UNIVERSIDADE ESTADUAL PAULISTA - UNESP

INSTITUTO DE BIOCIÊNCIAS - IBB

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS (ZOOLOGIA)

Efeitos do grau trófico e distância espacial entre sub-bacias alteram a distribuição de rotíferos em um grande rio?

Bárbara Araújo Martins

Botucatu

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Bárbara Araújo Martins

Tese apresentada ao Programa de Pós-Graduação em Ciências Biológicas (Zoologia) como pré-requisito para a obtenção do título de Doutora.

Orientador: Prof. Gilmar Perbiche Neves

Co-orientador: Prof. Marcos Gomes Nogueira

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Apresentação

Esta tese de doutorado analisou os rotíferos coletados na Bacia do rio da Prata, América do Sul, em trechos lóticos e reservatórios. Estão contidos em três capítulos: inventário de espécies, novas ocorrências no Brasil e na Argentina, utilização de espécies como bioindicadoras e atributos ecológicos e determinantes da diversidade beta. A tese está apresentada em artigos científicos visando facilitar a publicação, já na língua inglesa e formatados de acordo com as normas das revistas Biota Neotropica (capítulo 1), Hydrobiologia (capítulo 2) e Science of the Total Environment (capítulo 3).

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À minha família por confiar em mim e me apoiar nesse árduo caminho da vida acadêmica.

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À Olorum e toda espiritualidade, sem essa força eu nada seria!

A todos, meu muito obrigada!

"Eu não estou aceitando as coisas que eu não posso mudar, estou mudando as coisas que eu não posso aceitar"

Angela Davis

Sumário

Resumo

Foram estudados os rotíferos coletados na Bacia do Rio da Prata, a segunda maior da América do Sul, em janeiro (verão) e julho (inverno) de 2010, em 43 pontos, em trechos lóticos e reservatórios (zona de montante e próximo às barragens). As amostras foram realizadas por meio de arrasto vertical na coluna d'água com rede planctônica de malha de 50 µm. Os resultados foram divididos em três capítulos: 1. Composição e riqueza de rotíferos da Bacia do rio da Prata, 2. Influência do gradiente de nitrogênio, fósforo e clorofila-a na estrutura da comunidade de rotíferos em reservatórios da bacia do rio da Prata e 3. Determinantes da diversidade beta em rotíferos da Bacia do Rio da Prata. No capítulo 1 é apresentada a lista de espécies e a riqueza nas sub-bacias amostradas, assim como a diferença na riqueza entre os períodos amostrados. Neste capítulo foram registradas 106 espécies, e novas ocorrências foram encontradas no Brasil (Estado de São Paulo) e na Argentina. A sub bacia com maior riqueza foi do Baixo rio Paraná. No capítulo 2 foram utilizados apenas os pontos em 15 reservatórios da Bacia do Rio da Prata. Foi utilizada a análise TITAN com o objetivo de: i) avaliar qual é o limiar de concentração de variáveis relacionadas à eutrofização que alteram a estrutura da comunidade para rotíferos, ii) compreender quais espécies de Rotifera estão relacionadas positiva ou negativamente ao aumento dessas variáveis tendo sido encontradas 71 espécies e dessas 06 foram consideradas bioindicadoras, reforçando que rotíferos respondem às variáveis ambientais relacionadas diretamente com o nível trófico de ambientes aquáticos, especialmente em reservatórios. E no capítulo 3 a heterogeneidade, a diversidade beta e a influência de variáveis ambientais de rotíferos foi estudada em rios e reservatórios. Foram utilizadas as análises db-RDA, PERMANOVA, o coeficiente de dissimilaridade de Sorensen, ANOVA e a diversidade beta foi separada nos componentes substituição e diferenças na riqueza/abundância. Testamos as hipóteses: (i) os principais determinantes da diversidade beta dos rotíferos são variáveis ambientais relacionadas à eutrofização; (ii) devido à sua ampla distribuição geográfica em geral, o fator espacial não será importante; (iii) devido a heterogeneidade ambiental entre as sub-bacias, a substituição de espécies será mais importante do que a perda/ganho de espécies. Os resultados indicaram que a substituição de espécies explicou a maior porcentagem da dissimilaridade entre as sub-bacias, sendo as variáveis ambientais o principal fator determinante.

Palavras-chave: Bioindicador, Ecologia, Diversidade beta, Rotifera.

Abstract

Were studied the rotifers collected from La Plata River Basin, the second largest of South America, in January (Summer) and July (Winter) of 2010, in 43 sites, in lotic and reservoirs (upstream and dam stretches). Sampling were performed through vertical hauls of plankton net of 50 µm. The results were divided in three chapters: 1. Composition and richness of rotifers from La Plata River Basin; 2. Rotifers community structure controlled by nitrogen, phosphorus and chlorophyll-a in reservoirs from La Plata River Basin, and 3. Drivers of beta diversity of rotifers from La Plata River Basin. In the chapter 1 is presented the list of species and the richness in the sub basins sampled, as the difference in the richness among the periods sampled. In this chapter were registered 106 species, and new occurrences were found in Brazil (São Paulo State) and Argentina. The sub basin with the greatest richness was Lower Paraná Rivers. In the chapter 2 were used only the points of the 15 reservoirs of La Plata River Basin. The TITAN analysis were used with the objective: i) i) evaluate what is the concentration threshold of variables related to eutrophication that change the community structure of rotifers, ii) understand which Rotifera species are positively or negatively related to the increase in these variables. 71 species were found, and of these 06 were considered bioindicators, reinforcing that rotifers respond to environmental variables directly related to the trophic level of aquatic environments, especially in reservoirs. And in chapter 3 the heterogeneity, beta diversity and the influence of environmental variables of rotifers was studied in rivers and reservoirs. Were used the analysis db-RDA, PERMANOVA, Sorensen dissimilarity coefficient and ANOVA, and the beta diversity were divided in the components replacement and richness/abundance differences. We tested the hypothesis: i) the main determinants of the beta diversity of rotifers are environmental variables related to eutrophication; ii) due to its wide geographic distribution in general, the spatial factor will not be important; iii) due to environmental heterogeneity among sub-basins, species replacement will be more important than species loss/gain. The results indicated that species replacement explained the highest percentage of dissimilarity among the sub-basins, with environmental variables being the main determining factor.

Keywords: Bioindicator, Ecology, Beta diversity, Rotifera

CONSIDERAÇÕES INICIAIS

Em 2010, no verão e inverno, foi realizada uma coleta extensa na Bacia do Rio da Prata, a segunda maior da América do Sul. As amostras oriundas dessa coleta já geraram quatro teses de doutorado e uma dissertação de mestrado, acerca dos grupos de microcrustáceos (copépodes e cladóceros) e larvas de moluscos.

O projeto foi idealizado pela necessidade de resolver vários problemas taxonômicos e ecológicos, principalmente preenchendo as lacunas nos padrões de distribuição de espécies e entendendo assim, as fronteiras geográficas das espécies planctônicas.

A Bacia do Rio da Prata foi amplamente estudada, porém de modo geral os estudos são pontuais, focando em locais específicos, diferente da proposta do presente estudo, onde foram amostrados 43 pontos ao longo da bacia no Brasil, Argentina, Paraguai, Uruguai e Bolívia. Por ser uma área de coleta muito extensa e a mesma ter sido realizada pelo mesmo grupo de pesquisadores (foram percorridos 28.000 km e gastos 90 dias consecutivos na coleta), foi possível a realização de apenas duas campanhas em cada ponto, contudo geraram resultados importantes acerca da distribuição do zooplâncton.

Dentro do zooplâncton os rotíferos também foram amplamente estudados, e foi através de uma ampla base na literatura (e.g. JOSÉ DE PAGGI, 1978, 1990, 1996, MODENUTTI, 1998, AOYAGUI & BONECKER, 2004, LUCINDA et al 2004, BONECKER et al 2005, MATSUMURA-TUNDISI & TUNDISI, 2005, FRUTOS et al 2006, ROCHA et al 2006, LANSAC-TÔHA et al 2009, SOUZA-SOARES et al 2011, GARRAFFONI & LOURENÇO 2012, FERRANDO & CLAPS, 2016, PERBICHE-NEVES et al 2016, BRANCO et al 2018, ARROYO-CASTRO et al 2019, BAZZURI et al 2020, BRITO et al 2020) foi possível a discussão dos resultados encontrados. Todas essas referências e mais outras estão citadas no decorrer da tese.

Nesta tese foram analisados os organismos do filo Rotifera, especificamente da classe Monogononta, coletados em trechos lóticos e em reservatórios. No planejamento amostral não foram incluídos lagos ou lagoas marginais nos rios estudados. Para os reservatórios foram analisadas as regiões de montante e próximas às barragens, pois formam características distintas dos ambientes, podendo alterar a composição e abundância de rotíferos e dos demais organismos zooplanctônicos. Nos trechos lóticos foram analisados os trechos alto, médio e baixo, porém, para os trechos altos dos rios Paraná e Uruguai, somente os reservatórios foram amostrados. No rio Paraguai, em cujo canal central não há reservatórios, somente trechos lóticos foram amostrados.

Após as coletas, as amostras de zooplâncton foram triadas e identificadas em laboratório, com a utilização de microscópio ótico e literatura especializada. Detalhes da metodologia estão descritos nos capítulos.

A escolha de apresentar esta tese dividida em capítulos com artigos se dá pela praticidade e facilidade para a posterior publicação dos mesmos. Dessa forma, foi dividida em três capítulos, apresentados a seguir.

No capítulo 1 foi apresentada a composição das espécies em todos os pontos amostrados, gerando um inventário de espécies de rotíferos da Bacia do Rio da Prata. Além disso, foram utilizados dados de riqueza de espécies em cada sub-bacia e período amostrado. Uma análise de correlação de Spearman foi realizada, de modo a entender, de forma breve, a relação da riqueza com algumas variáveis ambientais. Por se tratar de um inventário, neste capítulo não foram utilizados os dados de abundância e nem análises ecológicas mais complexas. Os inventários nos dão um panorama da região amostrada, e com uma escala espacial tão ampla, esperava-se encontrar novas ocorrências, pois inclusive, algumas regiões não possuem estudos sobre a distribuição desses organismos.

No capítulo 2 foi apresentada a utilização de espécies de rotíferos como indicadores da qualidade da água de reservatórios através da análise TITAN. Essa análise determina limiar de variáveis que alteram a estrutura da comunidade. Como o foco foi a utilização de espécies como bioindicadoras, foram selecionados os nutrientes (nitrogênio e fósforo) e clorofila-a como as variáveis a serem analisadas. A previsão de limiares traz benefícios aos serviços ecossistêmicos e a identificação de potenciais limiares é um aspecto importante para o manejo de sistemas ecológicos.

No capítulo 3 foi avaliado os determinantes da diversidade beta desses rotíferos. Variáveis preditoras foram preparadas para a análise de redundância baseada na distância (db-RDA), selecionando quais variáveis seriam testadas. A heterogeneidade ambiental foi calculada por uma PERMANOVA, para verificar se a composição e distribuição das espécies entre as sub-bacias foram diferentes. Através do particionamento da diversidade beta total (dissimilaridade entre os locais) nos componentes β-Repl (*replacement*, substituição de espécies/traços entre as comunidades), e β-Rich/AbDiff (*richness/abundance diference,* diferença de riqueza/abundância que pode ser por perda ou ganho de espécies) (Podani & Schmera, 2011; Carvalho, Cardoso & Gomes, 2012) é possível diferenciar quais processos ecológicos, gradientes biogeográficos ou históricos estão atuando para estruturar as comunidades. Levando isso em consideração testamos entre as variáveis ambientais, espacial e temporal qual explicava mais a dissimilaridade entre as sub-bacias, entendendo como a heterogeneidade ambiental pode estar relacionada com a diversidade Beta.

Capítulo 1

Composition and richness of monogonont rotifers from La Plata River Basin, South America

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Abstract

We present here the first study that analyzed the composition and richness of rotifers of the entire La Plata River basin, the second largest in South America, based on simultaneous and standardized sampling. Fifteen large reservoirs and eight river stretches were selected in the upper, middle, and lower portions of the Paraná, Paraguay, and Uruguay Rivers, which are the major rivers of the La Plata basin. We took a total of 86 samples (open water habitats) in 2010. A mean of 27±11 species per sub-basin was found, with the highest richness in the Lower Paraná (41 species), followed by the Paranapanema (40 species) and Lower Uruguay (38 species). Low richness was observed in the Middle Uruguay and Middle Paraná. We found 106 species belonging to 21 families and two orders. The family with the highest number of species was Lecanidae (21), followed by Brachionidae (20), Trichocercidae (9), and Synchaetidae (8). The species with higher occurrences were *Conochilus dossuarius*, *Kellicottia bostoniensis*, *Keratella americana*, *Keratella cochlearis* and *Hexarthra mira*. New occurrences of rotifers were registered for Brazil (*Colurella adriatica*), São Paulo State (*Enteroplea lacustris*), and Argentina (*Gastropus hyptopus*, *Harringia rousseleti* and *Lecane thienemanni*). Spearman correlation between the number of species and physical and chemical variables demonstrated positive correlation with chlorophyll and temperature, and negative correlation with dissolved oxygen. We extend the distribution list for some native (*Lecane ludwigii*) and non-native species of rotifers (*K. bostoniensis*). We also list the monogonont rotifer species found at the sampling stations.

Keywords: *Biodiversity; Rotifera; Survey; New records; Lotic; Lentic environments.*

Composição e riqueza de rotíferos Monogononta da Bacia do Rio da Prata, América do Sul

Resumo

Apresentamos aqui o primeiro estudo que analisou a composição e riqueza de rotíferos de toda a bacia do Rio da Prata, a segunda maior da América do Sul, com amostragens simultâneas e padronizadas. Quinze grandes reservatórios e oito trechos lóticos foram selecionados nas porções alta, média e baixa dos rios Paraná, Paraguai e Uruguai, que atuam como os principais formadores da bacia do Prata. Coletamos um total de 86 amostras (habitats de águas abertas) em 2010. Foi encontrada uma média de 27 ± 11 espécies por sub-bacia, com maior riqueza no Baixo Paraná (41 espécies), seguido por Paranapanema (40 espécies) e Baixo Uruguai (38 espécies). Uma baixa riqueza foi observada no Médio Uruguai e no Médio Paraná. Encontramos 106 espécies pertencentes a 21 famílias e duas ordens. A família com maior número de espécies foi Lecanidae (21), seguida por Brachionidae (20), Trichocercidae (9) e Synchaetidae (8). As espécies com maior ocorrência foram *Conochilus dossuarius*, *Kellicottia bostoniensis*, *Keratella americana*, *Keratella cochlearis* e *Hexarthra mira*. Novas ocorrências de rotíferos foram registradas para o Brasil (*Colurella adriatica*), Estado de São Paulo (*Enteroplea lacustris*) e Argentina (*Gastropus hyptopus*, *Harringia rousseleti* e *Lecane thienemanni*). A correlação de Spearman entre o número de espécies e as variáveis físicas e químicas demonstrou correlação positiva com clorofila e temperatura, e correlação negativa com oxigênio dissolvido. Estendemos a lista de distribuição para algumas espécies nativas (*Lecane ludwigii*) e não-nativas de rotíferos (*K. bostoniensis*). Disponibilizamos também uma lista de espécies de rotíferos Monogononta encontrados nas estações amostradas.

Palavras-chave: *Biodiversidade; Rotifera; Levantamento; Novos Registros; Lótico; Ambientes lênticos.*

Introduction

Species inventories are important tools for conservation measures and management, especially in areas imperiled by human actions. It is also useful to show gaps in the scientific knowledge about zooplankton diversity and directions for future research.

There have been surveys of Rotifera diversity in the La Plata River basin, the second largest in South America. However, these surveys have focused on regions such as in the Upper Paraná floodplain (Lansac-Tôha et al. 2009), waterbodies of São Paulo State (Souza-Soares et al. 2011), and a few tributaries (Neschuk et al. 2002, Kuczynski 2017). There have been no basin-wide surveys that included all the countries drained by the basin.

The La Plata River basin has very distinct environments, with extensively dammed and undammed reaches. For example, there are reservoirs in more than half of the upper reaches in the Paraná River basin, leaving few truly lotic reaches; the opposite occurs in its middle and lower reaches (Agostinho et al. 2007). The situation is very similar for the Uruguay River. However, there are no reservoirs in the Paraguay River (Perbiche-Neves et al. 2016). This results in different habitats with distinct limnological features, which may favor differences in rotifer species composition among lotic and lentic regions.

There have been multiple studies of rotifer richness and distribution in Brazilian and Argentinian waters of the La Plata River basin. For example, Garraffoni & Lourenço (2012) surveyed rotifer species throughout Brazil. Other rotifer surveys were less extensive, such in Mato Grosso do Sul (Roche & Silva 2017), São Paulo (Souza-Soares et al. 2011), the Upper Tietê River basin (Lucinda et al. 2004), and Paranoá Reservoir (Padovesi & Andreoni 2011). Despite those surveys, the number of rotifer surveys are underrepresented (Souza et al. 2018), when compared to other groups of zooplankton such as copepods (Silva et al.2009, Matsumura-Tundisi & Tundisi 2011, Perbiche-Neves et al. 2014).

For Argentina, José de Paggi (1990) listed 279 rotifer taxa. Most rotifer surveys have been in the Paraná River floodplains (Aoyagui & Bonecker 2004) and La Plata River tributaries (Macluf et al. 1998, Modenutti 1998, Bazzuri et al. 2020). Recently, Ferrando & Claps (2016) updated the checklist of Argentinian Rotifera, including a reporting 35 species of monogonont rotifers. According to the authors, Ferrando & Claps (2016), the majority of reports were restricted to the provinces of Santa Fe (68% of the total records), Corrientes and Buenos Aires (50% of the total records), Río Negro and Formosa (30% of the total records). The rotifer species which are more commonly found in Argentinian Paraná River reaches and La Plata River tributaries were *Keratella cochlearis* (Gosse, 1851), *K. americana* Carlin, 1943 and *Brachionus calyciflorus* Pallas, 1776 (Modenutti 1998, Bonetto & Wais 2006).

Knowledge of the diversity and distribution of rotifers in the Paraguay River basin is scarce and concentrated in Brazil and Argentina, including rivers in the Pantanal (Branco et al. 2018, Brito et al. 2020) and those joining the Paraná River (Frutos et al.

2006). Similarly, few rotifer surveys have been conducted in the Uruguay River basin (e.g., José de Paggi 1978; Picapedra et al. 2019).

Therefore, we provide for the first time a spatially extensive survey of Rotifera species found in the lentic and lotic stretches of the La Plata River basin to characterize its species diversity patterns. In addition, we have expanded the distribution of some Rotifera species not yet reported in the literature, thus contributing to the general knowledge of the diversity of the group in the region.

Materials and Methods

1. Study area

The La Plata River basin has an area of 3.1 million km2 (Cuya et al. 2013) and drains portions of five countries: Brazil, Paraguay, Uruguay, Argentina, and Bolivia. The main sub-basins are the Paraná, Paraguay, and Uruguay River basins. The Paraná basin is the largest, covering 48.7% of the basin, followed by the Paraguay (35.3%) and Uruguay (11.8%) basins (Cuya et al. 2013).

2. Sampling

A total of 86 samples were collected at 43 stations, including 15 reservoirs (in dam and upriver zones) and 13 lotic stretches distributed in the three main sub-basins of La Plata River (Figure 1, Table 1). Sites (open water - littoral habitats were not included) were sampled in January (summer - wet season) and July (winter- dry season) 2010. Ten water quality variables were measured at each sampling station during each visit following Perbiche-Neves et al. (2016) and Nogueira et al (2020): total phosphorus and nitrogen, temperature, transparency, turbidity, conductivity, pH, dissolved oxygen, depth, and total chlorophyll.

We sampled rotifers through vertical hauls by using a 50 µm mesh conical plankton net. In deep sites, the maximum depth hauled was 40 m (Perbiche-Neves et al. 2019). The sampled rotifers were subsequently packed, labeled, and fixed with 4% formalin solution. Identifications were conducted with an optical microscope (Zeiss Axio Imager.A2m) and by using species keys (Edmondson 1959, Koste 1978, Nogrady et al. 1995, Segers & Dumont 1995, Smet & Pourriot 1997, Nogrady 2002, Wallace et al. 2019). Voucher specimens were deposited in the Laboratory of Continental Waters Ecology, Institute of Biosciences of Botucatu at the Universidade Estadual Paulista Júlio de Mesquita Filho (UNESP), Brazil. The number of species was correlated with water quality variables by using non-parametric Spearman correlation and a logarithmic transformation in R Cran Project 3.3.0 (2016) using the Hmisc package of R.

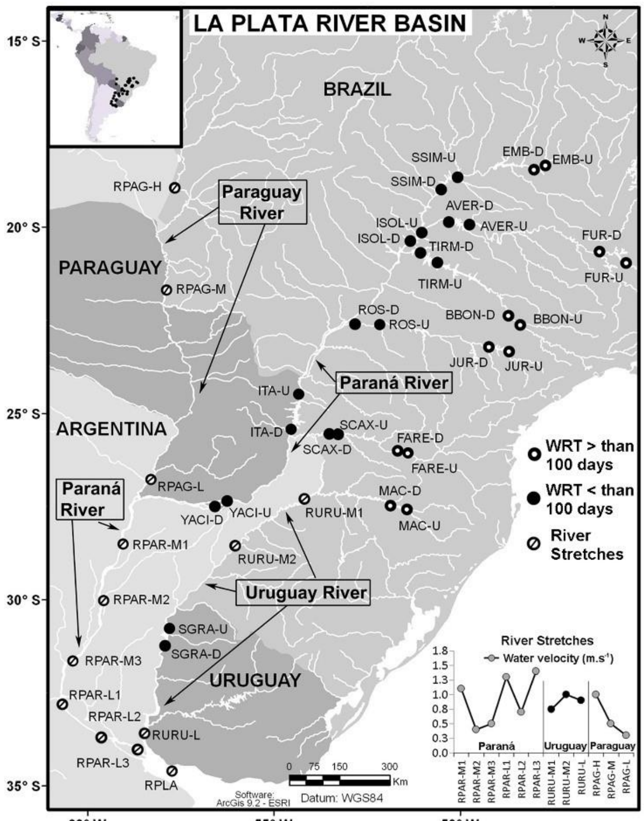

Figure 1. Locations of the 43 sites in La Plata River basin, with data of water retention time (WRT) and water velocity of the river stretches. For codes see Table 1. Adapted from Perbiche-Neves et al. (2016).

Table 1: Acronyms of the sampled sites, sub-basin, geographical coordinates and habitats sampled in La Plata River Basin. Number (n°) represents the sampling stations in the basin. Codes: ARG – Argentina, BRA – Brazil, PAR – Paraguay, URU – Uruguay.

Site	Sub-basin	Coordinates	Acronyms	N°	Habitat
Emborcação HPP – MG/GO – BRA	Paranaíba	18°26'28.43"S	EMB-U	1	Lentic
		47°58'59.59"W	EMB-D	2	Lentic
São Simão HPP – MG/GO – BRA	Paranaíba	19°00'04.51"S	SSIM-U	3	Lentic
		50°29'47.69"W	SSIM-D	4	Lentic
Furnas HPP – MG – BRA	Grande	20°39'38.30"S	FUR-U	5	Lentic
		46°18'01.65"W	FUR-D	6	Lentic
Água Vermelha HPP – MG/SP – BRA	Grande	19°51'58.67"S	AVER-U	7	Lentic
		50°19'11.62"W	AVER-D	8	Lentic
Ilha Solteira HPP – SP/MS – BRA	Upper Paraná	20°21'43.24"S	ISOL-U	9	Lentic
		51°21'14.53"W	ISOL-D	10	Lentic
Barra Bonita HPP – SP – BRA	Tietê	22°31'23.48"S	BBON-U	11	Lentic
		48°31'56.30"W	BBON-D	12	Lentic
Três Irmãos HPP – SP – BRA	Tietê	20°39'32.50"S	TIRM-U	13	Lentic
		51°16'56.16"W	TIRM-D	14	Lentic
Jurumirim HPP – SP - BRA	Paranapanema	23°13'02.15"S	JUR-U	15	Lentic
		49°13'26.89"W	JUR-D	16	Lentic
Rosana HPP – SP/PR - BRA	Paranapanema	22°36'02.03"S	ROS-U	17	Lentic
		52°51'07.39"W	ROS-D	18	Lentic
Itaipu HPP – BRA/PAR	Upper Paraná	25°24'21.09"S	ITA-U	19	Lentic
		54°34'02.38"W	ITA-D	20	Lentic
Foz do Areia HPP – PR – BRA	Iguaçu	26°00'23.84"S	FARE-U	21	Lentic
		51°39'45.76"W	FARE-D	22	Lentic
Salto Caxias HPP – PR - BRA	Iguaçu	25°32'25.00"S	SCAX-U	23	Lentic
		53°29'30.72"W	SCAX-D	24	Lentic
Yaciretá HPP – Ituzaingó - ARG	Middle Paraná	27°25'28.83"S	YACI-U	25	Lentic
		56°37'37.50"W	YACI-D	26	Lentic
Paraná River – Bella Vista - ARG	Middle Paraná	28°30'04.81"S	RPAR- M1	27	Lotic
		59°02'58.21"W	RPAR-M2	28	Lotic
			RPAR-M3	29	Lotic
La Plata River – Rosário - ARG	Lower Paraná	32°53'08.12"S	RPAR-L1	30	Lotic
		60°40'48.69"W	RPAR-L2	31	Lotic
			RPAR-L3	32	Lotic
La Plata River — URU/ARG	Lower Paraná	34°00'51.25"S			Lotic
		58°19'21.84"W	RPLA	33	
Machadinho HPP – SC - BRA	Upper Uruguay	27°31'12.35"S	MAC-U	34	Lentic
		51°47'05.01"W	MAC-D	35	Lentic

Porto Xavier – RS - BRA	Middle Uruguay	27°'52'17.26"S 55°07'25.49"W	RURU-M1 RURU-M2	36 37	Lotic Lotic
Salto Grande HPP – URU	Middle Uruguay	31°15'44.17"S 57°55'47.34"W	SGRA-U SGRA-D	38 39	Lentic Lentic
Uruguay River - Fray Bentos – URU	Lower Uruguay	33°21'02.20"S 58°25'49.97"W	RURU-L	40	Lotic
Paraguay River– Corumbá - BRA	Upper Paraguay	18°59'40.76"S 57°39'12.53"W	RPAG-H	41	Lotic
Paraguay River – Assunción - PAR	Middle Paraguay	25°28'24.65"S 57°33'40.53"W	RPAG-M	42	Lotic
Paraguay River – Paso de la Patria – PAR	Lower Paraguay	27°15'38.43"S 58°35'39.79"W	RPAG-L	43	Lotic

Results

The mean rotifer richness was 27±11 species. The sub-basins with higher richness were the Lower Paraná (41 species), followed by the Paranapanema (40 species) and Tietê (35 species). The basins with lower richness were the Middle Paraná and Lower Uruguay (Figure 2A).

The Rotifera fauna of the La Plata River basin was composed of 106 species, distributed in 21 families and 37 genera (Table 2, Figure 2B). The most representative family in the basin is the Lecanidae (21 species), followed by the Brachionidae (20), Trichocercidae (9), and Synchaetidae (8) (Figure 2B). The most speciose genera are *Lecane* Nitzsch, 1827 and *Brachionus* Pallas, 1766 with 21 and 10 species, respectively. We found 44 rotifer species in summer and 17 in winter. These seasonal periods share a combined 45 rotifer species (Figure 3).

Regarding individual sites, we found a wide range in species richness. Barra Bonita Reservoir (BBON-D; 12) in the Tietê River had the greatest species richness (22). The lowest richness was observed in the Lower (RURU-L; 40) and Middle (RURU-M1; 36) Uruguay River (3 species each; Table 2). The species occurring in >40% of the lotic and lentic sites evaluated were *Conochilus dossuarius* Hudson, 1885, *Kellicottia bostoniensis* (Rousselet, 1908), *Keratella americana* Carlin, 1943 *K. cochlearis* (Gosse, 1851) and *Hexarthra mira* (Hudson, 1871).

Our results indicate greater distribution ranges for several species. *Colurella adriatica* Ehrenberg, 1831, from the Foz do Areia Reservoir, is a new record for Brazil. *Gastropus hyptopus* (Ehrenberg, 1838) in the La Plata River and *Harringia rousseleti* de Beauchamp, 1912 and *Lecane thienemanni* (Hauer, 1938) in the Paraná River, are their first reports in Argentina. Finally, we expand the range of *Enteroplea lacustris* Ehrenberg, 1830, in São Paulo State (Brazil) and *Lecane ludwigii* (Eckstein, 1883) in Buenos Aires Province (Argentina).

Almost all the species are native, except *Kellicottia bostoniensis* which occurred in a new locality. Seven other species are Neotropical endemics (Table 2): *Brachionus dolabratus* Harring, 1914, *B. mirus* Daday, 1905, *B. zahniseri* Ahlstrom 1934, *K. americana*, *Lecane amazonica* (Murray, 1913), *L. proiecta* Hauer, 1956 and *Testudinella ohlei* Koste, 1972.

The mean ± standard deviations of water quality variables (Table 3) stratified by sub-basin reveals that the Tietê River has higher levels of total nitrogen, phosphorus, chlorophyll, and electrical conductivity.

The Lower Paraná River also demonstrates high values for these variables except for nitrogen. Higher temperatures were found in the Paraguay and Iguaçu Rivers. The lowest levels of dissolved oxygen occurred in the Paraguay River. Spearman correlations indicated that total chlorophyll and water temperature were positively correlated with species richness; dissolved oxygen demonstrated a negative correlation (Table 4).

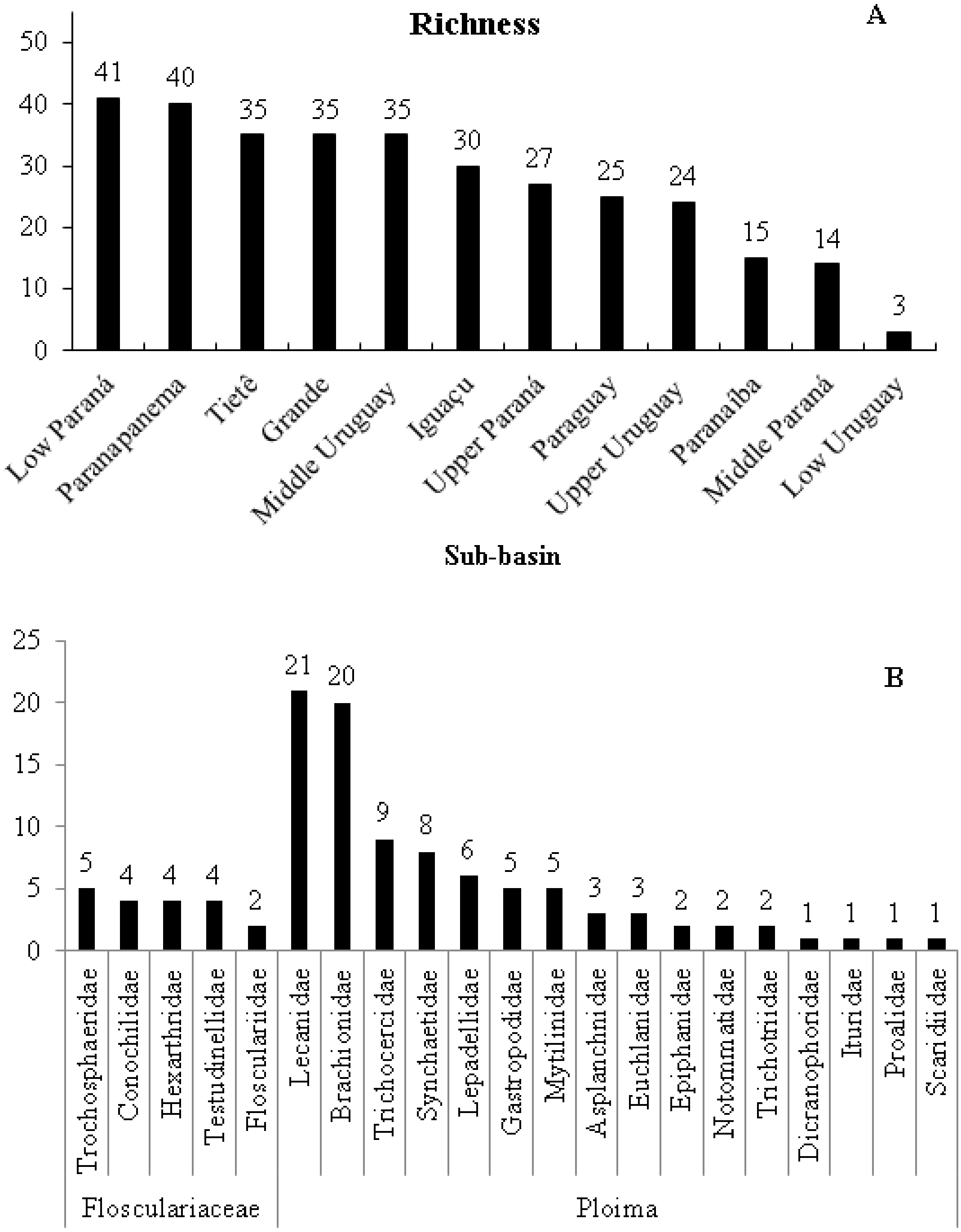

Figure 2. Rotifer richness per basin for species (A) and family (B).

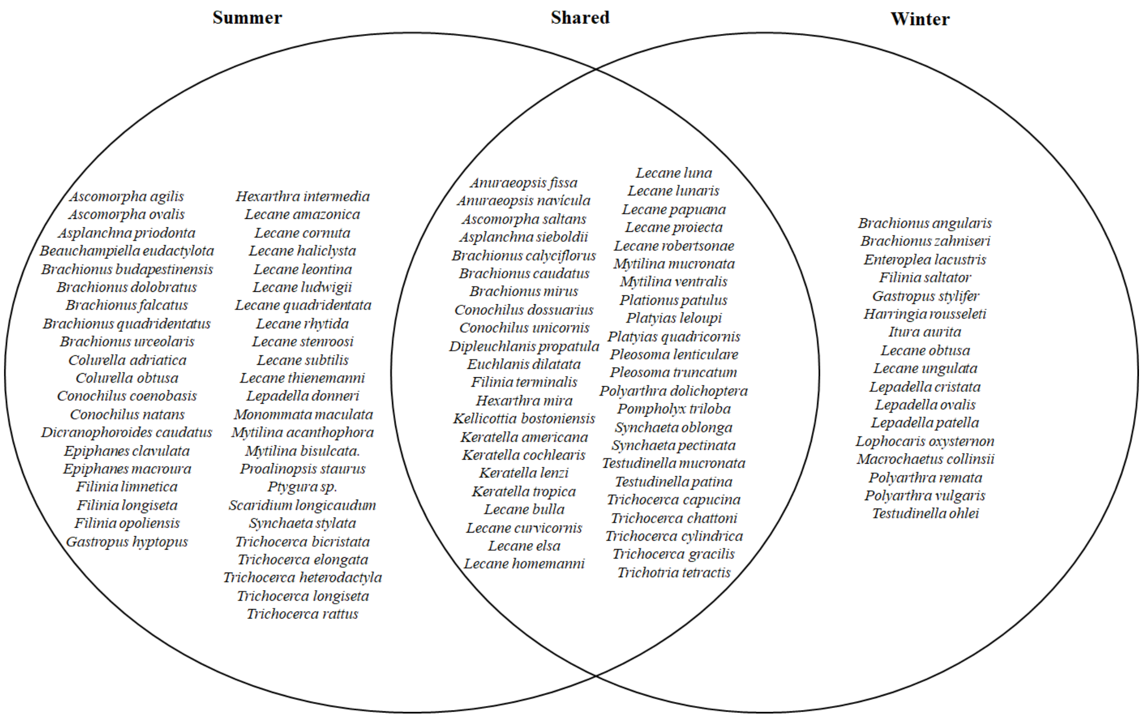

Figure 3. Species collected in the summer, winter and shared in both seasons.

Table 3. Mean±standard-deviation values of physicall and chemical variables of each sub-basin from our study.

Sub-basins	Total Nitrogen (µg.L^{-1})	Total Phosphorus (µg.L^{-1})	Chlorophyll (µg.L^{-1})	Depth Max. (m)	Transparency (m)
Paranaíba	196.1±43.38	9.60±3.08	1.21±0.67	61.61±16.29	4.13±1.64
Grande	311.78±53.54	8.53±1.16	2.45±1.60	44.32±25.01	3.31±1.42
Tietê	2131.05±1373.24	58.19±45.73	7.19±6.54	25.93±6.85	2.70±1.45
Paranapanema	463.92±115.72	16.94±5.21	1.51±0.72	21.66±6.89	1.41±0.64
Iguaçu	325.38±37.98	15.40±4.67	1.26±0.63	57.75±24.13	1.45±0.34
Upper Paraná	622.30±126.81	15.40±4.19	1.52±0.80	41.14±23.40	2.75±1.50
Middle Paraná	468.12±47.37	34.33±6.48	3.17±1.30	9.85±3.40	0.42±0.08
Low Paraná	415.29±79.69	54.60±13.93	3.74±1.63	11.8±5.80	0.56±0.09
Upper Uruguay	452.04±93.24	14.54±3.22	1.74±0.30	95.75±6.88	1.86±0.22
Middle Uruguay	780.90±70.22	22.07±5.80	3.12±1.96	22.67±15.43	0.66±0.11
Low Uruguay	650.35±108.47	36.10±9.01	2.97±1.36	16.93±5.40	0.67±0.15
Paraguay	426.44±225.85	43.00±18.71	2.41±0.87	10.1±4.37	0.81±0.32
Sub-basins	**Temperature (°C)**	**pH**	**Conductivity (µS.cm^{-1})**	**D.O. (mg.L^{-1})**	**Turbidity (NTU)**
Paranaíba	24.35±1.81	7.21±0.19	41.82±4.32	6.26±0.97	8.64±3.38
Grande	24.10±2.8	7.20±0.33	38.45±7.07	7.16±1.16	11.58±6.70
Tietê	24.11±3.10	7.27±0.30	182.42±43.98	6.92±1.54	12.1±6.46
Paranapanema	23.01±3.16	7.25±0.27	55.10±6.56	7.91±0.96	24.2±11.41
Iguaçu	25.14±3.37	7.34±0.14	51.26±4.74	7.57±0.79	20.52±7.70
Upper Paraná	21.73±3.69	7.19±0.32	46.31±6.44	7.80±1.12	12.75±4.91
Middle Paraná	23.21±6.19	7.36±0.22	64.64±4.96	7.98±1.36	40.49±7.56
Low Paraná	22.10±7.40	7.47±0.31	118.16±24.69	7.85±2.21	37.80±6.93
Upper Uruguay	17.71±1.77	6.86±0.13	32.26±2.13	8.68±0.46	14.51±2.12
Middle Uruguay	21.84±4.49	7.42±0.14	45.75±2.75	8.63±0.91	32.39±7.41
Low Uruguay	22.22±6.75	7.44±0.21	59.24±20.58	8.69±1.22	31.30±5.68
Paraguay	26.40±3.87	6.75±0.24	67.84±15.33	5.17±1.28	27.40±13.22

Table 4. Spearman correlations results (R^2 and p) among species richness and the physicall and chemical variables. In bold there are significant correlations.

Variables	**R2**	**P**	**Variables**	**R2**	**p**
Total Nitrogen	0.12	0.27	Temperature	0.27	**0.01**
Total Phosphorus	0.11	0.29	pH	-0.15	0.15
Chlorophyll	0.28	**0.00**	Conductivity	0.08	0.48
Depth	0.13	0.23	D.O.	-0.24	**0.02**
Transparency	0.02	0.87	Turbidity	-0.07	0.53

Discussion

We found 106 rotifer species in the La Plata basin. Our data represent 14% of the rotifer species richness known to Brazil (Garraffoni & Lourenço 2012), 37% of that for São Paulo State (Souza-Soares et al. 2011), 30% of that for the Upper Paraná (Lansac-Tôha et al. 2009), and 40% for the Upper Paraguay River (Branco et al. 2018). Data from other inventories show that the rotifer fauna in the La Plata River basin is richer than what was demonstrated in our study, possibly because we sampled in few Uruguay and Paraguay River stretches, and exclusively in open water habitats, not in littoral. Therefore, as recommended by Ferrando & Claps (2016), further investigations should be carried out to expand the distribution list of species in the La Plata River Basin.

The most diverse families were Lecanidae (21 spp.) and Brachionidae (20 spp.). These two families compose most rotifer species throughout Brazil and Argentina (Garraffoni & Lourenço, 2012; Ferrando & Claps, 2016), supporting our findings.

The higher summer (wet season) rotifer richness may be associated with the concentrated rainfall events that occur during this season.

Summer rains can carry nutrients and organic matter from the margins of aquatic environments resulting in increased food concentration and a reduction in competition for resources. The same tendency was observed for the rainy season in a study performed on a tropical lake in Mexico (Jiménez-Contreras et al. 2018). Richness may also be related to the sediment mixture caused by intense rains. This process provides a favorable condition for hatching of dormant stages (i.e., resting eggs), resulting in an increase in rotifer species richness.

Greater rotifer species richness was observed in the Lower Paraná sub-basin. Rotifers have low locomotion capacity and are carried by drifting through the central channel of the river and consequently the species richness increase towards downstream.

Barra Bonita Reservoir in the Tietê River sub-basin was the site with the greatest richness. Despite being a reservoir with a high degree of anthropogenic disturbance, including eutrophication (Tundisi et al. 2008), many studies have shown high biodiversity for other groups, which include rotifers (Matsumura-Tundisi & Tundisi 2005, Rocha et al. 2006). In the Barra Bonita Reservoir, Matsumura-Tundisi & Tundisi (2005) found 32 species of rotifers. However, in our work we found 22 species. The Spearman correlation suggested a positive relation between richness and chlorophyll levels, with Barra Bonita Reservoir demonstrating the highest values of observed chlorophyll. Presumably, this higher richness is a result of greater numbers of tolerant rotifer species (Allen et al. 1999).

The commonest species in the La Plata basin were *Keratella americana*, *K. cochlearis*, and *Hexarthra mira*. Others have reported the occurrence these species in the Uruguay (Di Persia & Neiff 1986), Paraguay (Frutos et al. 2006, Branco et al. 2018) and Upper Paraná Rivers (Bonetto & Wais 2006), indicating the wide distribution of these rotifers in the study area.

Colurella has been found in several inland waters (Arroyo-Castro et al. 2019, Tasevska et al. 2019, Wei et al. 2019). In the La Plata Basin we found two species of this genus: *Colurella adriatica* Ehrenberg, 1831 and *C. obtusa* (Gosse, 1886). *Colurella* *adriatica* originates in the Adriatic Sea and has been described as endemic (Ehrenberg 1831), but it is now widely distributed, including in Neotropical regions (Segers 2007). We found it in Foz do Areia Reservoir, in the Iguaçu sub-basin, Paraná State, which is its first record in Brazil.

Enteroplea lacustris is widely distributed in the Australasia, Neoarctic, Neotropical, Oriental, and Paleoarctic regions (Segers 2007). In Brazil, it occurs in Mato Grosso do Sul (Roche & Silva 2017) and Paraná States in the Paranapanema River basin (Dias et al. 2011, Roche & Silva 2017). We found it in Três Irmãos Reservoir, Tietê sub-basin, São Paulo State, near the Paraná River, indicating a gap in previous studies of this region.

For Argentina, Ferrando & Claps (2016) recorded 351 species of monogonont rotifers from lotic and lentic environments. Among the species they recorded, we found 43 (12.2%). Three other species of rotifers (*Gastropus hyptopus*, *Harringia rousseleti*, and *Lecane thienemanni*) found in our study are new records for Argentina. *Gastropus hyptopus* was found in the La Plata River Basin, in Rosario, Argentina. In Brazil, it had been registered in several regions (Serafim Jr. et al. 2003, Bonecker et al. 2005, Serafim-Júnior et al. 2010, Souza-Soares et al. 2011). *Harringia rousseleti* and *L. thienemanni* were recorded for the first time in Argentine reaches of the Paraná River, in the Bella Vista municipality. A new locality was found for *L. ludwigii*, which had been recorded in Corrientes Province (José de Paggi 1996); however, there is no previous record in the La Plata River estuary where we collected it.

We found a non-native species in the La Plata River basin, *Kellicottia bostoniensis* (Rousselet, 1908), which is native to North America (Edmondson 1959). For Argentina, José de Paggi (2002) first recorded the species in the Iguaçu River and Salto Grande Reservoir. We found the species in the La Plata River (Uruguay and Argentina reach), where there were no prior records of it. We thus extended the known distribution of *K. bostoniensis*. It is possible that its occurrence in the La Plata basin is related to aquaculture activities as has occurred in other regions (Coelho & Henry 2017). In many reservoirs of the La Plata basin, there are aquaculture activities, mainly with non-native fish species (Azevedo-Santos et al. 2011, Nobile et al. 2018). This rotifer may be introduced from cage aquaculture in upstream rivers (e.g., Grande and Paranapanema Rivers) and reached downstream areas where we captured it.

Seven Neotropical endemic species (sensu José de Paggi 1996) were found in the La Plata River basin. Their presence highlights the importance of preserving the condition of these ecosystems. However, anthropogenic stressors imperil many areas where these seven species occur. For example, in the Barra Bonita and Três Irmãos Reservoirs, where *Brachionus dolobratus, B. mirus*, and *L. proiecta* were captured, waters are polluted (Rodgher et al. 2005, Favaro et al. 2018). Similarly, eutrophic tributaries in the Grande River sub-basin (Melo et al. 2017) may affect endemic rotifer species. Another example is the occurrence of *L. amazonica* in the La Plata River; which also receives water from these polluted river basins. Conservation policies must be discussed for the entire La Plata system because of fluvial connectivity (Azevedo-Santos et al. 2019).

In conclusion, surveys covering wide spatial extents, such as in our study, are important for increasing the knowledge of species diversity and distribution. Our findings may contribute to future monitoring studies as well as management and conservation programs for the La Plata River basin. Finally, we recommend that future rotifer surveys should be concentrated in Paraguay and Uruguay River reaches because of the scarcity of data from them.

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Capítulo 2

Rotifers community structure controlled by nitrogen, phosphorus and chlorophyll-a in reservoirs from a large river basin

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Abstract

The rotifer community structure was studied in fifteen reservoirs of the second largest hydrographic basin in South America, with focus in indicators species and its relationships with limnological variables associated with eutrophication: nitrogen; phosphorus and chlorophyll-a, using Threshold Indicator Rate Analysis (TITAN). Considering that threshold prediction brings benefits to ecosystem services and the identification of potential thresholds is an important aspect to the management of ecological systems, we aimed to i) evaluate what is the concentration threshold of variables related to eutrophication that alter community structure for rotifers, ii) understand which Rotifera species are related positively or negatively to the increase of these variables. Most sampling sites were classified as oligotrophic, followed by mesotrophic and eutrophic. Seventy-one rotifer species were found and the three variables (nitrogen, phosphorus and chlorophyll-a) represented points of change on taxa and community levels according gradients of these variables, with values of 1118µg.L^{-1}, 22.44 µg.L^{-1} e 3.89µg.L^{-1}, respectively. Six species were considered as indicators of change in community composition, with significant responses to variation in at least one variable analyzed, most of them showing positive responses. Species with positive responses were *Keratella tropica, Plationus patulus, Filinia terminalis* and *Synchaeta oblonga.* We identified negative responses for two species, presented by *Conochilus unicornis* and *Synchaeta stylata*. The only species that presented the same response for all variable concentration was *Keratella tropica*. Our results reinforce the assumption that rotifers respond to the environmental variables related directly with the trophic level of aquatic environments, especially reservoirs.

Key-words**:** *Rotifera, bioindicator, TITAN, eutrophic, biomonitoring*

Influência do gradiente de nitrogênio, fósforo e clorofila-a na estrutura da comunidade de rotíferos em reservatórios da bacia do rio da Prata

Resumo

A estrutura da comunidade de rotíferos foi estudada em quinze reservatórios da segunda maior bacia hidrográfica do continente com foco em espécies indicadoras e suas relações com variáveis ambientais relacionadas a eutrofização: nitrogênio; fósforo e clorofila-a, usando a análise indicadora dos limites dos táxons (TITAN). Considerando que a previsão de limiares traz benefícios aos serviços ecossistêmicos e a identificação de potenciais limiares é um aspecto importante para o manejo de sistemas ecológicos, objetivamos: i) avaliar qual é o limiar de concentração de variáveis relacionadas à eutrofização que alteram a estrutura da comunidade para rotíferos, ii) compreender quais espécies de Rotifera estão relacionadas positiva ou negativamente ao aumento dessas variáveis A

maioria dos pontos de amostragem foi classificada como oligotrófica, seguida de mesotrófica e eutrófica. Foram encontradas 71 espécies de rotíferos e as três variáveis (nitrogênio, fósforo e clorofila-a) representaram pontos de mudança para abundância das espécies e ao nível de comunidade, com valores de 1118 µg.L^{-1}, 22.44 µg.L^{-1} e 3.89 µg.L^{-1}, respectivamente. Seis espécies foram consideradas como indicadores de mudança na composição da comunidade, com respostas significativas à variação em pelo menos uma variável analisada, a maioria delas apresentando respostas positivas. As espécies com respostas positivas foram *Keratella tropica*, *Plationus patulus*, *Filinia terminalis* e *Synchaeta oblonga*. Identificamos respostas negativas para duas espécies, apresentadas por *Conochilus unicornis* e *Synchaeta stylata*. A única espécie que apresentou a mesma resposta para todas as concentrações variáveis foi *Keratella tropica*. Os resultados reforçam o pressuposto que os rotíferos respondem às variáveis ambientais relacionadas diretamente com o nível trófico de ambientes aquáticos, especialmente em reservatórios.
Palavras-chave: *Rotifera, bioindicador, TITAN, eutrófico, biomonitoramento*

Introduction

In South America, more than 50% of electrical energy consumed come from hydroelectric plants supplied by reservoirs, however less than 20% of the water potential of hydrographic basins is used (Rudnick et al., 2008). Large hydroelectric reservoirs were built from the 1960s and 1990s, and to obtain and develop this energy model, the construction reservoirs on rivers is necessary, which have a considerable impact on freshwater ecosystems (Agostinho et al., 2007).

The filling of a reservoir cause physical changes, turning the previously lotic environment into lentic (Serafim-Júnior et al., 2016), and these new environment also modify the environment of the lotic system downstream of the dams, due to stratification (depending on the height of the water intake, it can send more cold water with little oxygen downstream - Naliato et al., 2009). Also the reservoir causes a decrease of the flow due to water retention, sediment and suspended matter retention , which leads to a seasonally and even daily heterogeneous environment, causing changes in the structure of aquatic communities (Agostinho et al., 2007; Naliato et al., 2009; Mantovano et al., 2015).

Reservoirs are complex systems with spatial and temporal gradients, generally compartmentalized in three distinct regions: fluvial, transition and lake (Matusumura-Tundisi et al., 1990; Nogueira et al., 2012). In addition, there are also two transversal regions: limnetica and littoranean (Esteves, 2011). All of these regions are not static, and can expand or contract according to the flow of water bodies and the operation of the reservoir, and differ in physical, chemical and biological properties, causing temporal and spatial heterogeneity and promoting the diversity of habitats, essential for biological diversity (Agostinho et al., 1999; Naliato et al., 2009).

The environmental heterogeneity of the reservoirs leads to changes in the composition and abundance of planktonic communities, important organisms in the cycling and flow of nutrients (Nogueira, 2000; 2001). According to heterogeneity-diversity hypothesis, heterogeneous environments provide greater diversity of niches than homogeneous ones, reflecting on the taxonomic (i.e. richness and abundance) and functional structure of communities (i.e. an increase in functional diversity) (Bomfim et al., 2018; Ortega et al., 2018). Zooplankton is composed of sensitive organisms that respond to a large number of environmental changes in relatively short periods, with fast reproduction and short life cycle, which make them good biological indicators of the evaluation of environmental water quality (Perbiche-Neves et al., 2016).

Many species of rotifers have wide spatial distribution and are considered good biological indicators, as the community persists over a year and is distributed across a wide variety of habitats. Also, they are considered opportunistic organisms, with increase of the number and abundance of tolerant species in situations of deteriorating ecosystem and represent the greater part of zooplankton of continental environments (Rocha et al., 1995). In this way, these organisms can be used to test the influence of environmental variable in a fine scale at values as also the point of change for taxa.

The increase in the trophy condition of the environment can also affect the structure of the rotifers community and cause the disappearance of species sensitive to eutrophication (Segers, 2008), causing an increase in the abundance of species considered tolerant (Balvay & Laurent, 1990; Landa et al., 2007; Da Silva et al., 2019). Species of *Brachionus* Pallas, 1766 and *Keratella* Bory de St. Vicent, 1822 genus, are commonly related to environments of higher trophy levels (Duggan et al., 2001; Perbiche-Neves et al., 2013; Wei et al., 2019).Levels of nitrogen, phosphorus and chlorophyll-a are related to trophy level. The Trophic State Index (TSI) formula for reservoirs use TSI for Chlorophyll and TSI for Total Phosphorus, showing the relations of these variables with the eutrophication of the environment.

In addition, nitrogen higher levels have been associated with increase in eutrophication of water bodies (Zhou et al 2020), and concentration of chlorophyll-a can be an indicator of biomass of planktonic algae, representing the food resources availability, which can affect the size of planktonic organisms and the recruitment of populations (Nicolle et al., 2011; Simões et al., 2012; Bomfim et al., 2018), thus we can consider these three variables as important when analyzing bioindicator species in zooplankton. Several studies use these variables with this purpose (Perbiche-Neves et al., 2016; De-Carli et al., 2018a). When we study the effect of gradient of variables in a community structure it is important the establishment of ecological thresholds, that are tools used to capture changes in attributes of biological communities along an environmental gradient (Baker & King, 2010).

Considering that threshold prediction brings benefits to ecosystem services (Martin et al., 2009, Tiburcio et al., 2021) and the identification of potential thresholds is an important tool for the management of ecological systems, we aimed to i) evaluate what is the concentration threshold of variables related to eutrophication that alter rotifer's community structure, ii) understand which Rotifera species are related positively or negatively to the increase of these variables. We expect to find species commonly used as bioindicators to be positively related with the increase of the variables directly related with eutrophication, confirming that the use of ecological thresholds can help to identify important changes in the structure of community. We suppose that increases in the concentration levels of variables directly related with the productivity of the reservoirs as nitrogen, phosphorus and chlorophyll-a are the main responsible for most species changes.

Material and methods

1. Study area

The La Plata River Basin is the second largest basin of South America, with the drainage area of 3.1 million km^2 (Cuya et al., 2013). Five countries are part of the basin, Brazil, Paraguay, Uruguay, Argentina and Bolivia. In relation to hydrography, it is formed by three main sub basins, where Paraná sub basin represents the greater drainage area, covering 48.7% of basin’s total area, followed by Paraguay River (35.3%) and Uruguay River (11.8%) (Cuya et al., 2013).

As for the basin hydrology, approximately 60% of UpperParaná River have dams, with a few lotic stretches, while the medium and low stretches the opposite occurs (Agostinho et al., 2007). In the Uruguay River the situation is very similar, different from Paraguay River, with no dams in its main course (Nogueira et al. 2021).

In addition to differences in the number of hydroelectric plants, there are also different trophic degrees throughout the basin. Important tributaries of the upper Paraná river have a series of cascading reservoirs downstream and their headwaters drain large cities, totaling more than 27 million people (e.g. São Paulo, Campinas, Curitiba, in Brazil) causing a longitudinal decrease of nutrients, chlorophyll and eutrophication along the course of the rivers (Nogueira et al., 2021). The same does not occurs with the other large rivers (Paraguay and Uruguay rivers) which do not have the influence of large cities at their headwaters, so the amount of nutrients and eutrophication is locally influenced, as in tributaries.

In this study, we sampled approximately 70% of the La Plata River Basin. Triplicate collections were performed at 30 points in the basin, during the summer and winter of 2010. Fifteen reservoirs were selected, all with water retention greater than 15 days (Figure 1, Table 1). The maximum distance among these reservoirs was 1,300 kilometers.

2. Sampling

Were measured the concentration of nitrogen, phosphorus and chlorophyll-a in each sampling campaign. The water samples were collected with a Van Dorn bottle for analysis in laboratory of total concentration of nutrients (nitrogen and phosphorus), and chlorophyll-a. Detailed information about limnological variables and major stressors in La Plata Basin, considering the same samplings, can be found in Nogueira et al. (2021).

Rotifers were sampled by means of vertical trawls in the water column, using a conical plankton net with 50 µm mesh size. The volume of filtered water ranged from 706 to 2826 L per sample, depending on the depth of each sampling stations (Perbiche-Neves et al., 2019). In deep sites, the maximum depth reached by vertical trawls in the water column was of 40 meters (Perbiche-Neves et al., 2019). Posteriorly, the sampled organisms were packed, labeled and fixed with 4% formalin solution.

The identification of the rotifers was carried out under an optical microscope, according to specialized bibliographies (Edmondson, 1959; Koste, 1978; Nogrady et al., 1995; Segers & Dumont, 1995; Smet & Pourriot, 1997).

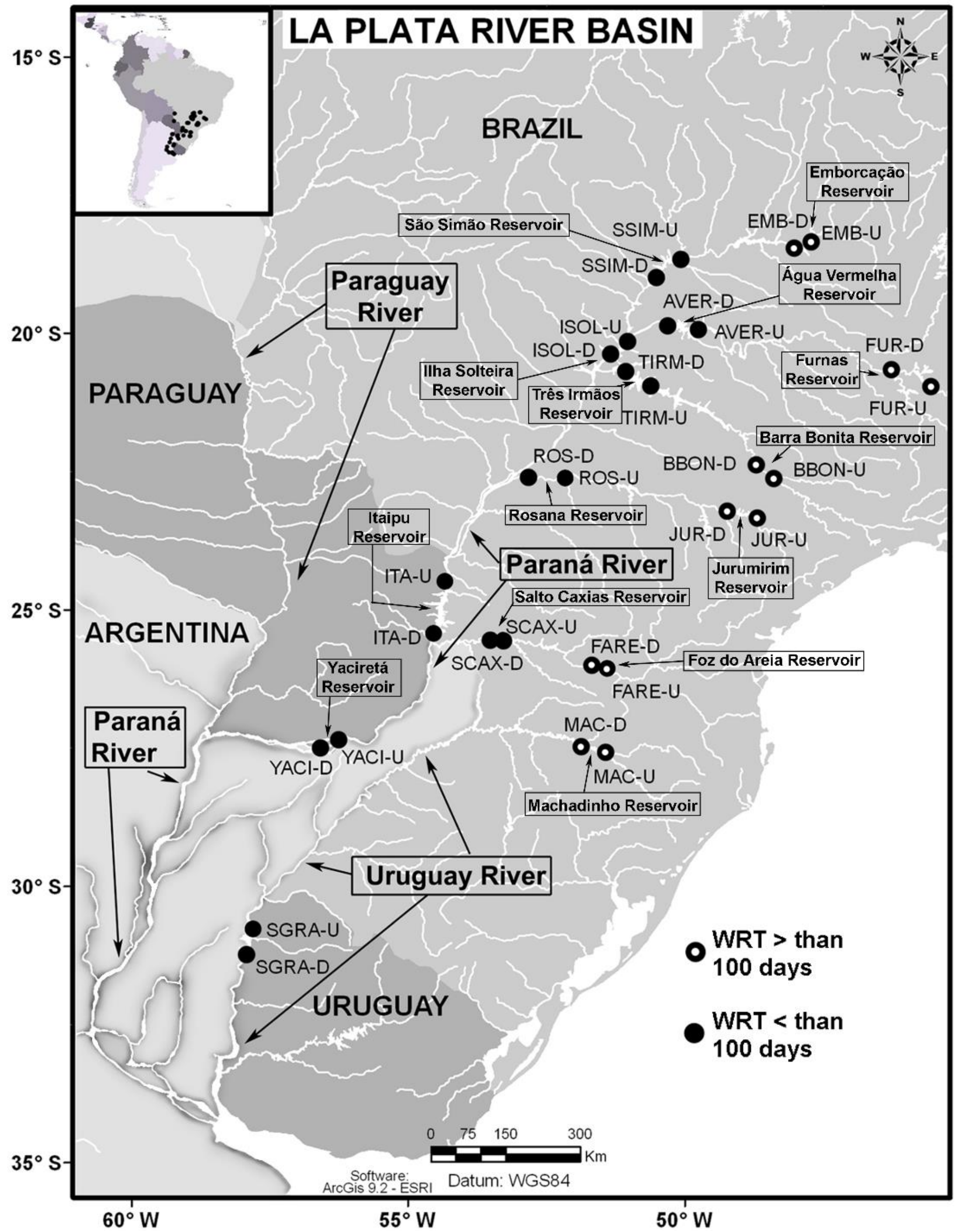

Figure 1. Map of sampling points with water time retention of reservoirs (WRT). The numbers represent the reservoirs, see table 1 for abbreviation and numbering.

Table 1. The La Plata Basin sampling points denomination, geographic coordinates, abbreviation, trophy and trophic state index (TSI). UO = ultraoligotrophic, O = oligotrophic, M = mesotrophic, E = eutrophic and SE = supereutrophic.

N°	Reservoir	Sub basin	Geographic coordinates	Code	Trophy	TSI
1	Emborcação Reservoir – Upstream	Paranaíba	18°22′40.47″S47°44′03.58″W	EMB-U	O	48.85
2	Emborcação Reservoir – Dam	Paranaíba	18°29′33.09″S47°58′17.22″W	EMB-D	UO	46.04
3	São Simão Reservoir – Upstream	Paranaíba	18°40′22.54″S50°04′17.76″W	SSIM-U	O	49.61
4	São Simão Reservoir – Dam	Paranaíba	18°59′15.59″S50°30′18.93″W	SSIM-D	O	51.30
5	Furnas Reservoir – Upstream	Grande	20°58′35.58″S45°31′24.18″W	FUR-U	O	51.54
6	Furnas Reservoir – Dam	Grande	20°39′36.51″S46°18′12.16″W	FUR-D	UO	46.26
7	Água Vermelha Reservoir – Upstream	Grande	19°55′42.17″S49°45′05.31″W	AVER-U	O	51.98
8	Água Vermelha Reservoir – Dam	Grande	19°52′03.73″S50°19′28.77″W	AVER-D	O	51.52
9	Ilha Solteira Reservoir – Upstream	Upper Paraná	20°10′29.60″S51°02′07.06″W	ISOL-U	M	55.43
10	Ilha Solteira Reservoir – Dam	Upper Paraná	20°22′10.87″S51°20′37.65″W	ISOL-D	M	52.85
11	Barra Bonita Reservoir – Upstream	Tietê	22°40′06.24″S48°21′06.42″W	BBON-U	SE	64.44
12	Barra Bonita Reservoir – Dam	Tietê	22°31′45.12″S48°31′27.90″W	BBON-D	E	59.23
13	Três Irmãos Reservoir – Upstream	Tietê	20°57′21.57″S50°36′34.83″W	TIRM-U	M	53.72
14	Três Irmãos Reservoir – Dam	Tietê	20°41′57.09″S51°05′58.43″W	TIRM-D	M	52.35
15	Jurumirim Reservoir – Upstream	Paranapanema	23°19′25.07″S48°42′11.07″W	JUR-U	O	50.96
16	Jurumirim Reservoir – Dam	Paranapanema	23°13′41.07″S49°13′28.03″W	JUR-D	O	50.72
17	Rosana Reservoir – Upstream	Paranapanema	22°36′28.27″S52°09′43.75″W	ROS-U	O	50.58
18	Rosana Reservoir – Dam	Paranapanema	22°36′04.71″S52°49′48.15″W	ROS-D	M	53.32
19	Itaipu Reservoir – Upstream	Upper Paraná	24°29′10.77″S54°19′42.38″W	ITA-U	O	49.37
20	Itaipu Reservoir – Dam	Upper Paraná	25°25′09.67″S54°32′14.47″W	ITA-D	O	49.53
21	Foz do Areia Reservoir – Upstream	Iguaçú	26°03′41.64″S51°24′02.25″W	FARE-U	O	49.68
22	Foz do Areia Reservoir – Dam	Iguaçú	25°59′57.06″S51°38′52.27″W	FARE-D	O	49.47
23	Salto Caxias Reservoir – Upstream	Iguaçú	25°30′32.11″S53°18′24.26″W	SCAX-U	M	53.12
24	Salto Caxias Reservoir – Dam	Iguaçú	25°31′50.96″S53°28′45.76″W	SCAX-D	O	50.31
25	Yaciretá Reservoir – Upstream	Middle Paraná	27°24′24.13″S56°15′19.86″W	YACI-U	O	48.73
26	Yaciretá Reservoir – Dam	Middle Paraná	27°30′09.12″S56°31′56.69″W	YACI-D	O	49.26
27	Machadinho Reservoir – Upstream	Upper Uruguay	27°32′26.71″S51°37′52.31″W	MAC-U	O	51.57
28	Machadinho Reservoir – Dam	Upper Uruguay	27°29′27.77″S51°46′26.50″W	MAC-D	M	52.18
29	Salto Grande Reservoir – Upstream	Middle Uruguay	30°46′27.52″S57°47′55.53″W	SGRA-U	M	56.01
30	Salto Grande Reservoir – Dam	Middle Uruguay	31°15′31.41″S57°55′33.66″W	SGRA-D	M	55.03

3. Data analysis

. We selected three variables that leads to eutrophication: total nitrogen, total phosphorus, and chlorophyll-a, to identify the concentration threshold of these variables, responsible for the abrupt changes in the frequency of occurrence and relative abundance of species, using the Threshold Indicator Rate Analysis (TITAN; Baker & King 2010). TITAN allowed us to identify the limits or points of change for each taxon and for the whole community along the environmental gradient and detect changes in the distributions of species. This analysis uses the value IndVal (Value Indicator) to identify these points of change. When the value obtained by IndVal is less than 0.05 and values of purity and reliability are greater than 0.95 a species is considered significantly associated with a positive (z +) or negative (z-) response. To determine the significant indicator taxa with high precision, data was permutated 500 times, and IndVal < 0.05 were retained. TITAN was implemented with the *TITAN2* package (Baker & King, 2010) of the R Environment (R Development Core Team, 2016), using the untransformed abundance of taxa with ≥ 3 occurrences (Baker & King, 2013).

Results

Were identified 71 species of rotifers. For details of list of species, see Martins et al., (2020), however in Martins et al., (2020), there were more sampling points, including lotic stretches. The following results are focused on ecological thresholds.

Inside some reservoirs, the sampled points showed different states of trophy. The reservoir with higher level of trophy (super eutrophic, 64.44) was Barra Bonita (Tietê River), which presented higher values of total nitrogen (4827.81 $\mu g.L^{-1}$), total phosphorus (145.23 $\mu g.L^{-1}$) and chlorophyll-a (17.67 $\mu g.L^{-1}$). In opposite the reservoir with lower trophy level (ultraoligotrophic, 46.04) were Emborcação (Paranaíba River), with lower values of total nitrogen (140.78 µg.L^{-1}), total phosphorus (5.07 µg.L^{-1}) and chlorophyll-a (0.70 µg.L^{-1}). As there was a great difference of limnological variables among the reservoirs, we can affirm that a wide variety of habitats were sampled (for limnological variables complete analysis see Nogueira et al. 2021).

Through TITAN, we identified significant points of change in the abundance of species in response to total nitrogen, total phosphorus and chlorophyll-a concentration (Table 2).

Table 2. TITAN results for rotifers species in response to variation in nitrogen, phosphorus and chlorophyll concentrations in reservoirs. Obs. = Observed change point; 5% and 95% = quartiles thresholds. Direction of the response given by z- (negative) and z + (positive).

Predictive variable	**Method**	**Point of change**		
		Obs.	*5%*	*95%*
Nitrogen	z-	286.33	254.86	652.78
	z+	1118	482.6	1365.3
Phosphorus	z-	9.1	8.69	16.53
	z+	22.44	11.02	31.45
Chlorophyll-a	z-	0.76	0.45	1.86
	z+	3.89	1.64	5.42

For the total nitrogen concentration, we identified the point of change for negative response (z-) at 286.33 µg L^{-1}, while the point of change for positive response (z+) was observed at a concentration of 1118 µg L^{-1} (Figure 2A and 2B). For the total phosphorus concentration, we identified the point of change for negative response (z-) at 9.1 µg L^{-1}, while the point of change for positive response (z+) was observed at a concentration of 22.44 µg L^{-1} (Figure 3A and 3B). And for the chlorophyll-a concentration, we identified the point of change for negative response (z-) at 0.76 µg L^{-1}, while the point of change for positive response (z+) was observed at a concentration of 3.89 µg L^{-1} (Figure 4A and 4B). We founded more positive than negative responses in all analysis, which indicates that the community structure of rotifers tends to have more effect with the increase of the variables related to eutrophication than with the decrease of these variables in the environment.

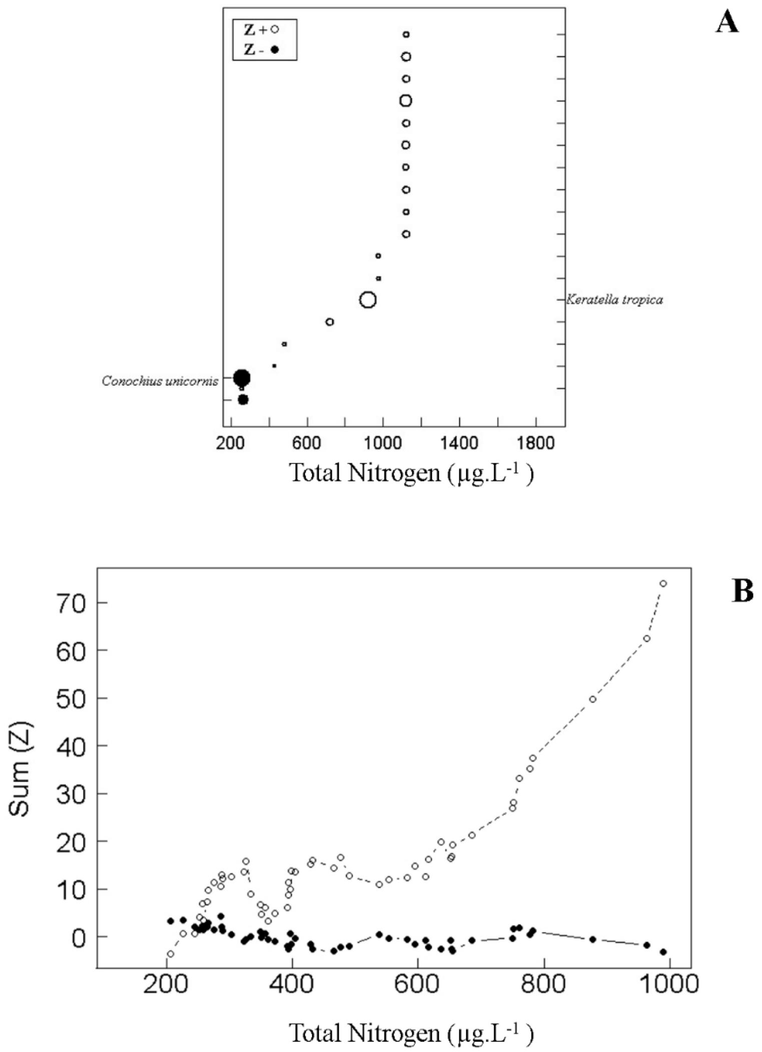

Figure 2 – Graphical representation based on the analysis of threshold indicators (TITAN) for Rotifers species that showed significance throughout the nitrogen concentration variation in reservoirs. Species that are negatively (z-) (black circles) and positively associated (z +) (white circles) suggest a negative and positive response to increasing nitrogen concentrations. The diameter of the circle is proportional to the magnitude of the response. A= species with p<0.05. B= concentration of nitrogen.

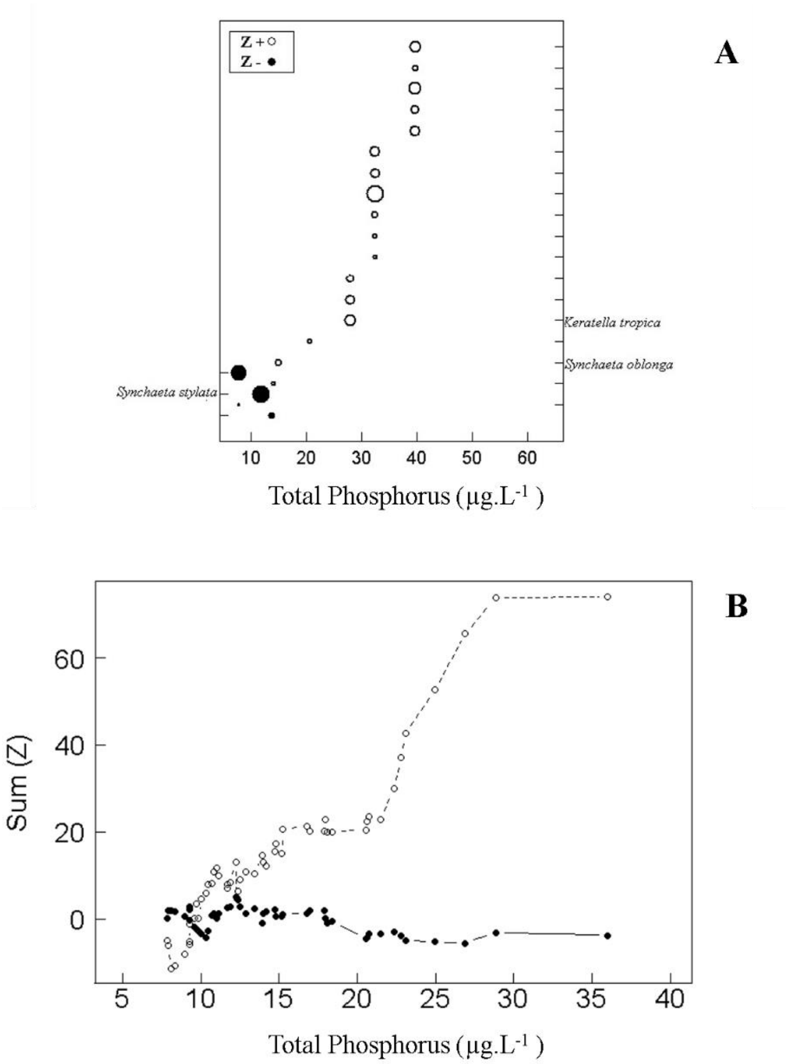

Figure 3 – Graphical representation based on the analysis of threshold indicators (TITAN) for Rotifers species that showed significance throughout the phosphorus concentration variation in reservoirs. Species that are negatively (z-) (black circles) and positively associated (z +) (white circles) suggest a negative and positive response to increasing phosphorus concentrations. The diameter of the circle is proportional to the magnitude of the response. A= species with p<0.05. B= concentration of phosphorus.

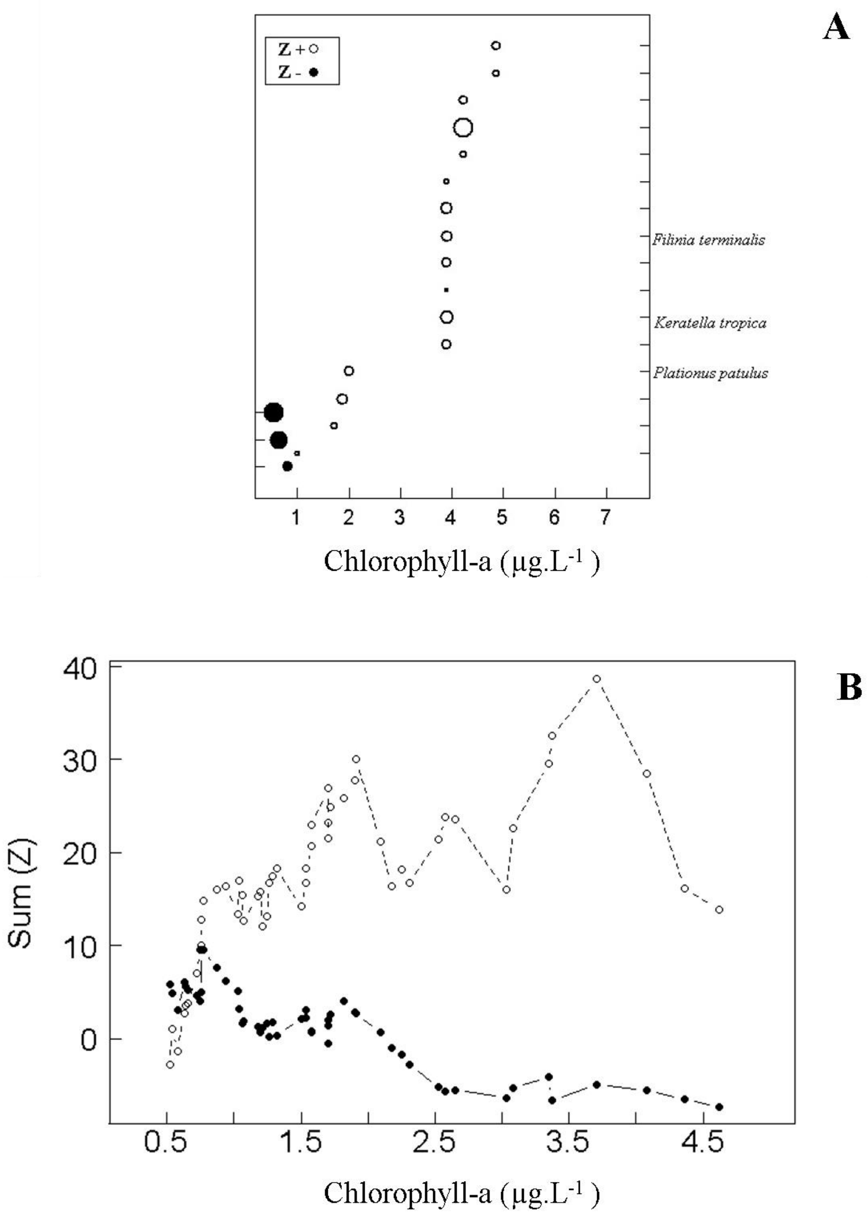

Figure 4 – Graphical representation based on the analysis of threshold indicators (TITAN) for Rotifers species that showed significance throughout the chlorophyll concentration variation in reservoirs. Species that are negatively (z-) (black circles) and positively associated (z +) (white circles) suggest a negative and positive response to increasing chlorophyll concentrations. The diameter of the circle is proportional to the magnitude of the response. A= species with p<0.05. B= concentration of chlorophyll-a.

We identified six species considered as indicators of change in community composition, with significant responses to variation in at least one variable analyzed ($p < 0.05$), most of them showing positive responses ($n = 4$). Species with positive responses were *Keratella tropica, Plationus patulus, Filinia terminalis* and *Synchaeta oblonga*, indicating their dominance in the high levels of the different variables. We identified negative responses for two species, *Conochilus unicornis* and *Synchaeta stylata*, indicating their dominance in the low levels of the different variables. The only species that presented the same response for all variables concentration was *Keratella tropica*.

Discussion

Six species of rotifers from a total of 71 found in reservoirs of La Plata River Basin, could be pointed as good indicator of total nitrogen, phosphorus and chlorophyll-a concentrations in reservoirs, varying positively or negatively according to the point of change for values of these three variables.

The relationship between rotifers and variables which indicated trophic conditions was also found by other studies in neotropical reservoirs (Matsumura-Tundisi & Tundisi, 2005; Serafim-Júnior et al., 2010) or rivers some of them under influence of reservoirs (Mantovano et al., 2019, Tiburcio et al., 2021). The nutrient concentration is responsible for phytoplankton biomass variation in reservoirs and lakes, what explains its influence on zooplankton structure (García-Chicote et al., 2019). In our study points of change values were provided, allowing to understand where the changes in total nutrients (nitrogen and phosphorus) and chlorophyll-a influence directly on some species within the community.

Dispersal generally governs species distribution in freshwater running waters, but recent studies using several approaches pointed to effects of environmental local variables in a finer scale (Yang et al., 2018). The presence of several reservoirs in a large river basin creates different environments where the local environmental variables can assume greater importance, reflecting the trophic state of the environment and the upstream and downstream positioning along the basin (Nogueira et al., 2008; Portinho et al., 2016; Mantovano et al., 2019; Perbiche-Neves et al., 2019).

Comparing with our species pointed as positively related to nutrients and other indicatives of eutrophication, Picapedra et al., (2021) found a species of *Keratella* indicating eutrophic waters. Picapedra et al., (2021) found positive correlations among chlorophyll-a, total dissolved solids, and total nitrogen concentrations with some rotifers as *Kellicottia bostoniensis, Conochilus* sp. and *Polyarthra* sp. *Keratella tropica* was one of the most abundant species in Barra Bonita Reservoir, characterized by high concentrations of total nutrients and chlorophyll (Matsumura-Tundisi & Tundisi, 2005), much higher than in other sampled reservoirs. Searching for zooplankton indicators in several reservoirs of La Plata Basin, but using cyclopoid copepods, five species were filtered from eleven found, and these species were separated in two main groups, from eutrophic and oligotrophic waters (Perbiche-Neves et al., 2021). García-Chicote et al. (2019) filtered 10 from 90 species as indicator of mesotrophic, eutrophic, and hypertrophic states of reservoirs in Spain. These authors found especially *K. tropica* and other brachionids as positively related with total phosphorus concentration, ciliate density, cyanobacteria abundance, phytoplankton biomass, and chlorophyll-a concentration.

Is important take in consider the behavior of species, as all species selected has some similar features. The body size and food behavior can be associated to the secondary productivity and nutrient cycling in the environment (Andersen & Hessen, 1991; Litchman et al., 2013; Hébert et al., 2016) which can be associated to the concentration of the analyzed environmental variables. All the four species with positive response to the increase of at least one variable has the same feed behavior (filter species) and similar body size (Braghin et al., 2018). Gilbert (1985) describes that when the available food is scarce in the environment, the population of species with greater body size, as cladocerans and copepods tends to increase, while smaller species (rotifers) tends to starve to death, it was the case of *Brachyinus calyciforus* and *Keratella cochlearis* in competition with *Daphnia sp*., but when the food is abundant, the competition decreases, and even rotifer species invest in population increase instead of only surviving (Simões et al., 2013). We could observe that the sampling site with more concentration of chlorophyll-a and nutrients was also the site with greater abundance of rotifers, especially the ones with bigger body size, as *K. tropica* It can show that the concentration of chlorophyll-a and nutrients is not the only variables that alter the structure of rotifer communities, when compared with other organisms of the plankton, as cladocerans and copepods, we could find different patterns. It could be interesting a study addressing nutrient and chlorophyll-a thresholds for microcrustaceans along rotifers communities in a large scale, so patterns could be stablished for the zooplankton.

The point of change of chlorophyll-a found in our study is narrow compared to the values that can be found in several reservoirs in the country, for example our positive point of change was 3.89 µg L^{-1}, but Matsumura-Tundisi & Tundisi (2005) found in a hypereutrophic reservoir mean values between 9.3 and 14.7 µg L^{-1}. Comparing with natural lakes, the values of chlorophyll-a point of change determined by Mantovano et al.

(2019) were also higher than ours, varying up to 42 µg L^{-1} as point of change using TITAN. In contrast, Picapedra et al. (2020) found values lower than the ones found by us (> 2 µg L^{-1}).This indicates that the concentration of chlorophyll-a vary in the environments, and even lower concentrations can alter the community structure of rotifers, and the use of ecological thresholds should be more disseminated among the researchers, understanding, this way, how abundance and frequency of occurrence of rotifers species responds to a gradient of this variable. In addition, the biogeographical scale in Mantovano et al. (2019) is smaller than the scale of our work, and other organisms of zooplankton were included (microcrustaceans), which can give a very different threshold than when only rotifers are studied. It give emphasis to the idea that the use of ecological thresholds of environment variables should be analyzed observing the local features of the study area and the community that is studied.

The points of change found in our study provide a wide view of rotifers in a large river basin, but value limits should not be considered solely and judiciously to set values for future guidelines. More studies are needed highlighting that environment variables and communities vary in space and time. Differences in nutrient and chlorophyll-a values are noted when comparing with other studies, and so far, there has not been a clear initiative to standardize the use of any trophic state index to facilitate comparison. For example, Picapedra et al. (2020) had values of total nitrogen close our means value, but Matsumura-Tundisi & Tundisi (2005) presented chlorophyll-a values considerably higher than ours.

Our results corroborate other studies suggesting the zooplankton as a metric to water monitoring in all the world (Yang et al., 2018; De-Carli et al., 2019; García-Chicote et al., 2019; Pomari et al., 2019). Independent of the filter or analysis used for water monitoring, it seems that this branch of limnology or aquatic ecology has advanced fast because the recent reference in last years (Perbiche-Neves et al., 2016, 2021; De-Carli et al., 2018b; Yang et al., 2018; García-Chicote et al., 2019), and in general the studies, individually, filter between 4 and 10 species as indicators within the community, as in our study.

Acknowledgements

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Capítulo 3

Drivers of beta diversity of rotifers from La Plata River Basin (South America)

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Abstract

The heterogeneity (composition and distribution), beta diversity and the influence of environmental variables of rotifers were studied in rivers and reservoirs of La Plata Basin in South America. Zooplankton samples were collected at 43 points, in two periods (Summer and Winter) of 2010. Predictive variables were prepared for the distance-based redundancy analysis (db-RDA), selecting the environmental (Env), spatial (Spa) and temporal (Temp) variables. The heterogeneity was calculated by a PERMANOVA. The component beta total (B-Total) was separated in the replacement (B-Repl) and richness/abundance differences components (B-Rich/AbDiff). In order to analyze the relative contribution of the pure and shared effects of the variables Env, Spa and Temp to explain the variation of beta diversity, we calculated analysis of partition of variance. The statistical significance of the pure fractions was tested using ANOVA ($p < 0,05$). We tested the following hypotheses: (i) the main determinants of beta diversity in rotifers are environmental variables related to eutrophication (e.g., nutrients, chlorophyll, turbidity), as these organisms respond to changes in water quality; (ii) due to its wide geographic distribution, in general, the spatial factor will not be important; (iii) due to the environmental heterogeneity between the sub-basins, the replacement of species will be more important than the gain/loss of species. The first ad the third hypotheses were confirmed, but the second was rejected. The results indicated that the B-Rich/AbDiff explained the highest percentage of dissimilarity between the sub-basins, with the environmental variables being the main determining factor. The sub-basins differed from each other, with the Paraguay basin exhibiting lower species richness. Despite the differences between the sub-basins, the large spatial scale is not the determining factor explaining the difference in species composition and distribution, but heterogeneity.

Keywords: Environmental variables, Heterogeneity, Rotifera.

Determinantes da diversidade beta de rotíferos da Bacia do Rio da Prata (América do Sul)

Resumo

A heterogeneidade (composição e distribuição), a diversidade beta e a influência de variáveis ambientais de rotíferos foram estudadas em rios e reservatórios da Bacia do Rio da Prata na América do Sul. Foram coletadas amostras de zooplâncton em 43 pontos em dois períodos (verão e inverno) de 2010. Variáveis preditoras foram preparadas para a análise de redundância baseada na distância (db-RDA), selecionando as variáveis ambiental (Env), espacial (Spa) e temporal (Temp). A heterogeneidade ambiental foi

calculada por uma PERMANOVA. O componente beta total (B-Total) foi separado nos componentes substituição (B-Repl) e diferenças na riqueza/abundância (B-Rich/AbDiff). Para analisar a contribuição relativa das variáveis preditoras puras e em conjunto na explicação da variação da diversidade beta, foi calculada a análise de partição da variância. A significância estatística das frações puras foi testada utilizando a ANOVA ($p < 0,05$). Testamos as seguintes hipóteses: (i) os principais determinantes da diversidade beta dos rotíferos são as variáveis ambientais relacionadas à eutrofização (e.g. nutrientes, clorofila, turbidez), por esses organismos responderem às mudanças na qualidade de água; (ii) devido à sua ampla distribuição geográfica, em geral, o fator espacial não será importante; (iii) devido à heterogeneidade ambiental entre as sub-bacias, a substituição de espécies será mais importante do que a perda/ganho de espécies. A primeira e a terceira hipóteses foram aceitas, porém a segunda foi rejeitada. Os resultados indicaram que a B-Rich/AbDiff explicaram a maior porcentagem da dissimilaridade entre as sub-bacias, sendo as variáveis ambientais o principal fator determinante. As sub-bacias diferiram entre si, sendo que a bacia do Paraguai se destacou das demais, a com menor riqueza de espécies. Apesar das diferenças entre as sub-bacias, a larga escala espacial não é o fator determinante para explicar diferenças de composição e distribuição de espécies, mas sim a heterogeneidade.

Palavras-chave: Variáveis ambientais, Heterogeneidade ambiental, Rotifera.

Introduction

Rotifers are simple and very common invertebrates present in aquatic environments, and in freshwaters environments frequently are the most abundant group in zooplankton (Lansac-Tôha et al., 2009; Sartori et al., 2009). Segers (2008) point 1,948 species in the world, of these 900 are endemic and 405 cosmopolitans, and there are 682 species in the Neotropical region (Central and South America).

The most important threats on rotifer diversity are the eutrophication and salinization, however for insecticides, for example, these organisms appear less sensitive than for cladocerans (Segers, 2008). Besides some studies point to problems in the association between rotifers species composition with trophic level (May & O'Hare, 2005) and point the use of trophy-based response to water quality (Oh et al., 2017), some species are widely recognized and used as indicators of water quality in reservoirs and other environments (Serafim-Júnior et al., 2010; Chen et al., 2012; Vázquez-Sánchez et al., 2014). Arruda et al., (2017)presented the effects of fish cage farm on rotifers structure and found five species as good indicators of water quality influenced by aquaculture, and among these, four species belong to *Brachionus* genus.

Metacommunities approaches are useful to understand the spatial dynamics of species in different scales with the integration between spatial and environmental predictors (Cottenie, 2005; Varzinczak et al., 2018; Gomes et al., 2020), since it considers how both regional processes and local interactions affect the local communities (Dias et al., 2016). Once this approach evaluates ecological processes at different spatial scales (Leibold & Norberg, 2004; Ryo et al., 2018), it can help the understanding of environmental changes and the effects on the zooplankton community in large spatial scales.

Several studies have been published aiming to understand which factors are the most important on zooplankton in large spatial scales (Nogueira et al., 2008; Pinel-Alloul et al., 2013; Heino et al., 2017; Perbiche-Neves et al., 2019), and within these studies the beta diversity metrics has been frequently used in ecological studies of aquatic organisms to explain the turnover or nestedness among the environments (Braghin et al., 2018; Soininen et al., 2018; Lopes et al., 2019; Perbiche-Neves et al., 2019; Rocha et al., 2020; Diniz et al., 2021). Using the metacommunity approach, Pinel-Alloul et al., (2013) found that the richness-energy theory explains diversity patterns of zooplankton in 1,665 lakes across Canada, pointing the solar radiation as the best predictor for regional species richness and community structure. In the same way, across the tenth largest river basin of the world, Perbiche-Neves et al. (2019) using four metrics of beta diversity found high turnover on microcrustaceans in sub-basins, suggesting a strong effect of eutrophication, and only for copepods the spatial distance, precipitation, and mean temperature of winter were important. These results suggest that geographic isolation drives speciation and endemism of copepods especially in the Neotropical region, with species or group of species distributed most times in few or delimited ecoregions or river basins (Perbiche-Neves et al., 2014).

However, Hessen et al., (2019) pointed that zoochory of living and resting species by birds can mistake the results of parameter effect, influencing dispersal and pos-dispersal species by changing the water quality and productivity. A same trend was found by Da Silva et al., (2019) for zooplankton metacommunities in ponds, also influenced by birds. Even considering the high number of endemic species, rotifers are easily dispersed by many ways, especially by humans Segers, (2008), as the case of *Kellicotia bostoniensis* in Asia (Yang & Min, 2020), Europe (Zhdanova & Dobrynin, 2011) and South America (Peixoto et al., 2010; Coelho & Henry, 2017).

With a large-scale spatial study, we can sample environments with different characteristics and significant environmental heterogeneity, thus comparing the contribution of local and regional processes in Beta diversity. High environmental heterogeneity can lead to greater beta diversity, as resource availability tends to be greater (Maloufi et al., 2016). Although the relationship between beta diversity and heterogeneity is under debate by many authors (Astorga et al., 2014; Bini et al., 2014; Lopes et al., 2014; Maloufi et al., 2016; Diniz et al., 2021), the joint study of beta diversity with metacommunity elements can help to establish patterns of species distribution (Wojciechowski et al., 2017; Diniz et al., 2021).

We studied rotifers across the tenth largest river basin in the world and the second largest in South America. Our aim was to identify major drivers acting on beta diversity of these organisms in a large-scale approach. we tested the following hypotheses: (i) the main determinants of beta diversity for rotifers are environmental variables related to eutrophication (e.g. nutrients, chlorophyll, turbidity), as these organisms respond to changes in water quality; (ii) due to its wide geographic distribution, in general, the spatial factor will not be important; (iii) due to the environmental heterogeneity between the sub-basins, the replacement of species will be more important than the gain/loss of species for the dissimilarity among the sub-basins.

Material and Methods

1. Study area

The La Plata River basin is the second largest hydrographic basin of South America, with a drainage area of 3.1 million km^2 (Cuya et al., 2013). Five countries are included in the basin: Brazil, Paraguay, Uruguay, Argentina, and Bolivia. In relation to the hydrographic network, the basin is formed by three main sub-basins: Paraná, Paraguay, and Uruguay, as well as several smaller sub-basins: Paranaíba River basin, Grande River, Tietê River, Paranapanema River, Iguaçu River, and Prata River (estuary).

In relation to the drainage area, the most representative sub-basin is Paraná River (2.583.000 km^2 extension area), followed by Paraguay River (365.592 km^2), Uruguay River (365.000km^2), Grande River (143.000 km^2), Paranapanema River (100.800km^2), Iguaçu River (62.000 km^2), Prata River, estuary (35.000 km^2), Paranaíba River (34.400 km^2) and Tietê River (1.150 km^2). In this study the nine sub-basins were sampled.

2. Sampling

A total of 86 samples were collected in 43 sampling stations, including 15 reservoirs and eight lotic stretches distributed in nine sub basins of La Plata River basin (sampling sites in maps and respective coordinates can be found in Nogueira et al., 2021; Perbiche-Neves et al., 2021). The samplings were performed in two periods, summer (January) and winter (July) of 2010. The rotifers were sampled by means of vertical hauls in the water column, using a conical plankton net with 50μm mesh size. In deep sites, the maximum depth reached by vertical trawls in the water column was 40 meters (Perbiche-Neves et al., 2019). The sampled rotifers were subsequently packed, labeled, and fixed with 4% formalin solution. The identification of the rotifers was carried out with an optical microscope (Zeiss Axio Imager.A2m) according to specialized bibliographies (Edmondson, 1959; Koste, 1978; Nogrady et al., 1995; Segers & Dumont, 1995; Smet & Pourriot, 1997; Nogrady, 2002; Wallace et al., 2006; Wallace et al., 2019; de Paggi et al., 2020). The analyzed material was deposited in the Laboratory of Ecology and Continental Waters, Institute of Biosciences of Botucatu at the Universidade Estadual Paulista Júlio de Mesquita Filho (Unesp), Brazil.

Ten physical and chemical variables of the water were measured for each sampling station according to the method of Perbiche-Neves et al. (2016) and Nogueira et al. (2021): total phosphorus and nitrogen, water temperature, transparency, turbidity, electrical conductivity, pH, dissolved oxygen, depth, and total chlorophyll.

3. Predictor variables

The environmental component was organized in a matrix of standardized limnological variables (log x+1, except the pH variable). Multicollinearity between environmental variables was verified by means of variance inflation factors (VIF) and variables that were strongly correlated were eliminated (VIF >5) before statistical analysis (Oksanen et al., 2020). Thus, predictive variables were prepared for the distance-based redundancy analysis (db-RDA), and then calculated Principal Coordinates Analysis (PCoA) with the packages "vegan" and "ape" in software R, to transform the incidence (presence and absence) and abundance of rotifers into distances.

To obtain the spatial component, the following steps were performed: 1) the distances in kilometers between all points of each sub-basin were determined, with the "path" function of "Google Earth"; 2) the distances were transformed into a triangular matrix; 3) the triangular matrix was transformed through Principal Coordinate Analysis of Truncated Distance Matrix (PCNM) creating a rectangular matrix, using the "pcnm" function. Thus, the three predictive variables for db-RDA were the environmental variables (Env), special variables (Spa) and temporal variables (Temp – summer and winter).

4. Data analysis

The heterogeneity of incidence and abundance of species were calculated by a PERMANOVA analysis for each component of Beta and pairwise. For that, we used the "adonis" function of package "vegan" of software R (R Core Team, 2019). The considered significance was $p<0,05$. The results were expressed in tables and NMDS figures. We calculated the components of beta diversity for incidence and abundance (matrix of dissimilarity between the sampling points) according to coefficient of dissimilarity of Sorensen. We applied the methodology proposed by Podani & Schmera, (2011) and Carvalho et al., (2012), where the beta total (B-Total) diversity is separated in the replacement (B-Repl) and richness/abundance differences components (B-Rich/AbDiff). The B-Repl refers to substitution in species identity and B-Rich/AbDiff refers to differences in loss and/or gain in species richness. Thus, three matrices of dissimilarity were created.

The distance matrices generated by the beta were used in the distance-based redundancy analysis (db-RDA, Legendre & Andersson, 1999). For the calculation of each db-RDA, the direct selection criterion was applied with “two stopping rules” to identify the final sets of environmental variables (Env), spatial variables (Esp) and temporal variables (Temp), that influence beta diversity (B-Total, B-Repl and B-Rich/AbDiff) in each sampled sub-basin (the variables selected are in tables 2 and 3). In order to analyze the relative contribution of the pure and shared effects of the variables Env, Spa and Temp to explain the variation of beta diversity, we calculated analysis of partition of variance (Peres-Neto et al., 2006). The statistical significance of the pure fractions was tested using ANOVA ($p < 0,05$). For this analysis, we used the packages "vegan", "FD", "stats" and "BAT" in software R.

Results

1. Environmental Heterogeneity

Incidence and abundance data showed significance heterogeneity, with the B-Repl of Incidence with the greatest distance from centroid (=3.32, pseudo F=3.52, p=0.001) and also for Abundance (=4.76, pseudo F =3.53 and *p*=0.001) (Table 1). The sub-basins showed a high heterogeneity, with different composition and distribution of species. The pairwise PERMANOVA showed that the Paraguay sub-basin was significantly different from the others (Figure 1; Table 1 MS), and Prata and Iguaçu were similar to each other, but different from the others sub-basins.

Table 1: PERMANOVA results. Df = degrees of freedom; SS = sum of squares; MS = mean square; F = F-value; R^2 = R-value; *p* = p-value. Values in bold means significant differences.

Data type	**Component**	**Df**	**SS**	**MS**	**F**	$\mathbf{R^2}$	***P***
	B-Total	8	1.621	0.203	3.423	0.262	**0.002**
Incidence	B-Repl	8	3.329	0.416	3.528	0.268	**0.001**
	B-Rich	8	1.621	0.203	3.423	0.262	**0.002**
	B-Total	8	7.891	0.986	3.777	0.282	**0.001**
Abundance	B-Repl	8	4.766	0.596	3.543	0.269	**0.001**
	B-AbDiff	8	0.663	0.083	3.902	0.288	**0.001**

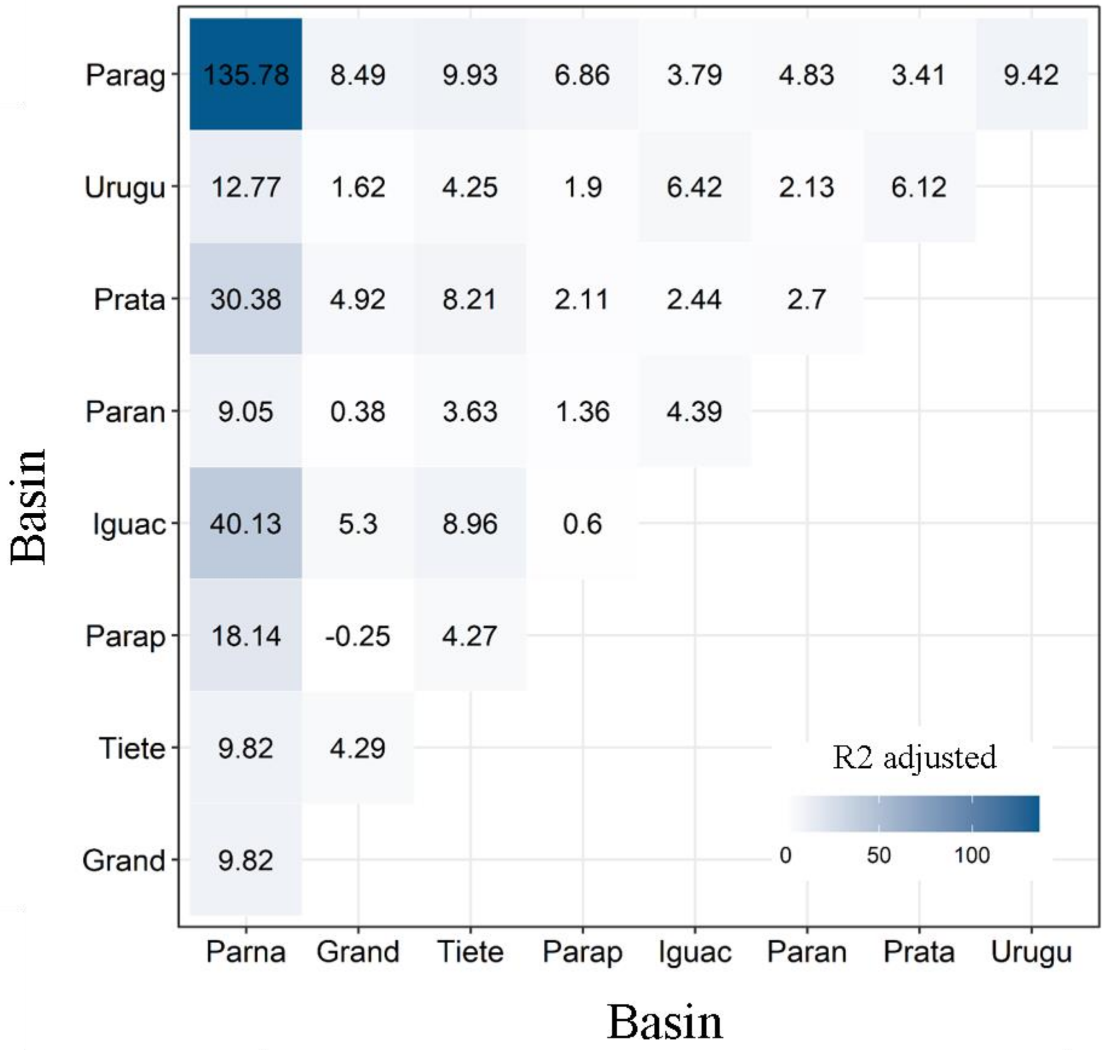

Figure 1. Pairwise PERMANOVA among the sub-basins, with values of R adjusted. Similar colors mean similar results.

2. Beta diversity

The B-Total showed similar results for both incidence and abundance data. The B-Repl component (substitution of species), were more representative of dissimilarities in incidence and abundance, indicating that the replacement of species explains more than the gain/loss of species. B-Rich/AbDiff was more representative of dissimilarities in abundance data (Figure 2).

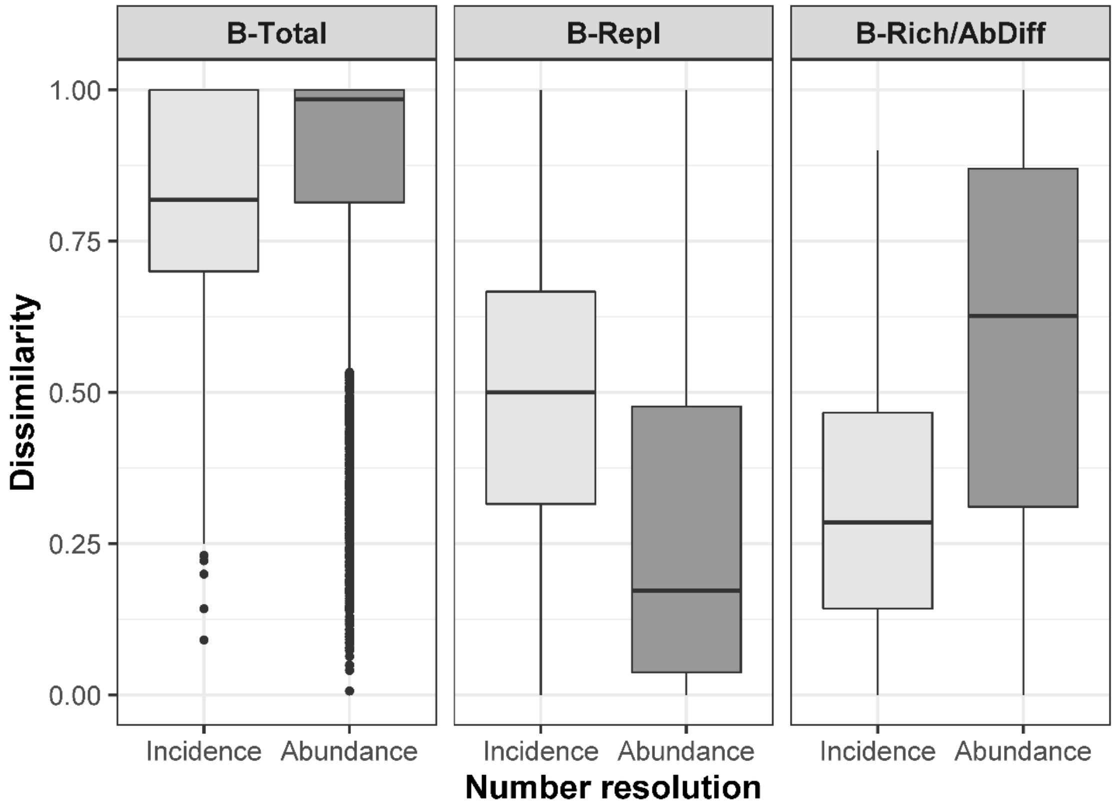

Figure 2. Boxplots of pairwise dissimilarity for total, replacement, and richness/abundance difference component of Rotifera incidence and abundance. The horizontal line describes the median value, box denotes first and third quartiles, whiskers denote minimum and maximum values, and dots indicate outliers.

3. Contribution of environmental, spatial, and temporal variables for Rotifera dissimilarity

The selected variables for each predictor variable (environmental, spatial, and temporal) for incidence and abundance, for B-Total and B-Repl. Nevertheless, the variables related to eutrophication (nitrogen and phosphorus) were selected by most of the components of beta diversity, along with water temperature, turbidity, suspended matter and pH. The temporal variable was considered a dummy variable, so it remained the same for all components (Tables 2; 3). The PCNM selected by B-Total and B-Repl were very similar for incidence and abundance. The B-Rich/AbDiff component selected only one environmental variable, and one PCNM for incidence, which shows that this component did not explain much of the dissimilarity among the sub-basins.

Table 2: db-RDA variable selection and cumulative adj. R^2 values obtained through forward selection for incidence data.

B-Total	Environment	Spatial	Temporal
	Silica	PCNM1	Dummy variable (Summer and Winter)
	Water temperature	PCNM2	
	Turbidity	PCNM3	
	Total suspended matter	PCNM4	
	pH	PCNM5	
	Total nitrogen	PCNM7	
	Total phosphorus	PCNM9	
		PCNM12	
Adj. R^2	0.16	0.18	0.06

B-Repl	Environment	Spatial	Temporal
	Silica	PCNM1	Dummy variable (Suumer and Winter)
	Turbidity	PCNM2	
	Water temperature	PCNM3	
	Total suspended matter	PCNM4	
		PCNM5	
		PCNM8	
		PCNM9	
		PCNM12	
		PCNM14	
Adj. R^2	0.22	0.3	0.1

B-Rich	Environment	Spatial	Temporal
	pH	PCNM7	Dummy variable (Summer and Winter)
Adj. R^2	0.08	0.06	0.03

Table 3: db-RDA variable selection and cumulative adj. R^2 values obtained through forward selection for abundance data.

B-Total	Environment	Spatial	Temporal
	Total phosphorus	PCNM1	Dummy variable (Suumer and Winter)
	Total nitrogen	PCNM2	
	pH	PCNM3	
	Total suspended matter	PCNM4	
	Turbidity	PCNM5	
		PCNM14	
Adj. R^2	0.11	0.18	0.03

B-Repl	Environment	Spatial	Temporal
	Water temperature	PCNM1	Dummy variable (Suumer and Winter)
	Turbidity	PCNM2	
	Total suspended matter	PCNM3	
	pH	PCNM4	
	Total phosphorus	PCNM14	
	Total nitrogen		
Adj. R^2	0.14	0.2	0.03

B-AbDiff	Environment	Spatial	Temporal
	Total phosphorus	PCNM5 PCNM7	Dummy variable (Summer and Winter)
Adj. R^2	0.06	0.16	0.01

3.1 db-RDA

Considering all the predictor variables, the B-Repl component showed the greatest percentage of explanation of dissimilarity, with values of 43% for incidence data and 32% for abundance data (Fig. 3b, e). Taking into consideration the variables separately, the spatial variable was the most important for the structure of the variation of the beta diversity, both incidence and abundance data (17%), followed by the environmental variable, that explained 9% on the abundance and 4% on the incidence. The temporal variable was significative only in B-Repl of incidence data, where it explained 3% of variation. In addition, the B-Rich/AbDiff component explained 13% of variation in the incidence data and 19% in the abundance data, in the latter, the spatial variable explained 12% of this variation. (Fig. 3 c, f).

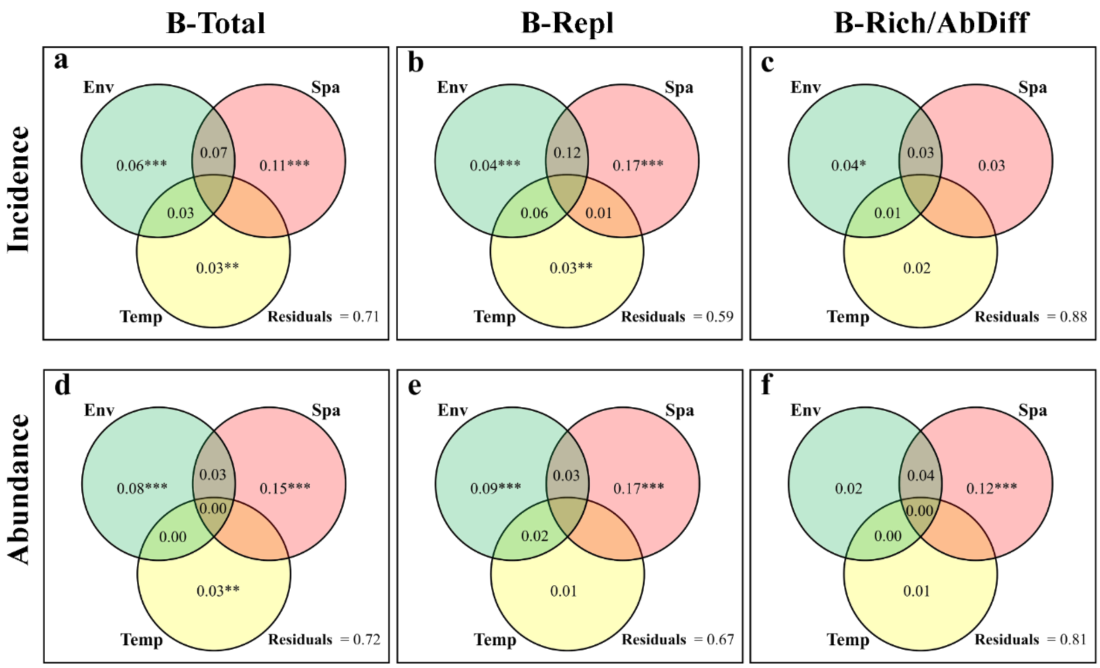

Figure 3. Venn Diagram based on the partition of variation showing the relative contribution of environment (Env), spatial (Spa) and temporal (Temp) variables of the beta diversity variation (B-Total, B-Repl and B-Rich/AbDiff) of presence and absence data and abundance data, a-c are the results of incidence data and d-f are the results of abundance data. *p<0.05; **p<0.1; *** p<0.001.

The composition of species was different among the sub-basins, and the way the species are distributed in the basins. In the B-Total for incidence, the species distribution dissimilarity was associated more with environmental variables than spatial, but the sub-basins that were closer to each other were more similar, showing a pattern of distribution of species according to the spatial scale. Similar results were showed for abundance data, but even with the effect of the spatial variable, the effect of environmental variables related to eutrophication were higher (phosphorus and nitrogen), and the Tiete sub-basin, with the highest value of trophy level, was strongly associated with these variables, in winter and summer.

In the B-Repl component, we could observe that Turbidity, Water temperature and suspended matter were very important in the incidence data, dividing the points according to physical proximity, the sub-basins located more to south were very related to water temperature, this region have colder water, and it can restrict the establishment of some rotifer species. For abundance data, this component explains less than for incidence, we did not find a pattern according to the spatial scale. The drivers were the environmental variables, as pH, water temperature, nitrogen and suspended matter. The B-Rich/AbDiff component, for both incidence and abundance, weakly explained the dissimilarities, which shows wide distribution of species. Even a clear pattern was not found, the composition of species varies with the biogeographical factors.

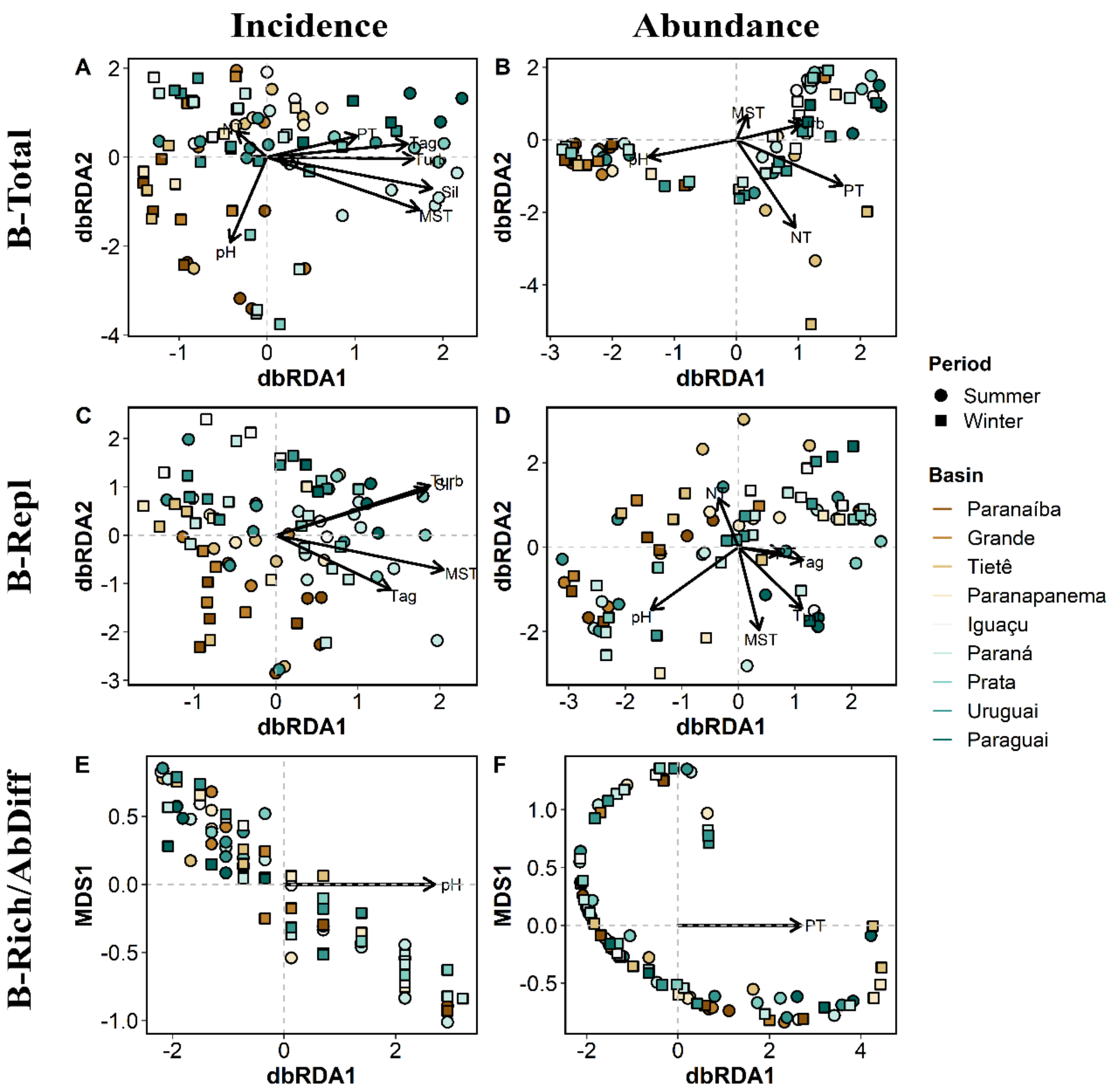

Figure 4. NMDS of db-RDA results of B-total, B-Repl and B-Rich/AbDiff environmental heterogeneity based on Euclidean dissimilarity between incidence and abundance data of Rotifera of La Plata River Basin.

Discussion

According to the hypothesis tested, the first one was confirmed, as in both incidence and abundance data, most environmental variables selected by db-RDA were related to eutrophication, as total phosphorus and total nitrogen, especially for B- Total, showing the influence of these variables in the beta diversity of rotifers. The second hypothesis was rejected; the large spatial scale was a very significant determinant of beta diversity, even with the wide geographical distribution of rotifer species, the composition and abundance of these species along the basin were affected by the location of each sampled point. The third hypothesis was confirmed, according to the sub-basin the composition of species was different, probably because of the different features of each sampled location.

Large spatial scale works tends to sample environments with different features (Pinel-Alloul et al., 2013; Heino et al., 2017; Soininen et al., 2018; Perbiche-Neves et al., 2019). In our study, the environmental heterogeneity was high among sub-basins, and as the sampling points features were different, the composition of species and the way as the species distribute among the sites were significant different. Similar results were found for microcrustaceans in the same La Plata River Basin (Perbiche-Neves et al., 2019). The heterogeneity-diversity hypothesis explain that heterogeneous environments provide greater diversity of niches than homogeneous ones, reflecting on the taxonomic structure of communities (Bomfim et al., 2018; Ortega et al., 2018), as we found in our results.

The PERMANOVA showed that the Paraguay sub-basin differs from the others. Analyzing by the features of this area, it was the sub-basin with lower number of reservoirs and more lotic environments, which may have effect on the composition and distribution of species. The environmental heterogeneity of the reservoirs leads to changes in the composition and abundance of zooplankton communities (Nogueira, 2000, 2001), and as this sub-basin presents a lower number of reservoirs sampled, what can justify the difference we found (Frutos et al., 2006).

The PERMANOVA also showed that Prata and Iguaçu sub-basins were similar between them, but different from the others. In these environments, we registered some rare species with low abundance, which is very important when analyzed the composition of species (Jain et al., 2014). Also in the spatial scale, these sub-basins are located in the south region, where the environment characteristics are very different (colder winters) from the others. In addition, as the Beta diversity showed, the spatial and environment variables are both important when explaining the dissimilarity among the sub-basins, and water temperature were selected by most components of beta diversity, and the mean values of this variable were lower in these two sub-basins, when compared to the others.

The analysis of beta diversity is important to understand differences in the assemblages composition among sampled sites or the extent of change in the assemblage composition along gradients (Legendre et al., 2005; Tuomisto & Ruokolainen, 2006; Heino et al., 2018). When the total beta is divided into replacement and richness differences components, the results focus in any variation related to richness differences between sites instead of nestedness-related patterns (Carvalho et al., 2012; Legendre, 2014; Heino et al., 2018). Our results showed that the replacement component was more important than the richness/abundance difference, in both incidence and abundance data, the same were registered by other studies that decomposed total beta diversity into the replacement and richness difference components, as in Heino et al., (2018). Even studies using the methodology of partition the beta diversity into the turnover and nestdness components (Baselga, 2010), it was observed that turnover component was clearly more important than the nestedness components, as in Soininen et al., (2018), that used a meta-analysis of 269 data points from freshwater, marine and terrestrial realms, in geographical areas from the tropics to near polar regions and with a wide range of organisms, from bacteria to mammals.

The B-Total component was determinate most for spatial variables, which shows that the difference among the locations were very important in the changes of composition of species, probably because the differences among the sub-basins, allows the establishment of different niches, leading to higher species replacement (Maloufi et al., 2016), as it is well described in the literature. In addition, the wide dispersion of rotifer species can enable a high exchange of species or propagules, which may favor an increase in replacement and beta diversity (Grabowska et al., 2014; Gianuca et al., 2017; Diniz et al., 2021). We found that geographical distance was the most important variable affecting differences in composition of species among sub-basins, which is very plausible given the large geographical area of this study (Roque et al., 2008; Landeiro et al., 2012; Heino et al., 2018; Tolonen et al., 2020). Followed by the environmental variables, that also vary along the sub-basins.

Many studies of zooplankton beta diversity found that the heterogeneity and spatial scale are the most determinants of beta diversity (Maloufi et al., 2016; Perbiche-Neves et al., 2019). In this study, we can confirm these findings, showing the importance of large spatial scale works, so we can have a better understanding on the ecological behavior of groups with high ecological importance, as rotifers. Our findings do point out that various factors should be taken into account in the conservation biogeography of highly diverse organism groups, in addition of large temporal scales. We highlight the need for further studies considering a large spatial scale over time to maximize the understanding of aquatic dynamics.

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Material Suplementar

Capítulo 1

Table S1: List of species of rotifers sampled in lotic and lentic habitats in La Plata River Basin, South America. Published in Martins et al., (2021).

Order/Family	Species	Local
Order Flosculariaceae		
Family Conochilidae	*Conochilus coenobasis* (Skorikov, 1914)	4
	Conochilus dossuarius Hudson 1885	1, 3, 5, 6, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 20, 21, 22, 23, 24, 28, 29, 30, 31, 33, 34, 36, 43
	Conochilus natans (Seligo, 1900*)*	7, 8, 15, 34
	Conochilus unicornis Rousselet, 1892	1, 2, 3, 4, 6, 7, 8, 12, 14, 15, 18, 28, 30, 32, 33, 34, 35, 39
Family Flosculariidae	*Ptygura sp.* Ehrenberg, 1832	15
Family Hexarthridae	*Hexarthra intermedia* (Hauer, 1929)	9, 16, 22
	Hexarthra mira (Hudson, 1871)	2, 5, 7, 8, 9, 10, 12, 15, 17, 21, 22, 23, 24, 27, 28, 30, 39, 43
Family Testudinellidae	*Pompholyx triloba* Pejler, 1957	16, 32
	Testudinella mucronata (Gosse, 1886)	15, 31, 32, 39, 41, 43
	Testudinella patina (Hermann, 1783)	12, 15, 18, 19, 28, 30, 32, 39, 40
Family Trochosphaeridae	*Filinia limnetica* (Zacharias, 1893)	21, 22
	Filinia longiseta (Ehrenberg, 1834)	7, 12, 21, 22, 30, 34
	Filinia opoliensis (Zacharias, 1898)	6, 7, 12, 16, 39, 43
	Filinia terminalis (Plate, 1886)	5, 6, 7, 8, 11, 12, 13, 16, 21, 33, 34, 39
Order Ploima		
Family Asplanchnidae	*Asplanchna priodonta* Gosse, 1850	12
	Asplanchna sieboldii (Leydig, 1854)	7, 12, 18, 22, 24, 25, 30, 34, 35, 39, 43
	Harringia rousseleti de Beauchamp, 1912	28
Family Brachionidae	*Anuraeopsis fissa* Gosse, 1850	12, 21
	Anuraeopsis navicula Rousselet, 1911	5, 15, 19
	Brachionus angularis Gosse, 1851	30
	Brachionus budapestinensis Daday, 1885	7
	Brachionus calyciflorus Pallas, 1766	2, 5, 7, 8, 11, 12, 13, 15, 16, 18, 30, 31, 33, 34, 35, 39
	Brachionus caudatus Barrois & Daday, 1894	29, 30, 31, 32, 37, 38, 39, 43

	Brachionus dolobratus Harring, 1914	5, 6, 8, 13, 16, 25, 34, 35, 37, 39
	Brachionus falcatus Zacharias, 1898	3, 5, 6, 7, 11, 12, 16, 23, 34, 35, 38, 39, 42, 43
	Brachionus mirus Daday, 1905	10, 11, 12, 14, 21, 30, 31, 34, 39, 42, 43
	Brachionus quadridentatus Hermann, 1783	32, 43
	Brachionus urceolaris Müller, 1773	39
	Kellicottia bostoniensis (Rousselet, 1908)	4, 5, 6, 11, 12, 15, 16, 21, 22, 23, 24, 25, 29, 32, 33, 34, 35, 36, 38
	Keratella americana Carlin, 1943	1, 5, 6, 7, 8, 9, 11, 12, 13, 14, 15, 21, 22, 24, 35, 36, 38, 39, 43
	Keratella cochlearis (Gosse, 1851)	3, 4, 5, 6, 7, 8, 9, 10, 12, 13, 15, 16, 18, 21, 22, 26, 34, 35, 38, 39, 41, 42
	Keratella lenzi Hauer, 1053	5, 8, 10, 11, 12, 13, 15, 34
	Keratella tropica (Apstein, 1907)	3, 4, 5, 6, 11, 12, 13, 14, 15, 16, 17, 21, 22, 35, 37, 38
	Plationus patulus (Müller, 1786)	11, 12, 13, 17, 21, 25, 26, 30, 32, 38, 39, 40, 42, 43
	Platyias leloupi (Gillard, 1957)	12, 17, 19, 27, 29, 30, 31, 32, 42, 43
	Platyias quadricornis (Ehrenberg, 1832)	17, 28, 29, 30, 43
Family Dicranophoridae	*Dicranophoroides caudatus* (Ehrenberg, 1834)	10
Family Epiphanidae	*Epiphanes clavulata* (Ehrenberg, 1832)	1, 11, 12, 15, 30, 43
	Epiphanes macroura (Barrois & Daday, 1894)	35
Family Euchlanidae	*Beauchampiella eudactylota* (Gosse, 1886)	30
	Euchlanis dilatata Ehrenberg, 1832	11, 12, 19, 25, 27, 32, 37, 41
Family Gastropodidae	*Ascomorpha agilis* Zacharias, 1893	39
	Ascomorpha ovalis (Bergendal, 1892)	34
	Ascomorpha saltans Bartsch, 1870	5, 9, 11, 15, 17

	Gastropus hyptopus (Ehrenberg, 1838)	30, 39
	Gastropus stylifer (Imhof, 1891)	17
Family Lecanidae	*Lecane amazonica* (Murray, 1913)	32
	Lecane bulla (Gosse, 1851)	12, 19, 21, 15, 30, 43
	Lecane cornuta (Müller, 1786)	43
	Lecane curvicornis (Murray, 1913)	11, 12, 17, 18, 19, 30, 32, 33, 39, 41, 42, 43
	Lecane elsa Hauer, 1931	40, 41
	Lecane haliclysta Harring & Myers, 1926	21
	Lecane hormemanni (Ehrenberg, 1834)	7, 8, 15, 25, 34
	Lecane leontina (Turner, 1892)	30, 39
	Lecane ludwigii (Eckstein, 1883)	33
	Lecane luna (Müller, 1776)	7, 19, 29, 21, 24, 32, 35
	Lecane lunaris (Ehrenberg, 1832)	20, 30, 39
	Lecane obtusa (Murray, 1913)	2, 15
	Lecane papuana (Murray, 1913)	7, 39, 42
	Lecane proiecta Hauer, 1956	5, 7, 8, 12, 19, 39
	Lecane quadridentata (Ehrenberg, 1830)	30
	Lecane rhytida Harring & Myers, 1926	17
	Lecane stenroosi (Meissner, 1908)	8
	Lecane subtilis Harring & Myers, 1926	18
	Lecane thienemanne (Hauer, 1938)	21, 28
	Lecane ungulata (Gosse, 1887)	42
Family Lepadelidae	*Colurella adriatica* Ehrenberg, 1831	21
	Colurella obtusa (Gosse, 1886)	21
	Lepadella cristata (Rousselet, 1893)	38
Family Mytilinidae	*Lophocaris oxysternon* (Gosse, 1851)	5
	Mytilina mucronata (Müller, 1773)	5, 7, 14, 19, 29
	Mytilina ventralis (Ehrenberg, 1830)	7, 8, 9, 12, 15, 16, 22, 27, 32, 35, 39
Family Notommatidae	*Enteroplea lacustris* Ehrenberg, 1830	13
	Monommata maculata Harring & Myers, 1930	30
Family Scaridiidae	*Scaridium longicaudum* (Müller, 1786)	30
Family Synchaetidae	*Pleosoma lenticulare* Herrick, 1885	21, 22, 24, 30
	Pleosoma truncatum (Levander, 1894)	5, 9, 15, 20, 21, 22, 23, 24, 34,39
	Polyarthra dolichoptera Idelson, 1925	5, 7, 8, 10, 11, 12, 13, 15, 16, 18, 21, 22
	Polyarthra remata Skorikov, 1896	2, 9, 15, 21, 22, 25, 29, 35
	Polyarthra vulgaris Carlin, 1943	10
	Synchaeta oblonga Ehrenberg, 1832	7, 9, 17, 18, 39
	Synchaeta pectinata Ehrenberg, 1832	5, 6, 7, 12, 15, 18, 30
	Synchaeta stylata Wierzejski, 1893	7, 26, 30, 34

Family Trichocercidae	*Trichocerca bicristata* (Gosse, 1887)	42
	Trichocerca capucina (Wierzejski & Zacharias, 1893)	1, 2, 6, 21, 8, 12, 15, 37, 39
	Trichocerca chattoni (de Beauchamp, 1907)	9, 21, 22, 23, 24, 34, 39
	*Trichocerca cylindrica (*Imhof, 1891)	5, 8, 12, 15
	Trichocerca elongata (Gosse, 1886)	30, 33
	Trichocerca gracilis (Tessin, 1890)	6, 12
	Trichocerca heterodactyla (Tschugunoff, 1921)	39
	Trichocerca longiseta (Schrank, 1802)	22
Family Trichotriidae	*Trichotria tetractis* (Ehrenberg, 1830)	20, 42

Capítulo 3

Table S1: PERMANOVA results showing the pairwise comparisons between basins for B-Total using incidence data.

Basin	Df	SS	MS	F	R^2	*p*
Paranaíba x Grande	1	0.638	0.638	3.170	0.209	**0.017**
Paranaíba x Tietê	1	0.638	0.638	3.170	0.209	**0.015**
Paranaíba x Paranapanema	1	0.875	0.875	3.370	0.219	**0.007**
Paranaína x Iguaçu	1	1.442	1.442	7.760	0.392	**0.001**
Paranaíba x Paraná	1	1.039	1.039	3.190	0.124	**0.004**
Paranaíba x Prata	1	1.243	1.243	5.080	0.297	**0.002**
Paranaíba x Uruguai	1	1.259	1.259	5.170	0.223	**0.001**
Paranaína x Paraguai	1	1.822	1.822	10.580	0.514	**0.004**
Grande x Tietê	1	0.304	0.304	1.420	0.092	0.187
Grande x Paranapanema	1	0.473	0.473	1.670	0.106	0.123
Grande x Iguaçu	1	0.900	0.900	4.090	0.226	**0.001**
Grande x Paraná	1	0.945	0.945	2.780	0.103	**0.012**
Grande x Prata	1	1.177	1.177	4.350	0.237	**0.001**
Grande x Uruguai	1	0.778	0.778	2.970	0.129	**0.001**
Grande x Paraguai	1	1.226	1.226	5.720	0.323	**0.001**
Tietê x Paranapanema	1	0.732	0.732	2.780	0.165	**0.011**
Tietê x Iguaçu	1	0.986	0.986	4.920	0.260	**0.001**
Tietê x Paraná	1	1.320	1.320	4.020	0.143	**0.001**
Tietê x Prata	1	1.574	1.574	6.270	0.309	**0.001**
Tietê x Uruguai	1	0.644	0.644	2.600	0.115	**0.002**
Tietê x Paraguai	1	1.360	1.360	7.100	0.371	**0.001**
Paranapanema x Iguaçu	1	0.352	0.352	1.300	0.085	0.229
Paranapanema x Paraná	1	0.315	0.315	0.850	0.034	0.567
Paranapanema x Prata	1	0.795	0.795	2.480	0.150	**0.008**
Paranapanema x Uruguai	1	0.546	0.546	1.840	0.084	**0.039**
Paranapanema x Paraguai	1	0.872	0.872	3.200	0.210	**0.003**
Iguaçu x Paraná	1	0.783	0.783	2.350	0.089	**0.022**
Iguaçu x Prata	1	0.901	0.901	3.500	0.200	**0.002**
Iguaçu x Uruguai	1	0.662	0.662	2.620	0.116	**0.005**
Iguaçu x Paraguai	1	1.125	1.125	5.650	0.320	**0.001**
Paraná x Prata	1	0.440	0.440	1.210	0.048	0.264
Paraná x Uruguai	1	1.122	1.122	3.320	0.099	**0.002**
Paraná x Paraguai	1	0.747	0.747	2.200	0.091	**0.026**
Prata x Uruguai	1	1.407	1.407	4.890	0.196	**0.001**
Prata x Paraguai	1	0.584	0.584	2.260	0.158	**0.023**
Uruguai x Paraguai	1	1.373	1.373	5.440	0.232	**0.002**

Table S2: PERMANOVA results showing the pairwise comparisons between basins for B-Repl using incidence data.

Basin	**Df**	**SS**	**MS**	**F**	**R^2**	***p***
Paranaíba x Grande	1	0.256	0.256	2.060	0.000	0.999
Paranaíba x Tietê	1	0.256	0.256	2.060	0.000	0.998
Paranaíba x Paranapanema	1	0.511	0.511	4.250	0.261	**0.015**
Paranaína x Iguaçu	1	0.548	0.548	7.190	0.374	**0.004**
Paranaíba x Paraná	1	0.538	0.538	4.040	0.155	**0.015**
Paranaíba x Prata	1	0.667	0.667	6.390	0.347	**0.004**
Paranaíba x Uruguai	1	0.322	0.322	2.910	0.139	**0.042**
Paranaína x Paraguai	1	0.197	0.197	2.290	0.186	0.097
Grande x Tietê	1	0.091	0.091	0.910	0.061	0.527
Grande x Paranapanema	1	0.162	0.162	1.030	0.068	0.467
Grande x Iguaçu	1	0.549	0.549	4.600	0.247	**0.001**
Grande x Paraná	1	0.105	0.105	0.680	0.027	0.668
Grande x Prata	1	0.728	0.728	5.080	0.266	**0.007**
Grande x Uruguai	1	0.481	0.481	3.500	0.149	**0.010**
Grande x Paraguai	1	0.827	0.827	6.150	0.339	**0.002**
Tietê x Paranapanema	1	0.364	0.364	3.740	0.211	**0.019**
Tietê x Iguaçu	1	0.587	0.587	9.850	0.413	**0.001**
Tietê x Paraná	1	0.551	0.551	4.650	0.162	**0.008**
Tietê x Prata	1	0.882	0.882	10.540	0.429	**0.003**
Tietê x Uruguai	1	0.429	0.429	4.490	0.183	**0.002**
Tietê x Paraguai	1	0.878	0.878	13.540	0.530	**0.002**
Paranapanema x Iguaçu	1	0.221	0.221	1.920	0.120	0.130
Paranapanema x Paraná	1	0.142	0.142	0.930	0.037	0.570
Paranapanema x Prata	1	0.616	0.616	4.410	0.239	**0.009**
Paranapanema x Uruguai	1	0.364	0.364	2.700	0.119	**0.032**
Paranapanema x Paraguai	1	0.390	0.390	3.000	0.200	**0.036**
Iguaçu x Paraná	1	0.364	0.364	2.810	0.105	0.066
Iguaçu x Prata	1	0.569	0.569	5.580	0.285	**0.006**
Iguaçu x Uruguai	1	0.475	0.475	4.380	0.179	**0.003**
Iguaçu x Paraguai	1	0.588	0.588	6.820	0.362	**0.004**
Paraná x Prata	1	0.295	0.295	2.060	0.079	0.152
Paraná x Uruguai	1	0.345	0.345	2.470	0.076	0.068
Paraná x Paraguai	1	0.045	0.045	0.330	0.000	0.886
Prata x Uruguai	1	0.906	0.906	7.230	0.265	**0.001**
Prata x Paraguai	1	0.024	0.024	0.210	0.017	0.807
Uruguai x Paraguai	1	0.849	0.849	7.230	0.286	**0.001**

Table S3: PERMANOVA results showing the pairwise comparisons between basins for B-Rich using incidence data.

Basin	**Df**	**SS**	**MS**	**F**	**R^2**	***p***
Paranaíba x Grande	1	0.508	0.508	27.310	0.694	**0.001**
Paranaíba x Tietê	1	0.508	0.508	27.310	0.694	**0.002**
Paranaíba x Paranapanema	1	0.194	0.194	4.560	0.275	**0.047**
Paranaína x Iguaçu	1	0.337	0.337	7.090	0.371	**0.011**
Paranaíba x Paraná	1	0.110	0.110	1.290	0.055	0.265
Paranaíba x Prata	1	0.112	0.112	2.290	0.160	0.168
Paranaíba x Uruguai	1	0.501	0.501	11.730	0.394	**0.005**
Paranaína x Paraguai	1	0.704	0.704	27.250	0.731	**0.001**
Grande x Tietê	1	0.042	0.042	0.965	0.064	0.350
Grande x Paranapanema	1	0.086	0.086	2.740	0.163	0.106
Grande x Iguaçu	1	0.025	0.025	0.690	0.047	0.468
Grande x Paraná	1	0.345	0.345	4.610	0.161	**0.020**
Grande x Prata	1	0.166	0.166	4.450	0.241	0.059
Grande x Uruguai	1	0.014	0.014	0.420	0.020	0.575
Grande x Paraguai	1	0.061	0.061	3.890	0.245	0.061
Tietê x Paranapanema	1	0.125	0.125	1.920	0.121	0.173
Tietê x Iguaçu	1	0.039	0.039	0.570	0.039	0.516
Tietê x Paraná	1	0.328	0.328	3.480	0.126	**0.041**
Tietê x Prata	1	0.201	0.201	2.840	0.169	0.108
Tietê x Uruguai	1	0.031	0.031	0.540	0.026	0.490
Tietê x Paraguai	1	0.030	0.030	0.560	0.044	0.522
Paranapanema x Iguaçu	1	0.026	0.026	0.460	0.032	0.563
Paranapanema x Paraná	1	0.077	0.077	0.890	0.035	0.393
Paranapanema x Prata	1	0.013	0.013	0.240	0.016	0.699
Paranapanema x Uruguai	1	0.063	0.063	1.280	0.060	0.264
Paranapanema x Paraguai	1	0.227	0.227	5.710	0.322	**0.023**
Iguaçu x Paraná	1	0.170	0.170	1.900	0.073	0.146
Iguaçu x Prata	1	0.073	0.073	1.170	0.077	0.282
Iguaçu x Uruguai	1	0.005	0.005	0.090	0.004	0.897
Iguaçu x Paraguai	1	0.107	0.107	2.390	0.166	0.119
Paraná x Prata	1	0.028	0.028	0.320	0.013	0.712
Paraná x Uruguai	1	0.331	0.331	4.240	0.123	**0.032**
Paraná x Paraguai	1	0.503	0.503	6.040	0.215	**0.017**
Prata x Uruguai	1	0.141	0.141	2.640	0.116	0.111
Prata x Paraguai	1	0.328	0..328	7.070	0.370	**0.010**
Uruguai x Paraguai	1	0.091	0.091	2.320	0.110	0.127

Table S4: PERMANOVA results showing the pairwise comparisons between basins for B-Total using abundance data.

Basin	Df	SS	MS	F	R^2	*p*
Paranaíba x Grande	1	0.714	0.714	2.560	0.176	0.060
Paranaíba x Tietê	1	0.714	0.714	2.560	0.176	0.060
Paranaíba x Paranapanema	1	1.043	1.043	3.090	0.205	**0.007**
Paranaína x Iguaçu	1	2.008	2.008	8.980	0.428	**0.003**
Paranaíba x Paraná	1	1.004	1.004	2.800	0.113	**0.020**
Paranaíba x Prata	1	1.404	1.404	5.310	0.306	**0.006**
Paranaíba x Uruguai	1	0.933	0.933	2.550	0.124	**0.006**
Paranaína x Paraguai	1	1.793	1.793	7.770	0.437	**0.003**
Grande x Tietê	1	0.583	0.582	1.550	0.099	0.110
Grande x Paranapanema	1	0.252	0.252	0.640	0.044	0.740
Grande x Iguaçu	1	0.679	0.679	2.320	0.142	0.080
Grande x Paraná	1	0.253	0.253	0.650	0.026	0.680
Grande x Prata	1	0.457	0.457	1.390	0.090	0.180
Grande x Uruguai	1	0.463	0.462	1.150	0.054	0.260
Grande x Paraguai	1	0.964	0.964	3.120	0.206	**0.020**
Tietê x Paranapanema	1	0.546	0.546	1.280	0.083	0.150
Tietê x Iguaçu	1	1.302	1.302	3.960	0.220	**0.001**
Tietê x Paraná	1	0.809	0.809	1.980	0.076	**0.040**
Tietê x Prata	1	0.937	0.937	2.570	0.155	**0.019**
Tietê x Uruguai	1	0.572	0.572	1.340	0.063	0.123
Tietê x Paraguai	1	0.982	0.982	2.790	0.188	**0.003**
Paranapanema x Iguaçu	1	0.529	0.529	1.540	0.099	0.080
Paranapanema x Paraná	1	0.227	0.227	0.540	0.022	0.880
Paranapanema x Prata	1	0.427	0.427	1.130	0.074	0.290
Paranapanema x Uruguai	1	0.391	0.391	0.900	0.043	0.560
Paranapanema x Paraguai	1	0.771	0.771	2.090	0.148	**0.008**
Iguaçu x Paraná	1	0.837	0.837	2.320	0.088	**0.030**
Iguaçu x Prata	1	0.340	0.340	1.210	0.079	0.270
Iguaçu x Uruguai	1	1.161	1.161	3.160	0.136	**0.002**
Iguaçu x Paraguai	1	0.797	0.797	3.130	0.207	**0.020**
Paraná x Prata	1	0.519	0.519	1.360	0.053	0.200
Paraná x Uruguai	1	0.477	0.477	1.140	0.036	0.250
Paraná x Paraguai	1	1.080	1.080	2.880	0.115	**0.008**
Prata x Uruguai	1	0.874	0.874	2.230	0.100	**0.020**
Prata x Paraguai	1	0.553	0.553	1.870	0.135	0.070
Uruguai x Paraguai	1	1.228	1.228	3.170	0.150	**0.001**

Table S5: PERMANOVA results showing the pairwise comparisons between basins for B-Repl using abundance data.

Basin	Df	SS	MS	F	R^2	*p*
Paranaíba x Grande	1	0.432	0.432	9.010	0.428	**0.040**
Paranaíba x Tietê	1	0.432	0.432	9.010	0.428	**0.030**
Paranaíba x Paranapanema	1	0.444	0.444	13.770	0.534	**0.006**
Paranaína x Iguaçu	1	1.053	1.053	32.820	0.732	**0.001**
Paranaíba x Paraná	1	0.522	0.522	8.890	0.287	**0.008**
Paranaíba x Prata	1	0.800	0.800	22.550	0.652	**0.005**
Paranaíba x Uruguai	1	0.404	0.404	10.620	0.371	**0.010**
Paranaína x Paraguai	1	0.596	0.596	79.490	0.888	**0.003**
Grande x Tietê	1	0.327	0.327	4.290	0.234	0.060
Grande x Paranapanema	1	0.017	0.017	0.250	0.018	0.740
Grande x Iguaçu	1	0.358	0.358	5.290	0.274	**0.021**
Grande x Paraná	1	0.029	0.029	0.380	0.015	0.640
Grande x Prata	1	0.347	0.347	4.910	0.260	0.060
Grande x Uruguai	1	0.100	0.100	1.610	0.074	0.350
Grande x Paraguai	1	0.451	0.451	8.490	0.414	**0.010**
Tietê x Paranapanema	1	0.267	0.267	4.260	0.233	0.070
Tietê x Iguaçu	1	0.561	0.561	8.950	0.390	**0.001**
Tietê x Paraná	1	0.270	0.270	3.630	0.131	0.100
Tietê x Prata	1	0.538	0.538	8.210	0.369	**0.005**
Tietê x Uruguai	1	0.249	0.249	4.240	0.175	0.070
Tietê x Paraguai	1	0.469	0.469	9.920	0.452	**0.002**
Paranapanema x Iguaçu	1	0.032	0.032	0.590	0.041	0.610
Paranapanema x Paraná	1	0.094	0.094	1.350	0.053	0.430
Paranapanema x Prata	1	0.120	0.120	2.100	0.130	0.380
Paranapanema x Uruguai	1	0.100	0.100	1.900	0.086	0.390
Paranapanema x Paraguai	1	0.257	0.257	6.850	0.363	**0.010**
Iguaçu x Paraná	1	0.304	0.304	4.380	0.154	**0.040**
Iguaçu x Prata	1	0.139	0.139	2.430	0.148	0.190
Iguaçu x Uruguai	1	0.339	0.339	6.410	0.242	**0.010**
Iguaçu x Paraguai	1	0.141	0.141	3.790	0.240	0.110
Paraná x Prata	1	0.191	0.191	2.690	0.101	0.170
Paraná x Uruguai	1	0.139	0.139	2.120	0.066	0.270
Paraná x Paraguai	1	0.297	0.297	4.830	0.180	0.060
Prata x Uruguai	1	0.336	0.336	6.110	0.234	**0.030**
Prata x Paraguai	1	0.138	0.138	3.410	0.221	0.060
Uruguai x Paraguai	1	0.391	0.391	9.410	0.343	**0.007**

Table S6: PERMANOVA results showing the pairwise comparisons between basins for B-AbDiff using abundance data.

Basin	**Df**	**SS**	**MS**	**F**	**R^2**	***p***
Paranaíba x Grande	1	0.057	0.057	0.360	0.029	0.730
Paranaíba x Tietê	1	0.057	0.057	0.360	0.029	0.750
Paranaíba x Paranapanema	1	0.166	0.166	0.650	0.051	0.630
Paranaína x Iguaçu	1	0.007	0.007	0.040	0.003	0.990
Paranaíba x Paraná	1	0.049	0.049	0.230	0.010	0.920
Paranaíba x Prata	1	0.030	0.030	0.170	0.014	0.790
Paranaíba x Uruguai	1	0.177	0.177	0.670	0.036	0.560
Paranaína x Paraguai	1	0.490	0.490	2.660	0.210	0.060
Grande x Tietê	1	0.135	0.135	0.730	0.049	0.570
Grande x Paranapanema	1	0.221	0.221	0.990	0.066	0.380
Grande x Iguaçu	1	0.061	0.061	0.420	0.029	0.720
Grande x Paraná	1	0.193	0.193	0.970	0.038	0.410
Grande x Prata	1	0.012	0.012	0.080	0.005	0.990
Grande x Uruguai	1	0.335	0.335	1.390	0.065	0.250
Grande x Paraguai	1	0.356	0.356	2.270	0.159	0.100
Tietê x Paranapanema	1	0.091	0.091	0.340	0.023	0.840
Tietê x Iguaçu	1	0.247	0.247	1.280	0.084	0.300
Tietê x Paraná	1	0.302	0.302	1.330	0.052	0.250
Tietê x Prata	1	0.118	0.118	0.580	0.040	0.650
Tietê x Uruguai	1	0.263	0.263	0.960	0.046	0.410
Tietê x Paraguai	1	0.107	0.107	0.500	0.040	0.700
Paranapanema x Iguaçu	1	0.227	0.227	0.980	0.066	0.390
Paranapanema x Paraná	1	0.130	0.130	0.520	0.021	0.700
Paranapanema x Prata	1	0.177	0.177	0.770	0.050	0.540
Paranapanema x Uruguai	1	0.083	0.083	0.270	0.013	0.890
Paranapanema x Paraguai	1	0.270	0.270	1.050	0.081	0.390
Iguaçu x Paraná	1	0.087	0.087	0.430	0.017	0.770
Iguaçu x Prata	1	0.043	0.043	0.270	0.018	0.720
Iguaçu x Uruguai	1	0.285	0.285	1.160	0.054	0.290
Iguaçu x Paraguai	1	0.575	0.575	3.470	0.224	**0.030**
Paraná x Prata	1	0.137	0.137	0.650	0.026	0.590
Paraná x Uruguai	1	0.154	0.154	0.600	0.019	0.630
Paraná x Paraguai	1	0.693	0.693	3.220	0.127	**0.010**
Prata x Uruguai	1	0.243	0.243	0.970	0.046	0.400
Prata x Paraguai	1	0.374	0.374	2.140	0.151	0.100
Uruguai x Paraguai	1	0.581	0.581	2.200	0.109	0.090