae				0 - 0.1					
Apareiodon ibitiensis					0		0		
Apteronotus brasiliensis					0 - 0.2		0 - 0.1		
Pimelodus paranensis						0	0 - 0.1		
Megalonema platanum							0 - 0.5	0 - 0.1	
Pimelodus absconditus							0 - 0.1	0 - 0.9	
Aphyocharax anisitsi							0 - 2.0		0 - 5.0
Brycon nattereri							0 - 0.7		
Corydoras ehrhardti							0 - 0.3		
Cetopsis gobioides							0 - 0.1		
Imparfinis schubarti							0 - 0.1		
Loricaria simillima							0		
Pimelodus microstoma							0 - 1.8		
Pseudopimelodus mangurus							0 - 0.2		
Trichomycterus diabolus							0 - 0.5		
Myloplus levis									0 - 0.1

Tab. 5. Distribution of long-distance migratory species in the cascade of reservoirs along the Paranapanema River (gray = presence), based on all studies (47 samples). Numbers are the relative abundance range (percentage, min-max), based on studies that provided abundance data (32 samples); the most abundant species in the cascade are highlighted in bold. Reservoir names (codes) are shown in Fig. 3.

Species	JU	CH	OU	SG	CA-II	CA-I	CP	TA	RO
Megaleporinus obtusidens	0 - 1.3	0 - 0.3	0.1	0 - 0.2	0 - 1.8	0 - 1.2	0.2 - 3.9	0.1 - 0.5	0 - 0.6
Pimelodus maculatus	**0 - 7.9**	**3 - 4.3**	**2.5**	**1.5 - 7.5**	**0 - 13.2**	**0 - 31.8**	**0.4 - 5.8**	**2.4 - 5.0**	**0 - 2.3**
Prochilodus lineatus	0 - 0.8	0 - 0.9	0.1	0	0 - 5.3	0 - 1.6	0 - 6.4	0.3 - 0.9	
Salminus hilarii	0 - 0.5		0.1	0	0	0	0 - 0.8	0 - 0.1	
Megaleporinus elongatus	0 - 1.1			0	0 - 6.1	0 - 2.5	0 - 2.8	0 - 0.3	0 - 1.0
Piaractus mesopotamicus	0 - 0.1			0	0	0	0 - 0.1		
Steindachneridion scriptum			0.1	0 - 0.1	0		0 - 0.3		
Rhinelepis aspera			0.4		0	0 - 0.6	0 - 0.1	0 - 0.7	0 - 0.1
Salminus brasiliensis					0 - 0.2	0 - 0.8	0 - 0.2	0 - 0.1	0 - 0.1
Pinirampus pirinampu					0 - 0.9	0 - 1.0	0 - 0.9	0.3 - 0.8	0 - 0.4
Pseudoplatystoma corruscans					0	0	0 - 0.1		
Rhaphiodon vulpinus							0 - 1.3	0 - 0.1	0 - 5.1
Zungaro jahu								0 - 0.2	
Brycon orbignyanus									0 - 0.08

Tab. 6. Distribution of non-native species in the cascade of reservoirs along the Paranapanema River (gray = presence), based on all studies (47 samples). Numbers are the relative abundance range (percentage, min-max), based on studies that provided abundance data (32 samples); the most abundant species in the cascade are highlighted in bold. Reservoir names (codes) are shown in Fig. 3.

Species	JU	CH	OU	SG	CA-II	CA-I	CP	TA	RO
Hyphessobrycon eques	**0 - 0.1**		**0**	**0**	**0 - 14.3**	**0 - 3.6**	**0 - 3.2**		**0 - 26.3**
Coptodon rendalli	0 - 1.0		0				0 - 0.3	0 - 0.7	
Metynnis lippincottianus	0 - 0.3			1.0 - 1.4	0.1 - 0.2	0.1 - 4.3	0 - 3.7	0.1 - 1.1	0 - 8.8
Cichla kelberi	0 - 0.7	0 - 0.8	0.1	0 - 0.4			0 - 5.5		0 - 4.3
Plagioscion squamosissimus		**2.9 - 7.6**	**1.9**	**1.6 - 1.7**	**0 - 11.8**	**0 - 10.0**	**0 - 9.4**	**3.3 - 8.7**	**0 - 37.9**
Oreochromis niloticus		0 - 11.4		0 - 0.1	0 - 1.1	0 - 0.1	0		0 - 0.1
Hypostomus auroguttatus		0 - 0.4		0 - 0.3	0 - 0.2			0 - 0.3	
Serrasalmus marginatus		0 - 0.1		0 - 0.2		0 - 0.2	0	0.4 - 5.1	0 - 15.5
Triportheus angulatus		0 - 6.5		0		0	0 - 1.7	0 - 0.1	
Steindachnerina brevipinna		0 - 1.6		0 - 1.2			0 - 2.1	0 - 0.2	0 - 2.0
Pimelodella avanhandavae		0 - 0.2		0 - 0.1			0 - 0.1		
Astronotus crassipinnis			0	0.2 - 0.2			0		
Schizodon borelli				0	0 - 0.2	0 - 0.4	0 - 1.8	0.3 - 0.6	0 - 12.0
Odontostilbe weitzmani	0 - 1.3								
Hoplias intermedius	0								
Hoplias lacerdae	0								
Gymnotus inaequilabiatus	0 - 0.4								
Triportheus nematurus	0 - 0.1	0 - 0.6							
Cyprinus carpio	0			0					
Hypostomus ternetzi		0 - 0.2	0.1						
Cichla piquiti		0 - 0.2		0 - 0.1					
Poecilia reticulata			0						
Hypostomus roseopunctatus			0						
Brachyhypopomus gauderio				0					
Megaleporinus macrocephalus				0 - 0.1	0	0			
Aphyocharax dentatus					0 - 0.9			0 - 0.1	
Pseudoplatystoma fasciatum						0			

Tab. 6. (continued).

Species	JU	CH	OU	SG	CA-II	CA-I	CP	TA	RO
Apteronotus cf. *caudimaculosus*						0	0 - 0.1		
Sorubim lima						0	0 - 0.1	0 - 0.1	
Tatia intermedia							0 - 0.1		
Corydoras paleatus							0 - 0.1		
Hypostomus myersi							0 - 0.1		
Hypostomus variostictus							0 - 0.1		
Pterygoplichthys ambrosetti									
Loricariichthys platymetopon							0 - 11.6	0.6 - 13.7	0 - 13.8
Clarias gariepinnus								0 - 0.1	
Roeboides descalvadensis								0.1 - 1.1	0 - 26.6
Rhamphichthys hahni								0 - 0.1	0 - 0.4
Auchenipterus osteomystax								6.2 - 8.8	0 - 9.3
Trachelyopterus galeatus								0.7 - 4.4	0 - 2.2
Pterodoras granulosus								0 - 0.3	0 - 0.3
Trachydoras paraguayensis								0 - 3.7	0 - 0.1
Pimelodus ornatus								0 - 0.1	0 - 0.5
Ossancora eigenmanni									0 - 0.4
Paraloricaria vetula									0 - 12.7
Loricariichthys labialis									0 - 0.1
Hypophthalmus edentatus									0 - 64.7
Catathyridium jenynsii									0 - 1.8
Potamotrygon cf. *motoro*									0 - 0.1
Satanoperca aff. *pappaterra*									0 - 7.2

Discussion

Our study is the first to compile data on fish diversity in the cascade of reservoirs along the Paranapanema River. This compilation, based on studies conducted in the last decades (1990 to 2012), revealed the presence of 161 species, being 111 native and 50 non-native. The accumulation curve indicated that most native species in the reservoirs were recorded, and we estimated total richness to range between 125 and 132 species. Previous estimates indicated 155 fish species in the Paranapanema river basin (Duke Energy, 2008), and 270 to 310 in the upper Paraná river basin (Agostinho *et al.*, 2007b; Langeani *et al.*, 2007). Impoundments in the Paranapanema River, therefore, hold a high number of fish species and contribute significantly to the basin species pool; a number that may increase if other environments are sampled (*i.e.*, downstream segments, streams, free-flowing stretches). We are aware that misidentifications, re-descriptions and taxonomic revisions may add uncertainty to estimates in impoundments, and we followed recent literature to avoid or minimize nomenclatural inconsistencies. Future studies may refine species lists and distribution ranges, including whole-basin monitoring programs, with standardized protocols and multi-gear sampling strategies.

The number of native species varied among reservoirs in the cascade system (range: 45 to 92), but most impoundments had similar values (*ca.* 50 species). Non-migratory fishes dominated assemblages, confirming our prediction and previous studies (*e.g.*, Agostinho *et al.*, 2007a). These species prevailed in richness, abundance and occurrence, especially small and medium-sized characids, a common pattern in Neotropical reservoirs (Barrella, Petrere Jr., 2003; Luiz *et al.*, 2005; Agostinho *et al.*, 2016). These values are higher than those reported by Agostinho *et al.* (2007a), which found between 20 and 40 species in Brazilian reservoirs. However, Agostinho *et al.* (2007a) estimates were based on gillnets, while studies gathered here used different sampling gears. In addition, some reservoirs were sampled multiple times over a considerable period (*e.g.,* Jurumirim, Salto Grande, Capivara, Rosana). We highlight also that impoundments in the Paranapanema River provide relevant habitats for small-sized species, such as submerged trees, aquatic macrophytes and lateral lagoons (*e.g.*, Casatti *et al.*, 2003; Pelicice *et al.*, 2005; Ferrareze, Nogueira, 2011). In particular, three reservoirs (*i.e.,* Ourinhos, Salto Grande and Capivara) were more species rich, but different mechanisms may be involved. Ourinhos (60 species), for example, was evaluated soon after its filling; in this stage, fishes are disoriented and populations are randomly distributed, with weak environmental selection. Previous studies have reported increases in species richness in the first years after river regulation, with declines in subsequent years (Agostinho *et al.*, 2007a). Salto Grande (67 species), on the other hand, is a small and old impoundment sampled with a variety of gears, what may result in surveys that are more complete. In addition, environmental heterogeneity may have played a role, considering that Salto Grande has relevant habitat diversity (Brandão *et al.*, 2009). This mechanism seems to be even more important in Capirava (80 species), which preserves remnant lotic areas and large tributaries (Hoffmann *et al.*, 2005; Pelicice, Agostinho, 2008; Bennemann *et al.*, 2013). The remaining reservoirs showed similar values of species richness (*ca.* 50 species), although we expected increasing values along the cascade system (*e.g.*, Oberdorff *et al.*, 1993; Araújo *et al.*, 2009; Foubert *et al.*, 2018). The convergence of species richness among impoundments (see also Agostinho *et al.*, 2007a) is probably linked to the loss of fluvial heterogeneity along the main channel, together with the creation of similar and homogeneous habitats (*i.e.,* impoundments). Neotropical fishes are primarily rheophilic, demanding specific habitats and flow conditions to survive and reproduce; few species evolved traits to cope with lentic habitats (Gomes, Miranda, 2001). Declines in species richness is a common pattern in rivers impacted by dams (*e.g.,* Barrella, Petrere Jr., 2003; Agostinho *et al.*, 2007a; Hoeinghaus *et al.*, 2009; Petesse, Petrere Jr., 2012; Araújo *et al.*, 2013). Long-term studies, in particular, have shown that fish assemblages in impounded areas are substantially different from the structure found in pristine conditions (Mol *et al.*, 2007; Orsi, Britton, 2014; Lima *et al.*, 2016). Future studies, therefore, must improve our understanding about factors that determine species richness in Neotropical reservoirs, as a means of improving predictions about diversity losses in new impoundments.

While most reservoirs were similar in respect to species richness, the composition of native non-migratory fishes changed considerably along the cascade. Some species were widely distributed, but each reservoir tended to have specific composition. Variation in fish composition along longitudinal gradients is a common pattern in large river systems (*e.g.*, Araújo *et al.*, 2009; Foubert *et al.*, 2018), usually in response to spatial and environmental components. Species are deleted/added to local assemblages, creating turnover and/or nestedness patterns along the river corridor. Impoundments, however, add discontinuity to the river continuum (Ward, Stanford, 1983) and provide common habitats irrespective to their position in the basin, usually associated with lentic conditions, shallow shores, vast water column and deep sites. These new environmental conditions select common traits and homogenize fish diversity in functional terms (Santos *et al.*, 2017). In this sense, reservoirs promote similar pressures upon the fish fauna and favor opportunistic or lentic-adapted species from the local species pool, forming simplified versions of the original riverine community. However, species are assembled from different species pools along the cascade system, resulting in divergent species composition among reservoirs. Therefore, even though species richness and functional traits are convergent among impoundments, taxonomical composition is divergent (*i.e.*, beta diversity), explaining the high species richness observed in the cascade system. However, the sequence of impoundments must have changed beta diversity patterns that characterize riverine networks (*e.g.*, Vitorino Jr. *et al.*, 2016), probably increasing the similarity among reservoirs (*e.g.*, Petesse, Petrere Jr., 2012). Data collected prior to river regulation is crucial to understand community assembling processes (*e.g.*, Araújo *et al.*, 2013; Lima *et al.*, 2016), but this type of data is rare in the Paranapanema basin.

As expected, migratory fishes showed low species richness and abundance in the cascade system. Although we recorded the presence of 14 species, especially in lower reaches, the abundance of migratory fishes was very low in all impoundments. The decline/collapse of migratory species is recurrent in regulated rivers (Petrere Jr., 1996; Okada *et al.*, 2005; Godinho, Kynard, 2008; Pelicice, Agostinho, 2008), since these fishes demand different fluvial habitats for feeding and reproducing, migrating over variable distances to complete their life cycle (Pompeu *et al.*, 2012). The cascade of dams along the Paranapanema River prevents long-distance migration and creates environments adverse to migratory fishes (*i.e.,* lentic areas, flow regulation). *Pimelodus maculatus* was the most important, but it also summed low abundance in most samples. This catfish is usually common in reservoirs of the upper Paraná basin, probably because it is small-sized, migrates over shorter distances and displays opportunistic feeding behavior (Lima-Junior, Gointein, 2004; Paschoalini *et al.*, 2013). Large-sized species, in particular, were recorded only downstream Salto Grande dam. This pattern may be related to biogeographic factors, since waterfalls were present in the area before dam construction, constraining fish movements. However, the position of reservoirs in the cascade must also be considered to explain the distribution of migratory fishes. The upper/middle reaches (between Jurumirim and Canoas I) are the most affected by river regulation, because 8 dams are distributed over 200 km. This sequence of impoundments creates sections where lotic segments are short or absent, with no critical habitat for migratory and rheophilic fishes (*e.g.*, lateral lagoons, backwaters, free-flowing stretches, tributaries). The area with greatest potential to support migratory fish populations is the upper section of the Capivara reservoir, which preserves large tributaries (Hoffmann *et al.*, 2005; Vianna, Nogueira, 2008; Bennemann *et al.*, 2013), especially the Tibagi river (Bennemann *et al.*, 2000; Shibatta *et al.*, 2007). This impoundment showed the highest species richness, including virtually all migratory species of the basin. Early life forms of large-size species have been recorded in the area, indicating the presence of spawning areas and nursery grounds (Orsi *et al.*, 2016). However, the construction of fish ladders at Canoas I and II dams affected the distribution of migratory fishes. Populations that recruited in the area of Capivara passed upstream and remained confined in short sections between Canoas I and Salto Grande dam (Lopes *et al.*, 2007; Pelicice, Agostinho, 2008; Britto, Carvalho, 2013). The greater abundance of migratory species in Canoas I and II indeed suggest that fishes migrated upstream and evaded Capivara reservoir soon after the installation of ladders, as indicated previously

(Pelicice, Agostinho, 2008; Britto, Carvalho, 2013). Another region with potential to maintain migratory fishes is the upper section of Rosana reservoir, which has a short lotic stretch with fluvial lagoons. However, Rosana dam is located *ca.* 25 km from the confluence with the Paraná river; this dam blocked upward fish movements and isolated the Paranapanema basin (Antonio *et al.*, 2007). In addition, Ferrareze, Nogueira (2011) captured no young migratory fish in lateral lagoons, possibly due to the lack of spawning grounds upstream. Similarly, Kipper *et al.* (2011) reported very low abundance of larvae across the reservoir, indicating that recruitment is negligible. Finally, large scale monitoring did not record eggs and larvae of important large-size species (*e.g., Piaractus mesopotamicus*, *Prochilodus lineatus*) in this reservoir (Orsi *et al.*, 2016). Therefore, migratory fish populations in reservoirs along the Paranapanema River are significantly disturbed, probably with low or no recruitment in many sections and impoundments, particularly in middle and upper reaches. The maintenance of migratory fish populations, much appreciated in riverine and floodplain fisheries, will depend on the preservation of lotic remnants and fluvial habitats (*e.g.*, Vianna, Nogueira, 2008; Suzuki *et al.*, 2013; Barzotto *et al.*, 2015), together with the revision of current management practices (*i.e.*, Pompeu *et al.*, 2012). In this sense, the area affected by Capivara reservoir should receive conservation efforts, particularly to maintain ecosystem functionality in tributaries (*e.g.*, Tibagi, Cinzas).

Another important result is the high number of non-native species in the impoundments (50 species), which accounted for 30.5 % of total richness. This is an impressive high number, confirmed by another recent study that reported 47 non-native species in the basin (Garcia *et al.*, 2018). This scenario is not an exception, considering that the upper Paraná river basin is highly invaded by multiple non-native species (*e.g.*, Britton, Orsi, 2012; Vitule *et al.*, 2012; Orsi, Britton, 2014; Ortega *et al.*, 2015). Our data showed that some species have wide distribution (*e.g.*, *P. squamosissimus*, *H. eques*, *O. niloticus*, *S. marginatus*, *Schizodon borelli*, *Metynnis lippincottianus*, *C. kelberi*), explaining why most reservoirs were similar in composition. However, many species were restricted to one or a few reservoirs, probably because of sporadic introductions that occurred in specific impoundments. This trend created a compositional turnover along the cascade, increasing the richness of non-native species at the basin level. In general, introductions occur due to different reasons (Ortega *et al.*, 2015; Azevedo-Santos *et al.*, 2015), but aquaculture, fish stocking, sport fishing, aquarium dumping, and the removal of natural barriers probably caused massive fish introductions in the Paranapanema River (Júlio Jr. *et al.*, 2009; Agostinho *et al.*, 2010; Britton, Orsi, 2012; Garcia *et al.*, 2018). These actions caused the release of species with high invasive risk, which are currently widespread (*e.g.*, *O. niloticus*, *Coptodon rendalli*, *C. kelberi*, *S. marginatus*, *P. squamosissimus*). It is not possible to confirm that all 50 species are established in these impoundments (*i.e.,* recruiting), but the presence of early life forms collected in different localities (Almeida *et al.*, 2018) indicate that some are reproducing. Furthermore, non-native species were abundant in most samples, summing relevant fraction or dominating local assemblages. Reservoirs located downstream were more invaded (*i.e.,* species richness and abundance), supporting previous studies that reported high invasion rates (Garcia *et al.*, 2018) or strong impacts (Orsi, Britton, 2014; Pelicice, Agostinho, 2009). Jurumirim reservoir was the less invaded and, consequently, has been considered a model for sustainable artisanal fisheries (Novaes, Carvalho, 2013), because fishing activities are based on native species, with higher prices, and may be sustained in the long term. The current scenario in the cascade of impoundments, therefore, demands immediate management actions to control populations (*e.g.*, selective fishing) and to prevent new introductions (*e.g.*, education, inspection), mainly because impoundments are vulnerable to new introductions (*e.g.*, Espinola *et al.*, 2010; Franco *et al.*, 2018). Non-native species impact native biodiversity in multiple ways, causing population declines, extirpation or homogenization, as recorded by studies conducted in the Paraná river basin (*e.g.*, Pelicice, Agostinho, 2009; Vitule *et al.*, 2012; Orsi, Britton, 2014; Daga *et al.*, 2015) and elsewhere (Cucherousset, Olden, 2011; Azevedo-Santos *et al.*, 2017). Equally important is the implementation of long-term monitoring in the cascade system, to perform robust studies about impacts, invasion dynamics (*e.g.,* establishment, invasion) and broad surveys. The difference in total richness between our study and Garcia *et al.* (2018), for example, suggests that the real number of non-native species is uncertain. Updated surveys are, therefore, crucial to understand biological invasions and minimize negative impacts.

In general, our results confirm trends reported in other regulated rivers (Petrere Jr. 1996; Barrella, Petrere Jr. 2003; Agostinho *et al.*, 2007b; Daga, Gubiani, 2012; Petesse, Petrere Jr., 2012; Agostinho *et al.*, 2016), where the diversity of migratory fishes is low and non-native species are common. The present study cannot infer about demographic trends and long-term dynamics, since our data come from multiple studies that applied different sampling methodologies. However, fish assemblage structure is probably stable in the studied reservoirs, especially because most are old, constructed decades ago. Specific environmental filters created by the impoundment constrain fish assemblages to persist in another state (Agostinho *et al.*, 2016; Santos *et al.*, 2017). In this sense, the current flow regime in the Paranapanema river, ruled by the cascade of dams, is the main force behind ecosystem state and dynamics, determining patterns of diversity and productivity. Conservation plans must consider this scenario to set appropriate management actions, especially because a number of studies have questioned the efficacy of current practices, *i.e.*, fish passages and stocking (Pelicice, Agostinho, 2008; Agostinho *et al.*, 2010; Pelicice *et al.*, 2015a; Lira *et al.*, 2017). Fish passages in Canoas dams, in particular, caused significant impacts on fish populations (Pelicice, Agostinho, 2008; Casimiro *et al.*, 2017), declining the conservation status of migratory fishes. In addition, stocking practices, conducted for decades (Agostinho *et al.*, 2010), contributed to introduce several non-native species (Britton, Orsi, 2012; Ortega *et al.*, 2015; Garcia *et al.*, 2018), but was unable to restore populations of migratory fishes in impoundments. This situation should concern authorities about the conservation of Neotropical fishes in light of severe human disturbances (Pelicice *et al.*, 2017), because rivers are extensively regulated, while the watershed is subjected to extensive agriculture and urban development, with activities that promote land cover changes and use non-native species (*e.g.*, aquaculture). Conservation will depend on measures that preserve fluvial remnants (*e.g.*, tributaries, such as the Tibagi and Cinza rivers), regulate human activities in surrounding areas, curb the introduction of non-native species, and control/eradicate populations already introduced (see Bennemann *et al.*, 2000; Britton, Orsi, 2012; Orsi *et al.*, 2016; Pelicice *et al.*, 2017). We emphasize that native fishes in these impoundments must receive conservation efforts, since they represent a relevant fraction of regional diversity, in addition to sustaining ecosystem services that are valued by artisanal and recreational fisheries.

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