Do river basins influence the composition of functional traits of fish assemblages in Neotropical reservoirs?

C. M. Muniz[a]* (ID), *A. Frota*[b] (ID), *M. J. M. Ganassin*[a] (ID), *A. A. Agostinho*[c] (ID) *and L. C. Gomes*[a] (ID)

[a]Universidade Estadual de Maringá – UEM, Departamento de Biologia, Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais, Laboratório de Ictiologia e Ecoestatística, Maringá, PR, Brasil

[b]Universidade Estadual de Maringá – UEM, Departamento de Biologia, Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais, Laboratório da Coleção Ictiológica do Nupélia, Maringá, PR, Brasil

[c]Universidade Estadual de Maringá – UEM, Departamento de Biologia, Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais, Laboratório de Ictiologia, Maringá, PR, Brasil

*e-mail: carolina_mendes_muniz@hotmail.com

Abstract

In aquatic environments, dams are considered one of the main threats to fish species, acting as an environmental filter for certain functional traits. Although there is some predictability in the composition of the functional traits in reservoirs, it is hypothesized that the environmental filters imposed by evolutionary processes, linked to the characteristics of the basins, are determinant for the functional composition of the traits in reservoirs. For this we performed a PCoA using the functional traits composition matrix of the reservoirs. We used PERMANOVA to test the difference in functional composition between basins. We performed the same process for the species composition matrix to compare the patterns. In this study, there were taxonomic and functional differences among reservoirs inserted in different basins. It was observed that the basin is a determining factor for the functional structure of fish assemblage in reservoirs. When compared, functional and taxonomic structures follow the same pattern, although functionally the reservoir tends to be more similar. These results reinforce the idea that reservoirs act as filters for functional traits (*e.g.*, related with reproduction, feeding and habitat use), although there is a great influence of evolutionary processes related to the basin's characteristics and origin of the ichthyofaunistic province.

Keywords: fish assemblage, ecoregions, environmental filter, functional structure, taxonomic structure.

As bacias hidrográficas influenciam a composição funcional da assembleia de peixes em reservatórios da região Neotropical?

Resumo

Em ambientes aquáticos, a construção de barragens é considerada uma das principais ameaças para as espécies de peixes, atuando como filtro ambiental para determinados traços funcionais. Assim, embora exista certa previsibilidade na composição dos traços funcionais em reservatórios, é hipotetizado que os filtros ambientais impostos pelos processos evolutivos, ligados as características das bacias, são determinantes para a composição funcional dos traços nos reservatórios. Para isso realizamos uma PCoA utilizando a matriz de composição de traços funcionais dos reservatórios. Utilizamos a PERMANOVA para testar a diferença da composição funcional entre as bacias. Realizamos o mesmo processo para a matriz de composição de espécies para comparar os padrões. Foi possível observar que a bacia hidrográfica é um fator determinante para a estruturação funcional da assembleia de peixe em reservatórios. Quando comparadas, a estrutura funcional e taxonômica, ambas seguem o mesmo padrão, embora funcionalmente os ambientes tendem a ser mais semelhantes. Esses resultados reforçam a ideia de que reservatórios atuam como filtros para determinados traços funcionais (*e.g.*, relacionados à reprodução, alimentação e uso de habitat), embora exista uma grande influência dos processos evolutivos ligados a característica da bacia e da origem da província ictiofaunística.

Palavras-chave: assembleia de peixe, ecorregiões, filtros ambientais, estrutura funcional, estrutura taxonômica.

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1. Introduction

The ecological patterns of distribution and abundance of fish species are the result of thousands of years of evolution (Lowe-McConnell, 1999; Harris, 1999). Throughout the evolution, species were pressured and had their dispersion and establishment limited by several environmental filters that acted hierarchically from continental to habitat scales (Tonn, 1990; Matthews, 1998). In this context, the delimitation of freshwater ecoregions captures the patterns produced by continental-and regional-scale filters and reflects the hydrological patterns, the distribution of fish species, and evolutionary processes (Tonn, 1990; Abell et al., 2008). Among the main broad-scale filters are the barriers to the dispersion of fish species, which form the basis that influence broad freshwater biogeographic patterns (*i.e.*, obligatorily aquatic species are confined in these regions and are unable to disperse between distinct basins) (Abell et al., 2008).

In addition to physical barriers, there are also physiological/adaptive-species barriers linked to environmental characteristics. In the case of river systems, the dynamics of the environment related to variability, predictability, and seasonality of floods are the key factors that structure fish assemblages (Southwood, 1977; Junk et al., 1989; Pool et al., 2010; Mims and Olden, 2012). Therefore, the primary selection driver of fish life strategies is the river dynamics, related to hydrological cycles of drought and flood and continuous water flow (Winemiller and Rose, 1992; Bunn and Arthington, 2002; Röpke et al., 2017). The structure of fish assemblages may be affected due to changes in the natural flow regime, usually promoted by human activities such as dams, leading to changes in species composition, selecting those that are pre-adapted to the new environmental conditions (Gomes and Miranda, 2001; Agostinho et al., 2016; Sanches et al., 2016).

The construction of dams alters river hydrology, causing changes in natural flow regime, changes in limnological conditions and spatial heterogeneity, affecting fish assemblage composition and ecosystem functioning (Webb et al., 2013; Agostinho et al., 2016). For instance, dams cause habitat fragmentation and blockage of fish movements (*e.g.*, mainly for migratory fish species, that use the route for reproduction), promote changes in water quality and reduce habitat heterogeneity (Agostinho et al., 2007; Poff et al., 2007; Zarfl et al., 2014; Pelicice et al., 2018). The success of species depends on their functional traits (*e.g.*, reproductive strategies, trophic specialization, habitat use, defense tactics, and physiology/metabolic; see Winemiller et al., 2015). It also depends on the characteristics of the reservoir, such as the presence of other reservoirs in the basin, type of dam operation, the surrounding land use, geomorphology and reservoir zone (Agostinho et al., 1999; Oliveira et al., 2004; Miranda and Krogman, 2015). Besides, the functional composition of the ichthyofauna of reservoirs may differ between basins because they have different origins and or are in distinct geographic regions,

each with its own limnological and geomorphological characteristics (Luiz et al., 2003; Pool et al., 2010).

Although reservoirs act as environmental filters for some functional traits of fish species (*e.g.*, decline of migratory species, characterized by seasonal spawning with small eggs, but in high numbers), it is hypothesized that the environmental filters imposed by evolutionary processes linked to basin characteristics (*i.e.*, ecoregion; Abell et al., 2008) are determinants for the functional trait composition of fish in reservoirs. We predict that there is a grouping of functional traits of the reservoirs studied concerning the basin in which it is located and that the assemblage's functional structure follows the same pattern as the taxonomic structure.

2. Material and Methods

2.1. Study area

We studied 29 reservoirs located in rivers of the Paraná State and neighboring states (Figure 1), south Brazil. Their ages ranged from 1-70 years when fish were sampled. Seven reservoirs are on the Paranapanema River; two on the Tibagi River, a tributary of the Paranapanema; two on the Ivaí River; two on the Piquiri River; 12 on the Iguaçu River; and four in the Coastal (or Litorânea) drainage basin (Table 1). Therefore, 25 reservoirs belonged to the Paraná River basin (Paranapanema, Tibagi, Ivaí, Piquiri, and Iguaçu rivers), and four to the Coastal basin. However, the Iguaçu basin is separated from the Paraná River by the Iguaçu Falls. The river basins where reservoirs are located belong to three ecoregions: Paranapanema, Tibagi, Ivaí and Piquiri rivers belong to the Upper Parana Ecoregion; the Iguaçu River belongs to the Iguassu Ecoregion; and the Litorânea basin rivers belong to the Ribeira de Iguape Ecoregion or Southeastern Mata Atlantica Ecoregion (for details, see Abell et al., 2008).

2.2. Data collection

All sampling surveys were conducted in the lacustrine zone (according to Thornton et al., 1990) of each reservoir in July and November of 2001. Fish assemblages were sampled in a standardized way at different depths (littoral, pelagic, and bathypelagic) using gillnets of different mesh sizes (2.4 to 14.0 cm between opposing knots), set for 24 hours, and checked in the morning, afternoon and night.

2.3. Fish assemblages and functional traits

The abundance of the species, by each sample, were indexed by the catch per unit of effort (CPUE; the number of individuals in $1000\ m^2$ of gillnets in 24 h). Species identification was based on Ota et al. (2018) for reservoirs of the Upper Paraná River, Baumgartner et al. (2012) for reservoirs of the Iguaçu basin, and Oyakawa et al. (2006) for reservoir of the Coastal basin, except for the families Clariidae and Ictaluridae (Burgess, 1989), Centrarchidae (Sigler and Sigler, 1987), and Cyprinidae (Cavender and Coburn, 1992) (see supplementary file S1, available only in the online version).

Data on traits were obtained from the literature (see supplementary file S2, available only in the online version).
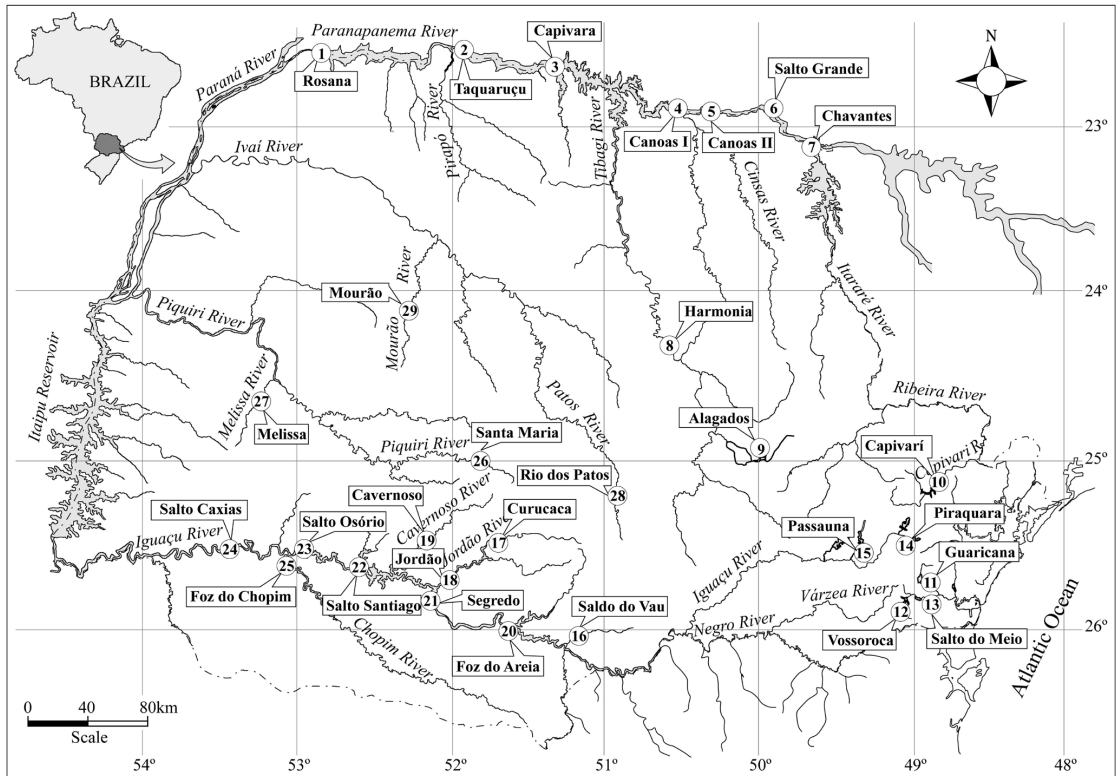
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Figure 1. Map of the Paraná State showing the locations of the study reservoirs. 1 = Rosana; 2 = Taquaruçu; 3 = Capivara; 4 = Canoas I; 5 = Canoas II; 6 = Salto Grande; 7 = Chavantes; 8 = Harmonia; 9 = Alagados; 10 = Capivari; 11 = Guaricana; 12 = Vossoroca; 13 = Salto do Meio; 14 = Piraquara; 15 = Passauna; 16 = Salto do Vau; 17 = Curucaca; 18 = Jordão; 19 = Cavernoso; 20 = Foz do Areia; 21 = Segredo; 22 = Salto Santiago; 23 = Salto Osório; 24 = Salto Caxias; 25 = Foz do Chopim; 26 = Santa Maria; 27 = Melissa; 28 = Patos; 29 = Mourão.

In cases where there was no data for the species we used data for the nearest related species (see supplementary file S3, available only in the online version). Functional traits selected to characterize fish species are related to trophic ecology (trophic category), life strategy (parental care, type of fecundation, spawning, migration and body size), use of habitats (body shape and position in the water column), and defense (cryptic behavior and presence of spine) (Table 2). In this study, functional traits were defined as biological characteristics that influence organism performance (Petchey and Gaston, 2006; Díaz et al., 2013) and that correlate with ecological processes and ecosystem stability through resistance and resilience (Villéger et al., 2010). The selection criterion used to survey the traits was to cover the largest number of functional traits related to the four niche dimensions proposed by Winemiller et al. (2015), *e.g.*, habitat use, life strategy, trophic ecology and defense.

2.4. Data analysis

In order to test our prediction that there is a grouping of functional traits of the reservoirs studied concerning the basin in which it is located, we performed an ordination (see *Functional structure of the fish assemblag*e session). After performing the ordering for the functional structure,

we performed an ordering for the taxonomic structure of fish assemblages (see *Taxonomic structure of the fish assemblage*). This step was necessary to compare the results to make sure they followed the same pattern.

2.5. Functional structure of the fish assemblages

The objective of this analysis was to verify if the traits composition depends on the hydrographic basin in which the reservoir is inserted. The functional composition of the ichthyofauna of the reservoirs may differ between the basins because they have different origins and/or are inserted in different geographic regions, which may differ in limnological and geomorphological characteristics. It was necessary to cross the n (local) vs. s (species) and s (species) vs. p (functional traits) to obtain the matrix n (local) vs. p (functional traits), which contains the mean of traits at the community level (Pillar et al., 2009). For this, the "matrix.t" function of the SYNCSA package was used in R (R Core Team, 2013). From the matrix n (local) vs. p (functional traits) it was generated a resemblance matrix using the Gower index, in which a Principal Coordinate Analysis was performed. (PCoA; Anderson et al., 2006). After the PCoA, a PERMANOVA was applied to verify if the basins (factor: Paranapanema, Tibagi, Piquiri, Ivaí, Iguaçu, and Litorânea basins) differed.

Table 1. Characteristics of the 29 study reservoirs located in the Paraná State, Brazil.

Reservoir	Basin	Year	Age	Age Classes	Basin Area	Area (km²)	Perimeter (km)	Max Dep (m)	RT	Volume (km³)	MAWT (°C)
Alagados	Tibagi	1945	56	Old	377	7.2	47.20	9.3	46	0.03	19.85
Canoas I	Paranapanema	1999	2	Recent	40920	30.85	74.64	26.0	6	207	23.95
Canoas II	Paranapanema	1999	2	Recent	39556	22.5	65.81	16.5	4.4	140	23.55
Capivara	Paranapanema	1975	26	Young	85000	419.3	738.93	52.5	126.8	10540	23.70
Capivari	Litorânea	1970	31	Old	-	12	123.50	43.0	48	156	19.95
Cavernoso	Iguaçu	1965	36	Old	1460	2.9	3.73	8.3	-	-	19.50
Chavantes	Paranapanema	1970	31	Old	27500	400	401.84	78.0	352.7	8795	21.90
Curucaca	Iguaçu	1982	19	Young	-	2	3.70	10.5	-	-	17.55
Foz do areia	Iguaçu	1980	21	Young	29900	139	288.67	135	102	5779	20.70
Foz do Chopim	Iguaçu	1970	31	Old	3800	2.9	5.25	6.0	-	-	20.05
Guaricana	Litorânea	1957	44	Old	-	7	7.20	17.0	13	-	19.95
Harmonia	Tibagi	1950	51	Old	-	3	7.49	12.0	-	8	20.90
Jordão	Iguaçu	1996	5	Recent	4700	3.4	21.74	60.0	-	110	18.45
Melissa	Piquiri	1962	39	Old	368	2.9	-	5.3	-	-	17.90
Mourão	Ivaí	1964	37	Old	573	11.3	60.00	12.7	70	0.06	20.95
Passauna	Iguaçu	1978	23	Young	-	14	35.30	-	420	-	16.50
Patos	Ivaí	1949	52	Old	1086	1.3	3.20	5.8	0.2	-	18.50
Piraquara	Iguaçu	1979	22	Young	-	3.3	40.00	18.0	438	0.5	19.90
Rosana	Paranapanema	1986	15	Recent	99000	220	230.32	26.0	18.6	1920	24.15
Santa Maria	Piquiri	1950	51	Old	-	0.1	-	4.3	-	-	16.70
Salto Caxias	Iguaçu	1998	3	Recent	57000	124	267.14	53.0	31	3573	21.80
Salto Grande	Paranapanema	1958	43	Old	38600	12	24.91	9.2	1.4	44.2	21.95
Salto do Meio	Litorânea	1931	70	Old	252	0.1	3.90	6.2	-	-	18.35
Salto Osório	Iguaçu	1975	26	Young	45800	51	180.16	43.0	16	1270	21.20
Salto Santiago	Iguaçu	1979	22	Young	43900	208	376.99	78.0	51	6753	21.60
Salto Segredo	Iguaçu	1992	9	Recent	-	82.5	-	100.0	47	-	21.80
Salto do Vau	Iguaçu	1959	42	Old	340	2	-	3.5	-	-	16.20
Taquaruçu	Paranapanema	1992	9	Recent	88000	80.1	156.35	26.5	7.9	672.5	23.60
Vossoroca	Litorânea	1949	52	Old	160	5.1	18.49	12.5	-	0.04	19.95

Year: year of reservoir formation; Age: the difference between 2001 (fish samplings) and the year of reservoir formation; Max Dep = maximum depth; RT = water retention time; MAWT = mean annual water temperature. Source: Gubiani et al. (2011).

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Table 2. Classes of traits, trait categories, functional traits, and abbreviations used in the analyses of fish species. The sources of these data are in Supplementary Files S2 and S3, available only in the online version. Fish species were classified as small (Ls < 150 mm), medium (150 < Ls < 400 mm) and large (Ls > 400 mm), respectively.

Trait	Traits classes	Traits categories	Abreviation
Trophic Ecology	*Trophic category*	Piscivore	PISC
		Detritivore	DETR
		Insectivore	INSEC
		Omivore	OMNI
		Invertivore	INVE
		Herbivore	HERB
Live strategy	*Parental Care*	Presence	PC
	Fertilization	Internal	FI
		External	FE
	Spawning	Total	TOT
		Multiple	MULT
		Continuous	CONT
	Migration	Presence	MIGR
	Body Size	Small	SMAL
		Medium	MEDI
		Large	LARG
Habitat use	*Position in the water column*	Benthopelagic	BENT
		Pelagic	PEL
		Demersal	DEME
	Body shape	Fusiform	FUSI
		Compressed	COMP
		Deep	DEPP
		Cylindrical	CYL
		Depressed	DEPP
		Low	LOW
Defense	*Criptic Behaviour*	Moderate	MOD
		Extreme	EXT
	Spine	Presence	SPI

2.6. Taxonomic structure of the fish assemblage

The objective of this analysis was to verify the distribution pattern of the species, from different river basins, in the multidimensional space. For this, we used the matrix n(local) vs. s(species). The Bray-Curtis index was used to construct a similarity matrix and later applied a Principal Coordinate Analysis (PCoA; Anderson et al., 2006). To verify if there were significant differences among basins, a PERMANOVA was applied, using basin as a factor. We consider this stage of the work important because although it is not part of our predictions, its results can provide insights regarding the processes related to the functional composition of the reservoirs. It is expected that the reservoirs inserted in different basins have different species, due to the evolutionary processes related to each region. However, when comparing these results with the results of the functional composition, we can verify if these two metrics follow the same trend (*e.g.*, variability and similarity/proximity between nearby basins) and thus verify how "strong" is the influence of the hydrographic basin on the taxonomic and functional composition of fish in reservoirs.

3. Results

3.1. Functional structure of the fish assemblages

The first two axes of the principal coordinate analysis (PCoA) represented 60.3% of the total data variation. The first axis represented 37.9% of the total variation, and

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the second axis represented 22.4% of the total variation (Figure 2). The PERMANOVA was significant for the factor basin (4,970 permutations; Pseudo-F = 10.13; P (perm) = 0.0002). The pair-wise test identified there were no significant differences only between Tibagi and Piquiri river basins (pair-wise test; p = 0.63) and between reservoirs Tibagi and Ivaí river basins (pair-wise test; p = 0.06). Some functional traits showed significant correlations with the first two axes of the PCoA (see supplementary file S4, available only in the online version), indicating large variability in the abundance of traits among basins. Functional traits such as omnivorous, depressed body, and multiple spawning were correlated with the Paranapanema, Tibagi, Ivaí, and Piquiri basin reservoir (inserted in the Upper Parana ecoregion). While traits such as fusiform body, deep and total spawning were related to the Iguaçu (Iguassu ecoregion) and Litorânea (Ribeira de Iguape and Southeastern Mata Atlantica ecoregions) river basins (both considered isolated basins).

3.2. Taxonomic structure of the fish assemblage

The first two axes of the principal coordinate analysis (PCoA) represented 42.2% of the total data variation (Figure 3). The first axis represented 27.8%, whereas the second represented 14.4% of the total variation in the structure (weighted by abundances) of the fish assemblages found in the study reservoirs. PERMANOVA test was significant for the factor basin (4,970 permutations; Pseudo-F = 10.904; P (perm) = 0.0001). There was no significant difference only between the reservoirs of Tibagi and Piquiri river basins (pair-wise test; p = 0.63) and between reservoirs of Tibagi and Ivaí river basins (pair-wise test; p = 0.06).
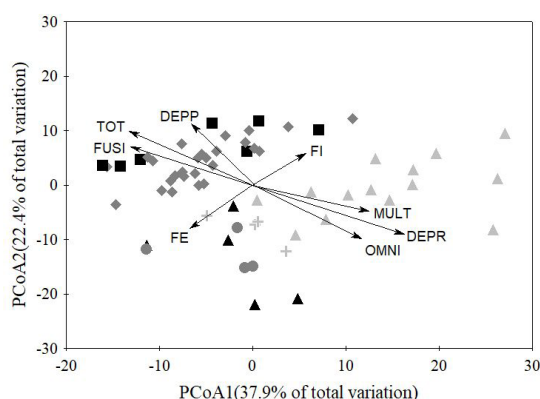

Figure 2. Result of PCoA analysis with Funcional structure of fish assemblages. Each point represents a reservoir at a given collection. Black Triangle: Tibagi; light grey triangle: Paranapanema; black square: Litorânea; dark grey quadrilateral: Iguaçu; light gray cross: Ivaí; dark grey circle: Piquiri. The arrow represents the direction of the effect (sign of the correlation) of the functional traits with significant correlation with the two first axis. TOT = Total spawning; DEPP = Deep body; FUSI = Fusiform body; FI = Internal Fertilization; FE = External Fertilization; MULT = Multiple spawning; DEPR: Depressed body; OMNI = Omnivore.

4. Discussion

In general, our findings shows that environmental filters imposed by evolutionary processes linked to basins' characteristics are determinant for the composition of functional traits in reservoirs. It was observed that the reservoirs inserted in the same basin/ecoregion were closer in multidimensional space (forming groups). Still, the patterns found by the functional structure were very similar to those found for the taxonomic structure: the reservoirs inserted in the Upper Parana ecoregion were closer to each other, while the reservoirs inserted in isolated basins (Iguassu ecoregion and Litorânea basin) were more closely related. Despite the similarities, the functional structure presented more considerable variability, and the reservoirs of different basins were closer in space, compared to the taxonomic structure. This result reinforces the idea that reservoirs act as environmental filters for functional traits that are related with fish niches (Agostinho et al., 1999; Santos et al., 2017; Arantes et al., 2019). For the reservoirs inserted in the Upper Parana Ecoregion (Paranapanema, Tibagi, Ivaí and Piquiri river basins) the functional traits that influenced the similarity between them were multiple spawning, omnivorous feeding habits and depressed body. The reservoirs of the Iguaçu and Litorânea basins were more similar in relation to functional traits related to fusiform and deep body and total spawning.

From these results we can verify the presence of distinct ichthyofaunas in the reservoirs of the main basins of the Paraná State, especially the set of rivers that flow to the upper Paraná River system (Langeani et al., 2007), such as Paranapanema River (Pelicice et al., 2018), Ivaí River (Frota et al., 2016a), Piquiri River (Cavalli et al., 2018) and Tibagi River (Shibatta et al., 2002, 2007). The same is true for those that drain to the Iguaçu River basin (Baumgartner et al., 2012; Frota et al., 2016b) and the Litorânea basin (Oyakawa et al., 2006; Frota et al., 2019).
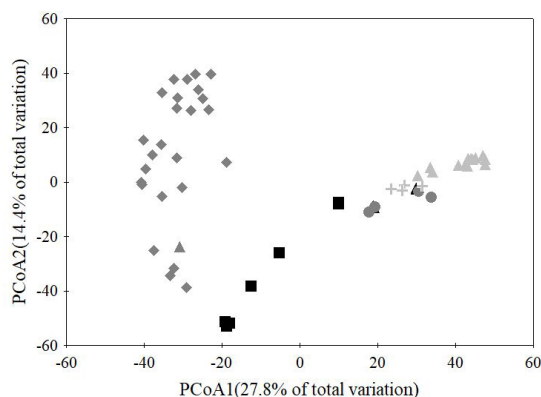

Figure 3. Result of PCoA analysis with Taxonomic structure of fish assemblages. Each point represents a reservoir at a given collection. Black Triangle: Tibagi; light grey triangle: Paranapanema; black square: Litorânea; dark grey quadrilateral: Iguaçu; light gray cross: Ivaí; dark grey circle: Piquiri.

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This difference in taxonomic and functional structure between basins is expected since the sampled reservoirs are inserted in different ecoregions. The ecoregions present several ecological and evolutionary processes, which result in different patterns of distribution and compositions of freshwater fish species (Abell et al., 2008).

From the point of view of the fish fauna, the upper Paraná River system comprises a complex area with its own geological history due to the tectonic activities undergone since the beginning of the Tertiary (Ab'Saber, 1998), and which in part is also shared with neighboring basins such as the coastal drainages and the Iguaçu River basin (Ribeiro, 2006). Besides that, the upper Paraná River system presents clear endemism (Langeani et al., 2007) and unique distribution patterns for its fish, which classify it as a natural ichthyofaunistic province (Géry, 1969; Abell et al., 2008). Therefore, the functional and taxonomic structure proximity evidenced for the drainage of the upper Paraná River system (*i.e.*, the Paranapanema, Piquiri, Ivaí, and Tibagi rivers) are expected within this biogeographic province. Still, this results reveal that even in the presence of a cascade of reservoirs, there is a close association of taxonomic composition with the last stretch of the upper Paraná River floodplain (see species in Ota et al., 2018), once they share most of their species (compare with Shibatta et al., 2002, 2007; Frota et al., 2016a; Cavalli et al., 2018; Pelicice et al., 2018).

The basins of the Tibagi, Ivaí and Piquiri rivers, despite the already installed dams, do not present reservoir cascades, which intensify the abiotic and biotic changes with pronounced consequences in the fish community and the composition of the traits (Miranda et al., 2008; Santos et al., 2017). This fact may explain the greater functional proximity of their analyzed reservoirs. Thus, the basins of these rivers still present certain integrity in their physical, chemical, and biological parameters. Thus, even the Paraná basin, with large number of reservoirs already installed (Agostinho et al., 2004), it is appropriate to emphasize the importance of basins free of reservoir cascades. They play a key role in maintaining the integrity of fish population in the basin (Affonso et al., 2015; Marques et al., 2018), especially the Ivaí (Affonso et al., 2015; Frota et al., 2016a), Tibagi (Shibatta et al., 2007; Pelicice et al., 2018), and Piquiri (Affonso et al., 2015; Cavalli et al., 2018) rivers.

Iguaçu and Litorânea basins harbor distinct fish assemblages (*i.e.*, the reservoirs of these basins were separated in the multidimensional space; Figure 3), but presented similar functional structure (*i.e.*, they overlapped in the multidimensional functional space; Figure 2). Distribution and phylogenetic patterns of their fish species suggest a close relationship among the rivers that flows directly into the Atlantic Ocean (Coastal drainage) and the adjacent upland crystalline shield that flow into the interior of the continent (Ribeiro, 2006). Recent surveys have revealed a composition of families and genera of similar fishes between the Iguaçu River (Baumgartner et al., 2012; Frota et al., 2016b; Larentis et al., 2016; Delariva et al.,

2018) and the Litorânea basin (Oyakawa et al., 2006; Frota et al., 2019), with predominance of Characidae, Loricariidae, Heptapteridae, Trichomycteridae, and Crenuchidae. This similarity appears in our study once there was some functional structure equality between these distinct drainage systems, but not necessarily for the same taxonomic composition. The basins of the Iguaçu and Litorânea rivers present similar hydrological characteristics. Many of their headwater regions run from high altitudes of some important geological structures, such as the Ponta Grossa Arch and the Serra da Esperança (Maack, 1981; Morais-Silva et al., 2018). Still, their mouths (Iguaçu and Litorânea) flowing into lowland or directly into the Atlantic Ocean (zero slopes). These hydrographic systems have large rapids and waterfalls (Oyakawa et al., 2006; Baumgartner et al., 2012). Therefore, due to their geomorphological and morphodynamic characteristics and their hydrographical relationships, the predominance of species with morphological structures capable of thriving in the high velocity functionally approximates these basins.

Although there is an intimate association with several ichthyofaunastic interchanges mainly between the upper Iguaçu River and the Litorânea basin (see Ribeiro, 2006), both basins behave as distinct riverine habitats with fast and rocky flows, which are local incubators of the diversification and biological specialization (Garavello and Sampaio, 2010; Roxo et al., 2017). Therefore, due the great geographic isolation of its distinct rapids and waterfalls (Oyakawa et al., 2006; Baumgartner et al., 2012), there is a high endemism of the fish species in both the Iguaçu River basin (Baumgartner et al., 2012; Frota et al., 2016b; Larentis et al., 2016; Delariva et al., 2018) and Coastal drainages (Oyakawa et al., 2006; Frota et al., 2019).

Regarding the functional structure, despite the identification of some differences between the sampled basins, they were closer in the multidimensional space. This result points to the fact that there is, independently of the species composition, a functional simplification of the fish communities in rivers where reservoirs are present (Oliveira et al., 2018). Because of the environmental changes imposed by dams, the remaining fish community presents functional traits that allow tolerance to the new environmental conditions (Ward and Stanford, 1995; Agostinho et al., 2008; Oliveira et al., 2018). Several studies have reported that after the formation of reservoirs, the fish fauna of these environments is dominated by species with generalist feeding habits, sedentary life strategy with parental care and small body size (Hoeinghaus et al., 2009; Agostinho et al., 2016; Santos et al., 2017; Oliveira et al., 2018). Consequently, even though species diversity remains high in reservoirs, there is a drastic change in dominance, with migratory fish becoming rare, while non-native species are common and dominant (Hoeinghaus et al., 2009; Daga et al., 2015; Santos et al., 2017; Pelicice et al., 2018). Thus, for all analyzed reservoirs, regardless of the ecoregion or drainage system, there was functional homogenization of the fish community (Daga et al., 2015; Oliveira et al., 2018), possibly imposed by the

environmental filters generated by the lentic waters of reservoirs (Santos et al., 2017).

A unique functional and taxonomic similarity was attributed among the reservoirs of the Tibagi River basin and the reservoirs of the Ivaí and Piquiri river basins. The functional similarity of these reservoirs was related to multiple spawning, omnivorous feeding habits and depressed body functional traits. Still the absence of species with internal fertilization in these reservoirs was responsible for their separation in the multidimensional space. For these basins, the taxonomic grouping evidenced has two plausible causes, which may be complementary. First, this similarity in composition is expected as both basins are inserted in the same Upper Parana Ecoregion, so their fish assemblages are part of the same ichthyofaunistic province (Langeani et al., 2007; Abell et al., 2008). Second, there is a huge spatial congruence of their fish faunas, mainly in the headwaters located in the interior of the Paraná State, which may characterize the upper stretches of the Tibagi, Ivaí and Piquiri rivers as endemic areas (Cavalli et al., 2018; Morais-Silva et al., 2018). These upper stretches presents interesting phylogeographic patterns of the resident fish fauna (Morais-Silva et al., 2018), with notable influence of geological formations of the Serra Geral, or Serra da Boa Esperança, as well as the Ponta Grossa Arch, which by virtue of their ancient origin (Creer, 1962; Karl et al., 2013) enabled vicariant patterns between the various sub-basins of the state (Frota et al., 2016a; Cavalli et al., 2018; Morais-Silva et al., 2018) and, through recent reactivations (Franco-Magalhaes et al., 2010) allowed faunistic exchanges (Cavalli et al., 2018; Morais-Silva et al., 2018; Frota et al., 2019).

Here, we investigate if the environmental filters imposed by evolutionary processes linked to basin characteristics are determinants for the functional trait composition of fish in reservoirs. Our results show that although reservoirs act as environmental filters for functional traits, the basin in which the reservoir is inserted has a great influence on the functional structure of a dammed environment. Furthermore, the functional structure follows the same patterns found for the taxonomic structure (*i.e.*, reservoirs inserted in different basins have high similarity if situated in the same ecoregion). These results reinforce the idea that environmental filters influence the local (*i.e.*, reservoir) functional structure in a hierarchical manner. Thus, although there is some predictability about the functional traits found in reservoirs, the ecoregion' ichthyofaunistic composition has a great influence on the final functional structure of the dammed environment. Finally, we highlight the necessity to integrate studies on the ichthyofaunistic structure and composition of the ecoregion in reservoir management and conservation projects.

Acknowledgements

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