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Adjacent environments contribute to the increase of zooplankton species in a neotropical river

Ambientes adjacentes contribuem no incremento de espécies zooplanctônicas em um rio neotropical

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Abstract: Aim: The distribution of the zooplankton community along the Paraná River and in adjacent environments (tributaries and lakes) was evaluated, as well as the contribution of the community present in these environments to the species composition of the Paraná River. It was expected that the ensemble of species found in the last sampling site of the Paraná River would represent the accumulation of species found in the upstream sites. **Methods:** The community was sampled at 25 sites, during 2013 and 2014, and the species richness and composition were determined. The similarity in the composition of the community between the environments was evaluated using cluster analysis, and the contribution of the species to the Paraná River was evaluated using nestedness analysis, using the NODF index. **Results:** Overall, 193 species were registered (116 rotifers, 48 cladocerans and 29 copepods), with the majority of species considered as rare (163 species). In general, the composition of the community in the river was dissimilar to the adjacent environments, although there was a relationship among communities. Rotifers presented broad distribution throughout the area. As expected, the zooplanktonic species presented a nested distribution, with the last river site representing a set of the species registered in the upstream sites. **Conclusion:** The results show the importance of the tributaries and lakes to the occurrence of species along the river. The distinct hydrological characteristics of the environments, as well as flow velocity, depth and connectivity, were responsible for the development of planktonic populations in the lakes that arrived in the main river through tributaries. With these results, we suggest the importance of the conservation of adjacent environments of the Paraná River for the maintenance of the zooplanktonic species in this system.

Keywords: species nestedness; spatial distribution; species dispersal; floodplain.

Resumo: Objetivo: A distribuição da comunidade zooplanctônica foi avaliada ao longo do rio Paraná e em ambientes adjacentes (tributários e lagoas), bem como a contribuição da comunidade presente nesses ambientes, para a composição de espécies no rio Paraná. Espera-se que o conjunto de espécies encontrados no último ponto do rio Paraná represente o acúmulo de espécies observadas nos pontos a montante. **Métodos:** A comunidade foi amostrada em 25 pontos, em 2013 e 2014. Foram determinadas a riqueza e composição de espécies. A similaridade da composição da comunidade entre os ambientes foi avaliada através da análise de Cluster, e a contribuição das espécies para o rio Paraná, através de uma análise de aninhamento, utilizando o índice NODF. **Resultados:** Foram registradas 193 espécies (116 de rotíferos, 48 de cladóceros e 29 de copépodes), sendo a maioria considerada como rara (163 espécies). Em geral, a composição da comunidade do rio foi dissimilar aos ambientes adjacentes, embora haja uma relação entre as comunidades. Os rotíferos apresentaram uma ampla distribuição em toda área. Como esperado, as espécies zooplanctônicas apresentaram distribuição aninhada, sendo que no último ponto do rio foi observado um conjunto de espécies registradas nos pontos a montante deste. **Conclusão:** Nossos resultados demonstraram a importância dos tributários e lagoas para a ocorrência de espécies ao longo do rio. As distintas características hidrológicas dos ambientes, como velocidade de fluxo, profundidade e conectividade, foram responsáveis pelo desenvolvimento de populações planctônicas nas lagoas, que depois chegaram ao rio através dos tributários. Com isso, sugerimos a importância da conservação dos ambientes adjacentes ao rio Paraná para a manutenção de espécies zooplanctônicas nesse sistema.

Palavras-chave: aninhamento de espécies; distribuição espacial; dispersão de espécies; planície de inundação.

1. Introduction

In freshwater ecosystems, the hydrology, connectivity, geomorphological complexity and nutrient input can be very distinct among environments, increasing the environmental heterogeneity (Bozelli et al., 2015). These characteristics enable the high diversity of species found in these fluvial systems (Naiman et al., 2000; Simões et al., 2012).

Furthermore, there is higher primary productivity (Thomaz et al., 2004), generally in the environments located in the lowland (such as tributaries and lakes), which contributes to a higher availability of feeding resources and favors higher species diversity. Thus, it can be affirmed that there is a tendency for such adjacent environments to function as a propagule source for the communities present in the main river of the floodplain (Braghin et al., 2015; Bomfim et al., 2015).

However, the construction of dams represents habitat fragmentation of this fluvial system, and therefore changes the environmental conditions of the whole system, altering both abiotic and interactions between organisms, thus affecting species diversity (Agostinho et al., 2008; Simões et al., 2015; Winemiller et al., 2016).

Many of the studies on the impact of reservoirs in fluvial systems discuss the effects upstream of the dam, as flow reduction creates an artificial lake, interrupting the system's natural flow. However, the impacts downstream of the dam are as important as those upstream, due to the volume and quality of water released by the reservoir's operation (Agostinho et al., 2008). These impacts can be even more intense when a floodplain is located downstream of the reservoir, as this system presents unique characteristics, with high species diversity and aquatic communities adapted to the fluviometric dynamics (Agostinho et al., 1994; Ward & Tockner, 2001).

Nevertheless, it is known that, as the river proceeds downstream of the reservoirs, it tends to regain its natural characteristics. This occurs mainly due to the contribution of the environments connected to it, such as lakes and tributaries, which have differing water masses that present distinct physical, chemical and biological characteristics (Ward & Stanford, 1995).

An important tool that has been used in the conservation and maintenance of systems is the concept of species nestedness (Baber et al., 2004). This concept is based on the non-random distribution of organisms (Worthen, 1996). The central idea is that a relatively poor biological assemblage is composed of a subset of the species that occur in a richer environment (Patterson & Atmar, 1986). A system is considered perfectly nested when any species found in a site is found in all sites with equal or higher richness, and any species absent in a particular site is absent from all sites with lower richness (Moore & Swihart, 2007). This means the difference in the species richness between sites is what determines the distribution pattern of the community.

The zooplankton community is among the most diverse in aquatic ecosystems and is composed by rotifers, cladocerans and copepods (Lansac-Tôha et al., 2009). These organisms have the capacity to colonize distinct environments according to their development strategies. Such strategies are related to feeding and reproductive habits (Allan, 1976) that characterize their ecologic niches both in central and littoral regions of the aquatic environments (Monakov, 2006; Colares et al., 2013). Zooplankton is also considered as an important link in the aquatic food chain, participating in various trophic relations (Auer et al., 2004).

However, the establishment of zooplankton organisms in the aquatic environment is driven firstly by their high dispersal capacity (passive and/or active) and then by environmental filters (Padial et al., 2014; Dias et al., 2016). This does not limit zooplankton distribution, as they quickly adapt to varied environmental conditions (Almer et al., 1974; Havens, 1991), and respond to oscillations through high renovation rates (Pontin & Langley, 1993), altering the number of organisms and/or species composition in the community (Bonecker et al., 2009; Lansac-Tôha et al., 2009). This idea complements the nestedness concept, because the heterogeneity and structure of the habitat influence the distribution and establishment of species and assemblage formation. Thereby, environments that are more complex support higher species richness than simpler environments (Hutchinson, 1959; Simões et al., 2012).

Considering the ability of these organisms to respond to variations in local factors, together with the different hydrological characteristics of the environments present in these aquatic systems, and the importance of lakes and tributaries in the increase of species for the system, we aimed to investigate the spatial distribution of the zooplankton community (rotifers, cladocerans and copepods), and whether adjacent environments contribute to the composition of species in the Paraná River, and if this increase is cumulative along this stretch of river.

Therefore, we hypothesized that the composition of species in the Paraná River, after the dam of Porto Primavera, is similar to those recorded in the lakes and tributaries, and that this contribution makes the communities further away from the dam a set of the species constituted by the subsets found in upstream sites.

2. Material and Methods

2.1. Study area

This study was carried out in the high Paraná River floodplain (Paraná River, Baia River and Ivinhema) and adjacent sub-basins (Ivaí, Piquiri, Amambaí and Iguatemi Rivers). This stretch encompasses an area of 230 km^2 free from damming and located between the Porto Primavera dam (São Paulo, Brasil) (22° 37´S, 53° 6´W) and the backwater of the Itaipu reservoir (Paraná, Brasil) (23° 55´S, 54° 8´W) (Figure 1). In this stretch, three conservation units are included (Área de Proteção Ambiental das Ilhas e Várzeas do Rio Paraná, Parque Estadual das Várzeas do Rio Ivinhema, and Parque Nacional de Ilha Grande).

The high Paraná River floodplain has an important social and economic role for local human communities, enabling tourism and fishery activities (Gubiani et al., 2007). Furthermore, the floodplain presents high biodiversity, including a high zooplankton diversity of rotifers, cladocerans and copepods (Lansac-Tôha et al., 2009).

2.2. Field sampling and laboratory analysis

A total of 25 sampling points were established, including 10 points in the Paraná River (P1 to P10), eight in tributaries (Paranapanema, Baia, Ivinhema, Ivinheminha, Ivaí, Amambaí, Iguatemi and Piquiri Rivers, T1 to T8), and seven in the lakes located at these river margins (Garças, Xirica, Ivaí, São João, Xambrê, Pavão and Saraiva Lakes, L1 to L7) (Table 1 and Figure 1). This study was carried out in August and November 2013 and February, May and August 2014, encompassing different phases of the region's hydrological cycle.

Zooplankton was sampled at the sub-surface of the pelagic region in each environment, with a motorized pump and plankton net (68 μm), filtering 600 liters of water per sample. The samples were conditioned in polyethylene flasks and preserved in 4% formaldehyde solution buffered with calcium carbonate.

Species identification was carried out according to specialized literature described in Lansac-Tôha et al. (2009), and zooplankton richness was analyzed in each sample until the curve of species-increase stabilized.

2.3. Data analysis

The frequency of species was determined considering the number of samples in which they occurred in relation to the total number of samples. This was calculated with the following formula: $C = p.100/P$, where C is the constancy index, p is the number of samples where the species occurred, and P is the total number of samples. Also, species were classified as constant (present in > 80% of samples), frequent (50-80%), common (20-50%) and rare (< 20%) (Castilho et al., 2016).

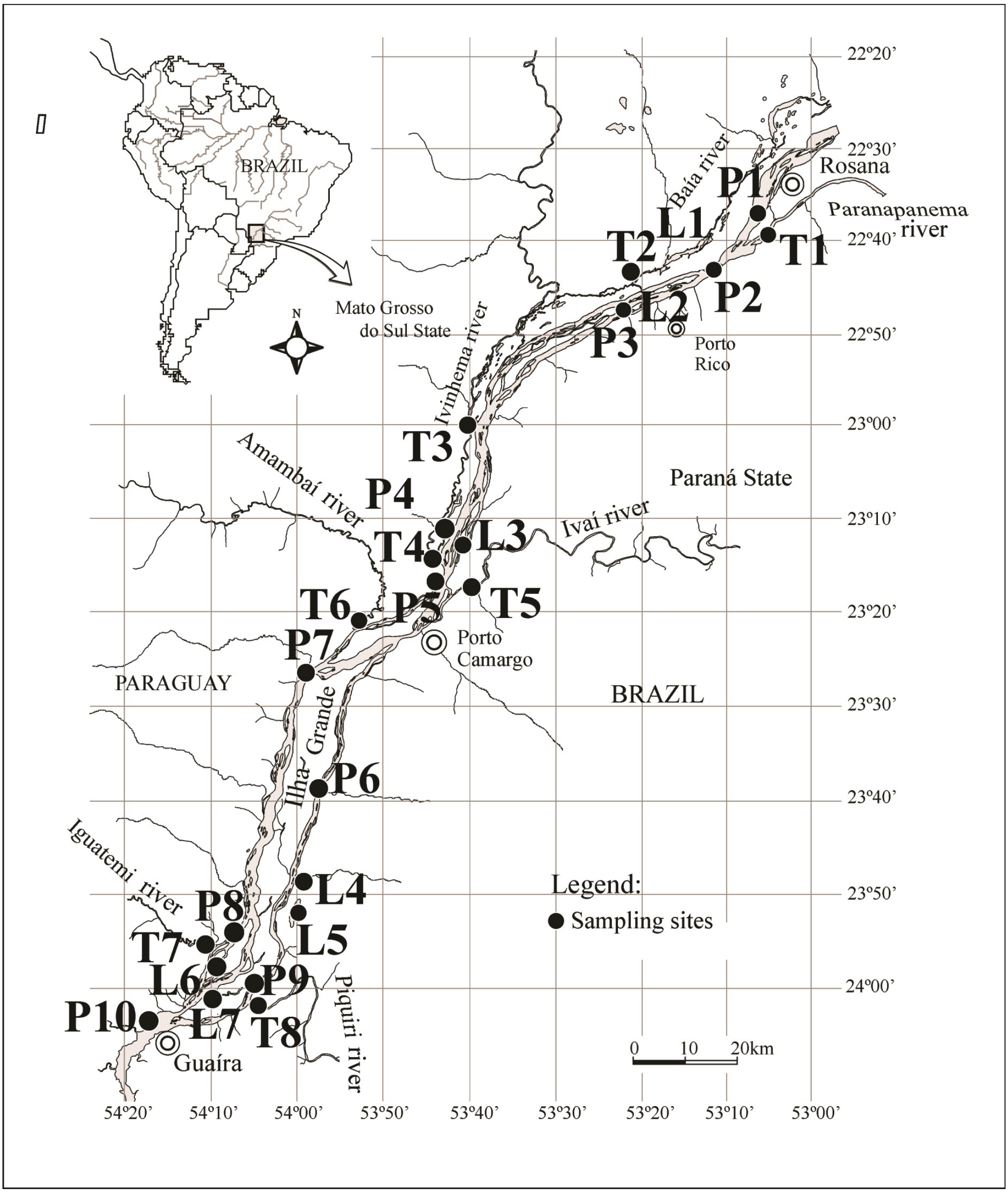

Figure 1. Study area between the Porto Primavera dam in Rosana city – SP and the beginning of the Itaipu dam, in Guaíra city – PR. P = sampling sites in the Paraná River; T = tributaries and L = lakes.

Nestedness was analyzed using the NODF index (nestedness metric based on overlap and decreasing fill), proposed by Almeida-Neto et al. (2008) and Ulrich et al. (2009). It was assumed that samples in the Paraná River would have an accumulation of species in the P1 to P10 direction, and that a set of the species found in the previous sites would be found in P10 (with higher species richness), as a result of the contribution of the species of the main river and adjacent tributaries and lakes. Thus, the results for NODF rows were analyzed.

This index calculates null models (randomly expected communities) and compares them with observed values for the real communities, providing a statistic confidence interval (*p*) to the results. An occurrence matrix was constructed for each zooplankton group (rotifers, cladocerans and copepods), where rows represented sampled sites and columns represented species. When a species was present in the site, we attributed the value 1, and when it was absent, we attributed the value 0. We ordinated the matrix decreasingly in relation to the sampled sites in the columns (P10 to P1).

To analyze the similarity in species composition between the environmental groups (Paraná River, lakes and tributaries), a cluster analysis was carried out using the Ward algorithm. Cluster analysis separated the environments according to the

Table 1. Characterization of sampling sites of the high Paraná River floodplain and, nearby subsystems*.

Environments	Environmental characterization
Paraná River (P1 to P10)	(22º 62´S, 53º 15´W; 24º 10´S, 54º 31´W): Non-dammed stretch extending for 230 km, from Porto Primavera dam to the backwater of Itaipu reservoir.
Garças Lake (L1)	(22º 79´S, 53º 24´W): Located in the Paraná River, with a length of 2.1 km, mean depth of 2.0 m, area of 150 m^2 and perimeter of 5 km.
Xirica Lake (L2)	(22º 47´S, 53º 21´W): Communicates with the Paraná River through a canal of approximately 200 m. Has an area of 10 m^2, perimeter of 1.31 km and mean depth of 1.12 m.
Ivai Lake (L3)	(23º 41´S, 53º 75´W): Has permanent communication with the Paraná River. Has an area of 100 m^2, perimeter of 2 km and mean depth of 2 m.
São João Lake (L4)	(23º 84´S, 53º 07´W): Communicates with the Paraná River through a canal of approximately 1.3 km. Presents an area of 2.21 km^2, perimeter of 6 km and mean depth of 1.70 m.
Xambrê Lake (L5)	(23º 51´S, 45º 1´W): Without communication with the Paraná River. Has an area of 4.78 km^2, perimeter of 12.3 km and mean depth of 3.6 m.
Pavão Lake (L6)	(24º 06´S, 54º 29´W): Communicates with the Paraná River through a canal of 150 m. Has an area of 4.5 km^2, perimeter of 770 m and mean depth of 2.7 m.
Saraiva Lake (L7)	(24º 12´S, 54º 19´W). Communicates with the Paraná River through a canal of approximately 1.5 km. Has an area of 1.14 km^2, perimeter of 19.5 km and depth of 1.6 m.
Paranapanema River (T1)	(22º 39´S, 53º 4´W): Tributary from the left margin of the Paraná River, has its headsprings in eastern São Paulo state. Has a total extension of 929 km and drained area of 100.800 km^2.
Baia River (T2)	(22º 46´S, 53º 19´W): Tributary from the right margin of the Paraná River, has varied width and mean depth of 3.2 m, with narrower stretches when margins are higher.
Ivinhema River (T3)/ Ivinheminha River (T4)	(22º 59´S, 53º 39´W/ 23º 14´S 53º 43´W): Tributary of the right margin of the Paraná River, has a length/width ratio of 22:1, flow velocity of approximately 0.85 $m\ s^{-1}$ and mean depth of 3.9 m.
Ivai River (T5)	(23º 17´S, 53º 40´W): Tributary of the left margin of the Paraná River, has its headwaters in Serra da Esperança, southeast Paraná state. Extends for approximately 685 km and has a drainage basin of more than 35,000 km^2.
Amambai River (T6)	(23º 21´S, 53º 53´W): Tributary of the right margin of the Paraná River, has its headwaters in Serra do Maracaju, Mato Grosso do Sul state. Has a hydrographic basin with total area of 10.206 km^2 and an extension of 354 km, flowing into the Paraná River at an altitude of 240 m.
Iguatemi River (T7)	(24º 01´S, 54º 9´W): Tributary of the right margin of the Paraná River, has its headwaters in the extreme South of Mato Grosso do Sul state. Extends for around 300 km. Has its headwater at an altitude of approximately 520 m and flows into the Paraná River at an altitude of 226 m.
Piquiri River (T8)	(23º 55´S, 54º 9´W): Tributary of the left margin of the Paraná River, has its headwaters in Serra do São João, in the border between the municipalities of Turvo and Guarapuava, Paraná state.

*Information extracted for the report *"Alto rio Paraná: gradiente longitudinal de variáveis ambientais e comunidades aquáticas no último trecho livre de barramentos entre UHE de Porto Primavera e reservatório de Itaipu/ PIE/PELD-CNPq"*, in which this study is inserted (Velho, 2016).

presence and absence of the species in a way that sites with a higher number of common species were grouped in the same block (Mingoti, 2005).

Both analyses were performed using software R 3.0 (R Development Core Team, 2014), with the *vegan* package (Oksanen et al., 2010).

3. Results

3.1. Characterization of the zooplankton community

The zooplankton community was represented by 193 taxa in the sampled sites: these were 116 rotifers, 48 cladocerans and 29 copepods. Species were distributed in 27 families, from which Lecanidae and Brachionidae were the most representative for rotifers (21 and 22 species, respectively); Chydoridae for cladocerans (27 species) followed by Daphniidae (6 species); and Cyclopidae were representative for copepods (19 species) (Table 2).

The frequency of occurrence of species showed the absence of constant species in the community. Copepods presented a higher number of frequent species (four), *Notodiaptomus henseni* (75%), *Notodiaptomus cearenses* (69.14%), *Thermocyclops decipiens* (59.57%) and *Thermocyclops minutus* (59.57%), plus three common and 22 rare species. For cladocerans, we registered the occurrence of three frequent species, *Bosmina hagmanni* (72.34%), *Daphnia gessneri* (72.34%) and *Bosminopsis deitersi* (53.19%), seven common, and 38 rare species. Finally, rotifers were represented by only two frequent species (50-80%), *Lecane bulla* (59.46%) and *Keratella cochlearis* (50.52%), 11 common species and 103 rare species (Table 2).

Species richness varied little among different environments, but was higher in lakes and tributaries. In lakes, the mean richness was 26 species, and the standard deviation was between 17 and 34 species (higher variation). In tributaries, the mean was 20 species, and the standard deviation was between 12 and 28 species. In the Paraná River, the mean was 19 species, and the standard deviation was between 13 and 25 species (Figure 2).

3.2. Clustering and nestedness

Cluster analysis indicated a separation of the sampling sites in the river, tributaries and lakes in two main groups A and B, according to species occurrences (Figure 3). For cladocerans and copepods, results were more evident, as group A was formed in its majority by sampling sites in the river (P1 to P10), and group B by sites in tributaries (T1 to T8) and lakes (L1 to L7). Although rotifer composition was also separated into two groups, we observed a lower dissimilarity than cladocerans and copepods, between sampling sites in the river, tributaries and lakes.

Nestedness analysis indicated that rotifers, cladocerans and copepods followed a nested distribution in this longitudinal stretch of the Paraná River. In P10, we observed a set of species composed of previous subsets (Figure 4), as was shown by significant values of the NODF row indexes of 65.65, 69.99, and 73.46, respectively, for each group (Table 3).

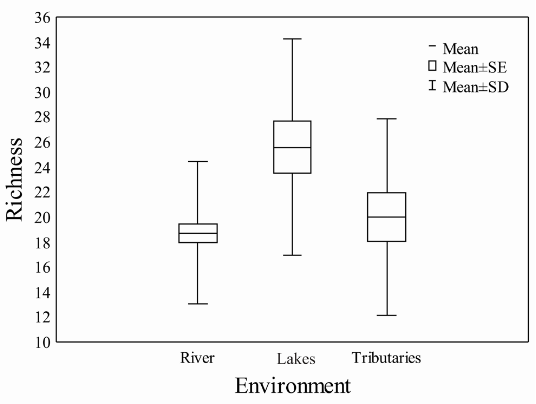

Figure 2. Zooplankton richness (mean and standard deviation) registered in the environments (river (Paraná), lakes and tributaries).

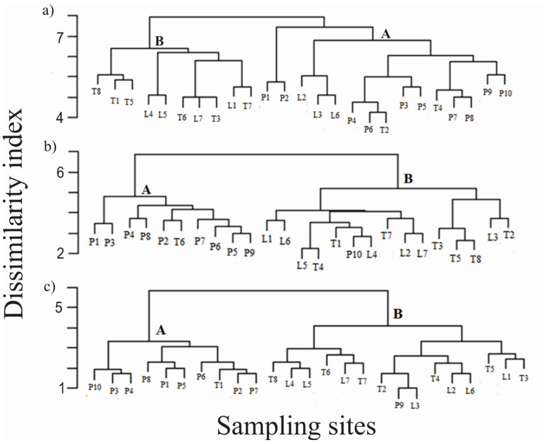

Figure 3. Cluster analysis dendrogram showing the similarity between zooplankton sampled environments, for (a) rotifers, (b) cladocerans and (c) copepods.

4. Discussion

The families that most contributed to the composition of the community (Lecanidae and Brachionidae for rotifers, Chydoridae for cladocerans, and Cyclopidae for copepods), are commonly registered in floodable areas in the neotropical region (Paggi & José de Paggi, 1990; Lansac-Tôha et al., 2009; Bozelli et al., 2015). The higher contribution of rotifer species to the zooplankton composition, including rare species, is due to these organisms being opportunistic, with short life cycles, and consuming a great variety of food items, from bacteria to other rotifers (Auer et al., 2004; Kalinowska et al., 2015). This varied diet favors the simultaneous presence of many species in the same environment, or of the same species in different environments (Neves et al., 2003), increasing their representativeness in sites with distinct characteristics (Branco et al., 2002; Lansac-Tôha et al., 2005).

The variation in species richness between the river, tributaries and lakes may be related to morphological heterogeneity and highly productive microhabitats (Thomaz et al., 2007), enabling variations in the zooplankton community. Thus, the variation in flow velocity may be important in structuring the community. The lowest flow, commonly found in lakes, favors the establishment and development of planktonic populations (Aoyagui & Bonecker, 2004). In general, there is also a higher phytoplankton biomass registered in these environments (Roberto et al., 2009), which

Table 2. Inventory of the species in the studied environments of the high Paraná River floodplain and adjacent sub-systems.

ROTIFERA	P	L	T		P	L	T
Lecanidae							
Lecane aculeata (Jakubski, 1912)+			X	*L. ungulata* (Gosse, 1887)+	X		X
L. bulla (Gosse, 1851)+++	X	X	X	*L. stenroosi* (Meissner, 1908)+	X		X
L. closterocerca (Schmarda, 1859)+	X		X	*L. signifera* (Jennings, 1896)+	X		
L. cornuta (Muller, 1786)+	X	X	X	*L. quadridentata* (Ehrenberg, 1832)+	X		X
L. curvicornis (Murray, 1913)++	X	X	X	*L. proeicta* (Hauer, 1956)+	X	X	X
L. elsa Hauer, 1931+	X	X	X	*L. papuana* (Murray, 1913)+	X	X	X
L. halyclista Harring & Myers, 1926+		X		*L. papuana* (Murray, 1913)+	X		
L. hastata (Murray, 1913)+	X			*L. mira* (Murray, 1913)+		X	X
L. hornemanni (Ehrenberg, 1834)+	X			*L. lunaris* (Ehrenberg, 1832)++	X	X	X
L. leontina (Turner, 1892)+	X	X	X	*L. lunaris* (Ehrenberg, 1832)++	X	X	X
L. ludwigii (Eckstein, 1883)+	X	X	X				
Brachionidae							
Brachionus angularis Gosse, 1851+	X	X	X	*Platyias leloupi* Gillard, 1967+	X	X	X
B. budapestinensis Daday, 1885+	X	X	X	*Plationus macrachantus* (Daday, 1905)+	X	X	X
*B. calyciflorus*Pallas, 1766++	X	X	X	*P. quadricornis* (Ehrenberg, 1832)+	X	X	X
B. calyciflorus spinosus Rousselet, 1901+		X		*P. patulus patulus*(Müller,1786)+	X	X	X
B caudatus Barrois & Daday, 1894+	X	X	X	*Keratella americana* Carlin, 1943++	X	X	X
B. c. personatus Ahlstrom, 1940+	X	X	X	*K. cochlearis* (Gosse, 1851)+++	X	X	X
B. dolabratus Harring, 1915+	X	X	X	*K. c. macracantha* (Lauterborn, 1900)+		X	
B. falcatus Zacharias, 1898+	X	X	X	*K. lenzi* Hauer, 1953++	X	X	X
B. forficula Wierzejski, 1891+	X	X		*K. tropica* (Apstein, 1907)++	X	X	X
B. mirus Daday, 1905+	X	X	X	*Kellicottia bostoniensis* (Rousselet, 1908)++	X	X	X
B. quadridentatus Hermann, 1783+	X	X	X				
B. urceolaris O. F. Müller, 1773+	X		X				
Trichocercidae							
Trichocerca agnatha Wulfert, 1939+		X		*T. stylata* (Gosse, 1851)+	X	X	
T. bicristata (Gosse, 1887)+	X	X	X	*T. similis* (Wierzejski, 1893)+			X
T. bidens (Lucks, 1912)+	X		X	*T. pusilla* (Jennings, 1903)+	X		X
T. capucina (Wierzejski & Zacharias, 1893)+			X	*T. porcellus* (Gosse, 1851)+			X
T. cylindrica (Imhof, 1891)+	X	X	X	*T. myersi* (Hauer, 1931)+	X		X
T. elongata (Gosse, 1886)+	X		X	*T. longiseta* (Schrank, 1802)+	X	X	X
T. gracillis (Tessin, 1890)+	X	X	X	*T. heterodactyla* (Tschugunoff, 1921)+		X	
Euchlanidae							
Dipleuchanis propatula (Gosse, 1886)+	X	X	X	*E. meneta* Myers, 1930+		X	
Euchlanis deflexa (Gosse, 1851)+			X	*E. i. mucronata* Ahlstrom, 1934+	X		X
E. dilatata Ehrenberg, 1832++	X	X	X	*E. incisa* Carlin, 1939+	X		X
Mytilinidae							
Mytilina acanthophora Hauer, 1939+	X			*M. ventralis* (Ehrenberg, 1830)+	X		
M. macrocerca (Jennings, 1894)+	X			*M. m.spinigera* (Ehrenberg, 1830)+	X		
M. mucronata (Muller 1773)+	X		X				
Testudinellidae							
Testudinella ahlstromi Hauer 1956+	X		X	*T. truncata* Gosse, 1886+			X
T. ohlei Koste, 1972+	X	X	X	*T. patina* (Hermann, 1783)+	X	X	X
T. mucronata (Gosse,1886)+	X						
Filinidae							
Filinia longiseta(Ehrenberg, 1834)+	X	X	X	*F. terminalis*(Plate, 1886)++	X	X	X
F. opoliensis(Zacharias, 1898)+	X	X	X				
Synchaetidae							
Ploesoma triacanthum(Bergendal, 1892)+	X			*Synchaeta oblonga* Ehrenberg, 1832++	X	X	X
P. truncatum (Levander, 1894)+	X	X	X	*S. pectinata* Ehrenberg 1832+	X	X	X
Polyarthra dolichoptera Idelson, 1925+	X	X	X	*S. stylata* Wierzejski,1893+	X	X	
P. vulgaris Carlin, 1943+	X	X	X				

The indication of each species' occurrence frequency considers +++ as frequent (50-80%), ++ as common (20-50%), and + as rare (< 20%). P= Parana river, L= lakes, T= tributaries.

Table 2. Continued...

ROTIFERA	P	L	T		P	L	T
Notommatidae							
Cephalodella forficula Ehrenberg, 1830+	X		X	*Monommata dentata* Wulfert, 1940+			X
C. mucronata Myers, 1924+	X			*Notommata copeus* Ehrenberg, 1834+	X		
C. obvia Donner, 1950+			X	*N. pachyura* (Gosse, 1886)+	X		
Lepadellidae							
Lepadella. oblonga (Ehrenberg, 1834)+	X		X	*L. patella oblonga* (Ehrenberg, 1834)+	X	X	X
L. ovalis (Müller, 1786)+	X		X	*L. triptera* (Ehrenberg, 1832)+	X		
L. patella (Muller, 1773)+	X						
Conochilidae							
Conochilus coenobasis (Skorikov, 1914)+	X	X	X	*C. natans* (Seligo, 1900)+	X	X	X
C. dossuaris (Hudson, 1885)+	X	X		*C. unicornis* Rousselet, 1892+	X	X	X
Gastropodidae							
Ascomorpha cf. agilis Zacharias, 1893+	X		X	*Gastropus hyptopus* (Ehrenberg, 1838)+		X	X
A. ecaudis Perty, 1850+		X	X	*G. stilifer* Imhof, 1891+	X	X	
A. ovalis Carlin, 1943+	X	X	X				
Dicranophoridae							
Aspelta angusta Harring & Myers, 1928+			X	*Dicranophorus forcipatus* (Müller, 1786)+			X
Dicranophoroides caudatus (Ehrenberg, 1834)+	X	X	X	*Dicranophorus epicharis* Harring & Myers, 1928+	X		
Trichotriidae							
Trichotria tetractis(Ehrenberg, 1830)+	X	X	X				
Hexarthridae							
Hexarthra intermedia intermedia (Wiszniewski, 1929)+			X	*Hexarthra mira* (Hudson, 1871)+		X	
Asplanchnidae							
Asplanchna priodonta Gosse, 1850+	X		X	*A. sieboldi* (Leydig, 1854)+	X	X	X
Epiphanidae							
Epiphanes clavulata (Ehrenberg, 1832)+	X	X	X	*E. senta* (Müller, 1773)+			X
E. macroura (Barrois & Daday, 1894)+	X		X				
Ituridae							
Itura myersi Wulfert, 1935+			X				
CLADOCERA							
Moinidae							
Moina micrura Kurz, 1874+		X	X	*M. reticulata* (Daday, 1905)+	X	X	
M. minuta Hansen, 1899++	X	X	X				
Bosminidae							
Bosmina hagmanni Stingelin, 1904+++	X	X	X	*Bosmina tubicen* Brehm, 1953+	X	X	X
Bosmina longirostris (De Melo; Herbert, 1994)+	X	X	X	*Bosminopsis deitersi* Richard, 1895+++	X	X	X
Daphniidae							
Ceriodaphnia cornuta Sars, 1886++	X	X	X	*Daphnia gessneri* (Herbst, 1967)+++	X	X	X
C. reticulata (Jurine, 1820)+			X	*D. lumholtzi* Sars, 1885++	X	X	X
C. silvestrii Daday, 1902+	X	X	X	*Simocephalus semisseratus* (Kock, 1841)+	X		
Sididae							
Diaphanosoma birgei Korinek, 1981++	X	X	X	*D. spinulosum* Herbst, 1967+	X	X	X
D. brevireme Sars, 1901+	X	X		*D. polyspina* Korovchinsky, 1982+		X	
D. fluviatilis Hansen, 1899+	X	X	X				
Ilyocryptidae							
Ilyocryptus spinifer Herrich, 1884++	X	X	X				
Macrothricidae							
Macrothrix elegans (Sars, 1901)+	X	X	X	*Macrothrix squamosa* Sars, 1901+	X	X	X

The indication of each species' occurrence frequency considers +++ as frequent (50-80%), ++ as common (20-50%), and + as rare (< 20%). P= Parana river, L= lakes, T= tributaries.

Table 2. Continued...

ROTIFERA	P	L	T		P	L	T
Chydoridae							
Acroperus tupinamba Sinev & Elmoor-Loureiro, 2010+	X		X	*Notoalona sculpta* (Sars, 1901)+	X	X	X
Alona dentifera (Sars, 1901)+		X	X	*Nicsmirnovius fitiztatricki* (Chien, 1970)+	X	X	X
A. glabra Sars, 1901+	X			*Leydigia ipojucae* Brehm, 1938+	X		
A.gutatta Sars, 1862++	X	X	X	*L. propinqua* Sars, 1903+			X
A. iheringula Sars, 1901+	X			*Karualona muelleri* (Richard, 1897)+	X	X	X
A. intermedia Sars, 1862+	X		X	*Graptoleberis occidentalis* Sars, 1901+	X		
Alonella clathratula Sars, 1896+	X		X	*Euryalona brasiliensis* Brehm & Thomsen, 1936+	X		X
A. dadayi Birge, 1910+	X	X	X	*Ephemeroporus. barroisi* (Richard, 1894)+			X
Anthalona verrucosa (Sars, 1901)+	X	X	X	*E. hybridus*(Dadayi, 1905)+	X	X	
Camptocercus australis Sars, 1896++	X	X	X	*E. tridentatus* (Bergamin, 1931)+		X	
Chydorus eurynotus Sars, 1901+	X	X	X	*Coronatella monocantha* (Sars, 1901)+	X	X	X
*Chydorus parvireticulatus*Frey, 1897+	X	X	X	*C. poppei* (Richard, 1897)+	X	X	X
Chydorus pubescens Sars, 1901+	X		X	*Dunhevedia odontoplax* Sars, 1901+	X	X	X
Chydorus cf. *sphaericus* (O. F. Müller, 1776)+	X						
COPEPODA							
Cyclopidae							
Acanthocyclops robustus (Sars, 1863)+	X			*T. minutus* (Lowndes, 1934)+++	X	X	X
Ectocyclops rubescens Brady, 1904+			X	*Thermocyclops decipiens* (Kiefer, 1929)+++	X	X	X
Eucyclops ensifer (Fischer, 1853)+	X	X	X	*Paracyclops chiltoni* (Thomson, 1883)+	X	X	X
Eucyclops prinophorus Kiefer, 1931+		X		*P. pilosus* Dussart, 1983+		X	
Eucyclops elegans (Herrick, 1884)+	X	X	X	*Microcyclops alius* (Kiefer, 1935)+	X		
Macrocyclops albidus (Jurine, 1820)+		X		*Microcyclops anceps* (Richard, 1897)+	X	X	X
Mesocyclops aspericornis (Daday, 1906)+	X	X		*Microcyclops finitmus* (Dussart, 1984)+		X	X
M. longisetus (Thiébaud, 1914)+	X			*Metacyclops laticornis*(Lowndes, 1934)+		X	X
M. meridianus (Kiefer, 1926)+	X	X	X	*Metacyclops mendocinus* (Wierzejski, 1892)+			X
M. ogunnus Onabamiro, 1957+							
Diaptomidae							
Argyrodiaptomus azevedoi (Wright, 1935)++	X	X	X	*N. coniferoides* (Wrigth, 1927)++	X	X	X
A. denticulatus (Pesta, 1927)+		X	X	*N. deitersi* (Poppe, 1891)+	X		
A. furcatus (Sars, 1901)+	X	X	X	*N. henseni* (Dahl, 1894)+++	X	X	X
Notodiaptomus cearensis Wright, 1936+++	X	X	X	*N. iheringi* (Wright, 1935)++	X	X	X
N. cf. *spinuliferus* Reid & Moreno, 1990+	X	X	X	*N. isabelae* (Wright, 1936)+	X	X	X

The indication of each species' occurrence frequency considers +++ as frequent (50-80%), ++ as common (20-50%), and + as rare (< 20%). P= Parana river, L= lakes, T= tributaries.

Table 3. Results of the nestedness analysis.

				NODF index			
Rotifers	**Statistic**	**Z**	**2.50%**	**50%**	**97.50%**	***P***	**Filling %**
N.columns	36.46	34.67	32.62	34.63	36.78	0.127	
N.rows	**65.65**	**34.23**	**30.37**	**34.31**	**37.60**	**0.001**	
NODF	36.64	34.66	32.62	34.62	36.78	0.071	36.60
Cladocerans							
N.columns	41.96	38.10	34.82	38.05	41.64	0.041	
N.rows	**69.99**	**37.62**	**32.28**	**37.65**	**42.24**	**0.001**	
NODF	42.75	38.09	34.88	38.06	41.61	0.017	36.96
Copepods							
N.columns	28.34	37.33	31.99	37.41	42.36	0.003	
N.rows	**73.46**	**37.17**	**30.63**	**37.15**	**43.73**	**0.001**	
NODF	32.33	37.31	32.20	37.41	42.31	0.055	36.12

The null model was generated through 999 randomizations and we adopted significance of $P < 0.05$.

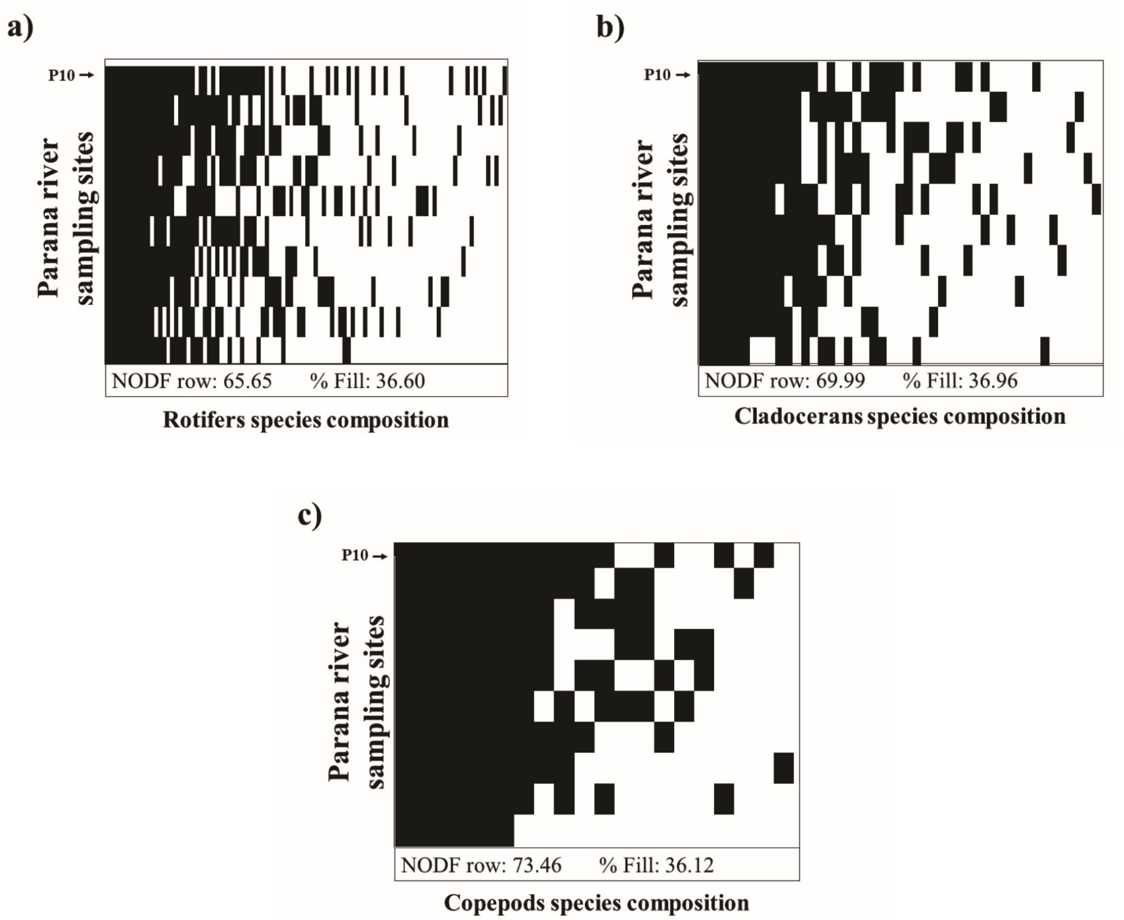

Figure 4. Distribution of presence (black) and absence (white) of rotifer (a), cladocerans (b), and copepod species (c) in the sites of the Paraná River. The most superior line represents the richest site (P10).

is an important feeding resource for zooplankton (Simões et al., 2012).

In the river, the flow is faster, and few species are able to stay in the water column, independent of the hydrological period (Lansac-Tôha et al., 2009). This relationship has also been reflected in the smaller variation in species richness in the river. On the other hand, in lakes, where variation in the number of species was higher, population fluctuations may occur according to the hydrological period. In general, in the drought periods, there is a high concentration of individuals, and in the flood, a higher dilution (Simões et al., 2013).

The relatively high species richness (25 species) in some sites of the Paraná River may be attributed to the contribution of the fauna of important tributaries present in these stretches, two of them being located inside conservation units. These tributaries also receive a contribution of the fauna of the lakes connected to them. Lakes have a high diversity of species (Lansac-Tôha et al., 2009), making them a source of propagules, and contribute to the increase in biodiversity of the whole system (Braghin et al., 2015; Bomfim et al., 2015). We believe that tributaries and lakes are increasing the species richness in the Paraná River, since the first sampling sites in this main river have few zooplankton species. Furthermore, the connectivity between the river and lakes, especially during the drought period, is preponderant for this dispersal, allowing a constant exchange of fauna among environments (Petry et al., 2003; Lansac-Tôha et al., 2009).

The results of the cluster analysis (species dissimilarity) highlighted that the microcrustacean species composition differs more clearly between the environments of the floodplain (lakes and tributaries) and the main river. This can be related to the differences between these environments and organisms' adaptations. The Paraná River has been suffering from the oligotrophization process, with a reduction in the concentration of nutrients and increasing water transparency in the last 15 years (Roberto et al., 2009), affecting aquatic communities, such as macrophytes, fishes, phytoplankton, and others (Thomaz et al., 2009; Fernandes et al., 2009; Rodrigues et al., 2009), and these changes reflect in the microcrustacean species establishment.

The cladocerans and copepods are more selective about their food resources and, have longer life cycles than rotifers (Allan, 1976). Thus, the reduced primary productivity in the main river, together with the higher flow velocity and increase in water transparency (Schwind et al., 2016), seem to have influenced the establishment of different species of these microcrustaceans in distinct environments (river and adjacent environments). Considering this, while the Paraná River is poor in food resources, the lagoons of this plain have high availability of foods, such as phytoplankton and protozoa (Bomfim, F. F. unpublished data), in addition to the physical differences between them.

The rotifers, on the other hand, presented a higher dispersal in the system, which is related to their opportunistic characteristics, such as short life cycle, higher niche amplitude, and smaller size of individuals (Allan, 1976; Bonecker et al., 2009). Therefore, some sites of the Paraná River were grouped to adjacent environments in the dissimilarity analysis.

The observed pattern of zooplankton species nestedness demonstrates the contribution of the adjacent environments to the increase of species along the river stretch (Moretto & Nogueira, 2003). This suggests that this environment has a tendency to return to some of its natural characteristics, such as species richness, which occurs from its connectivity with the lakes and tributaries of its margins (Ward & Stanford, 1995). The upstream reservoir (Porto Primavera) contributed to the composition of species in the first sampling points of the Paraná River, but during the 230 km to the last collection point (P10), there was an accumulation of species, which in this point (P10) was a set of species formed by subsets of the points before it. We thus emphasize that this is due to the contribution of the environments adjacent to this river.

Some studies have also found the same nestedness distribution pattern for the zooplankton community (Boecklen, 1997; Ramos-Jiliberto et al., 2009). More structured habitats favor the establishment of a higher number of species than more simple environments (Simões et al., 2012), and a nested distributive pattern implies that poorer sites are subsets of richer sites. Considering this, conservation practices must be concentrated in such environments and in species exchanges between them to protect the zooplankton diversity (De Meester et al., 2005).

Thus, our hypothesis was partially corroborated. Only the species composition of rotifers was similar between some sites of the main river and adjacent environments, due to the intrinsic characteristics of this group. However, the contribution of the fauna from lakes and tributaries for the river was determinant for the composition of species in this environment. This contribution was also responsible for the accumulation of species in the river, along the stretch to the beginning of the Itaipu reservoir (P10, with higher species richness).

Some physical characteristics of the environments (such as flow and depth) and the oligotrophization process of the main river have also influenced structuring of the community, but these factors were surpassed by the connectivity between the river and the lowland. With this, we suggest the importance of the conservation of environments adjacent to the main river for the maintenance of zooplankton species in the floodplain, considering the dynamics of this system and the important roles of the zooplankton in its trophic dynamics. Furthermore, the lowland environments support the restitution of the structure and dynamics of the Paraná River, which is highly impacted by damming, mainly in the stretch in which there is connectivity between the river and the conservation units in protected areas, like lakes, side channels and tributaries.

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