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Periphytic community structure of Ostracoda (Crustacea) in the river-floodplain system of the Upper Paraná River

Estrutura da comunidade de Ostracoda (Crustacea) perifíticos no sistema rio-planície de inundação do alto rio Paraná

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Abstract: Aim: We assessed the effect of environmental factors on the structure of periphytic ostracods communities along the river-floodplain system of the Upper Paraná River. We predict that the higher distance from Porto Primavera dam downstream would lead to higher diversity and density of the ostracods. **Methods:** Periphytic ostracods (associated with root systems of the floating *Eichhornia* spp) were sampled during November 2013 to May 2015. Three samples were collected at each sampling site (channel of the Paraná River, tributaries and lakes). *Eichhornia* plants were removed from the water by hand and the plants were placed in a plastic bucket. Roots were washed for the removal of ostracods, and samples were filtered through a hand net with 160 µm mesh size. **Results:** The faunistic survey recorded 44 ostracods species and richness estimators indicated that sampling effort appears to be suitable to reveal the diversity of ostracods in this studied area. The highest richness and density were observed in the stretch downstream of the dam in the main channel of Paraná River and in the lakes. Beta diversity was not significantly different along the longitudinal gradient downstream and higher similarity of ostracods species composition was observed in the lakes located in the stretch downstream of the dam. **Conclusions:** An increase in the richness and density of ostracods were recorded in the sections downstream of the Paraná River, evidencing the importance of undammed tributaries on the ostracods community. The similarity of beta diversity amongst sampling sites may be owing to permanent hydrological connectivity amongst these environments, favouring the exchange of organisms mainly through the drift of free-floating macrophytes, and owing to the passive dispersal of drought resistant eggs of ostracods. Local abiotic factors had significant effects on abundance and distribution of some ostracod species.

Keywords: microcrustaceans; macrophytes; regulated river; oligotrophication; connected lakes.

Resumo: Objetivo: Avaliou-se o efeito dos fatores ambientais sobre a estrutura da comunidade de ostrácodes perifíticos ao longo do sistema rio-planície de inundação do alto rio Paraná. Foi predito que quanto maior a distância a jusante da barragem de Porto Primavera, maior a diversidade e densidade de ostrácodes. **Métodos:** Ostrácodes perifíticos (associados aos sistemas radiculares da macrófita flutuante *Eichhornia* spp) foram amostrados durante novembro de 2013 a maio de 2015. Três amostras foram coletadas em cada ponto de amostragem (canal principal do rio Paraná, tributários e lagoas). Plantas de *Eichhornia* foram removidas da água manualmente e colocadas em balde plástico. As raízes foram lavadas para a remoção dos ostrácodes, e as amostras foram filtradas através de uma rede de mão de 160 µm de abertura de malha. **Resultados:** O levantamento faunístico registrou 44 espécies de ostrácodes e os estimadores de riqueza indicaram que o esforço amostral pareceu ser adequado para revelar a diversidade de ostrácodes nesta área de estudo. A maior riqueza e densidade foram observadas no trecho a jusante da barragem no canal principal do rio Paraná e nas lagoas. A diversidade beta não foi significativamente diferente ao longo do gradiente longitudinal a jusante e a maior similaridade na composição de espécies de ostrácodes foi observada nas lagoas localizadas no trecho a jusante da barragem. **Conclusões:** Um aumento na riqueza e densidade de ostrácodes foram registrados nas seções do rio Paraná, a jusante da barragem, evidenciando a importância dos tributários não represados sobre alguns atributos da comunidade de ostrácodes. A similaridade da diversidade beta entre os pontos de amostragem pode ser devido à permanente conectividade hidrológica entre estes ambientes, favorecendo a troca de organismos principalmente através da deriva de macrófitas flutuantes livres, e devido a dispersão passiva dos ovos de ostrácodes resistentes a seca. Os fatores abióticos locais tiveram efeitos significativos sobre a abundância e distribuição de algumas espécies de ostrácodes.

Palavras-chave: microcrustáceos; macrófitas; rio regulado; oligotrofização; lagoas conectadas.

1. Introduction

River-floodplain systems include both lentic and lotic habitats, such as rivers, canals, tributaries, permanently connected and isolated lakes (Thomaz et al., 2004; Higuti et al., 2010). The degree of connectivity between these environments and their hydrological dynamics maintain the integrity of the environments and their ecosystems (Poff et al., 1997; Wantzen et al., 2008).

One of the threats to global freshwater biodiversity is modification of water flow regime, caused by the construction of dams and the resulting human control of discharges of water for hydroelectric power production (Dudgeon et al., 2006).The construction of several reservoirs along a river (named "reservoirs in cascade"), might intensify the retention of sediment, organic matter and nutrients, turning the river water into an oligotrophic state downstream of the dam (Roberto et al., 2009; Vörösmarty et al., 2003), and leading to discontinuity in physical, chemical and biological characteristics (Ward & Stanford, 1995; Vannote et al., 1980). These effects can change the structure of aquatic communities, e.g. of macrophytes (Schwarz & Hawes, 1997), macroinvertebrates (King & Richardson, 2007) as well as the biomass of phytoplankton, zooplankton and of fish (Jeppesen et al., 2002).

Ostracods are small bivalved crustaceans (0.3-5.0 mm) with a calcified carapace. They can be found in most inland water bodies, where they abound in the benthic and aquatic vegetation (periphytic animal) communities (Martens & Behen, 1994; Martens et al., 2008).

Aquatic macrophytes are important biotopes for ostracods, which use this microhabitat for breeding, feeding and protection against predators (Higuti et al., 2007, 2010; Liberto et al., 2012; Szlauer-Łukaszewska, 2012; Higuti & Martens, 2016; Matsuda et al., 2015; Pereira et al., 2017).

Several studies have evaluated the effects of environmental factors on diversity, abundance and distribution of ostracod species in different aquatic ecosystems. The positive correlation of temperature, pH and dissolved oxygen with ostracods abundance was evidenced by Nagorskaya & Keyser (2005), whereas oxygen content and variables related with substratum and discharge showed negative influence on ostracod presence, abundance and species richness at a local scale (Poquet & Mesquita-Joanes, 2011). Besides the effect of the abiotic variables, also the presence and coverage of the vegetation can have significant effects on the distribution and abundance of ostracod species (Kiss, 2007), while the structural complexity of aquatic macrophytes might be an important determining factor for ostracod community composition (Matsuda et al., 2015).

Here, we assessed the effect of environmental factors on periphytic ostracod communities along the river-floodplain system of the Upper Paraná River. According to the Concept of Serial Discontinuity, tributaries are responsible for the addition of nutrients to the main river, contributing to the recovery of environments previous under oligotrophic conditions (Stanford & Ward, 2001). We hypothesize that ostracod communities will show higher diversities and densities, the further downstream they occur from the Porto Primavera dam.

2. Material and Methods

2.1. Study area

The Paraná River is formed by the junction of the rivers Grande and Paranaíba in South-central Brazil. The first third part of this basin is named Upper Paraná River and most of it runs inside the Brazilian territory. The Upper Paraná River presented an extensive floodplain on its west side, which is 230 km long and more than 20 km wide between the Porto Primavera Dam and the beginning of the Itaipu Reservoir. This represents the only extensive dam-free stretch of the Paraná River in Brazilian territory (Agostinho et al., 2004a). In this area, three conservation units were created: "Área de Proteção Ambiental das Ilhas e Várzeas do Rio Paraná" (Environmental Protection Area), the "Parque Nacional de Ilha Grande" (National Park), and the "Parque Estadual do Ivinheima" (State Park) (Agostinho & Zalewski, 1996; Agostinho et al., 2004a).

The study area is a river-floodplain system, which encompasses the main river (Paraná River), and several secondary rivers (named here tributaries), as well as connecting channels, isolated and connected lakes. We selected eight sampling points in the Paraná River (P1 to P8, distributed on the left (P1, P3, P6, P7) and right (P2, P4, P5, P8) banks of the Paraná River), four tributaries (P9: Baía, P10 and P11: Ivinhema, P12: Amambaí and P13: Iguatemi Rivers) and seven permanently connected lakes (P14: Garças, P15: Xirica, P16: Pombas, P17: Ivaí, P18: São João, P19: Pavão and P20: Saraiva) (Figure 1).

2.2. Sampling and laboratory analysis

Periphytic ostracods (associated with aquatic macrophytes, *Eichhornia crassipes* (Mart.) Solms and *E. azurea* (Swartz) Kunth were sampled between November 2013 and May 2015, totaling 7 collections in the dam-free stretch of the Upper Paraná River. In the upper section of the Paraná River (near the Porto Primavera Dam) there are no fixed and free floating aquatic macrophytes, only submerged plants. Therefore, ostracods associated with *Eichhornia* were sampled only in the lower section of the Paraná River. All the tributaries selected are located on the left bank (west side) of the Paraná River, because no fixed or free floating aquatic macrophytes were found in the tributaries of the right bank (east side) of the Paraná River during the whole collection period. The entire sampling period was characterized as dry hydrological period.

Three samples were collected at each sampling site (points of Paraná River, tributaries, lakes). Individual *Eichhornia* plants were removed from the water by hand and were immediately placed in a plastic bucket (Campos et al., 2017). The roots were washed in the bucket itself for the removal of ostracods (and other animals) and the sample was thoroughly washed through a hand net with 160 μm mesh size. The samples were preserved in 70° ethanol. The roots were stored in plastic bags, previously labelled and subsequently dried and weighted in the lab. The emerging parts of the plants were disguarded.

The ostracod samples were divided with the Folsom fractionator. ¼ of the samples were quantified and the remaining 3/4 were used to identify species that were absent from the first sub-sample. Ostracods were sorted under a stereoscopic microscope and the organisms were identified following Martens & Behen (1994) and articles comprised therein, Rossetti & Martens (1998), Higuti & Martens (2012a, b, 2014), Higuti et al. (2013).

In order to assess the abiotic environment, several chemical and physical variables were measured in the field, such as water temperature (°C) and dissolved oxygen (mg.L^{-1}) (both using YSI oximeter 550A), pH and electrical conductivity (μS.cm^{-1}) (both using YSI multiparameter 63) and turbidity (NTU, using turbidimeter). Alkalinity (μg.L^{-1}), total nitrogen (μg L^{-1}) and total phosphorus (μg L^{-1}) were determined according to methods proposed by Mackereth et al. (1978) in the Laboratory of Limnology of Nupelia from the State University of Maringá.

2.3. Data analysis

Ostracod densities were calculated as the number of individuals per gram of root dry mass (ind g^{-1} DW). Three estimators were used to describe values of species richness, in order to evaluate whether observed species richness in the present survey is representative of the total ostracod diversity for the dam-free stretch of the upper Paraná River. These estimators were Chao 1, Jackknife 1 (first order) and Bootstrap. The first one is based

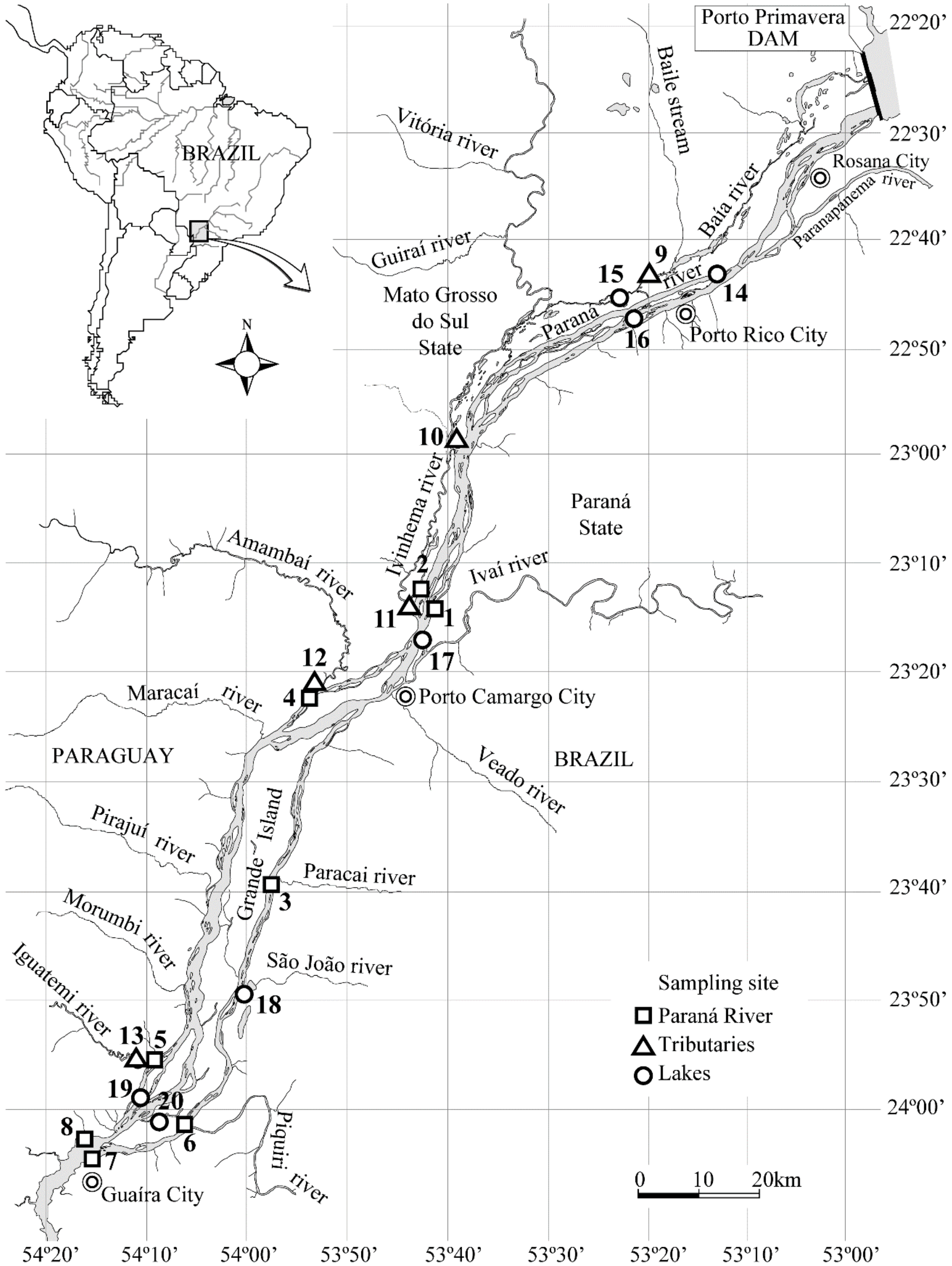

Figure 1. Sampling sites in the Paraná River (1-8), tributaries (9-13) and lakes (14-20) in the river-floodplain system of the Upper Paraná River. Locality codes are the same as shown in Table 1.

on species abundance and the other two species richness estimators are based on species incidence.

The environmental heterogeneity and beta diversity were analyzed through the Multivariate Permutational dispersion test (PERMDISP, Anderson et al., 2006) in each sampling sites of Paraná River, tributaries and lakes. Environmental heterogeneity was defined from the Euclidean distance of limnological variables (water temperature, dissolved oxygen, pH, electrical conductivity, turbidity, alkalinity, total nitrogen and total phosphorus). To evaluate species composition variability (beta diversity) we used a data matrix of presence / absence of the ostracod species.

PERMDISP calculates a centroid for each sampling sites, based on Jaccard distance. The test is based on the mean distance between the environmental variables (environmental heterogeneity) and their centroid group using a dissimilarity measure, within a dimensional space calculated through Principal Coordinate Analysis (PCoA, Legendre & Legendre, 1998). The same protocol was used to species composition (beta diversity). The higher average distance to the centroid corresponds to a higher environmental heterogeneity and higher dissimilarity in ostracod species composition. PERMDISP uses a 999 permutations ANOVA to test for significant differences ($p < 0.05$).

Rarefaction curves were performed according to the number of individuals, in order to compare the species richness amongst the sampling sites at comparable levels of density (Gotelli & Colwell, 2001).

A parametric analysis of variance (ANOVA) was performed to test for significance of differences in species richness, density, beta diversity and environmental heterogeneity amongst sampling sites in the Paraná River, tributaries and lakes. When the normality and homogeneity assumption required for ANOVA was not fulfilled, a non-parametric Kruskal-Wallis test was used. In case of significant differences; a Tukey test was performed a *posteriori*.

We performed a Redundancy Analysis - RDA (Legendre & Legendre, 1998) to evaluate the relationships between environmental variables and ostracod communities. This method is considered an extension of PCA, since the main axes are constrained to be linear combinations of the environmental variables. Multiple linear regressions of the ordination scores against environmental variables are then used to examine the relationship between community structure and the set of explanatory variables (Ramette, 2007). Significance was determined by 999 permutations. The model was selected with the environmental variables that best predict the characteristics of the community-using step forward (Blanchet et al., 2008).

Richness estimators, PCoA, PERMDISP and RDA were performed in the software R 3.2.4 (R Development Core Team, 2013) using the BiodiversityR (Kindt & Coe, 2005), vegan (Oksanen et al., 2017) and permute packages (Simpson, 2017). Analyses of variance and Tukey test were performed in Statistica 7.1 (Statsoft Inc., 2005).

3. Results

3.1. Abiotic variables and environmental heterogeneity

In general, an increase in turbidity and nutrient enrichment (nitrogen and phosphorus) and a decrease in pH were observed along the longitudinal downstream gradient of the Paraná River. Lower values of electrical conductivity were recorded in the tributaries, and more turbid waters in the Amambaí and Iguatemi rivers. Waters that are more alkaline, higher nutrient contents and lower dissolved oxygen concentrations were found in the lakes (Table 1).

The Paraná River and lakes were the most heterogenous environments. A trend in increasing environmental heterogeneity was observed downstream in the Paraná River and in the lakes. No significant differences were recorded amongst the sampling points of the Paraná River. The tributaries differed significantly ($F = 3.38$, $p = 0.01$) between Ivinhema (IV1) and Iguatemi, and significant differences were also found between the lakes Pavão and Pombas ($F = 2.84$, $p = 0.01$ - Figure 2)

3.2. Composition, diversity and density of ostracod communities

We recorded 44 species of ostracods associated with *E. crassipes* and *E. azurea*, between November 2013 and May 2015 in the dam-free stretch of the Upper Paraná River, between Porto Primavera and Itaipu reservoirs. The ostracod communities comprised five families: Cyprididae, Candonidae, Limnocytheridae, Ilyocyprididae and Darwinulidae. The family Ilyocyprididae was recorded for the first time in the Upper Paraná River, in addition, several new species of ostracods were found (see Table 2). Of the 44 species, 31 occurred in the Paraná River, 27 in the tributaries and 40 in the permanently connected lakes (Table 2). The most frequent species were *Cypricercus centrura* (Klie, 1940) and *Stenocypris malayica* Victor & Fernando, 1981 in the river-floodplain system of the Upper Paraná River. *Diaphanocypris meridana* (Furtos, 1936) and *C. centrura* were the most abundant species in Paraná River and lakes, apart from the high abundance of *Bradleytriebella lineata* (Victor & Fernando, 1981) in the lakes. *Cypretta costata* (G. W. Müller, 1898) and *Cytheridella ilosvayi* (Daday, 1905) were the most abundant species in the tributaries.

Species richness estimations were higher than the observed result (44 species), however, values of estimated richness were very close to observed

Table 1. Mean and standard deviation of the abiotic variables and type of substrate in the river-floodplain system of the Upper Paraná River.

	WT (°C)	pH	EC (μS.cm^{-1})	DO (mg.L^{-1})	TURB (NTU)	ALK (mEq.L^{-1})	TN (μg.L^{-1})	TP (μg.L^{-1})	Substrate
1. P1	25.57±3.44	7.30±0.30	57.97±8.65	6.52±0.48	4.94±1.16	585.99±173.72	830.85±187.93	17.22±3.11	Ea
2. P2	27.91±3.14	7.51±0.22	50.61±7.97	6.35±0.15	11.18±3.03	453.27±111.70	658.07±190.37	30.86±9.48	Ea
3. P3	25.61±3.25	7.07±0.59	48.98±11.11	7.01±0.81	7.74±2.14	584.38±202.19	699.62±150.94	22.83±7.72	Ea/Ec
4. P4	24.73±3.24	7.05±0.51	30.84±3.32	5.69±0.84	18.15±7.78	441.01±50.85	788.36±249.68	32.91±13.20	Ec
5. P5	26.65±3.42	6.79±0.36	40.50±15.51	6.24±0.82	12.34±3.52	442.42±122.04	726.36±247.29	24.48±4.16	Ec
6. P6	26.71±2.98	7.20±0.51	60.88±7.56	6.79±0.91	10.81±4.65	565.74±175.80	959.33±344.79	23.43±5.14	Ec
7. P7	24.03±2.52	6.60±0.26	49.61±6.19	6.23±1.12	30.38±23.48	566.93±197.02	993.37±262.85	35.17±13.73	Ec
8. P8	25.37±3.36	6.25±0.93	39.71±8.34	6.13±1.86	16.02±3.77	393.2±107.97	771.56±236.86	30.97±7.39	Ec
9. Baía	26.42±3.53	6.87±0.47	26.25±13.23	5.73±1.76	4.24±1.47	234.99±88.30	773.94±119.33	30.44±11.64	Ea/Ec
10. Ivinhema (IV1)	25.59±3.39	7.06±0.45	41.22±6.19	6.73±1.73	15.83±7.58	459.03±139.22	836.41±215.17	39.52±8.54	Ea/Ec
11. Ivinhema (IV2)	25.79±3.23	7.08±0.33	37.21±4.90	5.23±0.66	20.34±3.98	421.81±113.15	805.54±216.58	42.64±8.35	Ec
12. Amambai	24.60±3.19	7.00±0.49	28.62±7.19	6.05±1.08	44.43±23.54	299.42±115.14	850.99±129.05	37.55±14.70	Ea/Ec
13. Iguatemi	25.29±3.18	6.37±0.74	17.4±2.81	6.01±1.86	35.27±23.62	164.86±88.72	701.15±67.33	21.81±7.29	Ea/Ec
14. Garças	26.83±3.26	7.42±0.30	56.70±6.03	6.45±0.94	13.33±5.86	636.82±214.25	727.72±187.14	32.49±8.71	Ea/Ec
15. Xirica	25.44±4.58	7.32±0.29	48.15±11.45	5.12±1.87	10.77±4.10	458.45±131.77	934.46±194.20	47.76±15.29	Ea/Ec
16. Pombas	26.02±3.27	7.91±0.56	59.38±10.70	6.98±3.15	4.30±1.67	528.74±120.57	789.22±110.25	18.43±5.13	Ea
17. Ivaí	25.72±2.18	7.19±0.48	58.65±6.74	4.54±2.19	17.27±5.25	543.48±173.42	936.98±227.44	57.95±19.52	Ea/Ec
18. São João	26.22±3.40	6.66±0.33	33.33±4.00	5.74±1.68	15.21±4.97	271.07±69.61	784.95±333.69	26.66±10.62	Ea/Ec
19. Pavão	25.87±2.98	6.74±0.38	61.96±7.90	3.79±1.81	5.91±3.02	636.04±225.40	837.72±442.48	27.43±6.11	Ec
20. Saraiva	26.21±3.39	6.72±0.79	45.80±10.35	5.45±1.59	5.01±2.20	425.47±104.04	964.16±233.46	31.35±4.88	Ec

WT = water temperature; EC = electrical conductivity; DO = dissolved oxygen; TURB = turbidity; ALK = alkalinity; TN = total nitrogen; TP = total phosphorus; Ea = *Eichhornia azurea*; Ec = *Eichhornia crassipes*.

Table 2. Mean values of ostracod species density of the sampling sites (P1 to P8) of the Paraná River, tributaries and lakes.

	Paraná River								Tributaries					Lakes						
	P1	P2	P3	P4	P5	P6	P7	P8	BAI	IV1	IV2	AMA	IGU	GAR	XIR	POM	IVA	SJO	PAV	SAR
Family Cyprididae (Baird, 1845)																				
Diaphanocypris meridana (Furtos, 1936)	2.7	1.8	0.3		0.5	0.7	0.4	1.2	0.6	*0.0	0.2	†0.0		3.7	2.6	8.6	0.7	0.4	0.8	0.3
Stenocypris major (Baird, 1859)	0.2	0.3	0.9	0.1	0.6	0.8	0.2	0.2	†0.0	†0.0	0.2	*0.0	*0.0	0.1	0.1	0.2	0.2		*0.0	†0.0
Stenocypris malayica Victor & Fernando, 1981	0.4	0.2	0.3	0.3	0.6	0.8	0.7	0.6	0.1	0.3	0.2	0.4	0.3	0.2	0.7	0.2	0.3	0.2	*0.0	*0.0
Strandesia psittacea (Sars, 1901)									0.1						0.2	*0.0	*0.0			
Strandesia cf. *psittacea* sp. 2									*0.0								*0.0			
Strandesia mutica (Sars, 1901)								0.3	*0.0						*0.0		*0.0	†0.0	†0.0	†0.0
Strandesia variegata (Sars, 1901)									†0.0		†0.0								†0.0	
Strandesia bicuspis (Claus, 1982)																	*0.0			
Strandesia cf. *tolimensis* sp. 2	0.2														0.2	0.1	*0.0			
Strandesia lansactohai Higuti & Martens, 2013 (in Higuti et al., 2013)	0.1				0.1			0.3	*0.0	*0.0		†0.0		*0.0	0.1	0.3	0.1		0.3	†0.0
Strandesia velhoi Higuti & Martens, 2013 (in Higuti et al., 2013)			0.2	0.2	0.5										*0.0					
Strandesia nupelia Higuti & Martens, 2013 (in Higuti et al., 2013)			0.4		0.7			0.7	†0.0		†0.0				0.6		*0.0	†0.0	0.1	*0.0
Strandesia sp. 1 n.sp.					0.5								*0.0		*0.0		*0.0			
Strandesia sp. 2 n.sp.																		*0.0		
Strandesia sp. 3 n.sp.																06				
Bradleystrandesia trispinosa (Pinto & Purper, 1965)	0.9	0.1	0.2	0.3	0.9	0.2	0.7	0.1	0.1	0.1	*0.0		*0.0	*0.0	0.4	0.2	0.1	†0.0	0.6	1.2
Bradleytriebella lineata (Victor & Fernando, 1981)	2	1.6	0.2	0.3	0.7	0.2	1.2	*0.0	*0.0	†0.0	*0.0			3.5	0.8	1.2	0.9		0.1	*0.0
Cypricercus centrura (Klie, 1940)	4.1	0.4	0.5	1.8	0.5	0.2	2.2	0.7	0.7	0.1	0.3	*0.0	*0.0	7.3	2.8	7.7	3.4	14.4	3.1	10.4
Chlamydotheca deformis Farkas, 1958															†0.0	0.2				
Chlamydotheca iheringi (Sars, 1901)	0.7				0.1		0.2	†0.0	†0.0						*0.0	†0.0	0.3	0.1	0.1	*0.0
Chlamydotheca cf. *iheringi* sp. 2																	*0.0		0.2	
Chlamydotheca sp. 3																	†0.0			*0.0
Chlamydotheca spectabilis (Sars, 1901)															*0.0	*0.0				
Cypretta costata G. W. Müller, 1898	0.5	0.6	0.7	1.5	0.8	0.4	0.3	2.5	2.5	1.1	1.1	3.0	0.1	0.1	2.6		0.7	*0.0	2.0	*0.0
Cypretta sp. 3 n.sp.	0.1													0.8	*0.0	0.2				

BAI = Baía; IV1 and IV2 = Ivinhema; AMA = Amambaí; IGU = Iguatemi; GAR = Garças; XIR = Xirica; POM = Pombas; IVA = Ivaí; SJO = São João; PAV = Pavão; SAR = Saraiva.
†≤ 0.05; *≤ 0.005.

Table 2. Continued...

	Paraná River								Tributaries					Lakes						
	P1	P2	P3	P4	P5	P6	P7	P8	BAI	IV1	IV2	AMA	IGU	GAR	XIR	POM	IVA	SJO	PAV	SAR
Cypretta sp. 4 n.sp.				1.0																
Cypridopsis vidua (O. F. Müller, 1776)	0.2	0.6	0.1			0.2	0.1	0.2	0.2	†0.0	*0.0	†0.0		2.2	1.1	11.6	0.4	0.1		
Cypridopsis cf. *vidua* sp. 2	0.2						0.2										0.2		†0.0	
"*Cypridopsis*" n. gen. 1 n.sp.																			*0.0	*0.0
"*Cypridopsis*" n. gen. 2 n.sp.															*0.0				*0.0	*0.0
Cabelodopsis hispida (Sars, 1901)	0.3		0.9		0.6	0.6	0.1	*0.0	*0.0	†0.0	*0.0	†0.0	*0.0	1.5	0.3	0.1	1.5	0.1	1.4	0.8
Paranacypris samambaiensis Higuti et al., 2009																				
Family Candonidae (Kaufmann, 1900)																				
Candobrasilopsis brasiliensis (Sars, 1901)				0.1	0.7					†0.0	*0.0	0.1	*0.0				*0.0	*0.0	*0.0	*0.0
Candobrasilopsis rochai Higuti & Martens, 2012			0.1	0.2	0.5	0.4	0.5	0.1	0.1	0.1	0.1	0.4		*0.0			0.8	0.2	*0.0	*0.0
Candobrasilopsis elongata Higuti & Martens, 2014			0.1	0.4	0.2	0.1	0.2	0.1	0.1	0.1	0.3	0.2	0.3				0.5	0.5	0.1	1.0
Pseudocandona agostinhoi Higuti & Martens, 2014				0.6	1.0	0.3		*0.0	*0.0	0.1	*0.0	*0.0	*0.0				0.2	†0.0	1.0	1.1
Pseudocandona cillisi Higuti & Martens, 2014			0.2	0.3						†0.0	*0.0	*0.0	†0.0						†0.0	*0.0
Physocypria sp.1																				*0.0
Family Limnocytheridae (Kile, 1938)																				
Cytheridella ilosvayi Daday, 1905	1.0	0.4	0.3	0.1	0.2	0.1	0.8	1.0	1.0	*0.0	0.4	0.3	4.0	†0.0	1.0	0.2	14.5	1.5	6.9	6.5
Family Darwinulidae (Brady & Norman, 1889)																				
Darwinula stevensoni (Brady & Robertson, 1870)					0.9															
Alicenula serricaudata (Klie, 1935)	0.6	0.1		0.1	0.2	0.1	0.4	*0.0	*0.0	*0.0	0.5	0.5	*0.0		0.1		0.9	1.3	1.0	1.7
Vestalenula pagliolii (Pinto & Kotzian, 1961)		0.1	0.6	0.2	0.4	0.2	0.3	0.1	0.1	0.3	0.4	0.1		*0.0	*0.0		0.4	0.1	0.8	0.8
Penthesilenula brasiliensis (Pinto & Kotzian, 1961)	0.1		0.3	0.1	0.5	0.2	0.5	†0.0	†0.0	†0.0	*0.0	*0.0			*0.0		0.1	0.1	*0.0	0.1
Family Ilyocyprididae			0.2																	

BAI = Baía; IV1 and IV2 = Ivinhema; AMA = Amambaí; IGU = Iguatemi; GAR = Garças; XIR = Xirica; POM = Pombas; IVA = Ivaí; SJO = São João; PAV = Pavão; SAR = Saraiva.
†≤ 0.05; *≤ 0.005.

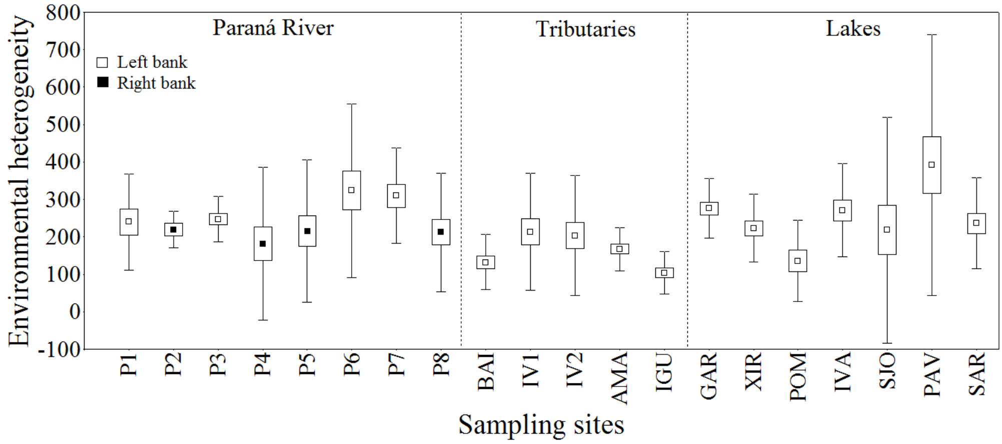

Figure 2. Mean values, deviation and standard error of environmental heterogeneity of the sampling sites in the river-floodplain system of the Upper Paraná River.

richness. The bootstrap estimations approached the observed species richness most closely (Figure 3).

The variation of richness and density of ostracods in different sampling sites (Paraná River, tributaries and lakes) is shown in Figure 4. Higher values of richness and density were recorded in lentic environments (lakes) followed by the lotic environments (rivers). In the main river we observed an increase in the values of both attributes according to the river longitudinal gradient from the upper to lower sections on the left (P1, P3, P6, P7) and right (P2, P4, P5, P8) banks of the Paraná River. Significant differences ($H = 28.02$, $p = 0.000$) were found for richness, mainly amongst sampling sites located in the upper (P2, P4) and lower (P8) sections of the right bank of the Paraná River, and. between the sampling points P6 and P7 on the left bank of the river ($H = 13.30$, $p = 0.004$). Density of ostracods differed significant ($H = 13.33$, $p = 0.004$) between points P2 and P8 on the right bank of the Paraná River.

On the other hand, richness and density were higher in the tributaries located in an upstream stretch of the Paraná River (Baía and Ivinhema (IV1 and IV2) rivers), when compared to the tributaries located further downstream (Amambaí and Iguatemi rivers) of the Paraná River. Significant differences were observed for richness ($H = 14.63$, $p = 0.005$) and density ($H = 20.70$, $p = 0.000$) between Iguatemi and Baía, and Iguatemi and Ivinhema (IV2).

Lower ostracod species richness was recorded in the lake Garças, Xirica and Pombas, while higher ostracod densities were found in the lakes Pombas (floodplain), Ivaí and Saraiva (downstream stretch of the Paraná River). Significant differences

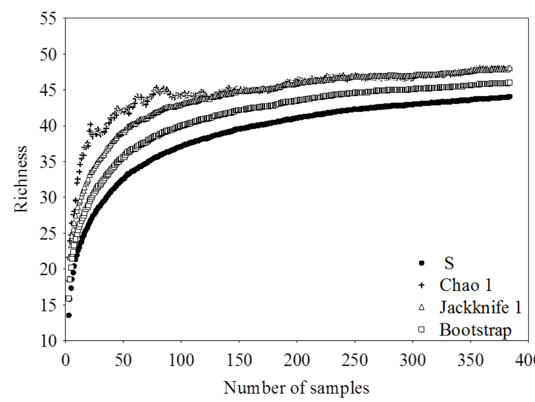

Figure 3. Accumulation curves of ostracods species resulting from different species richness estimators in the river-floodplain system of the Upper Paraná River.

($H = 64.97$, $p = 0.000$) were found only for ostracod species richness between the lakes Ivaí and Garças, Xirica, Pombas, São João, between Pavão and Garças, Xirica, Pombas, São João, and between Garças and Saraiva lakes.

The rarefaction curves showed that ostracod richness reached an asymptote in the sampling sites of Paraná River, tributaries and lakes. Higher numbers of ostracod species were recorded in the lakes, while species richness in the Paraná River and tributary sites were similar.

Beta diversities were similar in the Paraná River and no significant differences were observed amongst the sampling points. Higher diversities were recorded in the Iguatemi River, and significant differences ($F = 2.736$, $p = 0.033$) were found between Iguatemi and Baía rivers. Higher beta diversities were recorded in lakes Garças and Xirica, located in the upstream stretch of the Paraná River

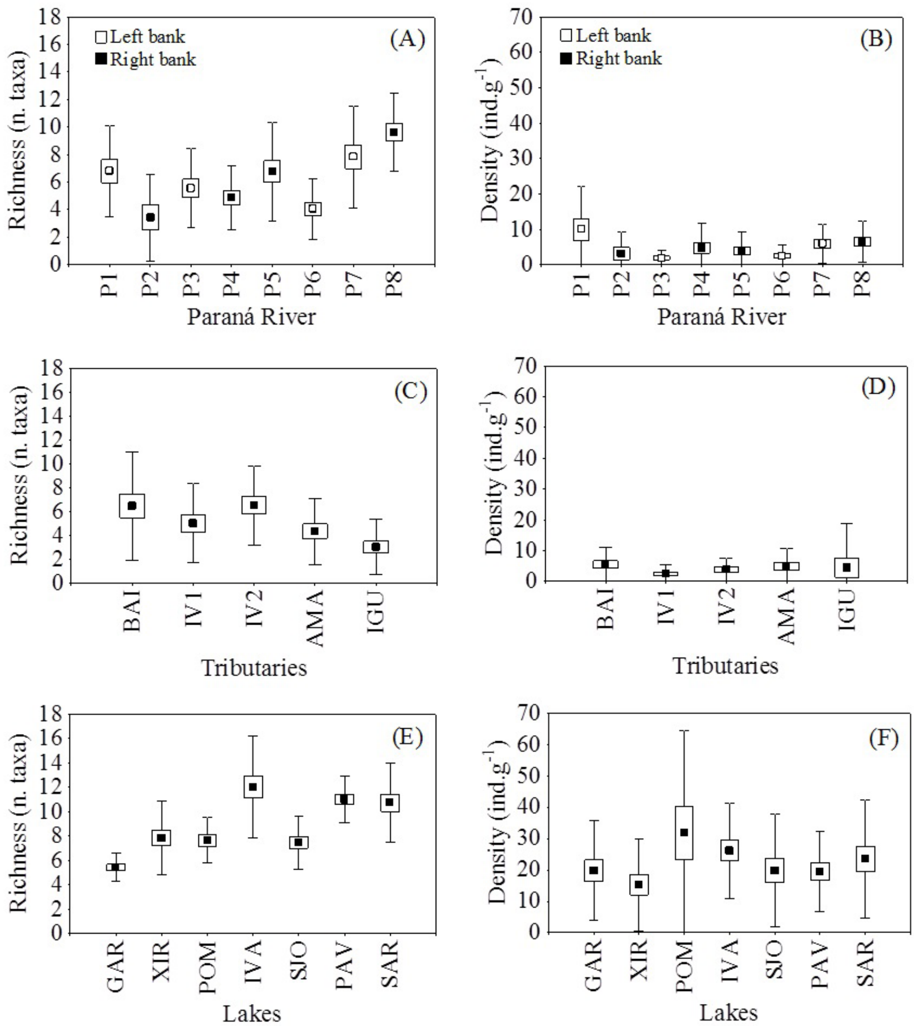

Figure 4. Mean values, deviation and standard error of richness and density of ostracods in (A, B) Paraná River, (C, D) tributaries and (E, F) lakes in the river-floodplain system of the Upper Paraná River.

(floodplain), which differed ($F = 7.70$, $p = 0.000$) than in lakes Ivaí and Saraiva, which are located in the downstream stretch of the Paraná River (Figure 5).

3.3. Environmental effects on the distribution of ostracods

First and second axes of RDA analyses which were performed using all environments (Paraná River, tributaries and lakes) together as well as each type of environment separately were all significant ($p<0.005$) and were retained for interpretation. The variables selected in the ordination explained 11.26% (all environments), 11.8% (Paraná River), 13.08% (tributaries) and 27.9% (lakes) of the species data variability. When all environments (Paraná River, tributaries and lakes) were analyzed together, turbidity, pH, water temperature, dissolved oxygen, electrical conductivity and total phosphorous were the factors that showed significant influence on ostracod distributions. Some associations between certain species of ostracods and limnological factors were observed when we analyzed the environments separately. In the Paraná River, *Diaphanocypris meridana*, *Cypricercus centura* and *Bradleytriebella lineata* were associated with higher values of electrical conductivity, whereas *Vestalenula pagliolii* (Pinto & Kotzian, 1961) and *Cypretta costata* were related to the lower values of this variable. *Stenocypris malayica* was associated with higher values of alkalinity in Paraná River. *Diaphanocypris meridana*, *Cypricercus centrura* and *Cypridopsis vidua* (O. F. Müller, 1776) were associated with lower turbidity values in Baía River. pH seems to have important effects

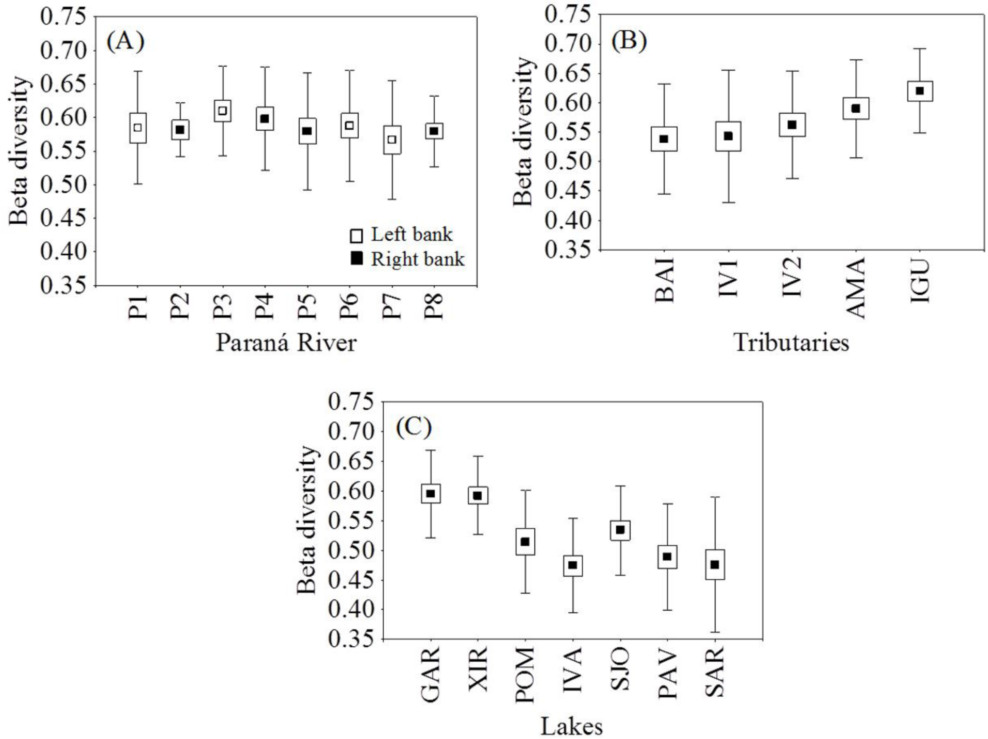

Figure 5. Mean values, deviation and standard error of beta diversity of ostracods in (A) Paraná River, (B) tributaries and (C) lakes in the river-floodplain system of the Upper Paraná River.

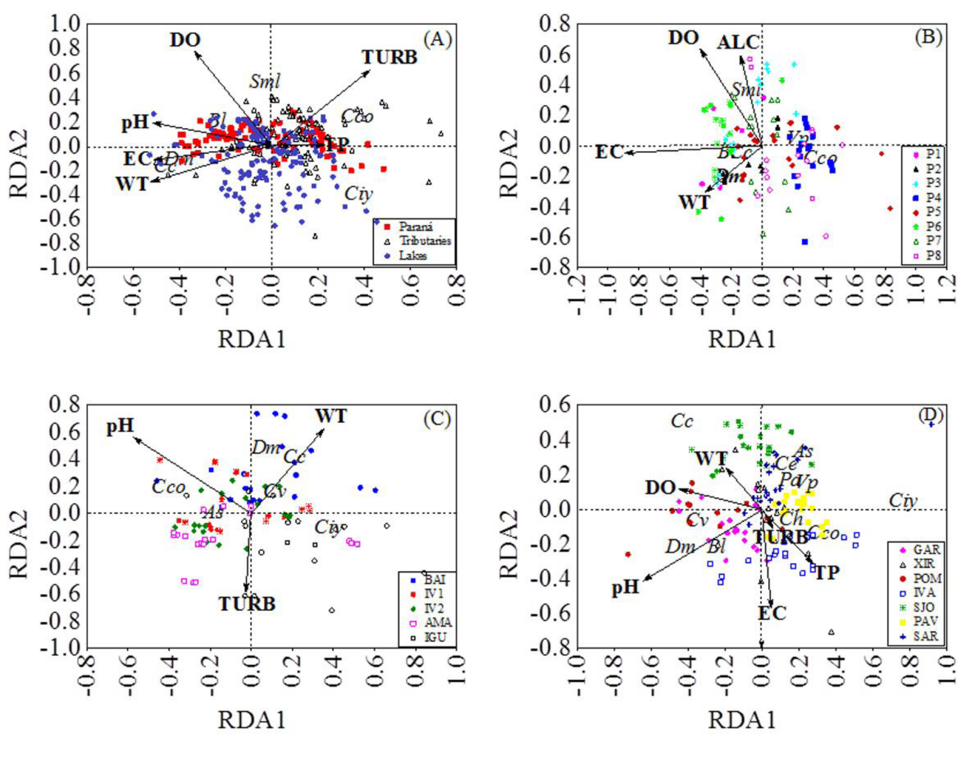

Figure 6. Biplot of the redundancy analysis (RDA) showing the association between ostracod community structure and limnological variables in (A) all environments, (B) Paraná River, (C) tributaries and (D) lakes. WT = water temperature, EC = electrical conductivity, DO = dissolved oxygen, TURB = turbidity, TP = total phosphorus. Dm = *Diaphanocypris meridana*, Cc = *Cypricercus centrura*, Bl = *Bradleytriebella lineata*, Sml = *Stenocypris malayica*, Cco = *Cypretta costata*, Cv = *Cypridopsis vidua*, Ciy = *Cytheridella ilosvayi*, Vp = *Vestalenula pagliolii*, As = *Alicenula serricaudata*, Pa = *Pseudocandona agostinhoi*, Ce = *Candobrasilopsis elongata*, Ch = *Cabelodopsis hispida*.

on the abundance and distribution of some ostracods species in the tributaries, such as *Cypretta costata* (Amambaí and Baía rivers) and *Cytheridella ilosvayi* (Iguatemi River). In addition, *D. meridana*, *B. lineata* and *C. vidua* were abundant in the lakes associated with higher pH (neutral-basic) and higher conductivity values. On the other hand, *Alicenula serricaudata* (Klie, 1935) and *Vestalenula pagliolii* (Darwinulidae), *Pseudocandona agostinhoi* Higuti & Martens, 2014 and *Candobrasilopsis elongata* Higuti & Martens, 2014 (Candonidae) were associated with lower pH values (neutral-acid) recorded in the lakes located downstream of Paraná River (Figure 6).

4. Discussion

4.1. Abiotic variables and environmental heterogeneity

The Upper Paraná River has four dams along its length, with Porto Primavera and Itaipu being the last dams in this part of the river (Stevaux et al., 2009). These cascade reservoirs act as filters retaining organic matter, thus increasing the water transparency and reducing the nitrogen and phosphorus concentrations of the water downstream (Roberto et al., 2009). The effect of the Porto Primavera dam on water quality and diverse aquatic communities of the Upper Paraná River floodplain has been widely reported (e.g. Agostinho et al., 2004b; Bovo-Scomparin et al., 2013). This effect would tend to increase along the longitudinal gradient, however, tributaries (without dams) and floodplains contribute organic and inorganic particulate matter to the river water, restoring the natural attributes that have been degraded by upstream reservoir regulation (Rice & Church, 2001; Stanford & Ward, 2001; Portinho et al., 2016). We observed a similar trend along the longitudinal gradient of the Paraná River in both banks (right and left), due the presence of several tributaries.

Environmental heterogeneity was similar in the Paraná River, the tributaries and the lakes. This is as expected, because the environments are connected to each other: tributaries and lakes are connected to the Paraná River. On the other hand, studies have shown that a lack of hydrological connectivity reduces the flow of organic and inorganic material (Thomaz et al., 2007), thus increasing the heterogeneity between them (Lopes et al., 2014; Bozelli et al., 2015). The confluence of tributaries with the main river channel minimizes these effects along the longitudinal gradient of the river, as it contributes to the increase of the organic and inorganic material, at the same time also increasing the environmental heterogeneity (Katano et al., 2009).

Flood pulses (sudden increases in water level, mainly owing to water release from the dams) are an important factor for limnological changes in floodplain lakes (Thomaz et al., 2004; Conceição et al., 2017a). During high waters, the lakes increase the extent of their margins, and thus also the decomposition of organic matter and with resulting increasing nutrient values (Thomaz et al., 2004). However, flood pulses of high amplitude, which were not observed during the present study, can reduce the environmental heterogeneity in floodplain lakes (GAR, XIR, POM, see Figure 4).

4.2. Composition, diversity and density of ostracod communities

Gamma diversity of freshwater ostracods was comparatively high in the river-floodplain system of the Upper Paraná River, as 44 species were recorded, compared to 48 species found in other studies about diversities of ostracods in this floodplain (Higuti et al., 2010, 2013). Sampling efforts appear to be suitable to reveal the diversity of ostracods, because of similar values amongst expected and observed estimators, while all richness estimators have already reached an asymptote.

The highest richness and densities were recorded in the lentic environments (approximately 91% of the total richness found throughout the study), compared to lotic environment (main channel of Paraná River and tributaries). This difference might be attributed to the lower water flow and higher stability within the lentic environments. This stability provides greater habitat complexity and larger food resources (Schindler & Scheuerell, 2002). Both of these features can lead to an increase of development of ostracods in the roots of aquatic macrophytes. On the other hand, in lotic environments, the water flow may affect the establishment of the organisms which could be washed out from amongst macrophytes (Grabowska et al., 2013).

The highest richness and density observed in the region downstream of the dam in the main channel of Paraná River (P6, P7, P8), may be attributed to effects of the tributaries, owing to the increase of environmental heterogeneity in these sampling sites. Several studies confirm the importance of the tributaries in attenuating the effects of oligotrophication in the main channels caused by dams. For example, the increase of taxonomic richness and density of macroinvertebrates along a longitudinal gradient in the Dam-regulated River in Japan was related to the confluence of a tributary, owing to the increase of environmental heterogeneity, food resources and recruitment of colonizers (Katano et al., 2009). In addition, an increase of nutrient concentrations in the main channel by the confluence of the tributaries showed a positive relation with density of macroinvertebrates downstream of the dam (Kiffney et al., 2006).

The similarity of beta diversity amongst Paraná River, tributaries and lakes may be owing to permanent hydrological connectivity amongst these environments, favouring the exchange of organisms and species. Low variation in beta diversity may then be caused by the absence of significant water flows during the dry season (Bonecker et al., 2005; Conceição et al., 2017b).

Higher environmental heterogeneity may lead to an increase in beta diversity (Anderson et al., 2006; Astorga et al., 2014). In contrast, our study did not show a positive correlation between environmental heterogeneity and beta diversity, which is in agreement with other studies (Heino et al., 2013; Bini et al., 2014; Heino et al., 2015; Zorzal-Almeida et al., 2017). Heino et al. (2015) postulate that environments with high dispersal rates can mask local environmental effects. This may therefore reduce the relationship between environmental heterogeneity and beta diversity amongst small regional units on a larger spatial scale.

Along the longitudinal gradient of Paraná River, its tributaries and lakes, one of dispersal routes of ostracods might be through drift of free floating macrophytes (and hitch-hiking pleustonic faunas) downstream, thus homogenizing the fauna. In addition, there are other dispersal ways such as wind (Vanschoenwinkel et al., 2008), birds (Brochet et al., 2010) and human (Waterkeyn et al., 2010) carrying the drought resistant eggs. Local abiotic factors probably had the largest influence on the variability of ostracod species composition amongst tributaries and amongst lakes, and less so in the main river channel.

4.3. Environmental effects on the distribution of ostracods

Physical and chemical properties of water are factors that generally have important effects on the distribution of ostracod species. However, we observed no such strong relationships in the river-floodplain system of upper Paraná River. Electrical conductivity ranges influenced the distributions of some ostracods species in the Paraná River and lakes, such as in other studies that showed conductivity as a factor determining ostracod communities (Liberto et al., 2012; Zhai et al., 2015).

The lotic environments have a higher flow velocity compared to the lentic environments. Consequently, this higher hydrodynamics increases sediment movement, making the water more turbid in the tributaries, except in the Baía River, where the current flow velocity is much smaller. Relatively transparent environments may benefit the abundance of some species with different strategies, e.g., swimming species (*D. meridana*, *C. centrura* and *C. vidua*), smaller species (*C. vidua*), or the presence of spines (*C. centrura*) to prevent predation.

Ostracods need to calcify their valves 9 times moult (during each moult) and this imposes important physiological stress if HCO_3 levels and pH are low (Higuti et al., 2010). pH seems to be the most important variable on abundance and distribution of some ostracods species in tributaries, despite the small amplitude of variation of this variable amongst the sampling sites. Liberto et al. (2012) also found a relation between the ostracods species with higher and lower pH variation. In addition, according Zhai et al. (2015), the range of pH tolerance depends on the niche of the species, some species tolerating higher and/or lower pH values.

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