

The variability in the hydrosedimentological regime supports high phytoplankton diversity in floodplain: A 12-year survey of the Upper Paraná River

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ABSTRACT

The alpha, beta, and gamma diversity are important tools for conservation studies, and the distribution of species in space and time is essential to provide insights regarding diversity patterns and processes that modify the ecosystem and the community responses to such changes. Thus, a long-term ecological data was used to evaluate in 12 biotopes the phytoplankton composition and diversity within selected habitats (alpha diversity), between habitats (beta diversity) and across the upper Paraná River floodplain (gamma diversity). We evaluate the environmental variability of the hydrosedimentological cycles (limnophase and potamophase) during 12 years, associated with the water level variability and with the environmental heterogeneity as drivers of the phytoplankton composition and diversity in the upper Paraná River floodplain. Remarkable gamma diversity was recorded especially in limnophase, however, years with intense flood presented high gamma diversity, and years with extreme drought presented low gamma diversity, although without significant differences. The alpha diversity was significantly different on spatial and temporal scales. The beta diversity showed high values, however with low temporal variability and without correlation with the hydrosedimentological regime of the Paraná River. Overall, these results indicate that the variability in the hydrosedimentological regime associated with the periodicity, duration, and amplitude of limnophase and potamophase, and the pattern of mosaic of habitats in this floodplain are essential for sustaining much of the phytoplankton diversity and ecosystem integrity, and that this approach is relevant and proved be useful to understand floodplain systems and associated phytoplankton community.

Key words: Biodiversity; long-term data; planktonic algae; spatial and temporal scale.

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INTRODUCTION

River-floodplain systems are characterized by a complex spatial and temporal hydrodynamic gradient between the main channel and surrounding wetlands, influenced by hydrosedimentological regime, represented by limnophase (low water level) and potamophase (high water level) (Neiff, 1990). Seasonal flooding is typical of these wetlands and may vary over time in intensity as well as in flood pulse duration (Milzow *et al.*, 2009). This variability, together with the gradients of connectivity, promotes different hydrological, geomorphological, biological and biogeochemical successional processes and results in a dynamic mosaic of habitats with high biodiversity (Ward *et al.*, 1999; Amoros and Bornette, 2002). These systems are among the most productive and diverse ecosystems on Earth, however are among the most threatened (Agostinho *et al.*, 2005; Dittrich *et al.*, 2016).

The study of biodiversity is a key tool for understanding how interactions between disturbance regimes and

habitat heterogeneity influence niche diversification and resource partitioning and for determining how functional processes integrate with spatio-temporal heterogeneity (Ward and Tockner, 2001). The distribution of species in space and time has provided insights regarding diversity patterns and processes that modify the ecosystem and the community responses to such changes (Magurran *et al.*, 2010). Thus, studies of biodiversity should emphasize multiple scales of distribution and variability (Giller *et al.*, 2004), once that the community diversity regulates ecological processes such as productivity and stability (Tilman and Downing, 1994; Weyhenmeyer *et al.*, 2013), which are important features especially due of the current intense anthropogenic pressure on natural ecosystems.

Thus, the alpha, beta, and gamma diversity are important tools for conservation studies. Alpha diversity represents the number of taxa occurring in a habitat, gamma diversity represents the total number of taxa in the region, and beta diversity represents the change in species composition along spatial or temporal gradients (Legendre *et al.*, 2005). Therefore, diversity may can be decomposed

into different components and provide information at both local and regional scales (Pinto *et al.*, 2015).

Phytoplankton is composed of organisms with high growth rates, and its ecology can help determine the effect that environmental modifications in floodplain systems have on diversity and ecosystem dynamics and functions. However, a more detailed understanding of the drivers of species richness and composition in phytoplankton communities is required (Özkan *et al.*, 2013). Evaluating the variability of phytoplankton diversity is essential for providing guidelines for conservation programs aimed at reducing biodiversity losses in conservation areas and understanding the relationship between biodiversity and environmental variables at spatial and temporal scales.

The upper Paraná River floodplain harbors high phytoplankton diversity (Train and Rodrigues, 2004). However, climatic events such as *El Niño* and *La Niña*, which are caused by the *El Niño*-Southern Oscillation (ENSO) cycles (McPhaden *et al.*, 2006) and habitat fragmentation resulting from the construction of Porto Primavera dam that prevent longitudinal connectivity, have changed the hydrosedimentological regime of the upper Paraná River and affected the phytoplankton diversity (Borges and Train, 2009; Bovo-Scomparin *et al.*, 2013; Rodrigues *et al.*, 2009, 2015; Bortolini *et al.*, 2014, 2016a) and others communities (Agostinho *et al.*, 2005; Bonecker *et al.*, 2013; Simões *et al.*, 2013).

Thus, this study aimed to evaluate the influence of hydrosedimentological regime, by the water level and environmental heterogeneity, on phytoplankton composition and diversity, encompassing different habitats in three sub-basins of the upper Paraná River floodplain in a long time period. We expect that the phytoplankton composition and diversity components presented different patterns as a response to conditions of each phase (limnophase and potamophase) of the hydrosedimentological cycles through time and of the mosaic of habitats in the floodplain.

METHODS

Study area

The Paraná River is the third largest river in South America, and it originates from the union of the Grande and Paranaíba Rivers in the south-central region of Brazil. In its upper third, referred to as the upper Paraná River, is a 230-km-long and 20-km-wide floodplain. This floodplain encompasses flooded areas on its right bank, including rivers, channels, lakes and backwaters. Backwaters (“ressacos”) are lentic water bodies connected to river originating from recently abandoned channels formed by sidebars (Souza Filho and Stevaux, 2004). Thus, floodplains can often be formed by set of habitats associated with a main river channel of a hydrological basin which

may be referred to as subsystems (Thomaz *et al.*, 2004; Padial *et al.*, 2012) or even as sub-basin as we follow in this study.

Sampling stations were established in 12 sites, including six floodplain lakes, one backwater and five lotic sites (two channel and three rivers) in three sub-basins on the floodplain stretch of the upper Paraná River: Paraná sub-basin (S1 and S3 - connected floodplain lakes, S2 - isolated floodplain lake and S4 - Paraná River), Baía sub-basin (S5 - connected floodplain lake, S6 - isolated floodplain lake, S7 - Curutuba channel and S8 - Baía River) and Ivinhema sub-basin (S9 - connected floodplain lake, S10 - isolated floodplain lake, S11 - Ipoitã channel and S12 - Ivinhema River) (Fig. 1).

Sampling scheme and samples analysis

Samplings were performed quarterly during the potamophase and limnophase periods between 2000 and 2011 (except in 2001 and 2003 when only two samples were taken in each year) as part of the Brazilian ‘Long Term Ecological Research Program. Daily water level (WL) data for the Paraná River were obtained from Itaipu Binational (Itaipu Binacional), the National Water Agency (Agência Nacional das Águas - ANA) and the Limnology, Ichthyology and Aquaculture Research Center (Núcleo de Pesquisas em Ictiologia, Limnologia e Aquicultura - Nupélia). As a reference, the flooding process of the Paraná and Baía sub-basins is considered to begin when the level of the Paraná River is above 3.5 m, and the Paraná River is considered to influence the Ivinhema sub-basin environments when its level is above 4.5 (Thomaz *et al.*, 2004). The upper Paraná River hydrological regime comprises periods of drought from June to September, and floods from October to February (Dittrich *et al.*, 2016). Extreme periods of drought occurred at the upper Paraná River during 2000 and 2001, which were influenced by *La Niña*, a climatic event responsible for negative anomalies in rainfall in the upper Paraná River (Borges and Train, 2009). Intense floods also occurred in 2005, 2007, 2010 and 2011, with the first three years influenced, even with less intensity, by climatic event *El Niño*, the presumable driver of positive rainfall anomalies recorded in this region (CPTEC, 2012). As our study did not aim to explain directly these climatic events, we can only speculate that these events seem to influence the precipitation levels and consequently the WL in this region. Besides that, the fragmentation of the Paraná River by upstream dams regulates the discharges and also influences the hydrosedimentological regime (Souza-Filho *et al.*, 2004).

For each year, pulse attributes (limnophase and potamophase days and connectivity index) were estimated using the software PULSO (<http://www.neiff.com.ar/> - Neiff and Neiff, 2003). The limnophase amplitude is the number of days when the WL was lower than the refer-

ence level, potamophase amplitude is the number of days when the WL was higher than the reference level, and connectivity index is the ratio of the number of days between the potamophase and limnophase performed to each year (Neff, 1990).

Samples of phytoplankton were collected at the sub-surface (20 cm) of the pelagic region of each site, and fixed with acetic Lugol's solution. Randomly selected fields were counted under an inverted microscope, according to Lund *et al.* (1958) and Utermöhl (1958) methods. The sedimentation of aliquot of the water sample (3, 5 or 10 mL) was established according to the algae and debris concentration present in each sample, and the sed-

imentation time according to the height of the sedimentation chamber, being at least three hours for each centimeter of height of the chamber (Margalef, 1983). The frequency of occurrence of the species (Constancy = C) was calculated according to Dajoz (2005), being classified as constant ($C \geq 70\%$), common ($30\% \leq C \leq 70\%$), sporadic ($10\% \geq C \leq 30\%$) or rare ($C \leq 10\%$).

Alpha diversity was estimated according to the species richness, *i.e.*, the number of taxa in each sample. Gamma diversity was estimated according to the total number of taxa in the study region (total and by period in each sub-basin) and nonparametric estimators of diversity (Chao, Jackknife 1 and 2, and Bootstrap) were

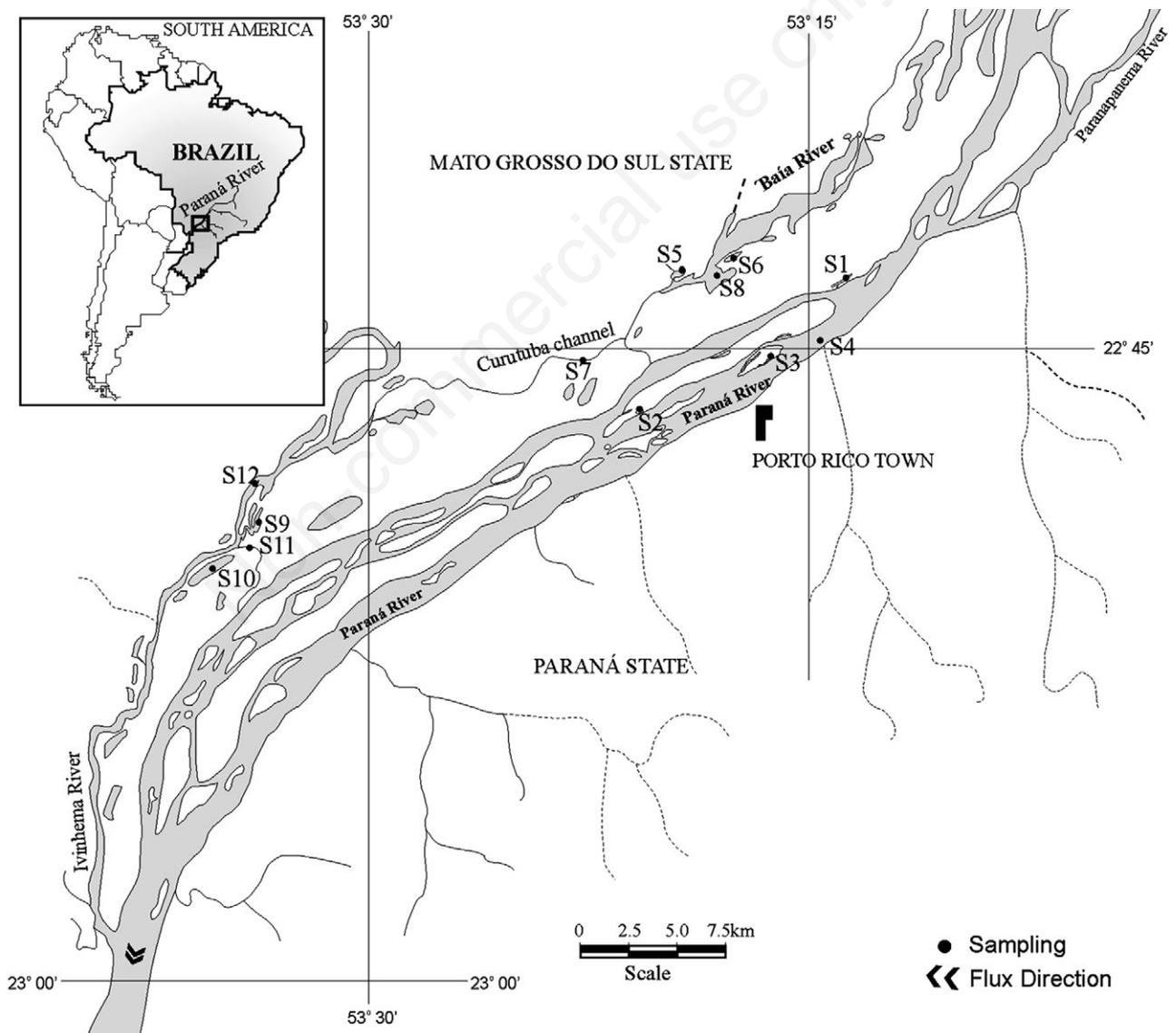


Fig. 1. Study area and sampling stations in the upper Paraná River floodplain. Paraná Sub-basin (S1 to S4); Baía sub-basin (S5 to S8); Ivinhema sub-basin (S9 to S12).

using to verify if the gamma diversity registered was approaching of the expected diversity. The change in species composition (beta diversity) was estimated between all sites of the study region in each sampling, using the Sorensen's (β_{sor}) and Simpson's (β_{sim}) indexes. β_{sim} is suitable for differentiating between turnover and nesting processes (Baselga, 2010).

The water temperature (WT, °C), pH, electric conductivity (EC, $\mu\text{S cm}^{-1}$), and dissolved oxygen (DO, mg L^{-1}) data were obtained using Digimed portable digital potentiometers. Water column transparency (m) was obtained using a Secchi disk, and the euphotic zone (Z_{eu} , m) was calculated as 2.7 times the depth of the Secchi disk (Cole, 1994). The soluble reactive phosphorus (SRP, $\mu\text{g L}^{-1}$; Golterman *et al.*, 1978), nitrate (NO_3^- , $\mu\text{g L}^{-1}$; Giné *et al.*, 1980), nitrite (NO_2^- , $\mu\text{g L}^{-1}$; Giné *et al.*, 1980) and ammonium (NH_4^+ , $\mu\text{g L}^{-1}$; Koroleff, 1978) levels were determined. The dissolved inorganic nitrogen (DIN) was determined from the NO_3^- , NO_2^- and NH_4^+ concentrations.

Data analysis

We first performed a Principal Component Analysis (PCA) to summarize the environmental variability at each sub-basin using the variables: WT, pH, DO, EC, Z_{eu} , SRP, DIN, and WL. Additionally, a Detrended Correspondence Analysis (DCA) was used to summarize the phytoplankton composition data and evaluate the temporal and spatial differences in each sub-basin. A presence/absence matrix was used for the DCA analysis, and it included species in all the different environments and sample periods within each sub-basin. Analysis of variance (ANOVA) were applied in the following situations: to the scores from the first two PCA axes to test temporal (hydrological period) and spatial (isolated and connected lakes, and lotic sites) differences in limnological conditions; to the scores from the first two DCA axes to test temporal (year and hydrological period) and spatial (isolated and connected lakes, and lotic sites) differences in the phytoplankton composition within each sub-basin; to test spatial (isolated and connected lakes, and lotic sites) and temporal (year and hydrological period) differences in the alpha diversity; and to test temporal differences in the gamma (year and hydrological period) and beta (year and hydrological periods) diversity. The relationship among beta diversity (β_{sor} and β_{sim}), environmental heterogeneity represented by the coefficient of variation of the abiotic variables (WT, pH, DO, EC, Z_{eu} , SRP and DIN) and water levels of the Paraná River in each sampling, was tested using Pearson's correlation coefficient. The PCA, DCA and ANOVA analyses were performed with the software R (R Core Team, 2012). Pearson's correlation coefficient was determined using the software Statistica (StatSoft, 2005).

RESULTS

Water level, connectivity and environmental variability in the sub-basins

Hydrosedimentological cycles in the Paraná River floodplain were characterized by extreme droughts in 2000 and 2001, and intense floods in 2005, 2007, 2010 and 2011 (Fig. 2). In the years 2007, 2009, 2010 and 2011 for both the Paraná and Baía sub-basins (reference level above 3.5 m) and for the Ivinhema sub-basin (reference level above 4.5 m) occurred more days under potamophase. The period of isolation of the lentic environments was longer for the Paraná and Baía sub-basins in 2001 and for the Ivinhema sub-basin in 2000, 2001 and 2004. At both the Paraná and Baía sub-basins, the highest connectivity index between lentic and lotic environments occurred in 2007, 2009, 2010 and 2011, whereas for the Ivinhema sub-basin, the highest connectivity index was observed in 2007 and 2010 (Tab. 1).

The first two PCA axes generated for the Paraná sub-basin explained 49% of the environmental variability. The Axis 1 was correlated with SRP (0.14), DO (-0.48), pH (-0.47), DIN (-0.45) and Z_{eu} (-0.43), while the second axis was correlated with WT (0.64), WL (0.54) and DO (-0.19). For this sub-basin was verified different between sites (axis 1 = $P < 0.05$; axis 2 = $P < 0.05$) and hydrological periods (axis 1 = $P < 0.05$; axis 2 = $P < 0.05$) (Fig. 3a).

For the Ivinhema sub-basin, the first two PCA axes explained 50% of the variability. The axis 1 was correlated with WL (0.47) and DO (-0.53). The second axis was correlated with Z_{eu} (0.43) and SRP (-0.58). For this sub-basin was verified different between sites (axis 1 =

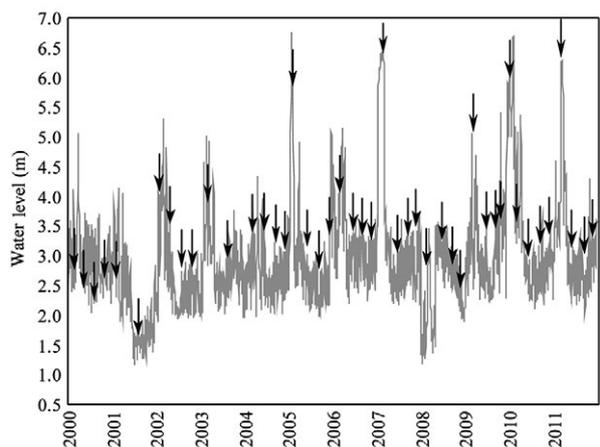


Fig. 2. Daily water levels of the Paraná River with their reference values for the flooding of the different sub-basins between the years 2000 and 2011. Arrows indicate sampling.

$P < 0.05$; axis 2 = $P < 0.05$) and hydrological periods (axis 1 = $P < 0.05$) (Fig. 3b).

In Baía sub-basin, 54% of the variability was explained by the two first PCA axes. The first axis was correlated with WL (0.48), WT (0.45) and DO (-0.53). The second axis was correlated with SRP (0.47) and Z_{eu} (-0.54). For this sub-basin, a discrete spatial separation, however significant (axis 1 = $P < 0.05$; axis 2 = $P < 0.05$) and a clear temporal separation (axis 1 = $P < 0.05$; axis 2 = $P < 0.05$) were observed (Fig. 3c).

Phytoplankton composition

A total of 753 sub-generic taxa distributed among the following taxonomical groups were identified: Chlorophyceae (207), Bacillariophyceae (129), Cyanobacteria (124), Euglenophyceae (121), Zygnematomphyceae (104), Xanthophyceae (28), Chrysophyceae (18), Cryptophyceae (10), Dinophyceae (10), Raphidophyceae (1) and Oedogoniophyceae (1). The genus *Trachelomonas* Ehrenberg had the highest number of taxa (60). High contribution of rare species was detected (92%), whereas sporadic (6%), frequent (2%) and constant (0.2%) species had low contributions to total of taxa. Constant species were just *Cryptomonas marssonii* Skuja and *Chroomonas acuta* Utermöhl, which had a frequency of occurrence (C) of 87% and 78%, respectively (Tab. 2).

Chlorophyceae were mainly represented by *Spermatozopsis exsultans* Korshikov (C=48%) and *Monoraphidium contortum* (Thuret) Komárková-Legnerová (C=40%). Bacillariophyceae were the second most represented group, and there was a high frequency of occurrence of

Aulacoseira granulata var. *granulata* (Ehrenberg) Simonsen (C=52%), *A. granulata* var. *angustissima* (O.F. Müller) Simonsen (C=36%) and *Aulacoseira distans* (Ehrenberg) Simonsen (C=41%). Cyanobacteria were mainly represented by *Synechocystis aquatilis* Sauvageau

Tab. 1. Pulse attributes of daily water levels of the Paraná in the upper Paraná River floodplain for each year of the study, with influence on the Paraná, Baía and Ivinhema sub-basins.

	Paraná and Baía			Ivinhema		
	ΣPP	ΣLP	CI	ΣPP	ΣLP	CI
2000	11	355	0.03	1	365	0.00
2001	3	362	0.01	0	365	0.00
2002	36	329	0.11	5	360	0.01
2003	27	338	0.08	3	362	0.01
2004	10	356	0.03	0	366	0.00
2005	54	311	0.17	29	336	0.09
2006	56	309	0.18	4	361	0.01
2007	60	305	0.20	55	310	0.18
2008	39	237	0.16	2	364	0.01
2009	93	272	0.34	28	337	0.08
2010	102	263	0.39	68	297	0.23
2011	81	284	0.29	35	330	0.11

CI, connectivity index; ΣPP , number of days under potamophase; ΣLP , number of days under limnophase.

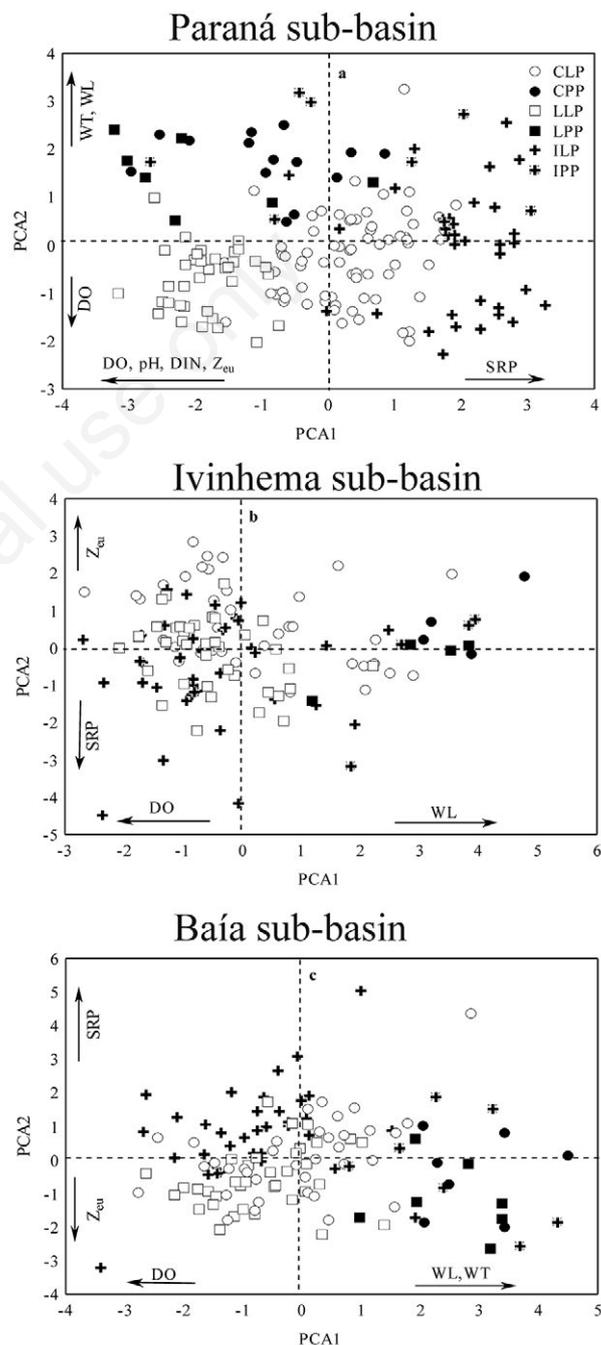


Fig. 3. Ordination of the first two axes of Principal Component Analysis for the sub-basins: a) Paraná, b) Ivinhema, c) Baía. CLP, connected lake in limnophase; CPP, connected lake in potamophase; LLP, lotic in limnophase; LPP, lotic in potamophase; ILP, isolated lake in limnophase; IPP, isolated lake in potamophase.

Tab. 2. Frequency of occurrence of constant, frequent and sporadic phytoplankton species in the upper Paraná River floodplain (asterisk indicates the occurrence). Rare species ($C \leq 10\%$) are not included.

	Frequency of occurrence		
	Constant	Common	Sporadic
Bacillariophyceae			
<i>Achnanthydium minutissimum</i> (Kützing) Czarnecki	-	-	*
<i>Aulacoseira ambigua</i> (Grunow) Simonsen	-	-	*
<i>Aulacoseira distans</i> (Ehrenberg) Simonsen	-	*	-
<i>Aulacoseira granulata</i> var. <i>angustissima</i> (O.F. Müller) Simonsen	-	*	-
<i>Aulacoseira granulata</i> var. <i>granulata</i> (Ehrenberg) Simonsen	-	*	-
<i>Aulacoseira herzogii</i> (Lemmermann) Simonsen	-	-	*
<i>Cyclotella</i> sp.	-	-	*
<i>Discostella stelligera</i> (Cleve & Grunow) Houk & Klee	-	*	-
<i>Fragilaria</i> sp.	-	-	*
<i>Gomphonema gracile</i> Ehrenberg	-	-	*
<i>Navicula</i> sp.	-	-	*
<i>Nitzschia palea</i> (Kützing) W. Smith	-	*	-
<i>Ulnaria ulna</i> (Nitzsch) P. Compère	-	-	*
<i>Urosolenia eriensis</i> (H.L. Smith) Round & R.M. Crawford	-	-	*
<i>Urosolenia longiseta</i> (O. Zacharias) Edlund & Stoermer	-	-	*
Cyanobacteria			
<i>Aphanocapsa delicatissima</i> West & G.S. West	-	-	*
<i>Aphanocapsa elachista</i> West & G.S. West	-	-	*
<i>Aphanocapsa holsatica</i> (Lemmermann) G. Cronberg & J. Komárek	-	-	*
<i>Aphanocapsa koordersii</i> K. Strøm	-	-	*
<i>Merismopedia tenuissima</i> Lemmermann	-	-	*
<i>Dolichospermum circinale</i> (Rabenhorst ex Bornet & Flahault) P. Wacklin, L. Hoffmann & J. Komárek	-	-	*
<i>Dolichospermum planctonicum</i> (Brunnth.) P. Wacklin, L. Hoffmann & J. Komárek	-	-	*
<i>Microcystis aeruginosa</i> (Kützing) Kützing	-	-	*
<i>Pseudanabaena</i> sp.	-	-	*
<i>Romeria gracilis</i> (Koczwara) Koczwara <i>in</i> Geitler	-	-	*
<i>Synechocystis aquatilis</i> Sauvageau	-	*	-
Chlorophyceae			
<i>Ankyra judayi</i> (G.M. Smith) Fott	-	-	*
<i>Chlamydomonas</i> sp.	-	-	*
<i>Closteriopsis scolia</i> A. Comas	-	*	-
<i>Closteriopsis</i> sp.	-	-	*
<i>Crucigenia tetrapedia</i> (Kirchner) Kuntze	-	-	*
<i>Desmodesmus armatus</i> (R. Chodat) E. Hegewald	-	-	*
<i>Dictyosphaerium pulchellum</i> H.C. Wood	-	-	*
<i>Eutetramorus fottii</i> (Hindák) Komárek	-	-	*
<i>Monoraphidium arcuatum</i> (Korshikov) Hindák	-	-	*
<i>Monoraphidium contortum</i> (Thuret) Komárková-Legnerová	-	*	-
<i>Monoraphidium griffithii</i> (Berkeley) Komárková-Legnerová	-	-	*
<i>Monoraphidium irregulare</i> (G.M. Smith) Komárková-Legnerová	-	-	*
<i>Monoraphidium komarkovae</i> Nygaard	-	-	*
<i>Monoraphidium minutum</i> (Nägeli) Komárková-Legnerová	-	-	*
<i>Monoraphidium tortile</i> (West & G.S. West) Komárková-Legnerová	-	-	*
<i>Scenedesmus ecornis</i> (Ehrenberg) Chodat	-	-	*
<i>Schroederia antillarum</i> Komárek	-	-	*
<i>Schroederia setigera</i> (Schröder) Lemmermann	-	-	*
<i>Spermatozopsis exsultans</i> Korshikov	-	*	-
<i>Tetrastrum komarekii</i> Hindák	-	-	*
Cryptophyceae			
<i>Chroomonas acuta</i> Utermöhl	*	-	-
<i>Cryptomonas brasiliensis</i> A. Castro, C. Bicudo & D. Bicudo	-	*	-
<i>Cryptomonas curvata</i> Ehrenberg	-	*	-
<i>Cryptomonas marssonii</i> Skuja	*	-	-
<i>Cryptomonas</i> sp.	-	*	-
Chrysophyceae			
<i>Mallomonas</i> cf. <i>akrokomos</i> Ruttner	-	-	*
<i>Mallomonas</i> sp.	-	*	-
Euglenophyceae			
<i>Euglena acus</i> (O.F. Müller) Ehrenberg	-	-	*
<i>Euglena</i> sp.	-	-	*
<i>Lepocinclis ovum</i> (Ehrenberg) Lemmermann	-	-	*
<i>Trachelomonas volvocinopsis</i> Svirenko	-	*	-
<i>Trachelomonas</i> sp.	-	-	*
Dinophyceae			
<i>Peridinium</i> sp.	-	-	*

(C=37%), *Dolichospermum planctonicum* (Brunnth.) Wacklin, L. Hoffm. & Komárek (C=25%) and *Merismopedia tenuissima* Lemmermann (C=24%), and Euglenophyceae were mainly represented by *Trachelomonas volvocinopsis* Svirenko (C=30%).

The DCA showed discreet spatial and temporal differences in phytoplankton composition for Paraná (axis 1 = 0.29 and axis 2 = 0.28), Ivinhema (axis 1 = 0.42 and axis 2 = 0.28) and Baía sub-basins (axis 1 = 0.28 and axis 2 = 0.20). A spatial variation was observed for the Paraná River and was primarily related to the presence of Cryptophyceae, Cyanobacteria and Bacillariophyceae (Fig. 4a-b). In the limnophase, the Ivinhema River and Ipoitã

channel were separated from the others, which was primarily related to presence of Bacillariophyceae (Fig. 4c-d) and for Baía sub-basin, the DCA distinguished the Baía River in limnophase due to presence of Chlorophyceae, Bacillariophyceae and Euglenophyceae (Fig. 4e-f).

The ANOVA evidenced spatial and temporal differences for the first two DCA axes for phytoplankton composition in Paraná and Ivinhema sub-basins and only temporal differences in the Baía sub-basin (Tab. 3).

Phytoplankton diversity

Was recorded high gamma diversity in the upper Paraná River floodplain, being the higher values recorded

Tab. 3. ANOVA three-way results for phytoplankton composition data represented by the scores of the first two axes of the DCA.

Variable	Effect	df	F	P
Paraná				
DCA 1	Environment	2	25.5067	<0.05
	Period	1	12.2694	<0.05
	Year	1	313.9687	<0.05
	Environment *Period	2	0.4293	0.6516
	Environment *Year	2	2.7425	0.0673
	Period *Year	1	12.7011	<0.05
	Environment *Period *Year	2	0.1471	0.8632
	DCA 2	Environment	2	26.6071
Period		1	1.6371	0.2025
Year		1	8.9708	<0.05
Environment *Period		2	0.2553	0.7749
Environment *Year		2	5.9638	<0.05
Period *Year		1	0.2825	0.5957
Environment *Period *Year		2	0.3883	0.6788
Ivinhema				
DCA 1	Environment	3	4.9065	<0.05
	Period	1	34.8999	<0.05
	Year	1	28.3088	<0.05
	Environment *Period	2	1.7633	0.1747
	Environment *Year	3	0.2652	0.8503
	Period *Year	1	2.4055	0.1228
	Environment *Period *Year	2	0.2416	0.7856
	DCA 2	Environment	3	14.3651
Period		1	12.8189	<0.05
Year		1	18.7539	<0.05
Environment *Period		2	1.7525	0.1766
Environment *Year		3	1.8503	0.1401
Period *Year		1	0.1457	0.7031
Environment *Period *Year		2	2.5546	0.0808
Baía				
DCA 1	Environment	2	1.2559	0.2875
	Period	1	1.8654	0.1738
	Year	1	63.7542	<0.05
	Environment *Period	2	0.8193	0.4425
	Environment *Year	2	0.4928	0.6118
	Period *Year	1	3.2826	0.0718
	Environment *Period *Year	2	0.0969	0.9077
	DCA 2	Environment	2	0.3005
Period		1	6.2615	<0.05
Year		1	1.1760	0.2797
Environment *Period		2	1.1440	0.3210
Environment *Year		2	0.7896	0.4557
Period *Year		1	2.6670	0.1043
Environment *Period *Year		2	1.1190	0.3290

df, degrees of freedom; F, statistical value F; Environment, connected lake, isolated lake, channel and river; Period, limnophase and potamophase; Year, 2000-2011; statistical significance level at $P < 0.05$.

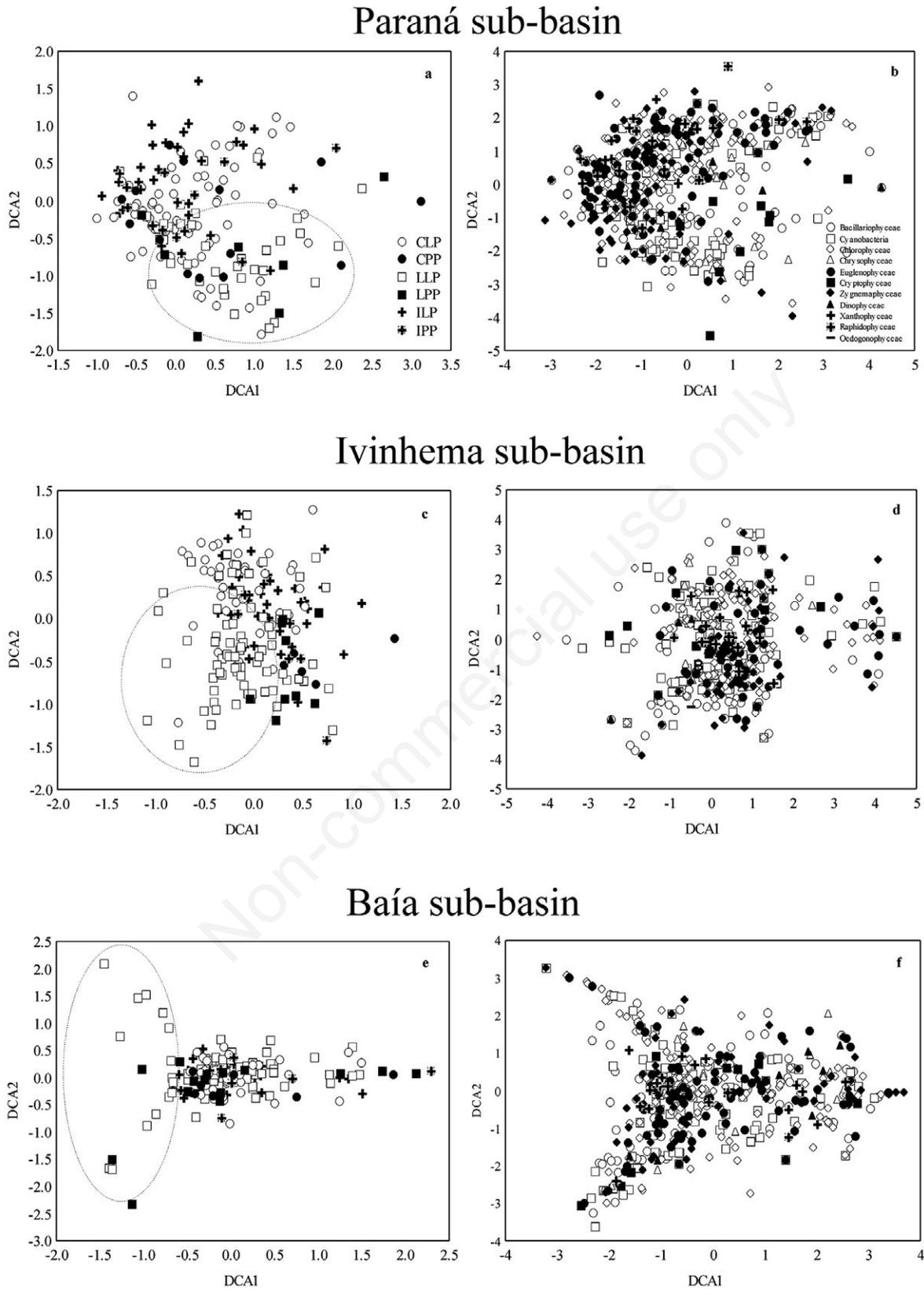


Fig. 4. Dispersion of scores over the first two axes of Detrended Correspondence Analysis for the sub-basins: a-b) Paraná, c-d) Ivinhema, e-f) Baía. CLP, connected lake in limnophase; CPP, connected lake in potamophase; LLP, lotic in limnophase; LPP, lotic in potamophase; ILP, isolated lake in limnophase; IPP, isolated lake in potamophase.

in limnophase, and the lowest in potamophase in all sub-basins, with significant differences ($P > 0.05$). In relation to the 12 years of study, the highest gamma diversity was recorded in 2007 (343 taxa), and the lowest in 2001 (206 taxa), however without significant differences ($P < 0.05$). The bootstrap estimator best reflected the gamma diversity, which produced values always above 80% of the values recorded throughout the entire study period (Tab. 4).

The highest mean alpha diversity values were observed in 2002 in Paraná sub-basin and in 2007 at both the Ivinhema and Baía sub-basins (Fig. 5a). The highest mean alpha diversity values occurred in connected lakes, followed by isolated lakes and the lowest values were recorded in lotic environments (Fig. 5b). The highest mean alpha diversity values in Paraná sub-basin occurred in the isolated lakes, whereas in Baía and Ivinhema sub-basins, such values were recorded in connected lakes (Fig. 5c). Overall, the highest mean alpha diversity values during the potamophase occurred in sites of Paraná sub-basin, followed by the Baía and Ivinhema sub-basins, while in the limnophase, the highest values were observed in sites of Baía sub-basin, followed by the Ivinhema and Paraná

sub-basins (Fig. 5d). Significant differences in alpha diversity were verified among sites ($P < 0.05$), hydrological periods ($P < 0.05$), and years ($P < 0.05$).

Between the lakes, the S2 (398 taxa), S5 (390 taxa) and S1 (382 taxa) had the highest total taxa number, whereas between lotic sites, the Baía River (289 taxa) had the highest total taxa number. Between the sub-basins, The Paraná sub-basin had the highest phytoplankton taxa (567), followed by the sub-basins of Baía (547) and Ivinhema (492).

The beta diversity presented high values (> 0.83 to B_{sor} and > 0.72 to B_{sim}) at both the potamophase and limnophase throughout the study period. The years 2001 (extreme drought) and 2011 (intense flood), presented the highest beta diversity ($B_{sor} = 0.85$ for both), and highest species turnover ($B_{sim} = 0.80$) in 2011. In relation to each sampling, the highest beta diversity ($B_{sor} = 0.91$) occurred in March 2010 in the potamophase, and the lowest in May 2002 in the limnophase ($B_{sor} = 0.83$). The highest species turnover ($B_{sim} = 0.85$) occurred in March 2006 in the potamophase, and the lowest turnover in May 2002 in the limnophase ($B_{sim} = 0.72$). Significant differences for beta

Tab. 4. Gamma diversity registered among periods (limnophase and potamophase) for each sub-basin and years (2000-2011), and gamma diversity expected through of the nonparametric estimators (Chao, Jackknife 1 and 2, and Bootstrap) and their relative contributions (%) in each period and year.

	Gamma diversity observed	S_{chao}	$S_{jackknife1}$	$S_{jackknife2}$	$S_{bootstrap}$
Period					
Paraná					
Limnophase	543	691.3 (78.54%)	705.8 (76.93%)	779.4 (69.66%)	618.3 (87.82%)
Potamophase	277	459.2 (60.32%)	408.3 (67.84%)	490.9 (56.42%)	333.8 (82.98%)
Baía					
Limnophase	498	707.1 (70.42%)	664.8 (74.90%)	764.9 (65.10%)	571.6 (87.12%)
Potamophase	313	471.5 (66.38%)	446.2 (70.14%)	522.6 (59.89%)	371.9 (84.16%)
Ivinhema					
Limnophase	442	617.1 (71.62%)	590.1 (74.90%)	675.2 (65.46%)	507.7 (87.05%)
Potamophase	238	444.9 (53.49%)	363.4 (65.49%)	448.1 (53.11%)	291.1 (81.75%)
Years					
2000	275	385.0 (71.40%)	385.6 (71.30%)	439.5 (62.60%)	324.9 (84.60%)
2001	206	351.7 (58.60%)	302.7 (68.00%)	364.6 (56.50%)	247.5 (83.20%)
2002	259	358.9 (72.20%)	343.2 (75.50%)	390.9 (66.30%)	296.1 (87.50%)
2003	260	387.6 (67.10%)	368.2 (70.60%)	428.0 (60.70%)	308.2 (84.30%)
2004	312	432.4 (72.10%)	422.6 (73.80%)	481.2 (64.80%)	362.2 (86.10%)
2005	298	383.5 (77.70%)	392.9 (75.80%)	434.3 (68.60%)	342.3 (87.10%)
2006	307	392.1 (78.30%)	417.6 (73.50%)	455.5 (67.40%)	359.3 (85.40%)
2007	343	473.5 (72.40%)	462.4 (74.20%)	525.9 (65.20%)	396.8 (86.40%)
2008	238	356.3 (66.80%)	327.1 (72.80%)	381.4 (62.40%)	277.3 (85.80%)
2009	242	328.0 (73.80%)	325.2 (74.40%)	367.2 (65.90%)	280.0 (86.40%)
2010	302	480.6 (62.80%)	434.1 (69.60%)	515.7 (58.60%)	359.3 (84.00%)
2011	295	490.5 (60.10%)	429.1 (68.70%)	515.4 (57.20%)	352.6 (83.70%)
Total	753	890.3 (84.60%)	911.6 (82.60%)	978.6 (76.90%)	828.1 (90.90%)

diversity were verified between the years ($B_{sor} - p < 0.05$ and $B_{sim} - P < 0.05$) but not between limnophase and potamophase ($B_{sor} - P > 0.05$ and $B_{sim} - P > 0.05$). In addition, were not found significant correlations between the WL of the Paraná River and beta diversity (Fig. 6a-b), as well as between the beta diversity and coefficients of variation of the abiotic variables, except a weak correlation between B_{sim} and conductivity ($r = -0.33$).

DISCUSSION

The results obtained through this long-term study showed that different hydrosedimentological cycles, represented by variability of water level and environmental heterogeneity, are determinants on phytoplankton composition and diversity in the floodplain. Fluctuations in WLs in the main channels are fundamental to structure, func-

tion and integrity of the surrounding floodplain environments (Leira and Cantonati, 2008). Lateral habitats may be flooded over short- or long-term periods, which were reflected in the interannual variability of the potamophase and limnophase amplitude in this floodplain. Disturbance intensity is closely related to the intensity, frequency and amplitude of the different phases as well as to the degree of connectivity in the lakes (Neiff, 2001). The synergistic action of these attributes affected the different habitats and phytoplankton community in the Upper Paraná River floodplain. The high potamophase amplitudes detected in 2005, 2007, 2009, 2010 and 2011 were contrasted with the lowest amplitudes recorded in 2000 and 2001. Therefore, the connectivity indexes showed limnological differences between the twelve hydrosedimentological cycles and influenced mainly the phytoplankton composition and alpha and gamma diversity.

The high interannual variability of the phytoplankton

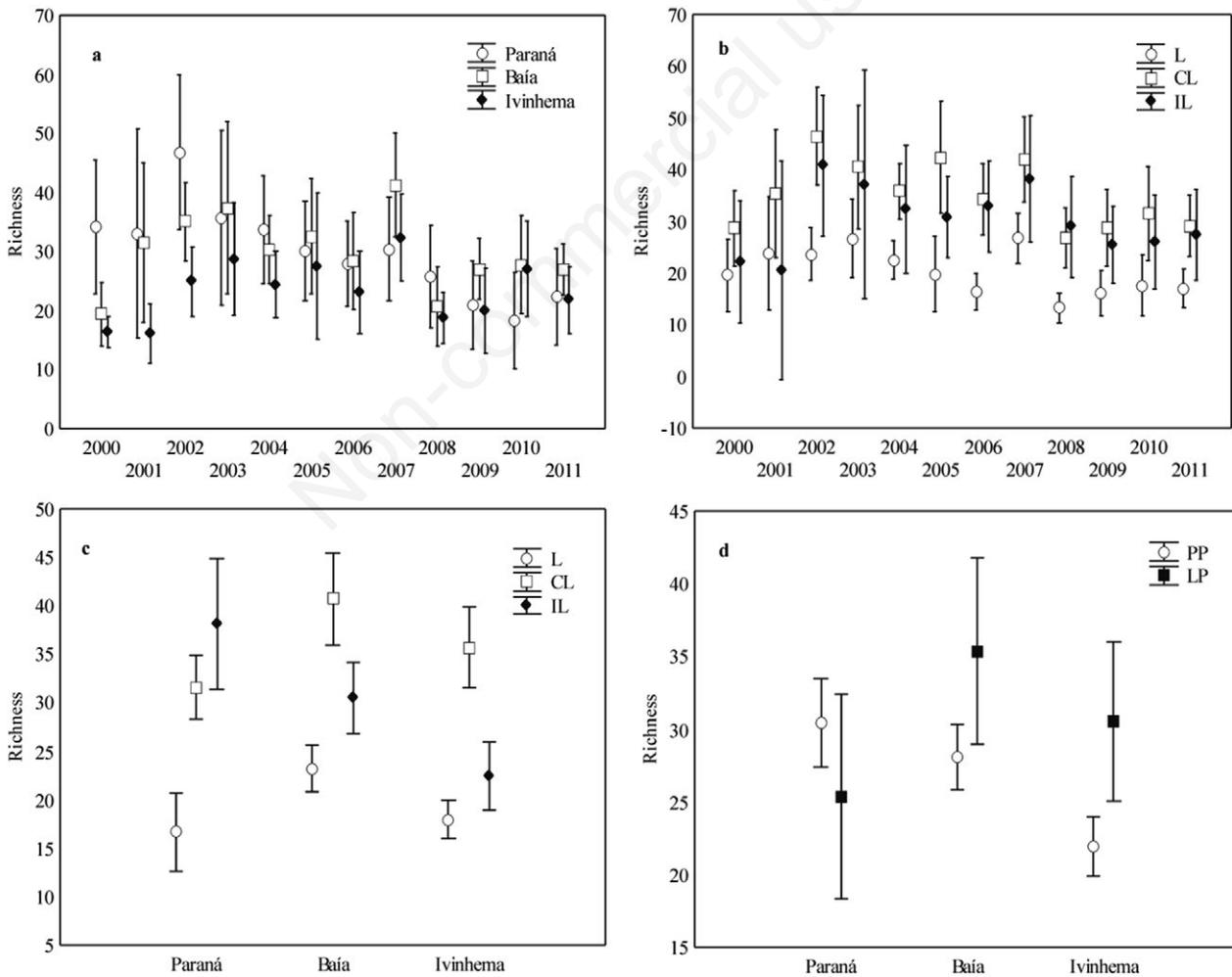


Fig. 5. Mean values and standard deviation of alpha phytoplankton diversity in the sites of the three sub-basins and periods between 2000 and 2011 in the upper Paraná River floodplain. CL, connected lake; IL, isolated lake; L, lotic; LP, limnophase; PP, potamophase.

composition was reflected by frequency of occurrence of species, with high contribution of rare species. Chlorophyceae presented the highest species richness, as reported in other studies of this floodplain (Train and Rodrigues, 1998, 2004; Bovo-Scomparin and Train, 2008; Borges and Train, 2009; Rodrigues *et al.*, 2009, 2015; Bortolini *et al.*, 2014, 2016a, 2016b), and it was mainly represented by cosmopolitan species. The Chlorophyceans are likely favored by the environmental conditions of limnophase periods (*e.g.* light and nutrient availability), that are common in this floodplain, besides their ecophysiological adaptations, which ensure that Chlorophyceae are successful in inland waters. Despite the high phytoplankton diversity, only *C. marssonii* and *C. acuta* were constant over time. These cryptophyceans are opportunists and mixotrophs organisms with a high

surface/volume ratio and high metabolism (Reynolds, 1998; Reynolds *et al.*, 2002; Padisák *et al.*, 2009) that most likely favor their permanence.

The spatial and temporal variability of species diversity illustrate the fundamental role of the sampling frequency for understanding ecological systems (Interlandi and Kilham, 2001) especially in a long-term. The high species diversity in floodplains is also related to the regional pool of species (Pinto *et al.*, 2015) in these ecosystems. Therefore, the high phytoplankton gamma diversity detected in this floodplain is a result of interactions between the structural heterogeneity of environments (isolated and connected lakes, and lotic sites) with different resources available (*e.g.*, nutrient, light), and the ability of planktonic algae to exploit such resources in each environment.

Although the gamma diversity presented significant differences between the hydrological periods, with higher values in the limnophase, and not between years, from a broader perspective, the highest gamma diversity recorded in 2007 may be related to intense potamophase and high hydrological connectivity in this year, which probably favored dispersion and exchange of phytoplankton inocula among sites, and later in low water level periods, these inocula are able to develop. In the other side, in 2001, a long limnophase (more than 360 days) associated with low connectivity prevailed and the lowest gamma diversity was recorded, probably limiting the dispersion and input of inocula in the sites of floodplain. Thus, these results confirm that regional-scale process, as the potamophase, contribute for the maintenance of local diversity (Ricklefs, 1987), and corroborate that the phytoplankton diversity can be favored, even if indirectly, with flooding and high WLS.

Alpha diversity was related to local and regional characteristics, resulting from hydrodynamic, chemical and biological variations (Borges and Train, 2009; Rodrigues *et al.*, 2009; Bortolini *et al.*, 2014), especially in the variations in the WL and environmental heterogeneity. The low mean alpha diversity values detected in lotic sites of the floodplain have been related to the greater instability of these lotic environments as well as to the greater flow velocity and lower water retention time (Train and Rodrigues, 2004). However, the highest mean values of phytoplankton richness founded in lakes connected, indicate the importance of the degree of connectivity between lakes and rivers as drivers of high phytoplankton richness in the upper Paraná River floodplain due to the easier exchange of inocula.

Previous studies have described human-induced degradation of the Paraná River and changes in limnological conditions over the last two decades, including degradation resulting from several dams built upstream of the study area, especially the Porto Primavera Dam (Souza

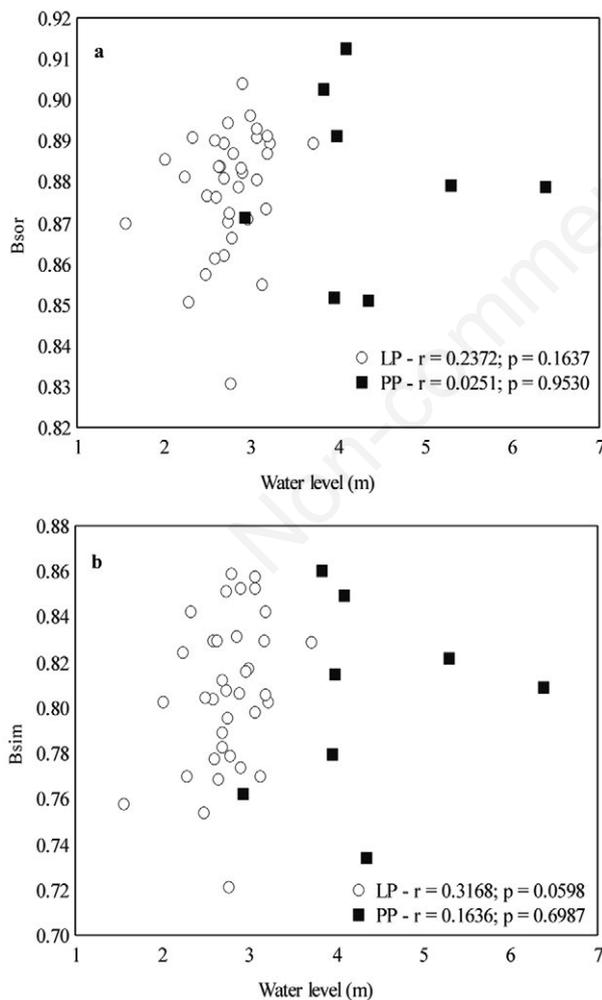


Fig. 6. Relationship between beta diversity, a) B_{sor} ; b) B_{sim} , and water levels of the Paraná River. LP, limnophase; PP, Potamophase; r, r of Pearson; p, significance level = $P < 0.05$).

Filho *et al.*, 2004; Souza Filho, 2009; Roberto *et al.*, 2009; Rodrigues *et al.*, 2009, 2015). Thereby, a clear decrease in phytoplankton alpha diversity in the main channel of the Paraná River has been documented and associated with alterations in transparency, nitrogen and phosphorus forms (Rodrigues *et al.*, 2015), as well as previous reports about the seston retention and sedimentation in the reservoir cascade upstream of the study site and high discharge rates (Roberto *et al.*, 2009; Bovo-Scomparin *et al.*, 2013). Despite this, the Paraná sub-basin still maintains high phytoplankton diversity, as seen in this study, due to the contribution of its associated lakes, which constituted, therefore, an important pool of species for this sub-basin, as well as for the floodplain as a whole. The establishment of phytoplankton species requires satisfactory conditions that allow them to disperse to a certain site and suitable environmental conditions for species survival and development (Reynolds *et al.*, 2012), including nutrient availability, light incidence and water column mixing.

The high beta diversity values observed in both the limnophase and potamophase, although without correlation with the abiotic variables related to hydrosedimentological regime of the upper Paraná River, may be related to other factors that not measured in our study. In addition, the absence of correlation between beta diversity and WLs of the Paraná River, unlike what is expected, with the homogenizing effect on aquatic communities (Thomaz *et al.*, 2007), is similar to other studies. Greater beta diversity in periods of higher WLs has been observed to phytoplankton also in the Araguaia River (Nabout *et al.*, 2007) and Amazon River lowlands (Nogueira *et al.*, 2010). Moreover, Simões *et al.*, (2013) reported that the zooplankton beta diversity was similar in an atypical dry year (2000) and in a year with a typical flood pulse (2010) in the upper Paraná River floodplain, as well as Ditttrich *et al.*, (2016) for fishes, macrophytes and zooplankton in a long-term study in this same floodplain. Borges and Train (2009) recorded dissimilarities in phytoplankton composition among habitats in this system but in their publication, only two years without potamophase were analyzed. Our results disagree Pinto *et al.* (2015) who observed greater beta diversity during the limnophase in the Pampean floodplain. This finding may be explained by the great length of the upper Paraná River as well as by the mosaic of habitats occurring in its floodplain, with distinct geomorphological and limnological characteristics and different degrees of anthropogenic action.

CONCLUSIONS

Our findings demonstrate that the variability in the hydrosedimentological cycles represented by water level variability and by conspicuous pattern of mosaic of habitats in this floodplain, are essential for sustaining phyto-

plankton diversity and ecosystem integrity. The hydrosedimentological regime of the upper Paraná River although it is regulated indirectly by climatic events that influence rainfall levels in the region, as well as by the operation of upstream dams, is an important factor in local and regional scale and must be sustained by the protection or restoration of natural hydrological regimes. This approach is relevant and proved be useful to understand floodplain systems and associated phytoplankton community, essential for management efforts and for conservation strategies.

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