INTER-ANNUAL VARIATION OF OSTRACOD (CRUSTACEA) COMMUNITIES IN THE UPPER PARANÁ RIVER FLOODPLAIN, BRAZIL

Running title: *Inter-annual variation of ostracod (Crustacea) communities*

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Abstract

Riverine floodplains have a large environmental heterogeneity, with lentic and lotic environments and a variety of aquatic macrophytes, providing habitat for various aquatic and terrestrial organisms. Here, we evaluate species composition and beta diversity of ostracod communities over a period of 14 years in two permanently connected lakes (Patos and Guaraná) and two rivers (Ivinhema and Baía) of the Upper Paraná River floodplain. We predict that the ostracod species composition differs in both types of environments amongst the years, and that beta diversity changes over time. Thirty-eight ostracod species were recorded, including new taxa that remain to be described. The change in ostracod species composition over time may be a result of natural or anthropogenic events occurring in the floodplain, in addition to the influence of local abiotic factors. The sequence of floods and droughts might also explain the difference in the contribution of replacement (turnover) and richness difference (loss or gain) components over time. These results show the importance of long-term research to understand the temporal dynamics of the communities, mainly in dam-regulated floodplains.

Keywords: macrophytes; micro-crustacean; species composition; turnover.

INTRODUCTION

Riverine floodplains, such as the Upper Paraná River floodplain, are suitable to investigate changes in aquatic communities since they have high environmental heterogeneity (e.g. permanent and isolated lakes, rivers, channels) and support high aquatic biodiversity. The importance of such floodplains for the conservation of biodiversity and for the maintenance of aquatic ecosystem functioning is widely recognized. Therefore, three conservation units were created in the Upper Paraná River floodplain, in addition to its inclusion as Atlantic Forest Biosphere Reserve by MAB/Unesco (Agostinho *et al*. 2004).

The dynamics of this ecosystem are influenced by the operation of several reservoirs located upstream. The changes in water levels in the Paraná River can occur on short time scales, such as daily and weekly oscillations owing to the demand for energy production by the reservoirs. Longer time scale dynamics, such as changes in the period and intensity of annual floods, also occur during the rainy season, when water is retained for use in the dry season (Agostinho *et al*. 2013).

Another factor that influences the dynamics of ecosystem processes in the Upper Paraná River floodplain is the precipitation variation caused by the El Niño-Southern Oscillation (ENSO) phenomenon. These natural events are of low recurrence (every three to seven years). Both groups of factors, the natural climatic oscillations such as the El Niño/La Niña sequences and the anthropogenic effects such as the water-level control by the reservoirs, can act in synergy on aquatic communities.

Short-term studies have shown that pleuston communities (living in root-systems of floating plants) are buffered against the effects of flood pulses in a lentic environment of the Upper Paraná River floodplain (Higuti *et al*. 2007). On the other hand, long-term studies (over seven years) in the same environment of this floodplain showed that the ostracod communities are persistent during regular pulses but variable during extreme floods (Conceição *et al*. 2018). In addition, extreme drought events (very low water levels) might influence ostracod metacommunities and may lead to a higher beta-diversity owing to the lower connectivity of the lakes (Campos *et al*. 2019).

One of the main questions in ecological studies is to identify the environmental (e.g. abiotic variables), biological (e.g. biological traits) and ecological (e.g. predation, interactions) factors that can affect changes in the attributes of aquatic communities at different temporal and spatial scales. For instance, the temporal variation of the community structure can be the result of gradual or abrupt changes in environmental conditions, including man-induced alterations (Shimadzu *et al*. 2015). Species composition can vary in time and space. However, few studies have investigated such changes over longer time frames, although such knowledge is relevant for the conservation and management of natural resources (Tilman 2000). Whittaker (1960) introduced the term “beta diversity” and defined it as ‘the extent of change in community composition’. Community ecology studies seek to understand the mechanisms of beta diversity (Anderson *et al*. 2011), which drive the distribution of diversity through space and time (Jurasinski *et al*. 2009) and the environmental patterns of variation during turnover (Anderson *et al*. 2006). Various ways to measure beta diversity have been developed. According to Baselga (2010) and Legendre (2014), beta diversity may actually comprise two different processes: species replacement (turnover) and richness differences (gain or loss of species).

Here, we investigate species composition of ostracod communities over a period of 14 years in two lentic and two lotic environments of the Upper Paraná River floodplain, as part of Long-Term Ecological Research, site 6. We assess the beta diversity through species replacement and richness differences. We predict that the variation in abiotic variables lead to differences in composition and beta-diversity over time. Besides, owing to such variation, ostracod species are replaced over time, so the replacement component of beta-diversity is the most important on ostracod community structure.

MATERIAL AND METHODS

Study area

The Paraná River is the tenth longest river in the world (4695 km) and has a drainage area covering 2.8 x 10^6 km^2. The Paraná River flows through Brazil into the La Plata River in Argentina, and it is formed by the confluence of the Paranaiba and Grande Rivers in south-central Brazil (Gomes & Miranda 2001, Agostinho *et al*. 2004). The Upper Paraná River includes approximately the first third of the Paraná River Basin. It has 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 Itaipu Reservoir. The Upper Paraná River floodplain is the last dam-free stretch of the entire Paraná River, where the 25 man-made reservoirs located into its basin affect 70% of the total length of the river. The floodplain includes areas that are vital to biodiversity conservation (Ward *et al*. 1999, Agostinho *et al*. 2000). In this area, three conservation units were created: “Área de Proteção Ambiental das

Ilhas e Várzeas do Rio Paraná” (100,310 ha; an Environmental Protection Area), the “Parque Nacional de Ilha Grande” (78,800 ha; National Park), and the “Parque Estadual do Ivinheima” (70,000 ha; State Park). The Paraná River floodplain, apart from the main channel of the Paraná River, also includes parts of the Ivinhema and Baía rivers (Agostinho *et al*. 2004). Here, we investigate two rivers (Ivinhema and Baía) and two permanently connected lakes (Patos and Guaraná; Figure 1).

Sampling and laboratory analysis

Periphytic ostracods (associated with aquatic macrophytes, *Eichhornia crassipes* (Mart.) Solms, *E. azurea* (Swartz) Kunth, *Hydrocotyle ranunculoides* L., *Limnobium laevigatum* (Humb. & Bonpl. ex Willd.) Heine, *Nymphaea amazonum* Mart. Et Zucc., *Pistia stratiotes* L., *Salvinia auriculata* Aubl., *S. herzogii* de la Sota., *S. minima* Baker and *Utricularia foliosa* L.) were sampled over a period of 14 years (between 2004 and 2018) in two lakes and two rivers of the Upper Paraná River floodplain. Samples were collected in March and November 2004, January/February 2011, July 2012, March and September 2017, and March and September 2018.

The aquatic macrophytes were hand collected and immediately placed in plastic buckets (Campos *et al*. 2017). The entire plants (*N. amazonum, Salvinia* spp., *U. foliosa*) and the roots (*Eichhornia* spp., *H. ranunculoides*, *L. laevigatum*, *P. stratiotes*) were washed in the bucket to remove the ostracods. The residuals were filtered in a hand net (mesh size c 160 µm). The samples were preserved in 70° ethanol buffered with sodium tetraborate (borax). The roots or whole plants were stored in labelled plastic bags, and subsequently dried and weighted in the lab to calculate ostracod densities. The emerging parts of the plants were disregarded.

Ostracods were sorted under a stereoscopic microscope. Specimens were identified using valve (Scanning Electron Microscopy) and appendage morphology (soft parts dissected in slides, studied with light microscopy), following Martens & Behen (1994) and articles comprised therein, Rossetti & Martens (1998), Higuti & Martens (2012a, b, 2014), Higuti *et al*. (2013) and Ferreira *et al*. (2020).

The physical and chemical variables of the water were measured *in situ* before the collection of ostracods, in macrophyte patches. Water temperature (WT, °C) and dissolved oxygen (DO, mg L^{-1}) were measured with a YSI 550A oximeter, pH and electrical conductivity (EC, µS cm^{-1}) with a YSI Model 63 meter. Water level data were obtained from the LTER program (Long Term Ecological Research, site 6 -

http://www.peld.uem.br) developed by researchers of the Centre of Research in Limnology, Ichthyology, and Aquaculture (Nupélia) from the State University of Maringá (UEM).

Data analysis

A principal component analysis (PCA) was applied to order the abiotic data set (water temperature (WT), dissolved oxygen (DO), electrical conductivity (EC), pH and water level (WL)) in lakes and rivers of the Upper Paraná River floodplain. Water levels were calculated from the daily means of six days preceding the sampling. According to Thomaz *et al*. (2004), the covariation between limnological variables and the water level is higher when considering the temporal average of water levels preceding the time of sampling. All values were log transformed, except for pH, to minimize the effect of the dimensionality of the abiotic data set. We standardize the abiotic data using the function decostand in the vegan package. Axes were selected by the broken-stick method and the two selected axes (1 and 2) were used as response variables. A Multivariate Permutational Variance Analysis (PERMANOVA) was performed to evaluate changes in the limnological variables over the years in lakes and rivers (Anderson 2006). We consider the limnological variables as predictor variables and used the Euclidean distance. A total of 999 permutations were performed to assess significance. We used a pair-wise PERMANOVA to assess significant differences amongst years.

The (dis)similarity in ostracod species composition was visualized between the lakes and rivers over the years by a Principal Coordinate Analysis (PCoA; Legendre & Legendre 1998), using a presence / absence matrix and the Jaccard index. A Multivariate Permutational Variance Analysis (PERMANOVA) was performed to evaluate changes in ostracod species composition over the years in lakes and rivers (Anderson 2006). A total of 999 permutations were performed to assess significance. We used a pair-wise PERMANOVA to assess significant differences amongst years.

Multiple regression analyses was carried out to test the influence of the limnological variables (water temperature, dissolved oxygen, electrical conductivity, pH and water level) on the ostracod species composition using both axes of the PcoA. The collinearity amongst the predictors was checked by the variance inflation factor (VIF < 5).

We used the partitioning beta-diversity framework to investigate the variation in ostracod community composition over time. This approach calculates the total variation in beta-diversity (B-total) and partitions it into a component attributed to species replacement (B-repl) and into a component attributed to richness differences (gain or loss of species, Rich-Diff). Firstly, we calculated three pairwise dissimilarity matrices (B-tot, B-repl and Rich-Diff, using Jaccard measures), based on species presence / absence, using the function *beta* in the BAT package (Cardoso *et al*. 2015). These matrices were calculated separately for each year and for each type of environment (lakes and rivers). Secondly, we calculated the mean values of dissimilarity (from a sample in relation to all the others) for each matrix. Finally, from these mean values, we used the parametric analysis of variance (ANOVA) to evaluated possible significant differences in B-total, B-repl and Rich Diff amongst the years. 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, post-hoc tests were performed.

Analyses were performed with the environment R 3.3.1 (R Development Core Team, 2019). PCA and PcoA used the vegan (Oksanen *et al*. 2019), permute (Simpson 2019) and lattice (Sarkar 2008) packages and PERMANOVA was performed according to the function “ADONIS” of the vegan package. B-tot, B-repl and Rich-Diff were calculated using the function *beta* in the BAT package (Cardoso *et al*. 2015). A parametric ANOVA and non-parametric Kruskal-Wallis were performed using the function aov and kruskal.test, respectively, of the vegan package in R environment.

RESULTS

The measured abiotic variables of the lakes and rivers are listed in Table 1. The highest water temperatures were measured in 2018; the lowest values in 2012. The lowest concentrations of dissolved oxygen were recorded in 2011 (lakes: 0.1 mg.L^{-1}, rivers: 1.7 mg.L^{-1}); the highest values in 2018 (lakes: 7.7 mg.L^{-1}, rivers: 8.5 mg.L^{-1}). In the lakes, the electrical conductivity ranged from 22.9 µS.cm^{-1} (2018) to 52.3 µS.cm^{-1} (2004) and in the rivers from 18.8 µS.cm^{-1} (2012) to 58 µS.cm^{-1} (2011). The pH varied from acid (in 2017) to neutral (in 2004).

Between 2004 to 2018, daily water level oscillations occurred, with five flood peaks (> 450 cm), as well as several short periods of drought and one period (2015 and 2016) of a more intense and prolonged drought (Figure 2). During the study period, the highest average water level was observed in 2011 and the lowest in 2018 (Table 1, Figure 2).

>>> Table 1

>>> Figure 2

The first two axes of the Principal Component Analysis (PCA) explained 63.3% of the variance of the abiotic data in the lakes and 65% in the rivers. Significant differences between the years were recorded in both the lakes (F= 9.90; p= 0.001) and in the rivers (F= 4.35; p= 0.006).

In the lakes, the correlated variables in the first axis (PC1 ($P \leq 0.5$)) were DO (R = -0.59), pH (R = -0.49) and WT (R = 0.49). In axis 2 (PC2) it was mainly EC (R = 0.84) (Figure 3A). The pairwise PERMANOVA showed significant ($P \leq 0.5$) differences between all years in the lakes (Table 2). The lowest concentration of oxygen was observed in 2011, while the highest mean value of pH and the lowest temperature were recorded in 2012 (Table 1).

In the rivers, the variables that contributed to the formation of the first axis were DO (R = -0.64), pH (R = -0.60) and of the second axis were WT (R = 0.75) and EC (R = 0.62) (Figure 3B). The pairwise PERMANOVA showed significant ($P \leq 0.5$) differences between all years in the rivers, except between 2014 and 2018 (Table 2). The lowest water temperature and conductivity values were observed in 2012 (Table 1).

>>> Table 2

>>> Figure 3

We recorded 38 species of ostracods, belonging to the families Cyprididae, Candonidae, Limnocytheridae and Darwinulidae (Table S1).

The result of the Principal Coordinates Analysis (PCoA), used to evaluate the (dis) similarity between the years, showed significant differences in species composition in both types of environment: in lakes (F = 2.0, P = 0.004) and rivers (F = 1.82, P = 0.001) (Figure 4). The pairwise PERMANOVA showed distinct ostracod species compositions in the lakes between 2004 and 2011 (P = 0.007), between 2004 and 2018 (P = 0.035), between 2011 and 2012 (P = 0.000), and between 2011 and 2018 (P = 0.006). On the other hand, the species composition of 2004 was significantly different from all other years, except from 2017 in the rivers (Table 3).

>>> Figure 4
>>> Table 3

The multiple regression analyses using all variables (global model) was not significant between abiotic variables and species composition in the lakes on axis 1 (Model, R^2= 0.179, P= 0.145), however it was significant on axis 2 (Model, R^2= 0.533, P< 0.000). Considering each variable separately in lakes, the multiple regressions were significant between species composition and water temperature, electrical conductivity on axis 1, and between composition and dissolved oxygen, pH, water temperature on axis 2 (Table 4). In the rivers, the multiple regression did not show relationships between species composition and any of the abiotic variables (global model) on both axes, axis 1 (Model, R^2= 0.157, P= 0.371) and axis 2 (Model, R^2= 0.206, P= 0.202). On the other hand, analysing each abiotic variable separately, the species composition in rivers were significantly correlated to water level on axis 1 and to dissolved oxygen on axis 2 (Table 4).

>>> Table 4

The results showed, in general, an increase in beta-total over time, with higher mean values in 2017, for lakes (0.80) and rivers (0.79) (Figure 5A, C). There was a significant difference in beta-total over time, for both types of environment (lakes: H = 14.8129; P = 0.0051 and rivers: H = 23.0289; P = 0.0001). Differences were found between 2004 and 2017, and 2012 and 2017 in the lakes, while in the rivers the beta-total differed between 2004 and all other years, excepted for 2011.

According to the components of beta-diversity, mean values of B-repl were usually higher than Rich-Diff (up to 0.640 in 2017, for the rivers), excepted in 2011 (lakes) and 2018 (rivers) (Figure 5B, D). There were significant differences in both of these components over time for lakes (B-repl: F = 3.1937; P = 0.0229; Rich-Diff: H = 19.1149; P = 0.0007) and rivers (B-repl: F = 10.2519; P = 0.00002; Rich-Diff: H = 18.5288; P = 0.0010). B-repl differences were found between 2004 and 2011 for lakes, and between 2017 and all other years for rivers. Rich-Diff differences were found between 2004 and all other years, excepted for 2012, for lakes; and between 2004 and 2018, and between 2017 and 2018 for rivers.

>>> Figure 5

DISCUSSION

Differences in ostracod composition and beta diversity over time might be associated with temporal variations at local scales, such as changes in environmental conditions, and regional scales, related to dispersal limitation throughout the Upper Paraná River floodplain. These factors have been considered important in structuring aquatic communities (Langenheder *et al.* 2011, Benone *et al*. 2018). In the Paraná river floodplain, water level variation (see Figure 2) can change the environmental heterogeneity within and amongst the environments over time (Conceição *et al*. 2018, Campos *et al*. 2019), and consequently the availability of habitats, generating niches where some species are favoured over others (Heino 2000). For example, while habitats are more isolated during low water periods, during flood periods there is a higher connectivity amongst them, leading to a homogenization in biological communities (Thomaz *et al*. 2007). Despite the importance of water level fluctuations and water flow, abiotic variables also influence biological (e.g. growth, reproduction) and ecological (e.g. composition, diversity, distribution) aspects of aquatic organisms, such as ostracods (Kim *et al*. 2015, Akita *et al*. 2016). Some variables such as dissolved oxygen, electrical conductivity, pH, water temperature and water level are known to be important for the composition of ostracod communities and our results confirm that. For instance, Kim *et al*. (2015), in experimental tests with *Heterocypris incongruens,* showed that higher pH levels lead to higher growth rates in populations. Similarly, Higuti *et al*. (2010) reported a positive relationship between pH and ostracods, especially owing to the importance of calcium for the formation of the shells. Also, water temperature affects the life story and body size of ostracods species (Aguilar-Alberola & Mesquita Joanes 2014) and electrical conductivity is commonly pointed as a factor that influences the distribution of ostracods, even in a great range of habitats (Akita *et al*. 2016, Külköylüoğlu *et al*. 2016, Castillo-Escrivà *et al*. 2017). Some studies have also found a correlation between ostracod community composition and dissolved oxygen (e.g. Conceição *et al*. 2017, Higuti *et al*. 2017). Even with the limited abiotic variables analysed in the present study, most of them had a significant effect on the species composition in ostracod communities. However, other (as yet unmeasured) variables could also affect these communities, such as nutrients, biotic interactions and substrate types (Schön *et al*. 2017).

The sequence of floods and drought might also explain the difference in the contribution of turnover and richness difference components over time. The fact that the B-repl component was the most important, compared to Rich-Diff, confirms that the environmental filtering (probably related to increases in the spatial variability in relation to abiotic factors during drought periods), replaced species from one environment to another in the Upper Paraná River floodplain. According to Zellweger *et al.* (2017), environmental filtering occurs owing to the species' physiological tolerances to abiotic environmental conditions. Hill *et al*. (2017) also obtained similar results in ponds of Leicestershire (UK), and the turnover was the main component influencing the beta diversity of macroinvertebrates, which was attributed mainly to environmental filtering. A high species replacement was also observed for zooplankton communities owing limiting similarity and habitat filtering in the lakes of the Upper Paraná River floodplain (Braghin *et al*. 2018).

The increase of total ostracod beta-diversity over time might be related to dam-controlled floods, together with climatic natural events, such as La Ninã phenomena (a phase of the ENSO-El Niño-Southern Oscillation - Berri *et al*. 2002, Grimm & Tedeschi 2009), which intensify, for example, extreme drought periods. Such intense and prolonged periods of low water levels have been common in the last decades and, in addition to the increase of environmental heterogeneity, might cause habitat isolation, and consequently species dispersal limitation. For instance, Campos *et al.* (2019), analysing ostracod metacommunities over time, found high values of beta-diversity in extreme drought periods, mainly related to spatial factors or dispersal limitation through the Paraná River region. Another feature that can affect the dynamics of ostracod communities is the production of resting eggs by these organisms, which can resist long periods of drought and can then be transported to and hatched from the sediments by several floods (Meisch 2000, Conceição *et al.* 2018, Chaparro *et al*. 2018).

In conclusion, the beta diversity and the species composition of ostracods change over the years in lentic and lotic floodplain environments owing, at least partly, to the variation in abiotic variables. The present study showed the importance of long-term ecological monitoring (PELD), mainly in large river ecosystems, which are regulated by dams and reservoirs (e.g. the Upper Paraná River). The potential effects of dams on biodiversity are here exemplified by changes in ostracod beta-diversity over time. In addition, the temporal changes observed in ostracod communities may reflect the dynamics of other communities, since these organisms form an integral part of the pleuston of root systems of floating plants, which interacts with both aquatic and terrestrial communities. Therefore, such long-term studies are valuable for future research, for example, but not exclusively, regarding biological interactions. We also stress that throughout this long-term study, new species and genera have been discovered, which can contribute to future biodiversity conservation strategies. The present results thus strongly emphasize the relevance of long-term monitoring in research on alpha and beta diversity.

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REFERENCES

Agostinho, A. A., Thomaz, S. M., Minte-Veral, C. V., & Winemiller, K. O. 2000. Biodiversity in the High Paraná River Floodplain. In: Gopal, B., Junk, W. J., & Davis, J. A. (Eds). Biodiversity in wetlands: assessment, junction and conservation. pp. 89--118. Leiden: Backhuys Publishers.

Agostinho, A. A., Gomes, L. C., Thomaz, S. M., & Hahn, N. S. 2004. The upper Paraná River and its floodplain: main characteristics and perspectives for management and conservation. In: Thomaz, S. M., Agostinho, A. A., & Hahn, N. S. (Eds.). The upper Paraná River and its floodplain: physical aspects, ecology and conservation. pp. 381--393. Leiden: Backhuys Publishers.

Agostinho, A. A., Gomes, L. C., Bonecker, C. C., & Thomaz, S. M. 2013. Padrões e variação de longo prazo na Planície de Inundação do Alto Rio Paraná. In: Tabarelli, M., Rocha, C. F. D., Romanowski, H. P., Rocha, O., & Lacerda, L. D. (Eds.). PELD – CNPq: dez anos do Programa de Pesquisas Ecológicas de longa duração do Brasil: achados, lições e perspectivas. p. 446. Ed.Universitária da UFPE: Série de publicações PELD.

Aguilar-Alberola, J. A., & Mesquita-Joanes, F. 2014. Breaking the temperature-size rule: thermal effects on growth, development and fecundity of a crustacean from temporary waters. Journal of Thermal Biology, 42(1), 15--24. DOI: 10.1016/j.jtherbio.2014.02.016

Akita, L. G., Frenzel, P., Wang, J., Börner, N., & Peng, P. 2016. Spatial distribution and ecology of the Recent Ostracoda from Tangra Yumco and adjacent waters on the southern Tibetan Plateau: a key to palaeoenvironmental reconstruction. Limnologica, 59(1), 21--43. DOI: 10.1016/j.limno.2016.03.005

Anderson, M. J. 2006. Distance–Based tests for homogeneity of multivariate dispersions. Biometrics, 62(1), 245--253. DOI: 10.1111/j.1541-0420.2005.00440.x

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.1461-0248.2006.00926.x

Anderson, M. J., Crist, T. O., Chase, J. M., Vallend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B., Stegen, J. C., & Swenson, N.,G. 2011. Navigating the multiple meanings of b diversity: a roadmap for the practicing ecologist. Ecology Letters, 14, 19--28. DOI: 10.1111/j.1461-0248.2010.01552.x

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography, 19(1), 134--143. DOI: 10.1111/j.1466-8238.2009.00490.x

Benone, N. L., Ligeiro, R., Juen, L., & Montag, L. F. A. 2018. Role of environmental and spatial processes structuring fish assemblages in streams of the eastern Amazon. Marine and Freshwater Research, 69(2), 243--252. DOI: 10.1071/MF17103

Berri, G. J., Ghietto, M. A., & García, N. O. 2002. The influence of ENSO in the flows of the upper Paraná River of South America over the past 100 years. Journal of Hydrometeorology, 3(1), 57--65. DOI: 10.1175/1525-7541(2002)003<0057:TIOEIT>2.0

Braghin, L. S. M., Almeida, B. A., Amaral, D. C., Canella, T. F., Gimenez, B. C. G., & Bonecker, C. C. 2018. Effects of Dams Decrease Zooplankton Functional β-Diversity in River-Associated Lakes. Freshwater Biology, 63(7), 721--30. DOI: 10.1111/fwb.13117

Campos, R., Conceição, E. O., Pinto, M. B. O., Bertoncin, A. P. S., Higuti, J., & Martens, K. 2017. Evaluation of quantitative sampling methods in pleuston: An example from ostracod communities. Limnologica (Jena), 63(1), 36--41. DOI: 10.1016/J.limno.2017.01.002

Campos, R., Conceição, E. O., Martens, K., & Higuti, J. 2019. Extreme drought periods can change spatial effects on periphytic ostracod metacommunities in river-floodplain ecosystems. Hydrobiologia, 828(1), 369--381. DOI: 10.1007/s10750-018-3825-3

Cardoso, P., Rigal, F., & Carvalho, J. C. 2015. BAT - Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. Methods in Ecology and Evolution, 6(2), 232--236. DOI: 10.1111/2041-210X.12310

Castillo-Escrivà, A., Valls, L., Rochera, C., Camacho, A., & Mesquita-Joanes, F. 2017. Disentangling environmental, spatial, and historical effects on ostracod communities in shallow lakes. Hydrobiologia, 787(1), 61--72. DOI: 10.1007/s10750-016-2945-x

Chaparro, G., Horváth, Z., O'Farrell, I., Ptacnik, R., & Hein, T. 2018. Plankton metacommunities in floodplain wetlands under contrasting hydrological conditions. Freshwater Biology, 63(4), 380--91. DOI: 10.1111/fwb.13076

Conceição, E. O., Higuti, J., & Martens, K. 2017. Variability in ostracod communities (Crustacea, Ostracoda) in connected and isolated tropical floodplain lakes. Annales de Limnologie - International Journal of Limnology, 53: 325--332. DOI: 10.1051/limn/2017016

Conceição, E. O., Higuti, J., Campos, R., & Martens, K. 2018. Effects of flood pulses on persistence and variability of pleuston communities in a tropical floodplain lake. Hydrobiologia, 807(1), 175--188. DOI: 10.1007/s10750-017-3392-z

Ferreira, V. G., Higuti, J., & Martens, K. 2020. Taxonomic revision of *Strandesia s.s.* (Crustacea, Ostracoda) from four Brazilian floodplains, with the description of three new species. Zootaxa, 4760(1), 1--74. DOI: 10.11646/zootaxa.4760.1.1

Gomes, L. C., & Miranda, L. E. 2001. Riverine characteristics dictate composition of fish assemblages and limit fisheries in reservoirs of the upper Paraná River basin. Regulated Rivers: Research & Management, 17(1), 67--76. DOI: 10.1002/1099-1646(200101/02)

Grimm, A. M., & Tedeschi, R. G. 2009. ENSO and extreme rainfall events in South America. Journal of Climate, 22(7), 1589--1609. DOI: 10.1175/2008JCLI2429.1

Heino, J. 2000. Lentic macroinvertebrate assemblage structure along gradients in spatial heterogeneity, habitat size and water chemistry. Hydrobiologia, 418(1), 229--242. DOI: 10.1023/A:1003969217686

Higuti, J., Velho, L. F. M., Lansac-Tôha, F. A., & Martens, K. 2007. Pleuston communities are buffered from regional flood pulses: the example of ostracods in the Paraná River floodplain, Brazil. Freshwater Biology, 52(10), 1930--1943. DOI: 10.1111/j.1365-2427.2007.01821.x

Higuti, J., Declerck, S. A. J., Lansac-Tôha, F. A., Velho, L. F. M., & Martens, K. 2010. Variation in ostracod (Crustacea, Ostracoda) communities in the alluvial valley of the upper Paraná River (Brazil) in relation to substrate. Hydrobiologia, 644(1), 261--278. DOI: 10.1007/s10750-010-0122-1

Higuti, J., & Martens, K. 2012a. On a new cypridopsine genus (Crustacea, Ostracoda, Cyprididae) from the Upper Paraná River Floodplain (Brazil). Zootaxa, 3391(1), 23--38. DOI: 10.11646/zootaxa.3391.1.2

Higuti, J., & Martens, K. 2012b. Description of a new genus and species of Candonopsini (Crustacea, Ostracoda, Candoninae) from the alluvial valley of the Upper Paraná River (Brazil, South America). European Journal of Taxonomy, 33(1), 1--31. DOI: 10.5852/ejt.2012.33

Higuti, J., Schön, I., Audenaert, L., & Martens, K. 2013. On the *Strandesia* Obtusata/Elliptica Lineage (Ostracoda, Cyprididae) in the Alluvial Valley of the Upper Paraná River (Brazil), with the description of three new species. Crustaceana, 86(2). DOI: 182--211. DOI: 10.1163/15685403-00003160

Higuti, J., & Martens, K. 2014. Five new species of Candoninae (Crustacea, Ostracoda) from the alluvial valley of the Upper Paraná River (Brazil, South America). European Journal of Taxonomy, 106(1), 1--36. DOI: 10.5852/ejt.2014.106

Higuti, J., Conceição, E. O., Campos, R., Ferreira, V. G., Rosa, J., Pinto, M. B. O., & Martens, K. 2017. Periphytic community structure of Ostracoda (Crustacea) in the river-floodplain system of the Upper Paraná River. Acta Limnologica Brasiliensia, 29(e.120). DOI: 10.1590/s2179-975x12217

Hill, M. J., Heino, J., Thornhill, I., Ryves, D. B., & Wood, P. J. 2017. Effects of dispersal mode on the environmental and spatial correlates of nestedness and species turnover in pond communities. Oikos, 126(11), 1575--1585. DOI: 10.1111/oik.04266

Jurasinski G., Retzer V., & Beierkuhnlein C. 2009. Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. Oecologia, 159 (1), 15--26. DOI: 10.1007/s00442-008-1190-z

Kim, Y., Mo, H., Son, J. Lee, Y., Lee, S., & Cho, K. 2015. Interactive effects of water pH and hardness levels on the growth and reproduction of *Heterocypris incongruens* (Crustacea: Ostracoda). Hydrobiologia, 753 (1), 97--109. DOI: 10.1007/s10750-015-2199-z

Külköylüoğlu, O., Yavuzatmaca, M., Sarı, N., & Akdemir, D. 2016. Elevational distribution and species diversity of freshwater Ostracoda (Crustacea) in Çankırı region (Turkey). Journal of Freshwater Ecology, 31(2), 219--230. DOI:10.1080/02705060.2015.1050467

Langenheder, S., Berga, M., Östaman, O., & Székely, A. Temporal variation of β-diversity and assembly mechanisms in a bacterial metacommunity. The ISME Journal, 6(6), 1107--1114. DOI: 10.1038/ismej.2011.177

Legendre, P., & Legendre L. 1998. *Numerical ecology*. Amsterdam: Elsevier Science.

Legendre, P. 2014. Interpreting the replacement and richness difference components of beta diversity. Global Ecology and Biogeography, 23(11), 1324--1334. DOI: 10.1111/geb.12207

Martens, K., & Behen, F. 1994. A checklist of the non-marine ostracods (Crustacea, Ostracoda) from the inland waters of South America and adjacent islands, Travaux Scientifiques du Musée d' Histoire Naturelle de Luxembourg 22, 1--81.

Meisch, C. 2000. Freshwater Ostracoda of Western and Central Europe. Berlin: Spektrum Akademischer-Verlag: p. 522.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. 2019. Vegan: Community Ecology Package. R Package Version 2.4-1.

R Development Core Team. 2019. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Rossetti, G., & Martens, K. 1998. Taxonomic revision of the Recent and Holocene representatives of the Family Darwinulidae (Crustacea, Ostracoda), with a description of three new genera. Bulletin de L´Institut Royal des Sciences Naturelles de Belgique, Biologie, 68(1), 55--110.

Sarkar, D., 2008. Lattice: Multivariate Data Visualization with R. New York: Springer.

Schön, I., Pieri, V., Sherbakov, D., & Martens, K. 2017. Cryptic diversity and speciation in endemic *Cytherissa* (Crustacea, Ostracoda) from Lake Baikal (Siberia). Hydrobiologia 800: 61--79. DOI: 10.1007/s10750-017-3259-3

Shimadzu, H., Dornelas, M., & Magurran, A. E. 2015. Measuring temporal turnover in ecological communities. *Methods in Ecology and Evolution,* 6(12), 1384--1394. DOI: 10.1111/2041-210X.12438

Simpson, G. L. 2019. Permute: Functions for Generating Restricted Permutations of Data. R package version 0.9-4.

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., & Hahn, N. S. (Eds.). The upper Paraná River and its floodplain: physical aspects, ecology and conservation. pp. 75--102. Leiden: Backhuys Publishers.

Thomaz, S. M., Bini, L. M., & 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

Tilman, D. 2000. Causes, consequences and ethics of biodiversity. Nature, 405(6783), 208--211. DOI: 10.1038/35012217

Ward, J. V., Tockner, K., & Schiemer, F. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers: Research & Management, 15(1), 125--139. DOI: 10.1002/(SICI)1099-1646(199901/06)15:1/3<125::AID-RRR523>3.0

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs, 30(3), 280--338. DOI: 10.2307/1943563

Captions of tables and figures

Table 1. Mean, standard deviation, minimum and maximum (between parentheses) values of the abiotic variables over time in lakes and rivers of the Upper Paraná River floodplain. Water temperature (WT), dissolved oxygen (DO), electrical conductivity (EC) and water level (WL). Water level measurements are from six days before sampling (see Thomaz *et al.*, 2004).

Table 2. Pairwise PERMANOVA of the limnological variables over time in the two lakes and two rivers of the Upper Paraná River floodplain.

Table 3. Pairwise PERMANOVA of the ostracod species composition over time in two lakes and two rivers of the Upper Paraná River floodplain.

Table 4. Results of multiple regressions between species composition and abiotic variables in two lakes and two rivers of the Upper Paraná River floodplain. Water temperature (WT), dissolved oxygen (DO), electrical conductivity (EC), water level – six days before sampling (WL).

Figure 1. Location of two lakes and two rivers of the Upper Paraná River floodplain.

Figure 2. Daily water levels of the Upper Parana´ River (in the field station of Porto Rico, Paraná) from 2004 to 2018. Arrows indicate the sampling periods.

Figure 3. Principal Component Analysis (PCA) ordination diagram derived from abiotic data of the two lakes (A) and two rivers (B) of the Upper Paraná River floodplain. Water temperature (WT), dissolved oxygen (DO), electrical conductivity (EC), and Water level (WL).

Figure 4. Principal Coordinate Analysis (PCoA) derived from ostracod communities in two lakes (A) and two rivers (B) of the Upper Paraná River floodplain.

Figure 5. Beta total, beta replacement (B-repl) and richness difference (Rich-Diff) of the ostracods over time, in the two lakes (A, B) and two rivers (C, D) of the Upper Paraná River floodplain.

Electronic supplementary material

Table S1. Ostracod species from the two lakes and two rivers of the Upper Paraná River floodplain studied in the present paper.

Table 1

Year	**Environmental type**	**WT (°C)**	**DO (mg.L^{-1})**	**EC (µS.cm^{-1})**	**pH**	**WL (cm)**
2004	Lakes	28.3±1.9	3.4±1.4	45.2±5.5	5.7±0.7	298.4±57.0
		(26.0-31.1)	(2.3-6.5)	(40.5-52.3)	(5.2-7.0)	(222-390)
	Rivers	28.0±1.9	4.8±1.3	37.5±6.2	6.2±0.5	298.4±57.0
		(25.8-30.5)	(3.1-6.5)	(30.9-46.6)	(5.7-7.0)	(222-390)
2011	Lakes	29.6±0.4	0.2±0.1	38.6±3.1	5.8±0.1	363.0±13.8
		(29.3-30.2)	(0.1-0.2)	(36.6-42.8)	(5.8-5.9)	(338-387)
	Rivers	36.0±14.9	2.3±1.1	30.2±0.5	5.6±0.6	363.0±13.8
		(27.3-29.5)	(1.7-4.0)	(30.6-58.0)	(5.2-6.5)	(338-387)
2012	Lakes	17.2±0.3	2.6±1.6	31.1±11.6	5.9±0.2	300.6±35.0
		(16.9-17.7)	(0.4-3.6)	(23.4-46.6)	(5.6-6.0)	(229-339)
	Rivers	18.3±0.9	5.1±2.0	25.3±10.0	6.4±0.1	300.6±35.0
		(17.2-18.9)	(3.8-7.7)	(18.8-38.3)	(6.2-6.6)	(229-339)
2017	Lakes	26.9±3.4	3.5±1.9	40.5±8.9	5.4±0.8	260.2±44.4
		(21.3-30.5)	(0.4-5.4)	(28.0-51.0)	(4.2-6.5)	(192-334)
	Rivers	27.7±3.3	5.7±1.0	39.2±11.2	5.3±1.1	260±44.4
		(24.0-32.0)	(4.7-7.1)	(24.9-53.0)	(4.2-6.3)	(192-334)
2018	Lakes	26.3±4.9	2.4±2.6	38.7±10.8	5.4±0.7	225.9±81.0
		(21.2-34.1)	(0.2-7.7)	(22.9-49.9)	(4.5-6.6)	(110-338)
	Rivers	26.4±4.9	4.8±2.7	34.7±13.8	5.6±0.4	225.9±81.0
		(22.0-31.3)	(2.7-8.5)	(20.3-49.9)	(5.0-6.0)	(110-338)

Table 2

Environment **Years**		**RIVERS**				
		2004	2011	2012	2017	2018
LAKES	2004		**0.000**	**0.000**	**0.014**	0.184
	2011	**0.010**		**0.000**	**0.000**	**0.001**
	2012	**0.000**	**0.000**		**0.001**	**0.014**
	2017	**0.020**	**0.047**	**0.000**		**0.032**
	2018	**0.020**	**0.002**	**0.000**	**0.007**	

Table 3

Environment Years		**RIVERS**				
		2004	2011	2012	2017	2018
LAKES	2004		**0.000**	**0.012**	0.183	**0.028**
	2011	**0.007**		0.284	0.080	0.063
	2012	0.570	**0.000**		0.358	0.142
	2017	0.434	0.483	0.400		0.600
	2018	**0.035**	**0.006**	**0.023**	0.060	

Table 4

Variables		**Lakes**				**Rivers**			
		Estimate	Standard error	T	*P*	Estimate	Standard error	T	*P*
PCoA1	WT	7.79	2.86	2.72	**0.009**	-3.98	3.49	-1.14	0.262
	DO	-3.83	7.49	-0.51	0.611	1.26	9.35	0.13	0.893
	EC	-3.80	1.70	-2.23	**0.003**	2.36	1.83	1.28	0.207
	pH	14.92	17.97	0.83	0.411	-23.99	16.45	-1.45	0.155
	WL	-0.44	0.22	-1.99	0.053	0.58	0.28	2.07	**0.047**
PCoA2	WT	-1.37	1.75	-0.078	0.435	-0.25	2.53	-0.10	0.919
	DO	11.61	4.58	2.53	**0.015**	-16.90	6.78	-2.49	**0.018**
	EC	-2.30	1.04	-2.22	**0.032**	0.93	1.33	0.70	0.487
	pH	26.43	10.99	-2.40	**0.020**	11.36	11.93	0.95	0.348
	WL	-0.19	0.13	-1.43	0.159	-0.06	0.20	-0.32	0.745

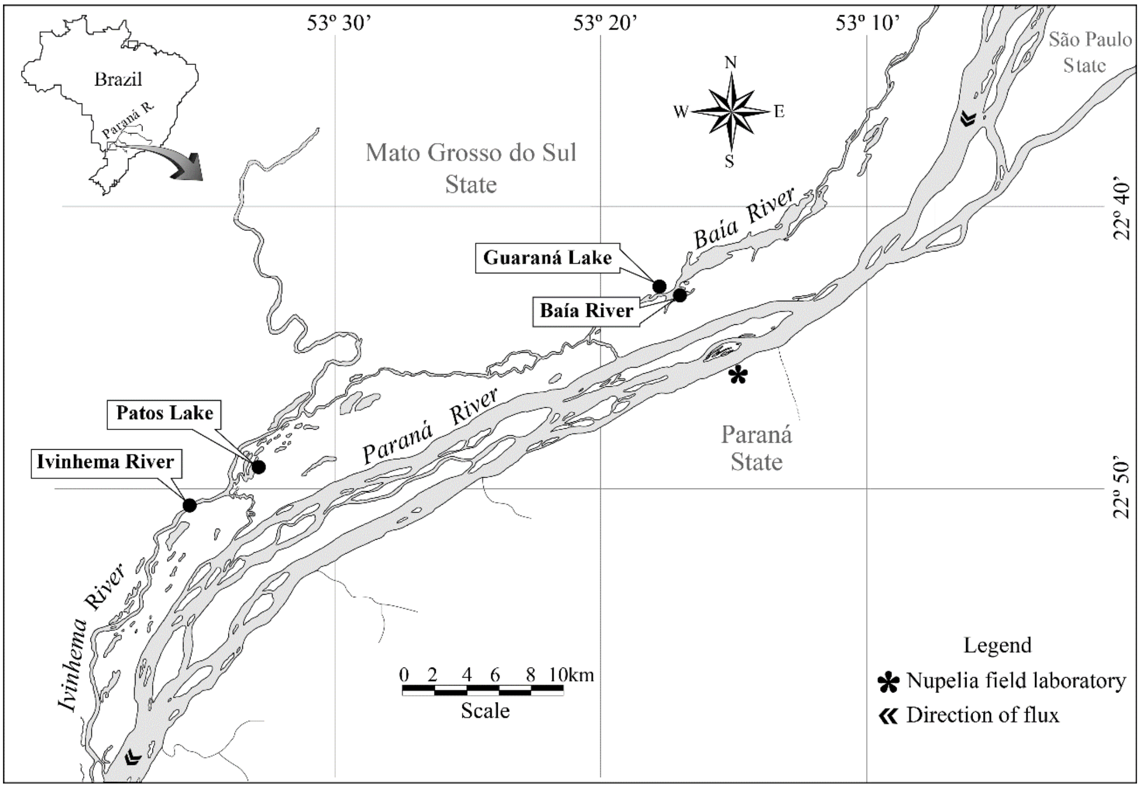

Brazil
Paraná R.
53º 30’
53º 20’
53º 10’
N
W
E
S
São Paulo State
Mato Grosso do Sul State
22º 40’
22º 50’
Baía River
Guaraná Lake
Baía River
Patos Lake
Ivinhema River
Paraná River
Paraná State
Ivinhema River
0 2 4 6 8 10km
Scale
Legend
✱ Nupelia field laboratory
« Direction of flux

Figure 1

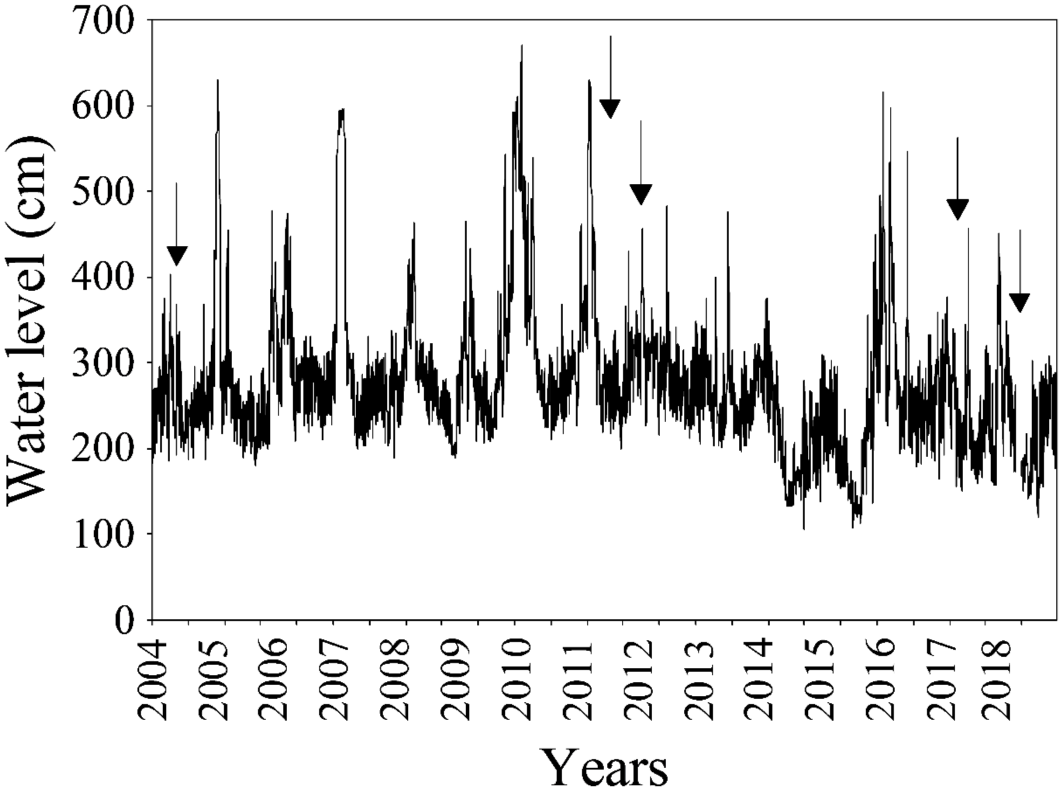

Water level (cm)
700
600
500
400
300
200
100
0
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
Years

Figure 2

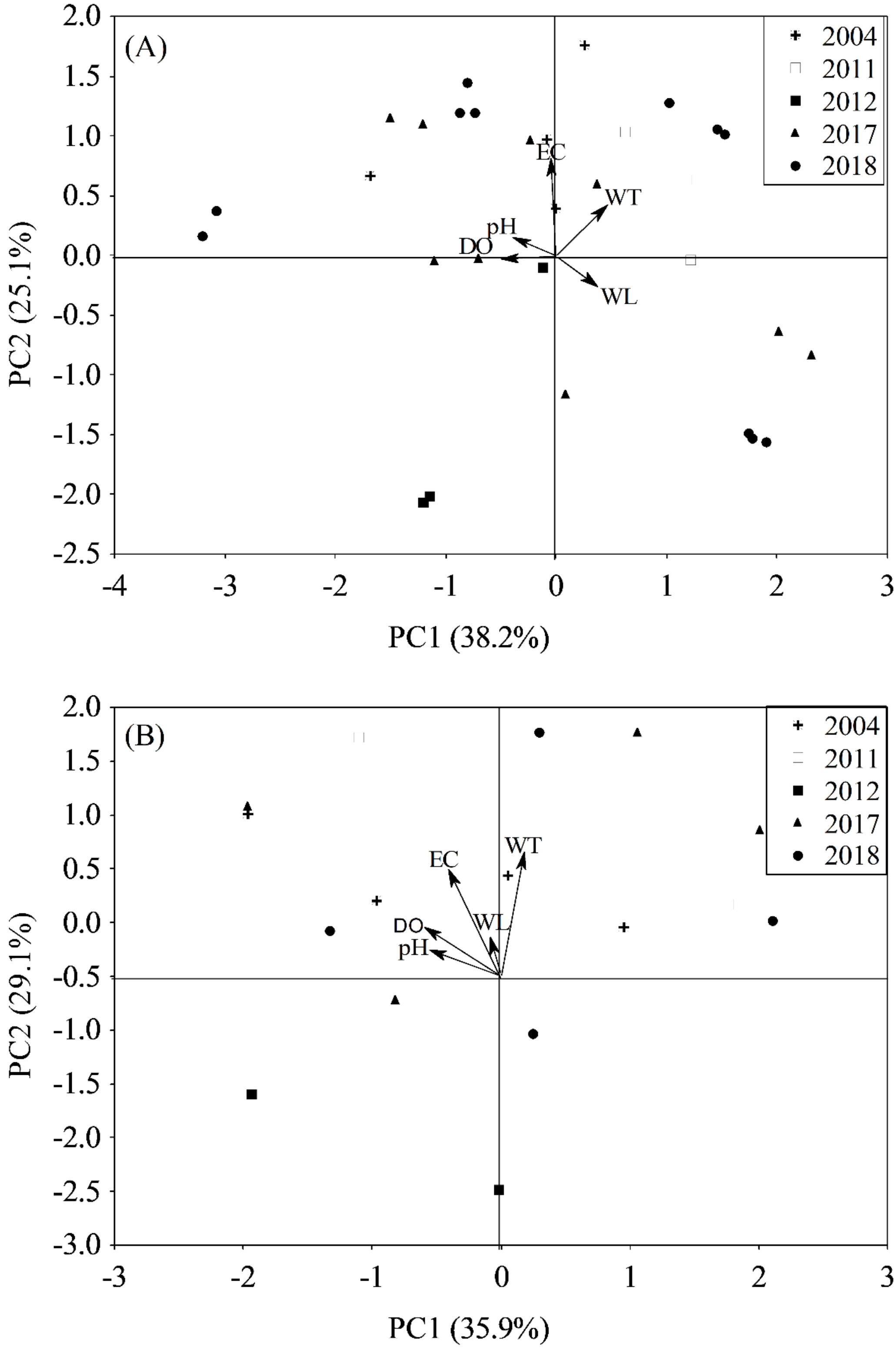

(A)
PC2 (25.1%)
PC1 (38.2%)
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
-4
-3
-2
-1
0
1
2
3
EC
WT
pH
DO
WL
2004
2011
2012
2017
2018
(B)
PC2 (29.1%)
PC1 (35.9%)
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
-3.0
-3
-2
-1
0
1
2
3
EC
WT
DO
WL
pH
2004
2011
2012
2017
2018

Figure 3

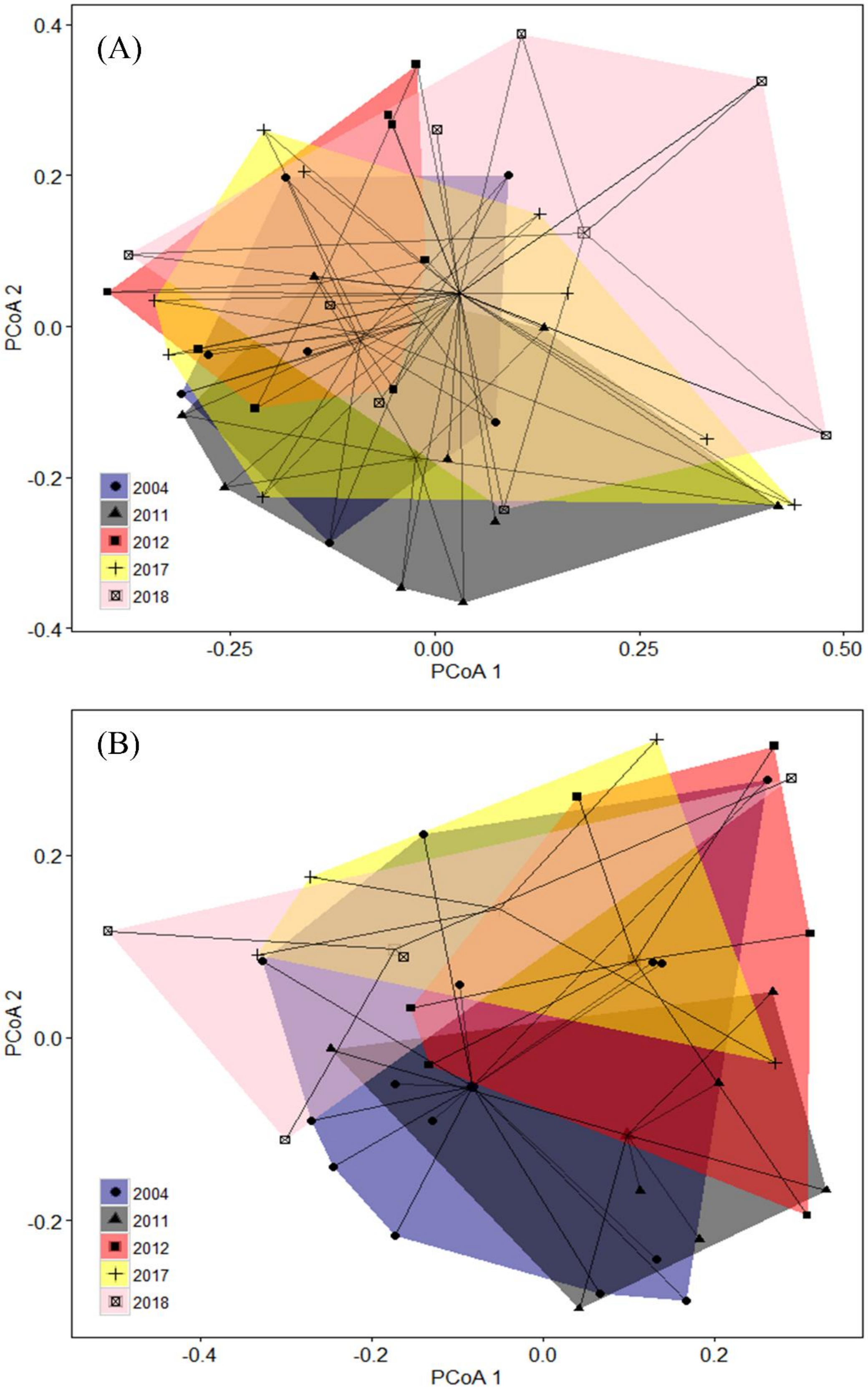
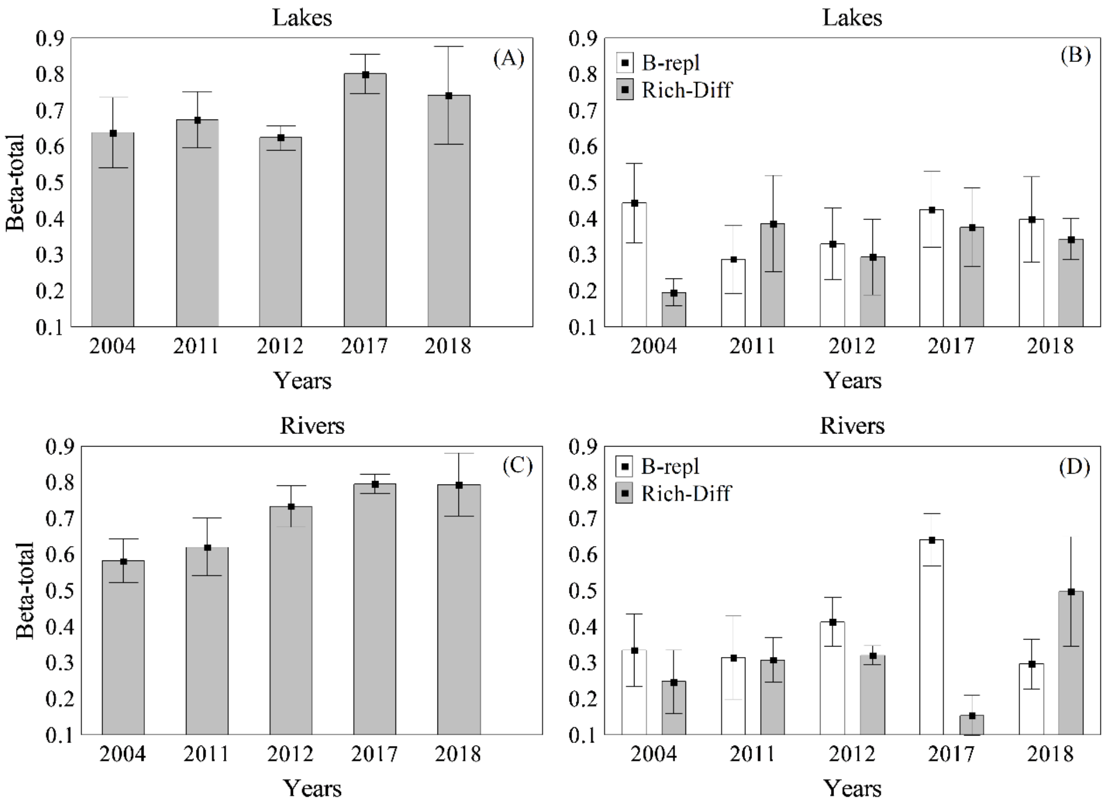

(A)
0.4
0.2
0.0
-0.2
-0.4
PCoA 2
-0.25
0.00
0.25
0.50
PCoA 1
2004
2011
2012
2017
2018
(B)
0.2
0.0
-0.2
PCoA 2
-0.4
-0.2
0.0
0.2
PCoA 1
2004
2011
2012
2017
2018

Figure 4



Lakes
(A)
Beta-total
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
2004
2011
2012
2017
2018
Years
Lakes
(B)
B-repl
Rich-Diff
Years
Rivers
(C)
Beta-total
Years
Rivers
(D)
B-repl
Rich-Diff
Years

Figure 5

Electronic supplementary material

Table S1

	Lakes					Rivers				
	2004	**2011**	**2012**	**2017**	**2018**	**2004**	**2011**	**2012**	**2017**	**2018**
Family Cyprididae Baird, 1845										
Bradleytriebella lineata (Victor & Fernando, 1981)			+		+	+				
Bradleytriebella trispinosa (Pinto & Purper, 1965)		+			+	+			+	+
Cabelodopsis hispida (Sars, 1901)	+	+	+	+	+	+	+	+	+	+
Chlamydotheca deformis Farkas, 1958	+				+	+				
Chlamydotheca iheringi (Sars, 1901)		+	+		+	+	+			
Chlamydotheca cf. *iheringi*				+	+	+				
Chlamydotheca sp. 2					+					
Cypretta costata G. W. Müller, 1898	+	+	+	+	+	+	+	+	+	+
Cypretta n. sp. 3						+				
Cypricercus sp. nov.	+	+	+	+	+	+	+	+	+	+
Cypricercus n. sp. 1									+	
Cypridopsis vidua (O. F. Müller, 1776)		+	+	+	+	+		+	+	
Cypridopsis cf. *vidua* sp.2	+		+	+	+	+	+	+		
Cypridopsis n.gen. 1 n. sp.1				+			+			
Cypridopsis n.gen. 2 n.sp.1		+		+			+		+	
Diaphanocypris meridana (Furtos, 1936)	+	+	+	+	+	+	+	+	+	+
Neocypridopsis nana (Sars, 1901)	+	+		+	+	+	+			
Stenocypris major (Baird, 1859)						+				
Stenocypris malayica Victor & Fernando, 1981						+		+	+	+
Strandesia nakatanii Ferreira *et al.*, 2020	+	+		+	+	+	+			+
Strandesia lansactohai Higuti & Martens, 2013	+		+	+	+	+	+	+		+
Strandesia mutica (Sars, 1901)	+	+	+	+	+	+	+			+
Strandesia nupelia Higuti & Martens, 2013	+	+	+	+	+	+	+	+	+	+
Strandesia psittacea (Sars, 1901)	+	+	+		+	+	+		+	+
Strandesia tolimensis Roessler, 1990					+					
Strandesia variegata (Sars, 1901)				+	+					
Strandesia velhoi Higuti & Martens, 2013					+					
Strandesia sp. 2					+					
Family Candonidae Kaufmann, 1900										
Candobrasilopsis brasiliensis (Sars, 1901)	+	+	+	+		+	+		+	+
Candobrasilopsis elongata Higuti & Martens, 2014	+	+	+	+	+	+	+		+	+
Candobrasilopsis rochai Higuti & Martens, 2012	+	+		+	+	+	+			+
Physocypria schubarti Farkas, 1958	+					+				
Pseudocandona agostinhoi Higuti & Martens, 2014	+	+			+	+				+
Pseudocandona cillisi Higuti & Martens, 2014	+	+		+		+			+	
Family Limnocytheridae Sars, 1925										
Cytheridella ilosvayi Daday, 1905	+	+	+	+	+	+	+	+	+	+

Family Darwinulidae Brady & Robertson, 1885										
Alicenula serricaudata (Klie, 1935)	+	+		+	+	+	+	+	+	+
Penthesilenula brasiliensis (Pinto & Kotzian, 1961)		+		+	+	+	+	+	+	+
Vestalenula pagliolii (Pinto & Kotzian, 1961)	+	+		+	+	+	+	+	+	+