SYNERGISTIC EFFECTS OF NATURAL AND ANTHROPOGENIC IMPACTS ON ZOOPLANKTON DIVERSITY IN A SUBTROPICAL FLOODPLAIN: A LONG-TERM STUDY

Claudia Costa Bonecker[1], Leidiane Pereira Diniz[1]*, Louizi de Souza Magalhães Braghin[1], Tatiane Mantovano[1], João Vitor Fonseca da Silva[2], Francieli de Fátima Bomfim[1], Dieison André Moi[1], Sabrina Deosti[1], Gabriela Naomi Tanaka dos Santos[3], Donisete Aparecido das Candeias[1], Anna Julya de Macedo Machado Mota[3], Luiz Felipe Machado Velho[1] & Fábio Amodêo Lansac-Tôha[1]

[1] Universidade Estadual de Maringá, Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais, Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Av. Colombo, 5790, CEP: 87020-900, Campus Universitário - Maringá - PR, Brazil.

[2] Universidade Estadual de Maringá, Programa de Pós-Graduação em Biologia Comparada- PGB, Núcleo de Pesquisas em Limnologia Ictiologia e Aquicultura, Av. Colombo, 5790, CEP: 87020-900, Campus Universitário - Maringá - PR, Brazil.

[3] Universidade Estadual de Maringá, Graduação em Ciências Biológicas, Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Av. Colombo, 5790, CEP: 87020-900, Campus Universitário - Maringá - PR, Brazil.

E-mails: claudiabonecker@gmail.com; leidianeediniz@gmail.com (*corresponding author); lobraghin@hotmail.com; mantovano.t@outlook.com; joaovitorbio@live.com; franbonfim.bio@gmail.com; dieisonandrebv@outlook.com; sabrinadeosti2@gmail.com; gnaomi97@gmail.com; donisetetiti@hotmail.com; annajulmm@gmail.com; felipe@nupelia.uem.br; fabio@nupelia.uem.br

Abstract: Large biological diversity can be observed in floodplains, which is linked to several ecosystem processes, such as productivity and nutrient cycling; among the species involved in these processes are zooplanktonic organisms. Here, we aimed to quantify the temporal trend of zooplankton, through changes in species richness and composition (β-diversity) and the abundance of individuals, in preserved and non-preserved sites of the Upper Paraná River floodplain during the last 19 years. 617 species (321 rotifers, 135 testate amoebae, 107 cladocerans, and 54 copepods) were recorded. The highest species richness was verified in 2002 and the lowest in 2016. Zooplankton richness and abundance in non-preserved sites show clear temporal homogenization, while preserved sites show cyclical fluctuations over time. The rarefaction curve showed the biodiversity potential in this floodplain. Three invasive species were recorded (*Kellicottia bostoniensis*, *Daphnia lumholtzi*, and *Mesocyclops ogunnos*). The variation in the hydrologic regime, the oligotrophication, and the reduced connectivity among the sites were the main factors interfering in the species composition over the years and leading to a reduction of the species richness and abundance. The preservation of the tributaries with pristine characteristics is very important for the mitigation of these synergistic effects under the community structure.

Keywords: Biodiversity; damming effect; invasive species; large rivers; oligotrophication.

INTRODUCTION

One of the challenges for the scientific community is to measure temporal changes in natural environments, including the accelerated loss of biodiversity in recent decades (Magurran & Dornellas 2010, Mace *et al.* 2010). One way to better understand how synergistic effects reduce biodiversity is through temporal monitoring, such as Long Term Ecological Research (LTER). This approach allows a systemic examination of the communities, providing a robust view of the past and present, which works as a theoretical framework to predict future trends of community change in the face of environmental impacts (Crawley 2007). Long-term studies are essential for the conservation and management of natural resources, such as water and biodiversity. Therefore, through long-term research it is possible to establish patterns to understand ecosystem dynamics and organisms' ecological roles (Franklin 1989, Field *et al.* 2009). However, long-term studies are scarce due to limited financial resources, especially in developing countries, and there are difficulties in standardizing temporal methodologies.

Among the communities that can be used as a model to understand the temporal dynamics of freshwater ecosystems, we highlight the zooplanktonic community, which consists of testate amoebae, rotifers, cladocerans, and copepods. This community presents a high abundance and species diversity (Lansac-Tôha *et al.* 2009, Bozelli *et al.* 2015), participating actively in the production and cycling of matter in freshwater ecosystems (Allan 1976, Auer *et al.* 2004). Also, due to their short life cycle and high reproductive efficiency, zooplankton species are considered excellent bio-indicators in aquatic environments, demonstrating the cumulative effects of environmental changes, either in the short or long term (Ovaskainen *et al.* 2019).

Zooplankton also presents a high taxonomic and functional diversity in floodplains (Arrieira *et al.* 2015, Braghin *et al.* 2018), as a result of spatial and temporal fluctuation in natural environmental conditions (environmental heterogeneity) (Junk *et al.* 1989, Thomaz *et al.* 2007, Ward & Tockner 2001, Opperman *et al.* 2010). In floodplains, the hydrological regime is the main force responsible for changes in the physical structure and water chemical characteristics, constituting the main factor in the organization of the aquatic communities (Junk *et al.* 1989, Neiff 1990, Opperman *et al.* 2010). However, these ecosystems have suffered from many anthropogenic impacts, including the construction of dams, which causes a reduction in nutrients due to sedimentation, a reduction in the water flow and control of the hydrologic regime, leading to changes in aquatic communities over time (Winemiller *et al.* 2016).

In the Upper Paraná River Floodplain, the retention in suspended particles after the reservoir formation was responsible for a drastic increase in water transparency and a reduction in the concentration of nutrients, such as total phosphorus and nitrogen (Thomaz *et al.* 2004, Roberto *et al.* 2009). Long-Term Ecological Research (LTER) in the Upper Paraná River Floodplain (site PIAP) monitors the effect of the hydrological regime and the regulations by dams upstream on the physical-chemical conditions and the biota of this floodplain. Based on these fluctuations in zooplankton community, due to natural and anthropogenic impacts (hydrological regime and dams, respectively), here we aimed to quantify the temporal trend of zooplankton through changes in species richness and composition (β-diversity) and the abundance of individuals, in preserved and non-preserved environments of this Neotropical floodplain over the last 19 years.

MATERIAL AND METHODS

Study area

The Upper Paraná River Floodplain (22º40'-22º50'S e 53º10'-53º40'W) (LTER/site PIAP) covers approximately 802,150 km². This ecosystem comprises three sub-basins, the Paraná sub-basin (main river), the Baía and Ivinhema sub-basins (tributaries), including numerous environments, such as connected and isolated lakes, backwater areas, channels and rivers. This distinct connectivity among the environments gives the floodplain high heterogeneity (Souza Filho 2009).

The PIAP site (Upper Paraná River Floodplain) is protected by three conservation units, two Federal Units: "Environmental Protection Area of the Islands and Varzeas of the Paraná River" and "Ilha Grande National Park" and one State Unit:
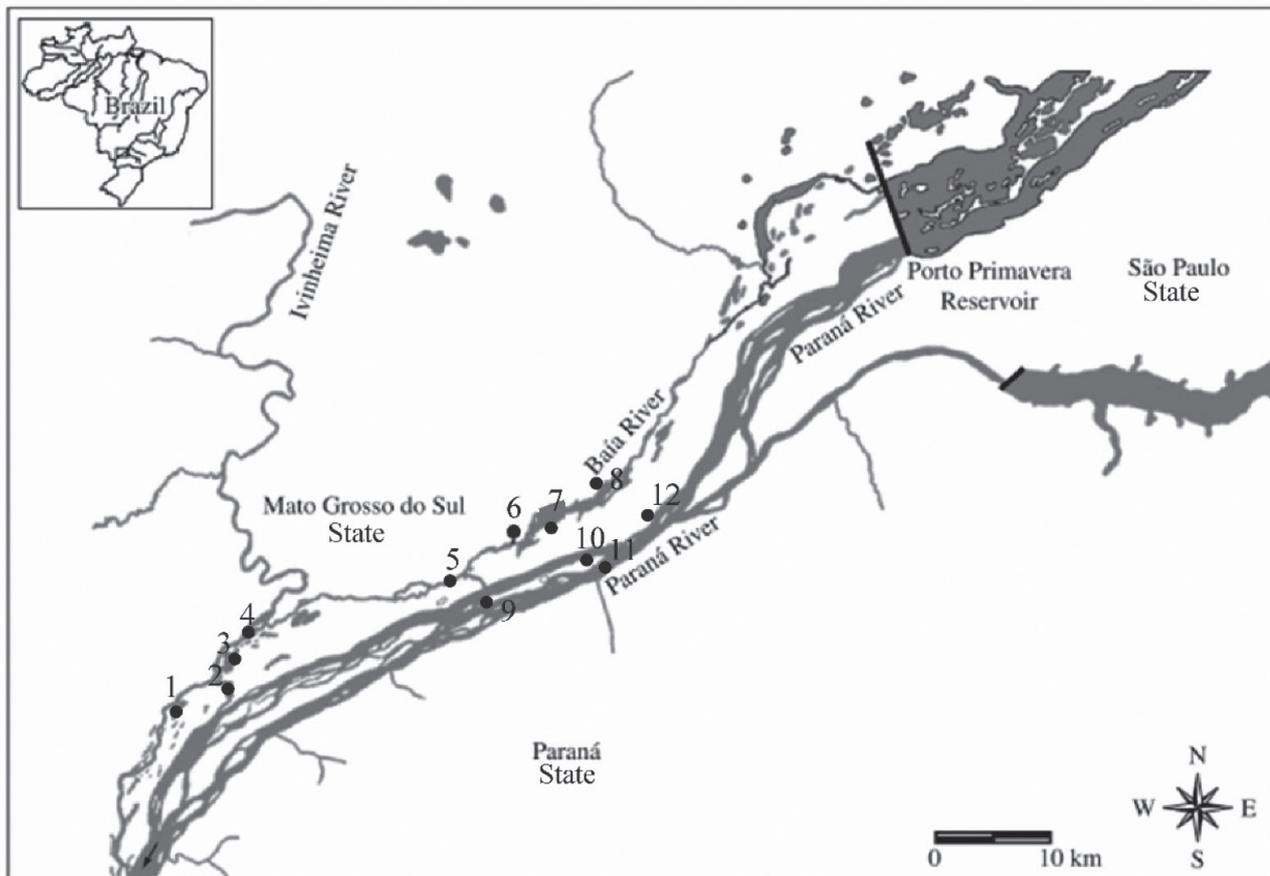
Figure 1 Map representing the sampled sites. From 1 to 4 belong to Ivinheima sub-basin, 5-8 to Baía sub-basin and, 9-12 are from the Paraná River sub-basin. Numbers 1, 7 and 9 are isolated lakes, 3, 6, 10 and 12 are connected lakes, 2 and 5 are channels. Numbers 4, 8 and 11 are the sampled sites in the rivers.

"State Park of Ivinhema River". The floodplain is the last non-dammed stretch of the Paraná River, restricted to 230 km between the Porto Primavera dam (São Paulo State, Brazil) and Itaipu reservoir (Paraná State, Brazil) (Figure 1). This system also has been suffering from the effects of oligotrophization of the numerous reservoirs built upstream (Roberto *et al.* 2009).

Sampling and laboratory analyses

The sampling occurred in 12 sites (comprising three rivers, two channels, four connected lakes and three isolated lakes), quarterly from 2000 to 2018. The zooplankton was sampled on the sub-surface of the pelagic region in each site. For that, a motorized pump and plankton net (68 μm mesh) were used, and 600 L of water was filtered per sample. The collected material was kept in flasks with formalin 4 % buffered with calcium carbonate. The species identification (testate amoebae, rotifers, cladocerans, and copepods), species richness and abundance (ind. m^{-3}) were

estimated according to the methodology described by Lansac-Tôha *et al.* (2009).

Hydrologic levels, total phosphorous and water transparency

The Paraná River hydrologic levels (2000-2018) were obtained on the left bank of the river in the town of Porto Rico. The overflow level (or the beginning of the flood) was considered to be when the Paraná River hydrologic level achieved 3.5 m (Souza Filho 2009). The physical and chemical variables were sampled simultaneously with zooplankton samplings. The water transparency (m) was estimated using a Secchi disk (black and white measuring 0.30 m in diameter). To estimate the total phosphorus (μg L^{-1}), the water was collected with a Van Dorn bottle and the samples were kept cool until the filtration in GF 52-C membranes (< 10 hours after sampling); after that, the samples were frozen (–20 °C) for further analyses in a spectrophotometer, according to Golterman *et al.* (1978).

Data analysis

To verify the efficiency in the sampling of zooplanktonic species over the years, a rarefaction curve was calculated using the "rarefy" function in R. To analyze the changes in the composition of zooplankton species during the last 19 years, we performed a multivariate homogeneity of groups dispersion test (PERMDISP; Anderson *et al.* 2006), which tested the variability of the zooplankton communities between sites in each year. A centroid was computed for each year and the distances between each sample and the centroid were considered the β-diversity. The significance (p < 0.05) of the differences in beta-diversity between each year was tested using a permutation test with 999 permutations. The results are shown in a *boxplot* built with the distances from the PERMDISP, using the "betadisper" function of "vegan" package in R (Oksanen *et al.*, 2018).

The tendencies in temporal variations in species richness and abundance of individuals over time were estimated through Generalized Mixed Effects Additive Models (GAMM –Wood 2017), using the type of site (river, channel, connected lake and isolated lake) as a factor in the random models. We performed mixed models because we have sites with distinct morphological and limnological characteristics, and it should be assumed that there is independence between the environments. Furthermore, to correct the possible temporal autocorrelation (as the sampling occurred on a temporal scale) auto-regressive model 1 from the GAM models was performed, using the "corAR1" of "nlme" package (Pinheiro *et al.*, 2019) and "acf" and "stats" functions using the R environment 3.6.2 (R Core Team, 2018).

As the sites present distinct impacts (anthropogenic effects such as damming, overfishing and pollution by urbanization, and preserved areas inside conservation units; Agostinho *et al.*, 2007) we separated the environments into two categories: preserved and non-preserved environments, according to literature observation and local experts' knowledge (Braghin *et al.*, 2015). Thus, we fitted a GAM model to evaluate temporal tendency in zooplankton richness and abundance of individuals for all sites together and for preserved and non-preserved sites separately. These models are indicated when looking for trends without a previous expectation of the relationship between the data, and they can be used to explore and obtain nonlinear adjustments for any data structure (Wood 2006). The species richness and abundance of individuals were log-transformed (log10) before the models' construction and the normal distribution was the one that best fitted the data.

In this way, the models to test the tendency between the data follow the generic equation:

$$g \text{ attribute} = b0 + s(time) + \alpha_i,$$

, where 'g' is the link function, 'attribute' is the richness and abundance, 'b0' is the intercept, 's' is the smoothing curve adjusted to the model (Wood 2006), 'α_i' is the random intercept (which is assumed to have a normal distribution with average 0 and variance equal to σenviroments ^{2}), and the 'time' corresponds to 65 samples (continuous and integer numbers from 1 to 65). The model adjustment occurred by the verisimilitude method. The tendency curve was obtained through the smoothing method - LOESS (Locally-Weighted Scatterplot Smoother), where for each point a surrounding point is defined and then the points are adjusted in a more robust and parsimonious way chosen from the data. For all GAM models, we used the "gamm" function in R.

All analyses were performed using the R environment 3.6.2 (R Core Team, 2018). The following packages were used: "*vegan*" (Oksanen *et al.,* 2018), "*mgcv*" (Wood 2017), "*stats*" (Wood 2017), and "*ggplot2*" (Wickham 2016).

RESULTS

The results of the hydrological levels of the Paraná River (2000-2018) revealed that periods of extreme flooding (≥ 6.0 m) were rare in the floodplain, and occurred only during 2005, 2009, 2010 and 2015. In contrast, droughts and extreme droughts (≤ 3.5m) were more common in the floodplain, mainly in 2001, 2014 and 2017 (Figure 2). Water transparency ranged from 1.85 m (SD ± 0.21 m, during 2001) to 5.73 m (SD ± 0.87 m, during 2009), while the total phosphorus ranged from 3.33 µg L^{-1} (SD ± 6.46 µg L^{-1}, during 2013) to 18 µg L^{-1} (SD ± 20.30 µg L^{-1}, during 2000) (Table 1).

Records were made of 619 species over the 19 years: 323 rotifers, 136 testate amoebae, 107
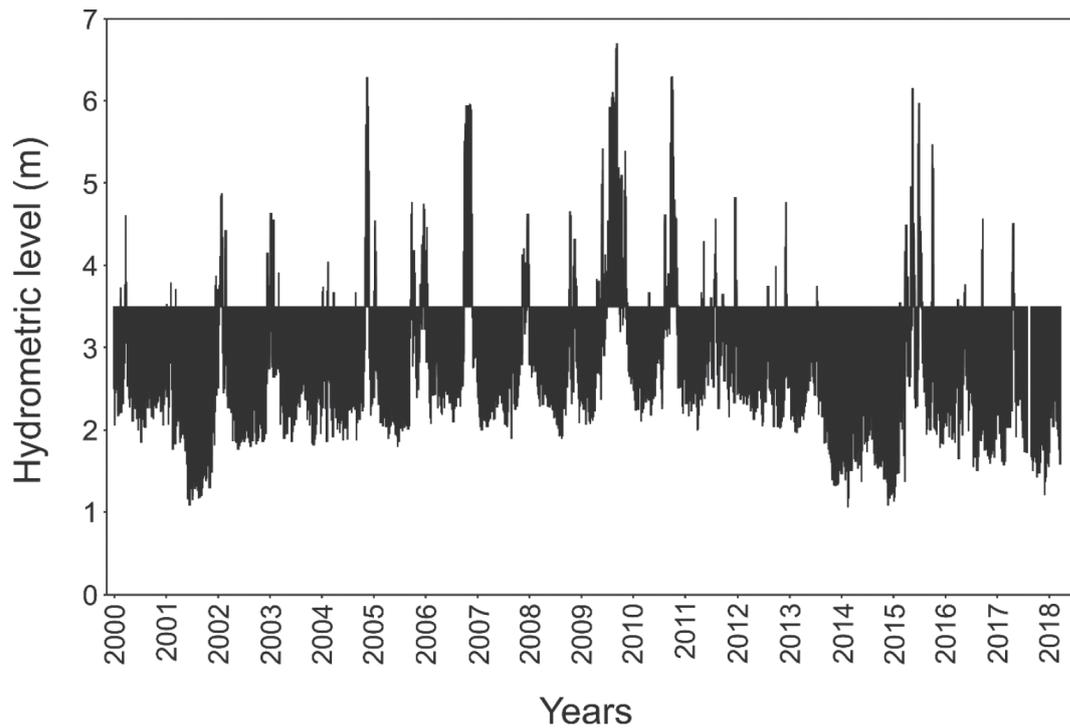
Figure 2. Hydrologic level of the Paraná River (town of Porto Rico) from 2000 to 2018. The cut in the hydrologic series represents the level in overflow and flooding above 3.5 m, and below 3.5 m represents drought periods.

Table 1. Minimum and maximum values, mean and deviation (SD) of phosphorus values (µg L^{-1}) and water transparency (Secchi = m) between 2000 and 2018 in the Upper Paraná River floodplain totaling 864 samples.

Year	Total Phosphorus (µg L^{-1})			Water transparency (m)		
	Range	Mean	SD	Range	Mean	SD
2000	3.00 – 47.00	18.00	20.30	1.50 - 3.40	2.44	1.03
2001	7.60 - 11.10	9.35	2.47	1.70 – 20.00	1.85	0.21
2002	9.84 - 12.47	11.4	1.38	1.55 - 2.50	2.18	0.58
2003	14.79 - 15.64	15.21	0.60	1.45 - 4.70	3.08	2.30
2004	9.93 - 18.21	13.64	3.48	1.70 – 4.00	2.94	0.99
2005	3.92 - 13.17	8.98	4.22	2.15 – 4.00	2.93	0.58
2006	5.59 - 14. 53	9.06	4.02	2.15 - 5.50	3.96	1.38
2007	6.59 - 17.30	11.61	4.69	1.40 - 4.80	3.65	1.60
2008	0.10 - 8.22	6.42	4.69	3.80 - 4.60	4.30	0.36
2009	9.48 - 13.85	10.10	2.85	4.50 - 6.40	5.73	0.87
2010	7.38 - 12.79	9.70	2.37	1.95 – 6.00	4.54	1.78
2011	7.30 - 16.62	10.89	4.20	3.20 - 7.50	5.10	2.09
2012	2.70 - 11.10	5.83	4.59	4.40 - 5.60	5.08	0.61
2013	0.10 - 13.01	3.33	6.46	3.40 - 4.50	4.09	0.51
2014	7.19 - 10.39	4.45	1.41	3.70 - 6.20	4.45	1.19
2015	8.85 - 18.38	12.28	4.31	0.70 - 4.80	3.01	1.85
2016	8.29 - 13.31	10.28	2.25	2.60 - 4.40	3.53	0.75
2017	14.07 - 17.47	15.77	3.20	4.10 - 4.35	4.23	0.18
2018	11.82 - 19.07	16.40	3.20	2.20 - 3.70	3.15	0.67

cladocerans and 53 copepods (Supplementary material, Table 1A). The rarefaction curve revealed elevated high number of species recorded in the samples over the years. Although there is a stabilization trend, the asymptote has not yet been reached (Figure 3), showing the biodiversity potential in the floodplain. The highest species richness was verified in 2002 (average of 57.3 ± SD 14.6 species) and the lowest in 2016 (average of 18.2 ± SD 8 species). The highest abundance was in 2001 (average of 369,951.1 ± SD 1,236,994.5 ind. m^{-3}) and the lowest in 2016 (average of 20,637.1 ± SD 52,693.1 ind. m^{-3}; Supplementary material, Table 1B).

The species composition (β-diversity) differed significantly over time in all sites together ($F = 6.74$; $p < 0.01$, Figure 4a), in preserved ($F = 5.24$; $p < 0.01$, Figure 4b) and non-preserved sites ($F = 2.69$; $p < 0.01$, Figure 4c), showing the same pattern of variation independent of site category. The differences in species composition increased from 2000 to 2007, and then after 2007 a decrease was observed, followed by a new increase observed from 2015 to 2018 (Figure 4).

There was a clear tendency toward reduction in the species richness and abundance of individuals from 2002 to 2018 considering all sites of the floodplain together, and these attributes differed significantly over time (richness: edf = 16.56, $F = 17$, $p < 0.01$; abundance: edf = 12.01, $F = 13.68$, $p < 0.01$) (Figure 5). Both zooplankton richness and abundance of individuals in preserved (richness: edf = 17.71, $F = 14.83$, $p < 0.001$; abundance: edf = 12.17, $F = 14.87$, $p < 0.01$) and non-preserved sites (richness: 12.14, $F = 3.57$, $p < 0.001$; abundance: edf = 10.61, $F = 3.91$, $p = 0.048$) also differed significantly over time (Figure 6). Zooplankton richness and abundance in preserved sites showed cyclic fluctuations over time, with the highest values during 2002 and decreasing after 2014 (Figure 6A, C). In non-preserved sites, abundance of individuals and species richness showed lower variation with a small peak during 2000 and 2002 (for abundances and richness respectively) but remained constant after 2004 (Figure 6B, D).

DISCUSSION

The environmental heterogeneity created by natural and anthropogenic influences has the power to change the species richness and composition as well as the abundance of individuals (Bomfim *et al.* 2017, Larsen *et al.* 2019).
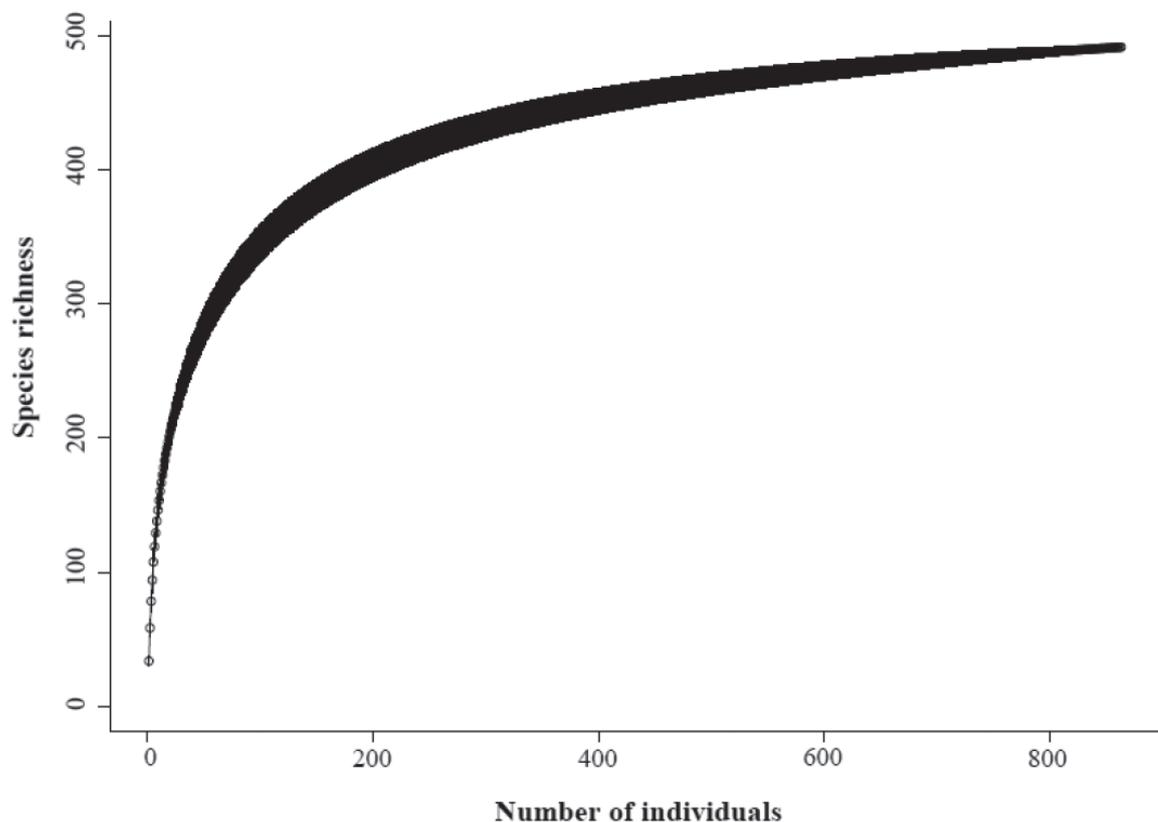
Figure 3. Rarefaction curve of the zooplankton community in the Upper Paraná River floodplain between 2000 and 2018.
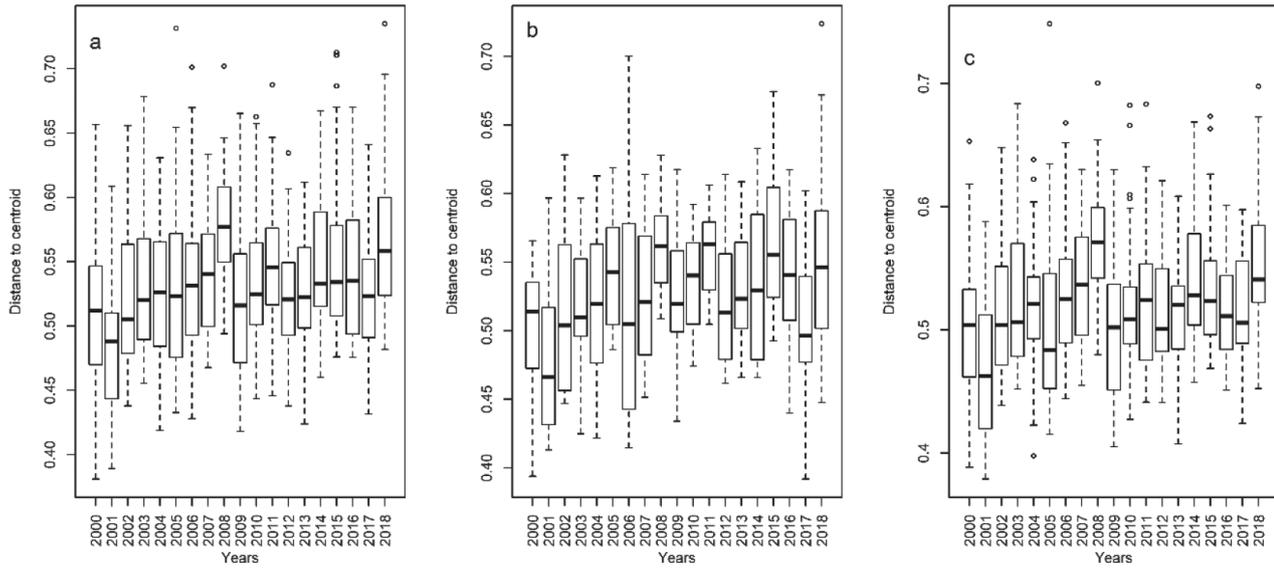
Figure 4. Difference in species composition, represented by the distance from the centroid using the PERMIDISP analysis, between 2000 and 2018. 'a' represents all sites together, 'b' represents the preserved sites and, 'c' represents the non-preserved sites.
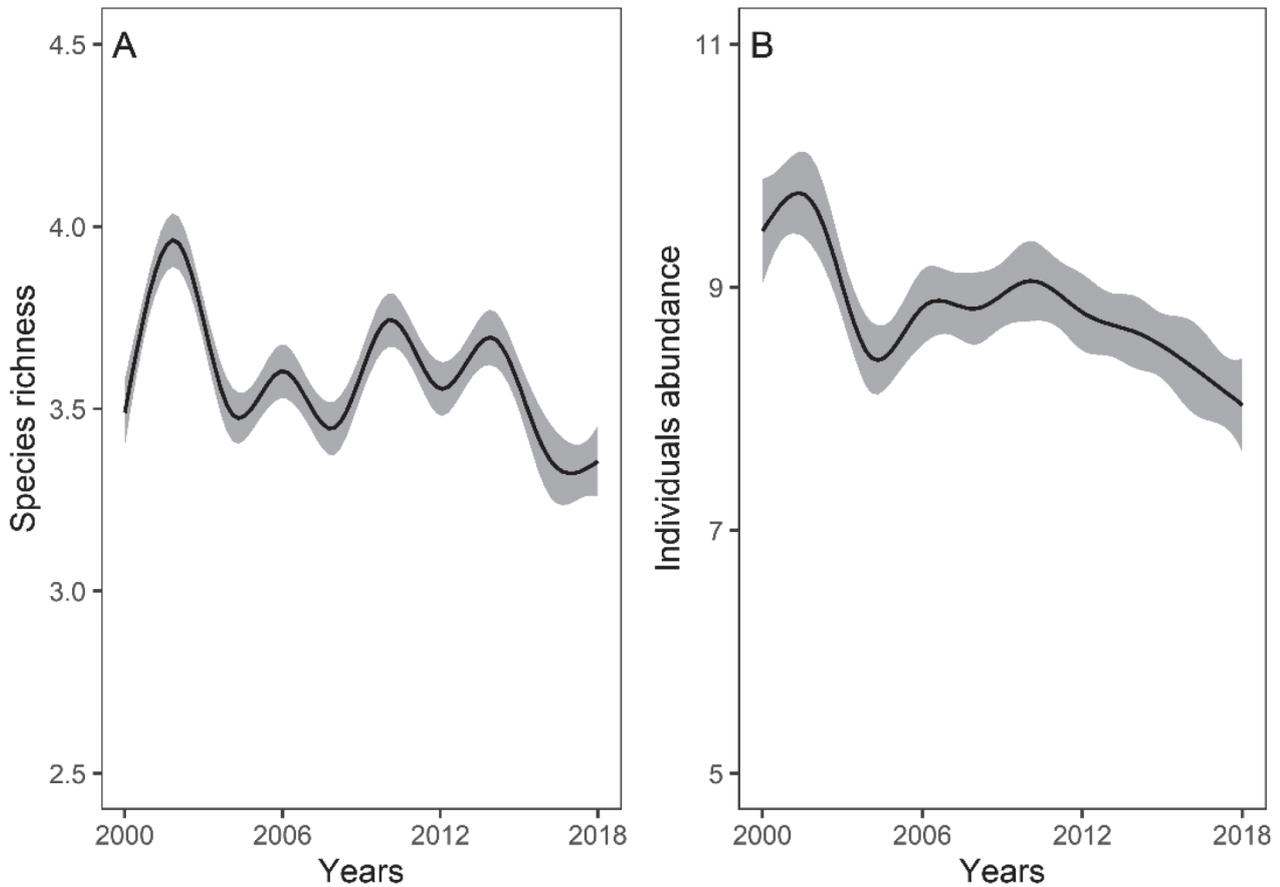
Figure 5. Smoothing curve displaying temporal fluctuations of species richness (A) and abundance of individuals (ind m^{-3}) (B) over time for all sites from the floodplain together. The shading in gray indicates the confidence interval of the adjusted data ± 95 %.
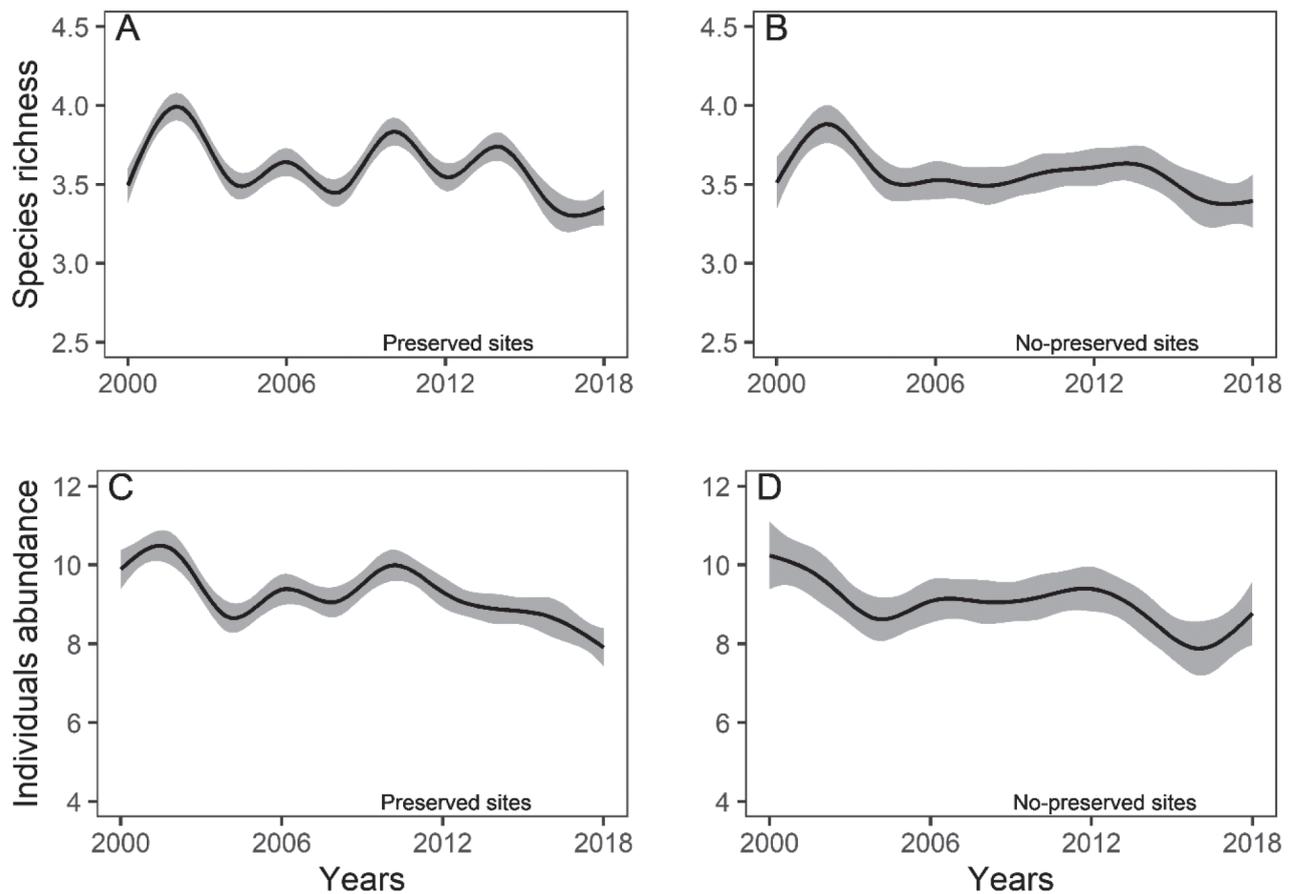
Figure 6. Smoothing curve displaying temporal fluctuations of species richness (A and B) and abundance of individuals (C and D) (ind m⁻³) over time in preserved (A and C) and non-preserved sites (B and D). The shading in gray indicates the confidence interval of the adjusted data ± 95 %.

Here, the zooplankton community showed high fluctuation over the last 19 years in the Upper Paraná River floodplain, with reduced species richness and abundance of individuals during the last four years. These changes were possibly driven by the combination of the hydrological regime and the dam regulation, which represents the natural and anthropogenic stressors (respectively) in this floodplain. Extreme floods and droughts alter the zooplankton dynamic by changes in the regional factors (such as the increase in the connectivity and dispersion) and in the local factors (such as food availability and predation) (Bozelli *et al.* 2015). However, the anthropogenic impacts promote greater environmental stress, compared to natural impacts, as they affect the species capacity in tolerating these disturbances, affecting the establishment of the communities (Loreau 2000, Hooper *et al.* 2005; Simões *et al.* 2015).

The high occurrence of zooplankton species in floodplains (Robertson & Hardy 1984, Lansac-Tôha *et al.* 2009) is related, among other factors,

to the presence of extensive aquatic macrophyte banks in the limnetic regions of the environments, especially in lakes (Brito *et al.* 2020). Submerged or free-floating macrophytes support a higher number of species in tropical lakes (Cazzanelli *et al.* 2008) by increasing the area for colonization, food availability, and refuge from predators (Meerhoff *et al.* 2007, Buosi *et al.* 2011). Some studies have shown that the habitat complexity, created by aquatic macrophytes, acts in these environments as a predictor of biodiversity, increasing the species richness and promoting a greater genetic pool (Lansac-Tôha *et al.* 2003, Cunha *et al.* 2012, Kovalenko *et al.* 2012, Padovesi-Fonseca & Rezende, 2017).

Rotifers, in general, represent the main contributors to the zooplankton diversity in floodplains (Sharma 2005, Lansac-Tôha *et al.* 2009, Chaparro *et al.* 2011, Bozelli *et al.* 2015). This fact is confirmed by our results, as rotifers contributed more than 52% of the total species observed over the last 19 years. In zooplankton evolutionary

history, rotifers may have been successful because they are opportunistic, have a fast life cycle, survive in adverse conditions of temperature and resource availability, and they are also less vulnerable to predation because of their small size compared to other zooplankton groups, such as cladocerans and copepods (Allan 1976, Segers 2008).

Concerning the factors acting on species establishment, flooding and dry periods are key factors in promoting ecosystem functioning and in determining biodiversity patterns in floodplains (Neiff 1990, Bunn & Arthington 2002). The oscillations in hydrometric levels maintain the connectivity among the sites in these ecosystems, determining the dynamics in the abiotic and biotic factors (Thomaz *et al.* 2004). The increase in the number and extension of drought periods, as well as the absence of prolonged floods after the Porto Primavera reservoir formation (1998), were possibly the main factors acting on the zooplankton community in the Upper Paraná River floodplain. Other studies in this floodplain have shown that the temporal variability in the limnological variables drives the variation in the intensity, regularity, and frequency of the flooding periods, which has changed the species occurrence (Bonecker *et al.* 2013).

Biological communities can oscillate naturally or under the influence of anthropogenic alterations, over time and space, and also in a dynamic and non-linear way (Angeler & Moreno 2007), as observed for composition, species richness and zooplankton abundance. However, observing the general trend over time, community attributes have decreased during recent years. This fact confirms the importance of long-term studies to better comprehend the tendency to see variations in communities over time and their influence on ecosystem processes, thus providing more than just a momentary picture of the community dynamics.

The species composition varied most in 2008, considering all sites together and separated by preserved and non-preserved sites. This variation occurred soon after an extensive flood period during 2007, reaffirming the influence of the hydrological level on zooplankton dynamics (the flood in 2007 lasted 43 days > 6.0 m in the hydrological level and 77 days > 3.5 m; the elasticity of the flood was 2.98; elasticity index = maximum hydrological level/ minimum hydrological level); the connectivity among the non-preserved sites was 0.27; and in preserved sites it was 0.17 (connectivity index = flood days/drought days; for more details please see Fernandes *et al.* 2009). In 2008, we also observed a decrease in total phosphorus, which might indicate lower biomass production; this ecosystem process is very important in wetlands (Van der Valk 2012). The reduction in primary productivity reflects lower energy availability for high trophic levels, affecting the entire ecosystem (Rodrigues *et al.* 2009, Mormul *et al.* 2012). Moreover, the increase in the water transparency (linked to fewer nutrients) allows the establishment of submerged macrophytes, which remove even more inorganic phosphorus from the water column, which contributes to a fall in the plankton biomass. All these changes have also implications for *varzea* fertility, because they can reduce inorganic nutrients available to *varzea* (Agostinho *et al.* 2008, Bonecker *et al.* 2013, Rodrigues *et al.* 2015).

The highest species richness recorded in 2002 is also related to a wide amplitude of flooding (55 days), which occurred after two years of drought (2000, 27 days of flooding and 2001, 10 days of flooding). The connectivity among the sites also increased in 2002 (connectivity index; $ci = 0.16$), after low values registered during 2000 ($ci = 0.08$) and 2001 ($ci = 0.03$; Lansac-Tôha *et al.,* 2009). Although the overflow was not so intense in 2002, there was a resumption in the flooding periods, with discharges of water in the Paraná River by the two reservoirs upstream, Porto Primavera (~88 % and ~51 % of the total discharge in the river) and Rosana reservoir (~12 % and ~49 % of the total discharge in the river; Meurer *et al.* 2005). It is known that the lentic region of the reservoirs allows a strong development of plankton, and discharges by the reservoirs allow the dispersion of these communities (Agostinho *et al.* 2009).

However, these same factors (flood and connectivity) led to a different response from the community, such as the high abundance of individuals and high similarity in the species composition during 2001. This year was characterized by a prolonged dry period (355 days), which allowed a greater concentration of individuals, intensifying the competition among the species and favoring the increase in the abundance of those species that are better competitors (Simões *et al.* 2012, Bozelli *et al.* 2015),

resulting in higher population peaks and a greater similarity in species composition. Furthermore, high values of phytoplankton biomass were recorded this year (Train & Rodrigues 2004), suggesting the contribution of the food resources to the development of the zooplankton community. The low hydrologic level in 2001 was also related to the second step in filling Porto Primavera (the first reservoir upstream), causing a large reduction in the flow rates in the Paraná River, far below the historical average.

During 2002 the zooplankton abundance and richness were high, probably related to the increased flooding, but the situation in 2016, which also presented high hydrologic levels (after five years without a large flood, maximum values up to 5.10 m), showed lower species richness and zooplankton abundance. These lower values might be a response to the dilution effect (Thomaz *et al.* 2007) and the accumulated effects of the dam over time. At the same time that the species could disperse among sites (with the increase in connectivity and water flow), the hardness of the sites could be selecting the species and establishment of organisms. Similar factors may have acted during 2018, because this period displayed high variation in zooplankton composition (considering all sites of the floodplain together), but lower zooplankton abundance and richness, probably due to the absence of extensive floods in 2017 and 2018 (12 days > 3.5m hydrological level in 2017 and 15 days in 2018). It is suggested that long drought periods have the power to select the species, acting as an environmental filter, which is reflected in a higher dissimilarity in the species composition (Thomaz *et al.* 2007, Bozelli *et al.* 2015).

Another impact of dam-building on large rivers is that reservoirs act as stepping-stones for the dispersal of exotic species across landscapes (Havel *et al.* 2005). We recorded three invasive species, *Kellicottia bostoniensis* (Rousselet, 1908) (rotifer) (Serafim *et al.* 2003), *Daphnia lumholtzi* Sars, 1885 (cladoceran) (Simões *et al.* 2009) and, *Mesocyclops ogunnos* Onabamiro, 1957 (copepod) (Lansac-Tôha *et al.* 2002). Although these species are not very frequent and occur in low densities, their occurrence causes concern, as they are better competitors than the native species and might cause biotic homogenization (Mack *et al.* 2000).

Because of the countless impacts in the floodplain, we flag the importance of preserving the tributaries, as they work as a source of propagules, helping in biodiversity maintenance and ecosystem functioning (Braghin *et al.* 2015, 2018, Bomfim *et al.* 2017). Besides, the tributaries can also play a role in reducing the oligotrophication effects, since they run in distinct areas and contribute nutrients and biota to the main river (Jati *et al.* 2017, Santana *et al.* 2017).

Finally, over the 19 years, it was possible to observe high zooplankton diversity and the response of the community to natural and anthropogenic impacts on the floodplain. The variation in the natural hydrologic regime, the oligotrophication (i.e., decrease in total phosphorus and increase in water transparency) due to upstream dams, and the reduced connectivity between the Paraná River and the *várzea*, were possibly the main factors interfering in the species establishment. In addition, the most intense and frequent periods of drought observed during the last 19 years in this floodplain might reduce species richness and abundance of individuals, making species composition more similar over time, which may have negative consequences for ecosystem functioning, as these species play important roles in the production and cycling of matter inside food-webs.

ACKNOWLEDGMENTS

REFERENCES

Agostinho, A.A., Gomes, L.C. & Pelicice, F.M. 2007. Ecologia e manejo de recursos pesqueiros em reservatórios do Brasil. EDUEM, Maringá. p. 501.

Agostinho, A. A., Pelicice, F. M., & Gomes L. C. 2008. Dams the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. Brazilian Journal of Biology, 68(4), 1119–1132. DOI: 0.1590/S1519-69842008000500019

Agostinho, A. A., Pelicice, F. M., & Marques, E. E. 2009. Reservatório de peixe angical: bases ecológicas para o manejo da ictiofauna. São Carlos: RiMa: p. 188.

Allan, J. D. 1976. Life History Patterns in Zooplankton. The American Naturalist 110, 971, 165–180. DOI:10.1086/283056 39

Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters, 9(6), 683–693. DOI: 10.1111/j.14610248.2006.00926.x

Angeler, D., & Moreno, J. 2007. Zooplankton community resilience after press-type anthropogenic stress in temporary ponds. Ecological Applications, 17(4), 1105–1115. DOI: 10.1890 / 06-1040

Arrieira, R. L., Schwind, L. T. F., Bonecker, C. C., & Lansac-Tôha, F. A. 2015. Use of functional diversity to assess determinant assembly processes of testate amoebae community. Aquatic Ecology, 49, 561–571. DOI: 10.1007/s10452-015-9546-z

Auer, M. T., & Powell, K. D. 2004. Heterotrophic Bacterioplankton Dynamics at a Site off the Southern Shore of Lake Superior. Journal of Great Lakes Research, 30, 214–229. DOI: 10.1016/S0380-1330(04)70387-1 40

Bomfim, F.F., Mantovano, T., Amaral, D.C., Palhiarini, W.S., Bonecker, C.C. & Lansac-Tôha, F.A. 2017. Adjacent environments contribute to the increase of zooplankton species in a neotropical river. Acta Limnologica Brasiliensia, 29, 1–14.

Bonecker, C. C., Simões N. R., Minte-Vera, C. V., Lansac-Tôha, F. A., Velho, L. M., & Agostinho, A. A. 2013. Temporal changes in zooplankton species diversity in response to environmental changes in an alluvial valley. Limnologica, 43, 114–121. DOI: 10.1016/j.limno.2012.07.007

Bozelli, R. L., Thomaz, S.M., Padial, A. A., Lopes, P. M., & Bini, L. M. 2015. Floods decrease zooplankton beta diversity and environmental heterogeneity in an Amazonian floodplain system. Hydrobiologia, 753(1), 233–241. DOI: 10.1007/s10750-015-2209-1

Braghin, L. S. M., Almeida, B. D. A., Amaral, D. C., Canella, T. F., Garcia, B. C. G. & Bonecker, C. C. 2018. Effects of dams decrease zooplankton functional β-diversity in river-associated lakes. Freshwater Biology, 63, 121–130. DOI: 10.1111/fwb.13117.

Braghin, L. S., Figueiredo, B. R., Meurer, T., Michelan, T. S., Simões, N. R., & Bonecker, C. C. 2015. Zooplankton diversity in a dammed river basin is maintained by preserved tributaries in a tropical floodplain, Aquatic Ecology, 49(2), 175–187. DOI: 10.1007/s10452-015-9514-7.

Brito, M. T. da S., Heino, J., Pozzobom, U. M. & Landeiro, V. L. 2020. Ecological uniqueness and species richness of zooplankton in subtropical floodplain lakes. Aquatic Sciences, 82, 1–13.

Bunn, S. E., & Arthington, A. H. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management, 30(4), 492–507. DOI: 10.1007/s00267-002-2737-0

Buosi, P. R. B., Pauletto, G. M., Lansac-Tôha. F. A., & Velho, L. F. M. 2011. Ciliate community associated with aquatic macrophyte roots: effects of nutrient enrichment on the community composition and species richness. European Journal of Protistology, 47, 86–102. DOI: 10.1016/j.ejop.2011.02.001.

Cazzanelli, M., Warming, T. P., & Christoffersen, K. S. 2008. Emergent and floating-leaved macrophytes as refuge for zooplankton in a eutrophic temperate lake without submerged vegetation. Hydrobiologia, 605(1), 113–122. DOI: 10.1007/s10750-008-9324-1.

Chaparro G., Marinone, M. C., Lombardo, R., Schiaffino M. R., & Guimarães A. S. 2011. Zooplancton succession during extraordinary drought-flood cycles. A case study in a South American floodplain lake. Limnologica, 41, 371–381. DOI: 10.1016/j.limno.2011.04.003

Crawley, M. J. 2007. The R book. Chichester, United Kingdom: Wiley. p. 1076.

Cunha, E. R., Thomaz, S. M., Mormul, R. P., Cafofo, E. G., & Bonaldo, A. B. 2012. Macrophyte Structural Complexity Influences Spider Assemblage Attributes in Wetlands. Wetlands 32, 369–377. DOI: 10.1007/s13157-012-0272-1

Fernandes, R., Agostinho, A. A., Ferreira, E. A.,

Pavanelli, C. S., Suzuki, H. I., Lima, D. P., & Gomes, L. C. 2009. Effects of the hydrological regime on the ichthyofauna of riverine environments of the Upper Paraná River floodplain. Brazilian Journal of Biology, 69, 669–680.

Field, R., Hawkins, B. A., Cornell, H. V., Currie, D. J., Diniz-Filho, J. A. F., Guégan, J. F., Dawn M. Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T. T., O'Brien, E. M. & John R. G. Turner. 2009. Spatial species-richness gradients across scales: a meta-analysis. Journal of biogeography, 36, 132–147. DOI: 10.1111/j.1365-2699.2008.01963.x

Franklin, J. F. 1989. Importance and justification of long-term studies in ecology. In: Long-term studies in ecology. Ed. by G. E. Likens. Springer, New York, 3–19.

Golterman, H. L., Clyno, R. S., & Ohnstad, M. A. M. 1978. Methods for physical and chemical analysis of freshwaters. 2nd ed. Blackwell, Oxford. p. 315.

Havel, J. E., Lee, C. E., & Zanden, J. V. 2005. Do reservoirs facilitate invasions into landscapes? BioScience, 55(6), 518–525. DOI:10.1641/0006-3568(2005)055[0518:DRFIILorgeous2.0.CO;2

Hooper, D. U., Chapin, F. S., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeen, S., Schmid, B., Seta, L. A., Symstad, A. J., Vandermeer, J., & Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs, 75(1), 3–35. DOI: 10.1890/04-0922

Jati, S., Bortolini, J. C., Moresco, G. A., Paula, A. C. M. D., Rodrigues, L. C., Iatskiu, P, Pineda, A., Zanco, B. F., da Silva, M. V., Souza, Y. R. 2017. Phytoplankton community in the last undammed stretch of the Paraná River: considerations on the distance from the dam. Acta Limnologica Brasiliensia, 29, e112.

Junk, W. J., Bayley, P. B., & Sparks, R. E. 1989. The flood pulse concept in river-floodplain systems. Canadian special publication of fisheries and aquatic sciences, 106(1), 110–127.

Kovalenko, K. E., Thomaz, S. M., & Warfe, D. M. 2012. Habitat complexity: approaches and future directions. Hydrobiologia, 685, 1–17. DOI: 10.1007/s10750-011-0974-z

Lansac-Tôha, F. A., Bonecker, C. C., Velho, L. F. M., Simões, N. R., Dias, J. D., Alves, G. M., & Takahasi, E. M. 2009. Biodiversity of zooplankton communities in the Upper Paraná River floodplain: interannual variation from long-term studies. Brazilian Journal of Biology, 69(2), 539–549. DOI: 10.1590/S1519-69842009000300009

Lansac-Tôha, F. A., Velho, L. F. M., & Bonecker, C. C. 2003. Influência de macrófitas aquáticas sobre a estrutura da comunidade zooplanctônica. In: Thomaz, S. M. and Bini, L. M. (Eds.). Ecologia e Manejo de Macrófitas Aquáticas. pp. 231–242. Maringá: Eduem.

Lansac-Tôha, F. A., Velho, L. F. M., Higuti, J., & Takahashi, E. M. 2002. Cyclopidae (Crustacea, Copepoda) from the upper Paraná River floodplain, Brazil. Brazilian Journal of Biology, 62(1), 125–133. DOI: 10.1590/S1519-69842002000100015

Larsen, S., Karaus, U., Claret, C., Sporka, F., Hamerlík, L., Tockner, K. 2019. Flooding and hydrologic connectivity modulate community assembly in a dynamic river-floodplain ecosystem. PLoS ONE, 14, 1–22.

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos, 91(1), 3–17. DOI: 10.1034/j.1600-0706.2000.910101.x

Mace, G. M. 2010. Drivers of biodiversity change. In: Leader-Williams, N., Adams, W. M. & Smith, R. J. (Eds.). Trade-offs in conservation: deciding what to save. pp. 349–364. Wiley Blackwell, Oxford.

Mack, R. N., Simberloff D., Lonsdale, W. M., Evans, H., Clout, M. & Bazzaz, F. 2000. Biotic Invasions: causes, epidemiology, global consequences and control. Ecology, 10(3), 689–710. DOI:10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2.

Magurran, A. E. & Dornellas, M. 2010. Biological diversity in a changing world. The Royal Society, 365, 3593–3597. DOI: 10.1098/rstb.2010.0296 38.

Meerhoff, M., Iglesias, C., De Mello, F. T., Clemente, J., Jensen, E., Lauridsen, T. L., & Jeppesen, E. 2007. Effects of habitat complexity on community structure and predator avoidance behavior of littoral zooplankton in temperate versus subtropical shallow lakes. Freshwater Biology, 52(6), 1009–1021. https://doi.org/10.1111/j.1365-2427.2007.01748.x

Meurer, M., Martins, D. P., & Souza Filho, E. E. 2005. Dinâmica das vazões reguladas pelas usinas de Porto Primavera e Rosana, na região do Pontal

do Paranapanema, no período 1999-2003. Geosul 20 (40): 147–166.

Mormul, R. P., Ahlgren, J., Ekvall, K. M., Hansson, L-A., & Brönmark, C. 2012. Water brownification may increase the invasibility of a submerged non-native macrophyte. Biological Invasions, 14(10), 1–9. DOI: 10.1007/s10530-012-0216-y

Neiff, J. J. 1990. Ideas para la interpretacion ecologica del Parana. Interciencia, 15(6), 424–441. DOI: 0378-1844/90/06-424-18

Oksanen. J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner E. 2018. vegan: Community Ecology Package. R package version 2.5-3. https://CRAN.R-project.org/package=vegan

Opperman, J. J., Luster R., McKenney, B. A., & Meadows, A. W. 2010. Ecologically Functional Floodplains: Connectivity, Flow Regime, and Scale. Journal of the American Water Resources Association (JAWRA), 46(2), 211–226. DOI:10.1111/j.1752-1688.2010.00426.x.

Ovaskainen, O., Weigel, B., Potyutko, O. & Buyvolov, Y. 2019 Long-term shifts in water quality show scale-dependent bioindicator responses across Russia – Insights from 40 year-long bioindicator monitoring program. Ecological Indicators, 98, 476–482. DOI: 10.1016/j.ecolind.2018.11.027.

Padovesi-Fonseca, C., & Rezende, R. D. S. 2017. Factors that drive zooplankton diversity in Neo-Tropical Savannah shallow lakes. Acta Limnologica Brasiliensia, 29, e15. DOI: 10.1590/s2179-975x1817

Pinheiro J, Bates D, DebRoy, S., &Sarkar,D, R Core Team (2020). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-145, https://CRAN.R-project.org/package=nlme.

R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Roberto, M. C., Santana, N. F., & Thomaz, S. M. 2009. Limnology in the upper Paraná River floodplain: large-scale spatial and temporal patterns, and the influence of reservoirs. Brazilian Journal of Biology, 69(2), 717–725. DOI: 10.1590/S1519-69842009000300025. PMid:19738977.

Robertson, B. A., & Hardy, E. R. 1984. Zooplankton of Amazonian lakes and Rivers. In Sioli, H. (Ed.). The Amazon: limnology and landscape ecology of a might tropical river and its basin. pp. 337–352. Dordrecht: Junk Publishers.

Rodrigues, E. H. C., Barreto, L. N., Ferreira-Correia, M. M., & Silva, M. R. C. 2015. Variação temporal do fitoplâncton em um rio tropical pré-amazônico (Rio Pindaré, Maranhão, Brasil). Ciência e Natura, 37(2), 241–251. DOI: 10.5902/2179460X14855

Rodrigues, L. C., Pivato, B. M., Vieira, L. C. G., Bovo-Scomparin, V. M., Bortolini, J. C., Pineda, A., & Train, S. 2018. Use of phytoplankton functional groups as a model of spatial and temporal patterns in reservoirs: a case study in a reservoir of central Brazil. Hydrobiologia, 805(1), 147–161. DOI: 10.1007/s10750-017-3289-x

Rodrigues, L. C., Train, S., Bovo-Scomparin, V. M., Jati, S., Borsalli, C. C. J., & Marengoni, E. 2009. Interannual variability of phytoplankton in the main rivers of the Upper Paraná River floodplain, Brazil: influence of upstream reservoirs. Brazilian Journal of Biology, 69(2), 501–516. DOI: 10.1590/S1519-69842009000300006

Santana, N. F., Pereira, L. S., Roberto, M. D. C., Gomes, S. E. D. A., Pagioro, T. A., & Mormul, R. P. 2017. Longitudinal gradient in limnological variables in the Upper Paraná River: a brief description and the importance of undammed tributaries. Acta Limnologica Brasiliensia, 29, e116. DOI: 10.1590/s2179-975x0217.

Segers, H. 2008. Global diversity of rotifers (Rotifera) in freshwater. In Freshwater Animal Diversity Assessment. Springer, Dordrecht, 595, 49–59. DOI: 10.1007/s10750-007-9003-7

Serafim, J. R. M., Bonecker, C. C., Rossa, D. C., Lansac-Tôha, F. A. & Costa, C. L. 2003. Rotifers of the upper Paraná River floodplain: additions to the checklist. Brazilian Journal of Biology, 63(2), 207–212. DOI: 10.1590/S1519-69842003000200005

Sharma, B. K. 2005. Rotifer communities of floodplain lakes of the Brahmaputra basin of lower Assam (N.E. India): biodiversity, distribution and ecology. Hydrobiologia, 533(1-3), 209–221. DOI: 10.1007/s10750-004-2489-3.

Simões, N. R., Nunes, A.H., Dias, J. D., Lansac-Tôha, F. A., Velho, L. F. M., & Boecker, C.C. 2015. Impact of reservoirs on zooplankton diversity and implications for the conservation of natural aquatic environments. Hydrobiologia, 758, 3–17. DOI 10.1007/s10750-015-2260-y

Simões, N. R., Lansac-Tôha, F. A., Velho, L. F. M., & Bonecker, C. C. 2012. Intra and inter-annual structure of zooplankton communities in floodplain lakes: a long-term ecological research study. Revista de Biologia Tropical, 60(4), 1819–1836. DOI: 10.15517/rbt.v60i4.2183.

Simões, N. R., Robertson, B. A., Lansac-Tôha, F. A., Takahashi, E. M., Bonecker, C. C., Velho, L. F. M., & Joko, C. Y. 2009. Exotic species of zooplankton in the upper Paraná river floodplain, Daphnia lumholtzi Sars, 1885 (Crustacea: Branchiopoda). Brazilian Journal of Biology, 69(2), 551–558. DOI: 10.1590/S1519-69842009000300010.

Souza Filho, E. E. 2009. Evaluation of the Upper Paraná River discharge controlled by reservoirs. Brazilian Journal of Biology, 69(2), 707–716. DOI: 10.1590/S1519-69842009000300024.

Thomaz, S. M., Bini, M. L., & Bozelli, R. L. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. Hydrobiologia, 579(1), 1–13 DOI: 10.1007/s10750-006-0285-y.

Thomaz, S. M., Pagioro, T. A., Bini, L. M., Roberto, M. C., & Rocha, R. R. A. 2004. Limnological characterization of the aquatic environments and the influence of hydrometric levels. In Thomaz, S. M., Agostinho, A. A. and Hahn, N. S. (Eds.). The Upper Paraná River and its floodplain: physical aspects, ecology and conservation. pp. 75–102. Leiden: Backhuys Publishers.

Train, S., & Rodrigues, L. C. 2004. Phytoplankton assemblages. The Upper Paraná river floodplain: physical aspects, ecology and conservation. Netherlands: Backhuys, 103–124.

Van der Valk, A. G. 2012. The biology of freshwater wetlands. Oxford University Press. 2nd ed. p. 296.

Ward, J. V., & Tockner, K. 2001. Biodiversity: towards a unifying theme for river ecology. Freshwater Biology, 46(2), 807–819. DOI: 10.1046/j.1365-2427.2001.00713.x

Wickham, H. (2016). ggplot2: elegant graphics for data analysis. Springer. p. 213.

Winemiller, K. O., Mcintyre, P. B., Castello, L., Fluet-chouinard, E., Giarrizzo, T., Nam, S., Baird, I. G., Darwall, W., Lujan, N. K., Harrison, I., Stiassny, M. L. J., Silvano, R. A. M., Fitzgerald, D.B., Pelicice, F. M., Agostinho, A. A., Gomes, L. C., Albert, J. S., Baran, E., Petrere Junior, M., Zarfl, C., Mulligan, M., Sullivan, J. P., Arantes, C. C., Sousa, L. M., Koning, A. A., Hoeinghaus, D. J., Sabaj, M., Lundberg, J. G., Armbruster, J., Thieme, M. L., Petry, P., Zuanon, J., Vilara, G. T., Snoeks, J., Ou, C., Rainboth, W., Pavanelli, C. S., Akama, A., Soesbergen, A., & Saenz, L. 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. Science, 351(6269), 128–129. PMid:26744397. DOI: 10.1126/science.aac7082.

Wood, S.N. 2017. Generalized Additive Models: An Introduction with R, 2nd ed. Boca Raton, FL: CRC Press. p. 496. DOI: 10.1201/9781315370279

Wood, S. N. 2006. Generalized Additive Models: An Introduction with R. Chapman & Hall/CRC. p. 410.

Supplementary Material: Table 1A. Species inventory of the zooplanktonic community in different environments of the upper Paraná river floodplain, from 2000 to 2018.

Supplementary Material: Table 1B. Species richness and organisms' abundance (ind. m^{-3}) recorded in the different environments of the upper Paraná river floodplain during 19 years.