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LEIDIANE PEREIRA DINIZ

Patterns of β diversity in aquatic ecosystems at different spatial and temporal scales

Maringá
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Tese apresentada ao Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais do Departamento de Biologia, Centro de Ciências Biológicas da Universidade Estadual de Maringá, como requisito parcial para obtenção do título de Doutora em Ecologia e Limnologia.
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COMISSÃO JULGADORA

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“...São tantos caminhos pra se seguir
E lugares pra se descobrir
E o sol a girar sobre o azul deste céu
Nos mantem neste rio a fluir...”
O Rei Leão

“O aspecto mais impressionante do mundo vivo é a sua diversidade...para onde olharmos na natureza encontramos singularidade”
Ernst Mayr

Padrões de diversidade β em ecossistemas aquáticos em diferentes escalas espaciais e temporais

RESUMO

As espécies estão distribuídas de forma heterogênea e alterações ambientais, como a construção de reservatórios ou eventos climáticos extremos, podem modificar a dinâmica dos organismos aquáticos. Entender os processos que impulsionam a diversidade, em longos períodos de tempo, pode auxiliar no estabelecimento de medidas de conservação cada vez mais precisas. Esta tese avaliou os padrões de diversidade β e estrutura de metacomunidade em diferentes escalas espaciais e temporais em três estudos independentes na planície de inundação do Alto rio Paraná, Brasil. No primeiro foi analisado a variação sazonal da diversidade β e Elementos da Estrutura da Metacomunidade [EMS] do zooplâncton, durante quatro anos (dois anos de seca prolongada e dois anos com inundação extrema), e em uma menor (sub-bacias) e maior escala (planície de inundação). Independente do período hidrológico e da escala, a estrutura da metacomunidade do zooplâncton se manteve praticamente constante ao longo dos quatro anos, com predomínio do padrão Clementsiano. A predominância desse padrão sugere que as associações de espécies responderam de forma semelhante ao gradiente ambiental e que as respostas diferiram entre os grupos de espécies. No segundo foi determinado a singularidade ecológica taxonômica (LCBD-t) e funcional (LCBD-f) do zooplâncton ao longo de 19 anos em lagos e sistemas lóticos de duas sub-bacias (represada e não represada), além de investigar quais processos (temporais, ambientais e biológicos) impulsionam a LCBD-t e LCBD-f. Independentemente das características de cada sub-bacia, os maiores LCBD-t e LCBD-f foram relacionados a menor riqueza de espécies e de traços, respectivamente. Os processos temporais foram os principais impulsionadores da singularidade ecológica do zooplâncton, sendo mais importante do que os processos biológicos (biovolume do fitoplâncton e biomassa dos peixes, representando recurso alimentar e potencial predador, respectivamente). Por último, foi testado se em uma sub-bacia represada, um período de seca prolongada torna as comunidades aquáticas (fitoplâncton, zooplâncton e peixes) mais semelhantes ao longo do tempo do que um período com inundações extremas. Apenas o zooplâncton sofreu homogeneização nesse período. A diversidade β do fitoplâncton e dos peixes não diferiu entre os períodos hidrológicos, indicando que o tipo de dispersão (passivo ou ativo) não interfere na homogeneização da seca. Como a resposta entre os grupos biológicos foi diferente, sugere-se que os grupos não são substitutos uns dos outros. A maior diversidade β no período com inundações extremas mostra, pelo menos para o zooplâncton, a importância do pulso de inundação, reduzindo os efeitos negativos da seca prolongada em uma sub-bacia represada. Os resultados mostraram a predominância de um padrão de metacomunidade resultante de alto turnover (Clementsiano), indicando que medidas de conservação devem incluir um maior número de locais, inclusive aqueles com menor riqueza, uma vez que podem ter composição distinta (> LCBD). Reforçamos também a importância de considerar diferentes escalas, uma vez que cada uma pode fornecer *insights* exclusivos. É importante que estudos de biodiversidade considerem a diversidade β para compreender os mecanismos que impulsionam as metacomunidade diante das alterações ambientais, especialmente em escalas temporais mais longas.

Palavras-chave: Zooplâncton. Planície. Traços funcionais. EMS. LCBD. Fitoplâncton. Peixe.

Patterns of β diversity in aquatic ecosystems at different spatial and temporal scales

ABSTRACT

Species are heterogeneously distributed and environmental changes, such as the construction of dams or extreme climate events, can modify the dynamics of aquatic organisms. Understanding the processes that drive diversity, across long time periods, can help in the establishment of increasingly accurate conservation measures. This thesis evaluated the patterns of β diversity and metacommunity structure at different spatial and temporal scales in three independent studies in the Upper Paraná river floodplain, Brazil. The first analyzed the seasonal variation of zooplankton β and Elements of Metacommunity Structure [EMS] of zooplankton, over four years (two years of prolonged drought and two years of extreme flooding), and on a smaller (sub-basins) and a larger scale (floodplain). Regardless of the hydrological period and spatial scale, zooplanktonic metacommunity structure remained practically constant throughout the four years, with the predominance of the Clementsian pattern. The predominance of the Clementsian pattern suggests that the associations of zooplankton species in the floodplain responded similarly to the environmental gradient and that the responses differed among species groups. In the second, the taxonomic (LCBD-t) and functional (LCBD-f) ecological uniqueness of zooplankton over 19 years was determined in lakes and lotic systems of two sub-basins (dammed and free-flowing), in addition to investigating which processes (temporal, environmental and biological) drive LCBD-t and LCBD-f. Regardless of the characteristics of each sub-basin, the highest LCBD-t and LCBD-f were related to lower species and trait richness, respectively. The temporal processes were the main drivers of the ecological uniqueness of zooplankton, and they were more important than the biological processes (phytoplankton biovolume and fish biomass, representing food resource and potential predation, respectively). Finally, it was tested whether, in a dammed sub-basin, a prolonged drought makes aquatic metacommunities (phytoplankton, zooplankton, and fish) more similar over time than a period that includes extreme flood events. Only zooplankton underwent homogenization during this period. The β diversity of phytoplankton and fish did not change between different hydrological periods, indicating that the dispersion type (passive or active) does not interfere with drought homogenization. The response between the biological groups was different, reinforcing that the groups are not surrogates of each other. The greater β diversity in the period with extreme floods shows, at least for zooplankton, the importance of the flood pulse, reducing the negative effects of prolonged drought in a dammed sub-basin. The results showed the predominance of a metacommunity pattern resulting from high turnover (Clementsian), indicating that conservation measures should include a greater number of sites, including those with less richness, as they may have a different composition (> LCBD). We also emphasize the importance of considering different scales, as each can provide unique insights. It is important that biodiversity studies consider β diversity to understand the mechanisms that drive the metacommunity in the face of environmental changes, especially over longer time scales.

Keywords: Zooplankton. Floodplain. Functional traits. EMS. LCBD. Phytoplankton. Fish.

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SUMMARY

1 GENERAL INTRODUCTION

Which processes are responsible for changing aquatic biota over space and time? How do species respond to different stressors? Which processes govern β diversity patterns in aquatic metacommunities? How do the spatio-temporal dynamics affect the structuring of the metacommunity? Although there is no unified answer to these questions, since classic works, such as Forbes (1887) "The lake as a microcosm", a great advance has been observed in ecological studies trying to unveil these questions. These advances are largely due to the loss of biodiversity in the Anthropocene (SINGH, 2002). The regulation of water flow by reservoirs in natural systems is one of the main factors responsible for the loss of biodiversity in freshwater ecosystems, since they homogenize the dynamics of rivers, affecting all aquatic biota (AGOSTINHO et al., 2004). Given the loss of biodiversity and the heterogeneous distribution of species on the globe (GASTON, 2000), understanding changes in species composition and distribution patterns, over time or in space, allows us to assist in conservation measures in the face of global changes (SOCOLAR et al., 2016).

In this context, studies that consider the relationships between β diversity and environmental changes, such as the impact of dams and extreme climate events, are important in the context of current environmental degradation, climate change, and loss of biodiversity (PETSCH, 2016; MORI et al., 2018; BOMFIM et al., 2021). Thus, β diversity, which for a long time was a little-explored facet of biodiversity, has been receiving considerable interest in recent years (SOCOLAR et al., 2016; MORI et al., 2018). Metrics to estimate β diversity have changed over time, and the choice of metric depends on the objective of each study (BASELGA, 2010; PODANI & SCHMERA, 2011; CARVALHO et al., 2012; LEGENDRE & DE CÁCERES, 2013). Regardless of which approach is taken, β diversity studies have become increasingly prominent, especially those that in addition to considering the identity of the species also address the ecological functions performed by them (BRAGHIN et al., 2018; SIMÕES et al., 2020; DINIZ et al., 2021).

Functional β diversity, variation in the composition of traits between sites or within a site between times, has been gaining prominence because it is often more sensitive in detecting environmental changes than the taxonomic approach. In addition, this approach can provide a better understanding of ecosystem functioning (LITCHMAN et al., 2013; BRAGHIN et al., 2018; DINIZ et al., 2021). This is because although two species may be taxonomically similar if they present different functional strategies (that is, functional divergence), the impact of losing these species would be greater than if they performed the same ecosystem function

(VILLÉGER et al., 2012; LOISEAU et al., 2017). Thus, the loss or gain of some species may have greater functional implications than others for the ecosystem (CADOTTE et al., 2011).

Understanding β diversity patterns is critical in understanding many ecological processes, including the principles of structuring a metacommunity (CHASE et al., 2020). A metacommunity is traditionally defined as a set of local ecological communities potentially connected by dispersion (LEIBOLD & NORBERG, 2004; LEIBOLD et al., 2004). Thus, the fundamental idea of metacommunity ecology is that a community should not be understood in isolation from the network of communities in which it interacts. Therefore, it is widely known that several factors can influence the structuring of the metacommunity, highlighting both deterministic and stochastic processes. The deterministic theory includes the environmental filter and the biotic interactions themselves as being determinants for diversity patterns (CHASE et al., 2020), while stochastic theories involve random events, such as ecological drift and colonization, and extinction at random (CHASE & MYERS, 2011).

However, the main challenge for ecologists has been to interpret the observational data and, from that, to infer the processes that are likely to structure the metacommunity (OVASKAINEN et al., 2019). Many studies have assumed that metacommunity assembly processes are relatively stable over time. This is problematic because patches have their temporal dynamics and it is difficult to try to categorize them within a single paradigm (such as patch-dynamic, species-sorting, mass effects, or neutral perspective), since they are not exclusive (LOGUE et al., 2011). Holyoak et al. (2020) address three types of temporal variation that can alter the dynamics and structure of a metacommunity and that need to be considered in ecological studies: (i) *stochastic and unpredictable*, which occurs quite often and therefore organisms can respond well; (ii) *predictable temporal variation*, such as seasonality or flood pulses, which can be overcome by the evolution of the life history of organisms; (iii) *stochastic and infrequent temporal variation*, such as extreme climatic events or even the damming of a river.

The assessment of the dynamic β diversity and structuring of metacommunities through long time scales is recent and there is still a lot to be explored (RUHÍ et al., 2017; SARREMEJANE et al., 2017; WOJCIECHOWSKI et al., 2017; SILVA et al., 2021). Many ecological studies have been conducted in the snapshot. In this case, it is considered that the dynamics of the organisms are stable over time and, because they show only one of the different stages of that metacommunity, they may not represent well the reality of the natural biota (MEYNARD et al., 2013; FERNANDES et al., 2014). Furthermore, the same event can lead to different patterns of metacommunity and β diversity, depending on the spatial and temporal scale considered, especially in highly dynamic environments such as a floodplain (LANSAC-TÔHA et al., 2021; PETSCH et al., 2021). Thus, because biodiversity changes over time and space, it is necessary to consider different scales to obtain clearer ecological responses and more robust conservation measures (MAGURRAN et al., 2019).

Floodplains are highly dynamic systems that support one of the largest biodiversities in the world, attributed mainly to their high spatial and temporal variability (JUNK et al., 1989; TOCKNER & STANFORD, 2002; CHAPARRO et al., 2019). Even so, this system is among the most threatened in the world, with flood control through the construction of dams and the introduction of exotic species among the most common impacts (TOCKNER & STANFORD, 2002; AGOSTINHO et al., 2005). The Paraná River, in Brazil, for example, is considered the system most affected by dams in Brazil (AGOSTINHO et al., 2008), resulting in changes in biodiversity, functioning, and ecosystem services of the entire floodplain (AGOSTINHO et al., 2008; OLIVEIRA et al., 2018). Even so, the Upper Paraná River floodplain represents a highly dynamic system with high biodiversity (AGOSTINHO et al., 2004; BONECKER et al., 2020), and ecological studies of β diversity and metacommunity that help define management and conservation strategies are increasingly necessary.

Zooplankton is highly diverse in floodplains (BONECKER et al. 2020) and has a wide variety of morphology, strategies, and ecological functions (LITCHMAN et al., 2013). In addition, as it has passive dispersion and phylogenetically distinct groups, also to responding quickly to environmental changes, it is excellent for testing ecological theories (FRISCH et al., 2012; DIAS et al., 2016). Zooplankton also plays an important role in the trophic web, being a link between primary producers and other trophic levels (ALLAN, 1976). Thus, they can directly or indirectly influence other biological groups, such as phytoplankton and fish (LI et al., 2020; MAO et al., 2020; DEOSTI et al., 2021). Therefore, to maintain the multifunctionality of aquatic ecosystems it is necessary to conserve the different trophic groups (MOI et al., 2021). Although zooplankton is used as a model in ecological studies, it is important to emphasize that one group is not a surrogate of another, and that certain patterns can be specific only to certain groups

Based on this, this thesis evaluated the patterns of β diversity and metacommunity structure at different spatial and temporal scales in three independent studies in the Upper Paraná River floodplain. In the first study (Manuscript 1), we investigated the seasonal variation of β diversity and the zooplanktonic metacommunity structure (using the Elements of Metacommunity Structure "EMS" approach) over four years (two years of prolonged drought and two years with extreme flood events) and on two spatial scales (sub-basins and floodplain;

smaller and larger spatial scales, respectively), considering 29 lakes. In the second study (Manuscript 2), the aim was to determine the taxonomic (LCBD-t) and functional (LCBD-f) ecological uniqueness of zooplankton over 19 years in lakes and river systems of two sub-basins (one that was dammed in 1998 and the other free-flowing), in addition to investigating which processes (temporal, environmental, and biological) drive the LCBD-t and LCBD-f. Lastly, in the third study (Manuscript 3), we tested whether a prolonged drought period makes aquatic metacommunities more similar over time than a period that includes extreme flood events. For this, three distinct biological groups (phytoplankton, zooplankton and fish) and ten lakes, over four years (two years of prolonged drought and two years with extreme flood events) were studied.

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Zooplankton β diversity dynamics and metacommunity structure depend on spatial and temporal scales in a Neotropical floodplain*

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2 ZOOPLANKTON β DIVERSITY DYNAMICS AND METACOMMUNITY STRUCTURE DEPEND ON SPATIAL AND TEMPORAL SCALES IN A NEOTROPICAL FLOODPLAIN

Abstract

1. Both β diversity and metacommunity structure vary in time and space. It is necessary to examine different scales, especially in the face of extreme hydrological conditions.

2. We investigated seasonal variation in β diversity and Elements of Metacommunity Structure [EMS] of zooplankton during four years (two years of prolonged drought and two years with extreme flood events) and at two spatial scales (sub-basins and floodplain; smaller and larger spatial scale, respectively).

3. We sampled 29 lakes quarterly during four years in the Upper Paraná River floodplain, Brazil. We estimated the replacement component of β diversity using the Jaccard dissimilarity index. We also used EMS to determine the metacommunity pattern of zooplankton distribution in each period and spatial scale.

4. The flood peak observed in the snapshot sampling drove the homogenization of zooplanktonic assemblages. However, β diversity was not reduced in the two years with extreme flood events compared to the period of prolonged drought at either of the spatial scales (floodplain and sub-basins), except for a single sub-basin. This finding shows the importance of longer-term ecological studies to better capture the dynamics of the zooplanktonic metacommunity.

5. Regardless of the hydrological period and spatial scale zooplanktonic metacommunity structure remained practically constant throughout the four years, with a predominance of species range turnover (Clementsian). At the smallest spatial scale (sub-basins), we found quasi-structural patterns (quasi-Clementsian and quasi-Gleasonian). The predominance of the Clementsian pattern suggests that the associations of zooplankton species in the floodplain responded similarly to the environmental gradient and that the responses differed among species groups. 6. Over time, the smaller spatial scale (sub-basin) better represents the dynamics of β diversity than the larger spatial scale (floodplain), and better represents the structure of the zooplankton metacommunity. However, we emphasize the need for further studies to consider different biological groups and larger spatial scale over time to maximize the understanding of aquatic metacommunities dynamics.

Keywords: Clementsian pattern, elements of metacommunity structure, limnophase, Paraná river, potamophase.

2.1 Introduction

The world is facing a biodiversity crisis, and the forecast scenarios show that extreme hydrological periods will be more and more frequent (Singh, 2002). Given this scenario, studies involving conservation are essential (Socolar et al., 2016). When the intention is to study extreme patterns or variations in ecological patterns in dynamic systems, floodplains stand out because they undergo significant changes in a single year and are also influenced by extreme climatic events, such as *El Niño* and *La Niña* (Borges & Train, 2009; Fernandes et al., 2014). The hydrological cycle, characterized by periods of floods and droughts, is a crucial factor in maintaining ecological processes and diversity patterns in floodplains (Junk et al., 1989; Neiff, 1990; Thomaz et al., 2007). By increasing the river's water level and, thus, the connectivity between sites, floods act as homogenizers of habitats and aquatic communities (Thomaz et al., 2007), thus decreasing β diversity at the landscape scale. In contrast, during extreme droughts, higher environmental heterogeneity is recorded and both biotic relationships and environmental conditions seem to be more important in maintaining community structure (Simões et al., 2013). This higher environmental heterogeneity, in the drought period, sometimes leads to a greater β diversity since the availability of resources tends to increase along with environmental heterogeneity (Maloufi et al., 2016). However, this relationship between environmental heterogeneity and β diversity is still under debate in the literature (Astorga et al., 2014; Bini et al., 2014; Lopes et al., 2014; Maloufi et al., 2016).

Most studies have sought to understand variations in β diversity patterns through analyses that verify the contribution of local and regional processes (metacommunity mechanistic approach) (Heino, Nokela et al., 2015; Leibold et al., 2004; Logue et al., 2011). However, it is also important to focus on identifying species distribution patterns (Heino, Soininen et al., 2015; Leibold & Mikkelson, 2002; Presley et al., 2010) and, since β diversity can provide information about the organization of metacommunities, studies that consider these two approaches simultaneously - β diversity and elements of metacommunity structure (EMS)- are necessary (Wojciechowski et al., 2017). EMS is a handy approach in searching for general rules that will determine the organization of metacommunities (Leibold & Mikkelson, 2002; Presley et al., 2010). Although EMS has received some criticism regarding its consistency in determining specific idealized patterns (Schmera et al., 2018; Ulrich & Gotelli, 2013), many researchers consider that the cautious use and interpretation of EMS results is very useful and allows a better understanding of patterns in metacommunities (Alves et al., 2020; Heino, Nokela, et al., 2015). EMS investigates hierarchically three elements to determine spatial and/or temporal patterns of species distribution in a metacommunity: *coherence*, *species range* *turnover*, and *boundary clumping*. Coherence shows how species respond to an environmental gradient, while species range turnover is related to species replacement. The last element, boundary clumping, evaluates the overlap of species distribution limits along a gradient (i.e. it indicates the distinctiveness of blocks of species). Based on the evaluation of these elements, five ecological patterns can be recognized that summarize the distribution of species among communities: Clementsian, Gleasonian or evenly spaced (for cases of positive coherence and species range turnover), nestedness (positive coherence and negative species range turnover), and random distribution (non-significant coherence) (Leibold & Mikkelson, 2002; Presley et al., 2010). Previous studies have considered the checkerboard (negative coherence) pattern in their EMS analyzes. However, we did not consider this pattern in our research since it was recently discovered that EMS has methodological limitations for identifying checkerboard pattern (Presley et al., 2019).

The Clementsian (Clements, 1916) and Gleasonian (Gleason, 1926) gradients are related to a very old debate on ecology, regarding the attempt to understand whether groups of species respond in a similar way to an environmental gradient (Clementsian gradient) or if they respond individualistically (Gleasonian gradient). Over time, other species distribution patterns have also been recognized, in addition to these two gradients. An evenly spaced gradient, for example, may arise in the face of strong interspecific competition between species (Tilman, 1982). By contrast, the nested pattern occurs if the sites with the fewest species represent subsets of the richest sites, arising, for example, from changes in environmental heterogeneity or simply from dynamic extinction-colonization (Patterson & Atmar, 1986). However, if the organisms do not respond to any of these patterns, their distribution is not coherent, in which case the distribution will be taken as random (Leibold & Mikkelson, 2002). Most of these patterns can form quasi-structures, when a species niche breadth extended beyond the range in which species turnover is significant. In this case, although quasi-structures represent the same attribute as its corresponding structure (quasi-Clementsian and Clementsian, for example), due to weaker structural forces it is not significant. Thus, quasi-structures indicate weaker structuring mechanisms than structures where species range turnover is significant (Presley et al., 2010).

For freshwater communities, the patterns observed have been Clementsian, Gleasonian, nestedness, or random distribution (see Alves et al., 2020; Fernandes et al., 2014; Heino, Melo et al., 2015; Henriques-Silva et al, 2013; Petsch et al., 2017; Tonkin et al., 2016). One way to explore these patterns is through β diversity (Wojciechowski et al., 2017). The predominance of the Clementsian and Gleasonian patterns, for example, may be a result of high values of β diversity, since they are driven by a positive species range turnover. Thus, even though it is difficult to make accurate predictions for the EMS approach, greater environmental variability and/or dispersal limitation can generate high β diversity and, consequently, lead to a positive turnover gradient (e.g., Clementsian, Gleasonian, or evenly spaced) (Presley et al., 2010; Wojciechowski et al., 2017).

Factors such as the degree of connectivity, dispersal limitation, or the environmental filter itself can influence patterns of β diversity and metacommunity distribution in highly dynamic ecosystems such as floodplains (Fernandes et al., 2014). However, in addition to understanding which environmental predictors are important, it is necessary to examine the scale at which each phenomenon occurs (Chaparro et al., 2018; Meynard et al., 2013). This is an important factor in determining the species distribution pattern found (Viana & Chase, 2019). On a large spatial scale, greater environmental variability can be captured and will determine changes in the species composition. However, at a smaller spatial scale, environmental heterogeneity will be less important, and stochastic processes will tend to be stronger (Chase, 2014; Garzon-Lopez et al., 2014). Thus, when we consider a smaller spatial scale, as it does not cover all heterogeneity and availability of resources, weaker EMS patterns (i.e. quasi-structures) could be expected. This contrasts with larger spatial scales where all environmental heterogeneity can be captured. Thus, a stronger relationship between β diversity and its predictors is expected (Melchior et al., 2017), as well as significant EMS patterns (i.e. patterns without quasi-structures).

In addition to spatial scale, temporal scale is also important since many ecological phenomena only become noticeable in larger temporal periods (e.g., extreme drought and flood events; Lindenmayer et al., 2012; Reich & Lake, 2015). Snapshot studies assume that the dynamics of organisms are stable over time and, therefore, often they may not represent the reality of nature well because they show only one of the different stages of a community (Chaparro et al., 2018; Fernandes et al., 2014; Meynard et al., 2013). Thus, snapshot or long-term studies can detect different patterns (Fernandes et al., 2014). In this sense, it is essential to evaluate biological data in a spatio-temporal context (Dornelas et al., 2013). However, most studies have considered only spatial scale (Braghin et al., 2018), and few studies have incorporated the influence of temporal variation on β diversity and metacommunity structure (EMS) (e.g. Fernandes et al., 2014; Wojciechowski et al., 2017). In the case of Neotropical floodplains, where the flood pulse is a key factor in their structure and functioning (Junk et al., 1989; Neiff, 1990), monitoring spatial and temporal variation becomes even more important. This is because, in addition to sustaining high biodiversity, attributed to spatial heterogeneity and temporal variability, they are threatened by human actions, such as regulation of water flow by reservoirs (Agostinho et al., 2004; Lansac-Tôha et al., 2009). Thus, understanding the processes that affect β diversity and metacommunity patterns in these highly dynamic ecological systems is extremely necessary to consolidate political and environmental strategies and, thus, assist in the management of floodplain ecosystems (Chase et al., 2020).

In floodplains, aquatic organisms are adapted to live in floating environments, and zooplankton are especially suitable for analyzing the effects of extreme environmental conditions at different spatial and temporal scales (Leibold & Norberg, 2004). This is related to the fact that they have a short life cycle (Allan, 1976) and can respond quickly to physico-chemical changes in water sources, being highly sensitive to environmental variability (Simões et al., 2013). Furthermore, because they have different dispersal capacity and comprise phylogenetically distinct groups, zooplankton are considered ideal for testing ecological theories, using β diversity or metacommunity concepts (Dias et al., 2016; Frisch et al., 2012).

We investigated seasonal variation of β diversity and zooplankton metacommunity structure (using an EMS approach) during 4 years (2 years of prolonged drought and 2 years with extreme flood events) and on two spatial scales (sub-basins and floodplain). We tested the following hypotheses: (1) Flooding reduces β diversity, both in snapshots (single collections) and at a 2-year time scale with extreme flood events. (2) Regarding the temporal scale, in the 2-year period of extreme flooding, β diversity is lower and the random distribution predominates, while in the 2-year period of prolonged drought, β diversity is higher and the Clementsian or Gleasonian pattern dominates, especially at a larger spatial scale (Figure 1). The predominance of the random distribution in the period of extreme floods is expected because flood events increase dispersal rates, decreasing β diversity and allowing species to be distributed more widely and randomly (Bortolini et al., 2017). By contrast, in years of drought, heterogeneity becomes higher, resulting in greater niche variability, thereby increasing turnover between species. Therefore, in periods of prolonged drought, we expect the predominant metacommunity patterns to be related to high turnover values (i.e. Clementsian or Gleasonian). Although the evenly spaced pattern can also be found when the range species turnover is significant, it is associated with cases of high competition, which we do not believe to be the case for planktonic organisms where coexistence through niche partitioning is more common than competition (see the paradox of the plankton – Hutchinson, 1961). (3) At a larger spatial scale (floodplain), significant metacommunity patterns predominate, while at a smaller spatial scale (sub-basins), quasi-structures predominate (Figure 1). Because a smaller scale does not cover all environmental heterogeneity of a region, fewer established EMS patterns with a predominance of quasi-structures are to be expected. Finally, we also tested whether the hydrological period, environmental heterogeneity, and water level influence β diversity at all spatial scales over time.

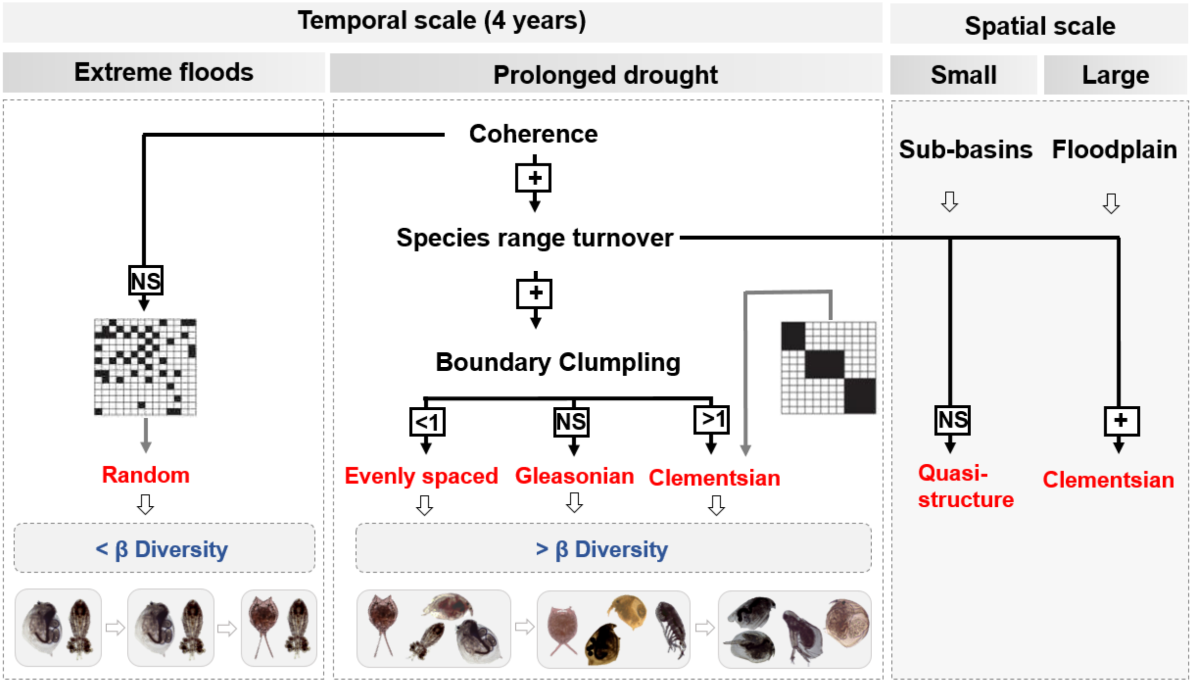

Figure 1 Conceptual model illustrating our main hypotheses. In blue and red are the expected patterns of β diversity and metacommunity structure (EMS), respectively, for each period and spatial scale. The prolonged drought period (2 years, 2000-2001) and the extreme flood period (2 years, 2010 - 2011) correspond to our time scale. The different time scales reference the comparison between snapshot collections (at the peak of the flood) and extreme flood period (2 years). The spatial scale is related to floodplain (larger spatial scale) or to each sub-basin separately (smaller spatial scale).

2.2 Methods

2.2.1 Study area

The Upper Paraná River floodplain (22°40′-22°50′S and 53°10′-53°40′W) is located between the states of Paraná and Mato Grosso do Sul, Brazil. This floodplain constitutes the last stretch of the Paraná River free of dams in Brazilian territory, situated between the Porto Primavera (São Paulo) and Itaipu (Paraná) dams (Figure 2). The Upper Paraná River floodplain represents a highly dynamic ecosystem with high biodiversity (Agostinho et al., 2004; Lansac-Tôha et al., 2009). The hydrological regime is characterized by flood pulses and alternating drought events, responsible for increasing the heterogeneity between the habitats (Thomaz et al., 2007) and a key factor in the structure and functioning of the floodplains (Junk et al., 1989; Neiff, 1990). However, after the construction of the Porto Primavera reservoir (1998), the patterns of the natural dynamics of the floodplain changed, causing drought events to become more intense (> 2 m from the level of the Paraná River) while events of extreme flooding (~ 6m) became less and less frequent (Figure 3). In addition to altering the natural dynamics, the effect of flow control and sediment retention, as a consequence of the construction of a reservoir, alters the biodiversity, functioning and ecosystem services of the entire floodplain (Agostinho et al., 2008; Oliveira et al., 2018).

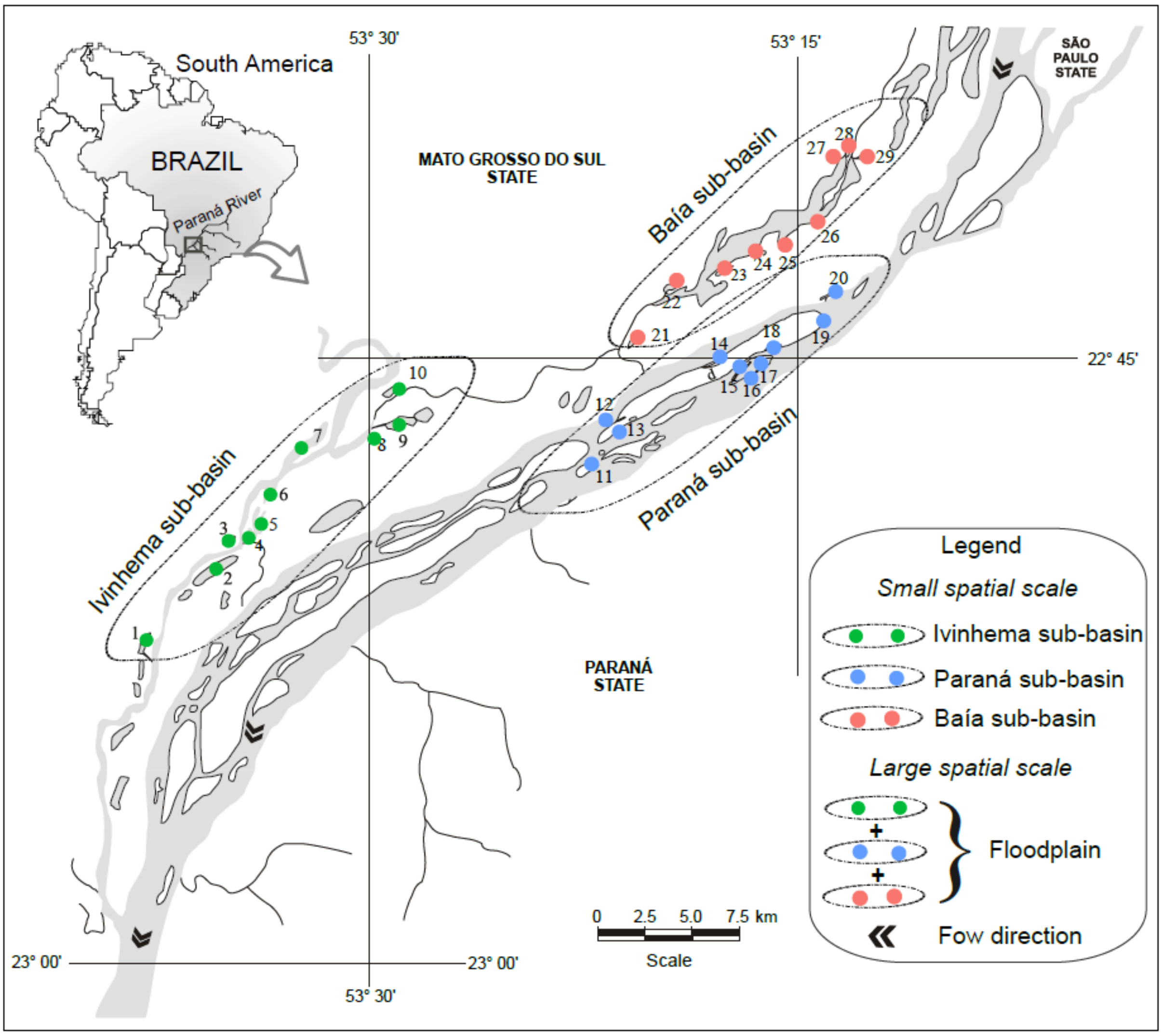

Figure 2 Location of the 29 floodplain lakes studied in three sub-basins of the Upper Paraná River Floodplain, Brazil. *Ivinhema*: 1 - Peroba; 2- Ventura; 3 –Zé do Paco; 4 –Boca de Ipoitã; 5 –Patos; 6 –Capivara; 7 –Finado Raimundo; 8 –Jacaré; 9 –Sumida; 10 – Cervo. *Paraná*: 11 - Pombas; 12 - Manezinho; 13 - Osmar; 14 - Bilé; 15 - Leopoldo; 16 - Genipapo; 17 - Clara; 18 - Pau Véio; 19 - Pousada; 20 - Garças; *Baía*: 21 - Traíra; 22 -Guaraná; 23 - Fechada; 24 - Garças; 25 - Porcos; 26 - Aurélio; 27 - Maria Luiza; 28 - Gavião; 29 - Onça.

The studied area includes three sub-basins: Paraná, Baía, and Ivinhema. The Paraná River sub-basin is considered impacted due to a series of reservoirs upstream, suffering from the oligotrophication process. The sub-basin of the Baía River flows parallel to the sub-basin of the Paraná River and, therefore, is considered partially regulated. Finally, the sub-basin of the Ivinhema River is considered to be conserved, being inserted in a conservation unit and free of dams (State Park *Várzeas do rio Ivinhema*) (Agostinho et al., 2008; Oliveira et al., 2018).

Sampling was carried out in 29 lakes: 10 lakes were located in the sub-basin of the Ivinhema river; 10 in the sub-basin of the Paraná River, and nine in the sub-basin of the Baía River (Figure 2). Some lakes remain connected to the main river, and others are temporarily isolated. Still, they connect to the main river during periods of flooding. The depth of the lakes varied from 0.6 to 4 m, in the period of prolonged drought, and from 1.1 to 4.7 m in the period of extreme floods (see Table S1 in Appendix A).

This study is part of the project "Long-Term Ecological Research" site 6 (PIAP–PELD/CNPq), which involves sampling of different aquatic communities in the Upper Paraná River floodplain, since 2000. The main aim is to monitor the biodiversity of the region over time.

2.2.2 Water level

To test our hypothesis comparing contrasting hydrological periods of the Upper Paraná River floodplain, we chose 2 years of prolonged drought (2000 and 2001) and 2 years with extreme floods (2010 and 2011; Figure 3). The years categorized as a prolonged drought period were influenced by the *La Niña* climatic event when below-normal rainfall occurred (Borges & Train, 2009), while years with extreme floods were affected by the *El Niño* climatic event, with above-average rainfall levels for lowland (CPTEC, 2012). The water level considered was referent to Paraná River. We used the 3.5 m water level as the reference value for the overflow and the consequent beginning of the flood period (Souza Filho, 2009; Thomaz et al., 2004). Over the four years of study, the Paraná river level varied between 1.2 and 5.1 m (period of prolonged drought) and between 2.0 and 6.7 (period with extreme flood events; Figure 3).

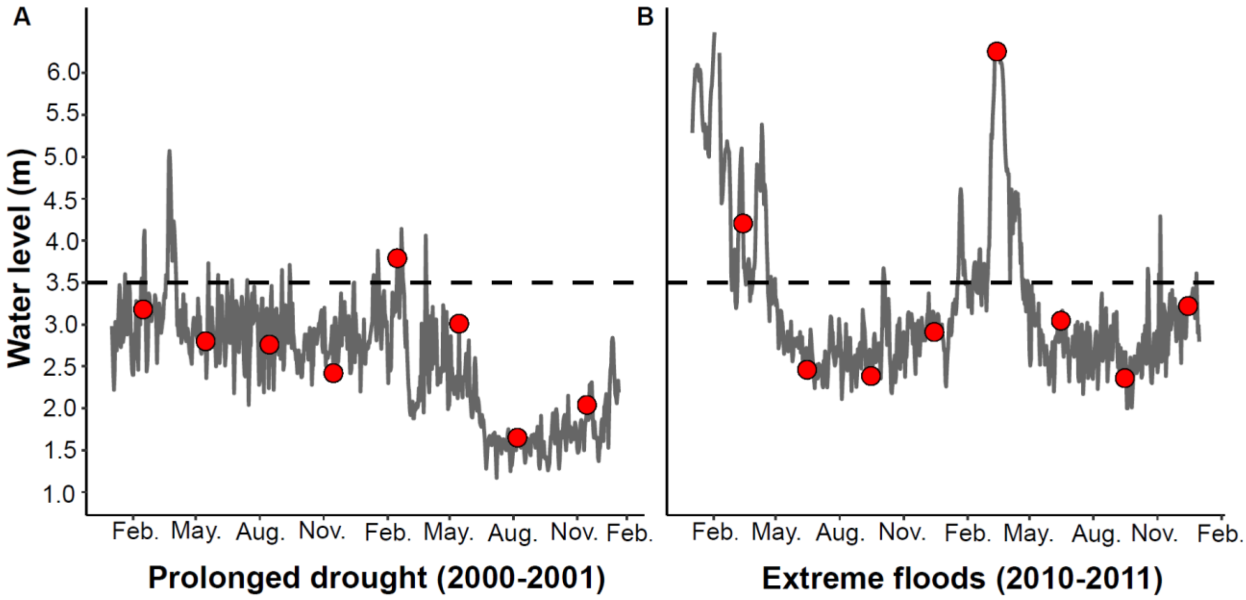

Figure 3 Daily levels of water volume in the Paraná River in periods of prolonged drought (2000-2001; A) and periods with extreme flood events (2010-2011; B). The red dots represent the water level at the time of each collection.

2.2.3 Zooplankton sampling and analysis

Zooplankton collections were carried out quarterly during 4 years, totaling 16 sampling occasions: eight during the period of prolonged drought (2000-2001) and eight during the period with extreme flood events (2010-2011). All samples were obtained from the sub-surface of the pelagic zone of each lake, always in the morning, with the aid of a motor-pump and 68µm plankton net, with 600 L of water being filtered per sample. To obtain a representative sample of each lake, we standardized the sampling effort applied with the boat always moving at a constant speed. All samples were fixed with a 40% formaldehyde solution, buffered with calcium carbonate, and preserved with 4% formalin solution.

In the laboratory, zooplankton organisms were observed under an optical microscope and identified from specific literature (Elmoor-Loureiro, 1997; Koste, 1978; Matsumura-Tundisi, 1986; Reid, 1985). For each sample, quantification was performed by subsampling with a Hensen-Stempell, with at least 10% of the sample being counted in Sedgwick-Rafter chambers (Bottrell et al., 1976).

2.2.4 Environmental variables sampling and analysis

Each lake, with the same periodicity of collections from the zooplankton community, was characterized in terms of environmental conditions, using the following descriptors: depth (m; portable depth sounder), water temperature (°C; YSI digital portable), pH (digimed digital potentiometer), dissolved oxygen (mg L^{-1}; YSI digital portable), electric conductivity (µS cm^{-1}; digimed digital potentiometer), turbidity (NTU; portable turbidimeter), nitrate (µg L^{-1}; Giné et al., 1980), phosphate (µg L^{-1}; Golterman, Clymo & Ohstad, 1978) and chlorophyll-*a* concentrations (µg L^{-1} ; Golterman, Clymo & Ohstad, 1978). As the phytoplankton community has a strong trophic relationship with zooplankton and influences its dynamics (Striebel et al., 2012), we used the chlorophyll-*a* concentration to represent phytoplankton. Many studies have also used chlorophyll-*a* concentration as a resource proxy for zooplankton (Dias et al., 2016; Ulloa, 2004). However, we emphasize that this is only an estimate of this trophic relationship, since chlorophyll-*a* may also include cyanobacteria or large diatoms that may not be palatable for some zooplanktonic species, such as *Daphnia* (Ferrão-Filho et al., 2014).

2.2.5 Data analysis

To calculate β diversity, we used a permutational analysis of multivariate dispersions (PERMDISP, function *betadisper*; Anderson et al., 2006). This test is based on the distance between the variables and their centroid in the multivariate space (here, principal coordinate analysis). Thus, the greater the mean distance to centroid, the greater the β diversity. We transformed the incidence matrix of zooplankton species into a Jaccard dissimilarity matrix. Then, we partitioned β diversity into its component richness differences and replacement, following the approach of Podani and Schmera (2011) and Carvalho et al. (2012) (function *beta*; Cardoso et al., 2018). We considered only the replacement component for our β diversity analyses since the EMS approach includes species range turnover as one of its elements. Thus, we sought to minimize the effect of the difference in species richness in estimating β diversity and obtained only the replacement of species among sites. We chose to calculate β diversity with this approach because it has the advantage of not weighting one of the β diversity components (in this case, replacement) too highly and because it is theoretically and algebraically correct (Carvalho et al., 2012). These analyses generated a value of environmental heterogeneity and β diversity, for each of the 16 sampling occasions. In addition to investigating whether β diversity would be higher in periods of prolonged drought, we were interested in verifying the spatial scale of each phenomenon. For this reason, we performed PERMDISP considering both the largest spatial scale (floodplain) and the smallest spatial scale (sub-basins separately).

We also used PERMDISP to calculate environmental heterogeneity at both spatial scales (i.e. floodplain and sub-basins). We obtained environmental heterogeneity from Euclidean distances of environmental variables (depth, water temperature, pH, dissolved oxygen, electrical conductivity, turbidity, nitrate, and phosphate) and resource (concentrations of chlorophyll-*a*). All variables were standardized for z-scores before analysis.

To test the hypotheses that flooding reduces β diversity, both in snapshots (single collections) and in a 2-year time scale with extreme flood events (hypothesis 1) and that β diversity is greater in the prolonged drought period (hypothesis 2) we used beta regression models (function *betareg*, Cribari-Neto & Zeileis, 2010). Estimates were obtained through maximum likelihood (ML). We chose this procedure because the values of β diversity estimated using PERMDISP vary from zero to one. We standardized the environmental predictors (environmental heterogeneity also estimated using PERMDISP and water level) for z-scores before analysis to make slope coefficients comparable. We visually inspected the assumptions of normality and homoscedasticity. As the data do not show temporal autocorrelation (tested using the autocorrelation function (ACF) analysis, using the *acf* function; Figure S1), we believe it was not necessary to use a model that considered time correction. β regression models were also used to test whether environmental predictors (environmental heterogeneity, water level, and hydrological period) influence β diversity over time in all spatial scales.

To test the predominant metacommunity pattern in each hydrological period (hypothesis 2) and to verify if in the smallest spatial scale quasi-structures predominate (hypothesis 3), we used the EMS (Leibold & Mikkelson, 2002; Presley et al., 2010). A metacommunity pattern is obtained by hierarchically evaluating coherence, species range turnover, and boundary clumping elements in the distribution of species, which result in five possible distribution patterns: random, nestedness, Clementsian, Gleasonian, and evenly spaced (Leibold & Mikkelson, 2002; Presley et al, 2010; 2019; Figure 4). In addition to these distribution patterns, corresponding quasi-structures may occur when the species range turnover is not significant. Thus, each quasi-structure (quasi-nested, quasi-Clementsian, quasi-Gleasonian, and quasi-evenly spaced) has the same essential characteristics as its associated idealized structure, except that species range turnover is not significant (Presley et al., 2010).

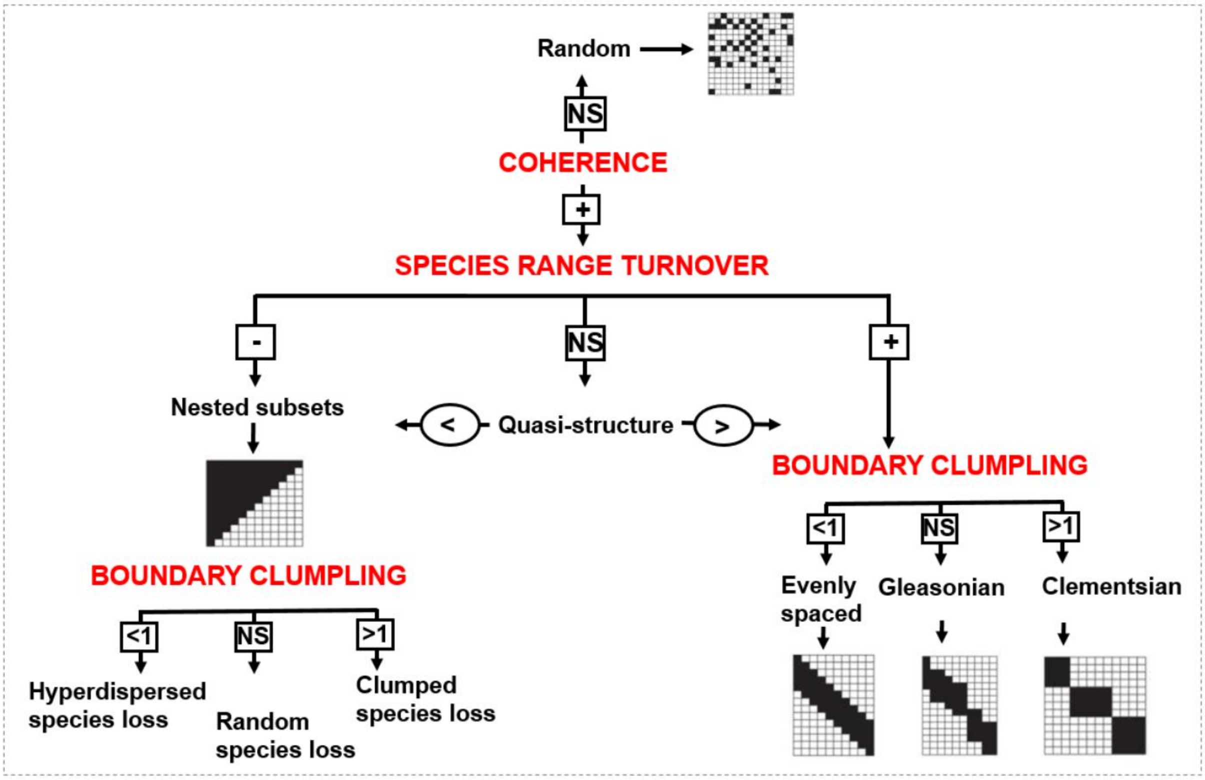

Figure 4 Representation of the elements of metacommunity structure approach that can result in six patterns of species distribution (Leibold & Mikkelson, 2002) or six patterns of quasi-structures (Presley, Higgins & Willig, 2010). (-) negative value, (+) positive value, (NS) non-significant value and (<1 or <1) correspond to the results of the Morisita index. Figure adapted from Presley et al., (2010).

To calculate the EMS we followed the *range perspective* in the analysis (Presley et al., 2010). We used the fixed-proportional null model (*r1* method) to investigated the significance of coherence and species range turnover. The fixed-proportional null model keeps the species richness of each lake (i.e. the sums of the lines remain fixed). However, species ranges (i.e. columns) are determined through on their marginal probabilities. This null model has also been widely used and indicated because it is not highly sensitive to type I or II errors (Alves et al, 2020; Heino, Nokela et al., 2015; Presley et al., 2010; Wojciechowski et al., 2017).

We ordered a presence and absence matrix using reciprocal averaging. Firstly, we analyzed the coherence, which is related to how much the species respond to the same environmental gradient or to the number of embedded absences, which can be defined as an absence found for a species between two locations in the ordered array (Braga et al., 2017). We compared the number of embedded absences in the ordered matrix, by reciprocal average, with the empirically observed value of embedded absences to a null distribution created from a simulation with 1000 randomly ordered matrices (Braga et al. 2017; Presley et al., 2010). If the coherence is not significant, the species distribution is not different from the null model and, therefore, occurs at random. However, if it is significantly positive, the species range turnover is analyzed. The significance of the species range turnover was also tested using a fixed-proportional null model, as in other recent studies (Alves et al., 2020; Heino, Nokela et al., 2015; Wojciechowski et al., 2017). When the species range turnover (positive or negative) is not significant, the resulting pattern will be a quasi-structure (Figure 4). Quasi-structures were incorporated to solve the problem of lack of identification of a pattern when the species range turnover was not significant (Presley et al., 2010). If turnover is significantly negative, it indicates a nested pattern. If it is positive, regardless of whether it is significant or not, the third element is analyzed, boundary clumping. Significance of boundary clumping is given by the Morisita index, which is determined using a χ^2 test. If the Morisita index is significantly lower than one ($I < 1$), it indicates an evenly spaced gradient (or quasi-evenly spaced). However, if the index is significantly higher than 1 ($I > 1$), the pattern is Clementsian. But, if the value is not significant, the EMS framework suggests a Gleasonian distribution (Figure 4). Finally, to check whether the EMS pattern changes depending on the spatial extent, we calculated the EMS on the largest spatial scale (i.e., considering all the lakes on the floodplain) and on the smallest spatial scale (i.e. considering the lakes of each sub-basin separately).

All analyses were performed in R (R Core Team, 2019), using the following packages: *vegan* (Oksanen et al., 2019), *metacom* (Dallas, 2014), *betareg* (Grün et al., 2012), *BAT* (Cardoso et al., 2018), and *ggplot2* (Wickham, 2016).

2.3 Results

Environmental heterogeneity did not differ between the period of prolonged drought (2000-2001) and the period of extreme floods (2010-2011), neither at the largest spatial scales ($F_{(1,28)} = 0.83$; $p = 0.37$) nor the smallest. The only exception occurred for one of the sub-basins (Ivinhema), the smallest spatial scale, which showed a slightly higher heterogeneity in years of prolonged drought (mean distance to centroid = 2.72) than in years with extreme flood events (mean distance to centroid = 2.25; $F_{(1,8)} = 4.52$; $p = 0.03$). Over time, the largest spatial scale does not seem to cover a greater heterogeneity than the smallest spatial scale (Figure S2; Appendix A).

We recorded a total of 352 zooplankton species, including 224 rotifers, 90 cladocerans, and 38 copepod species (Table S2; Appendix A). We observed that β diversity, represented here by the replacement component, fluctuated between periods and spatial scale (Figure 5).

Water levels significantly reduced β diversity (pseudo $R^2 = 0.60$, $p < 0.001$) (Table 1). Accordingly, the flood peak (6 m) coincided with the lowest β diversity value in the flood period, both for floodplain and sub-basins (Figure 6). Thus, the flood peak (snapshot) decreased β diversity. However, when considering a larger time scale, β diversity does not differ between hydrological periods at any spatial scale (floodplain and sub-basins). The only exception was registered at the smallest scale (for one of the sub-basins only (Ivinhema)), where the period of prolonged drought showed the lowest values of β diversity (Pseudo $R^2 = 0.41$, $p = 0.015$) (Figure 6; Table 1).

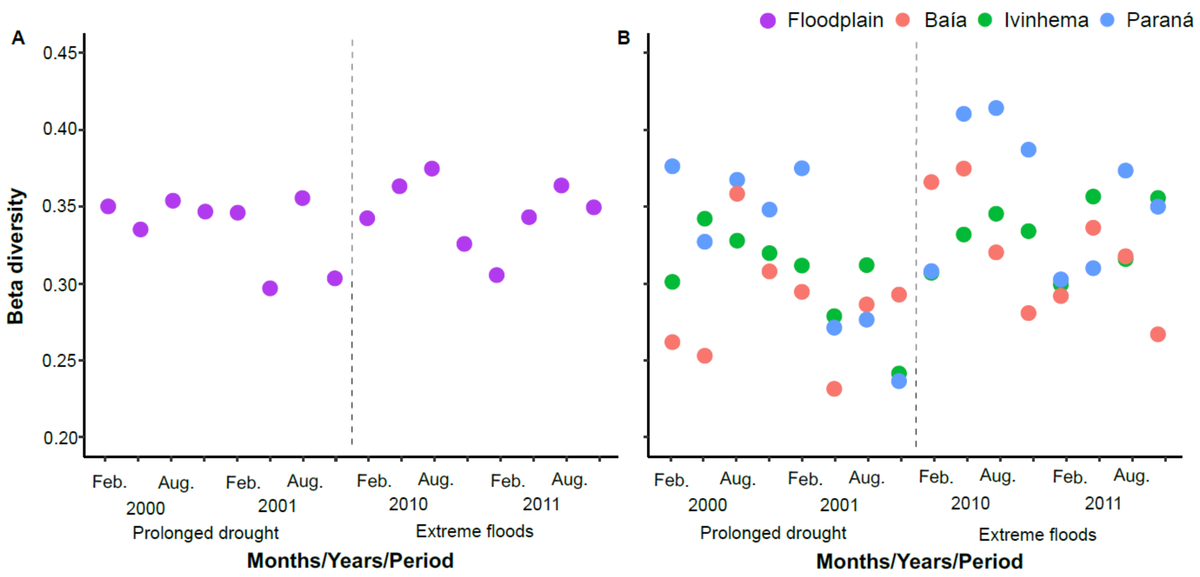

Figure 5 β diversity variation over time considering the largest (A) and the smallest spatial scale (B) of the Upper Paraná River floodplain, between the period prolonged droughts (2000-2001) and the period with extreme flood events (2010-2011). The blue color represents the sub-basin of Paraná, green the Ivinhema, pink the Baía, and purple the floodplain.

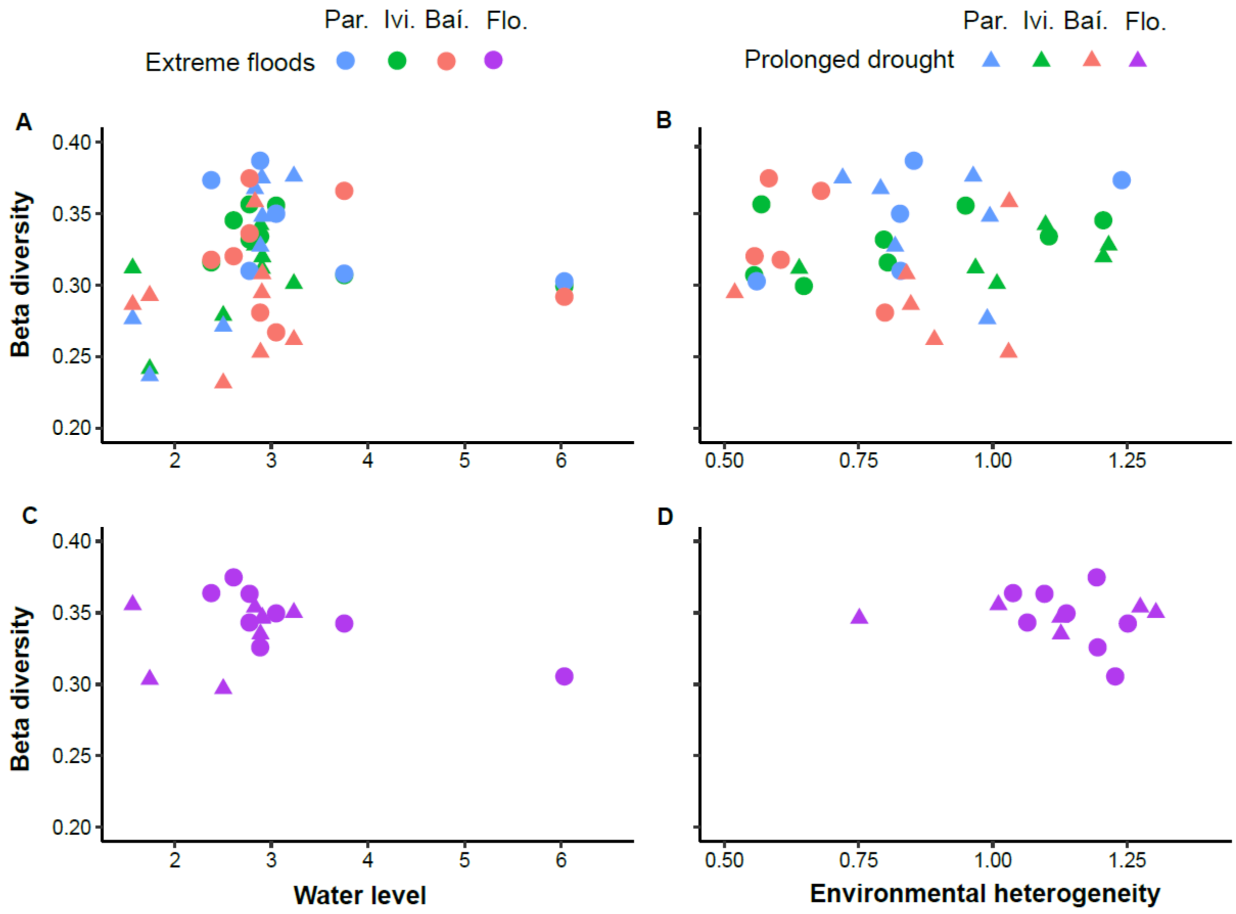

Figure 6 Relationship between β diversity with water level (m) and environmental heterogeneity, considering the smallest spatial scale (sub-basins) (A and B) and the largest spatial scale (floodplain) (C and D) of the Upper Paraná river floodplain. The triangles represent the periods of prolonged drought (2000-2001) and the circles the periods with extreme flood events (2010-2011). The blue color represents the sub-basin of Paraná, green the Ivinhema, pink the Baía and purple the floodplain. Par – Paraná; Ivi – Ivinhema; Baí. – Baía; Flo. – Floodplain.

Table 1 Result of β regression models considering the largest spatial scale (floodplain) and smallest spatial scale (Paraná, Ivinhema and Baía sub-basins) of the Upper Paraná River floodplain. In bold, variables that were significant. *Reference level for period comparison is the period of prolonged extreme flood.

Spatial spatial	**Environment**	**Predictor variables**	**Estimate**	**Error**	***z***	**P**
Large	Floodplain	(Intercept)	-0.616	0.017	-35.747	< 0.001
		Env. heterogeneity	0.008	0.014	0.599	0.549
		Water level	-0.063	0.015	-4.332	**<0.001**
		*Period	-0.024	0.027	-0.901	0.368
Small	Paraná	(Intercept)	-0.580	0.061	-9.532	< 0.001
		Env. heterogeneity	0.063	0.063	1.005	0.315
		Water level	-0.014	0.058	-0.251	0.802
		*Period	-0.083	0.092	-0.894	0.371
	Ivinhema	(Intercept)	-0.695	0.024	-28.862	< 0.001
		Env. heterogeneity	0.028	0.021	1.352	0.177
		Water level	-0.035	0.019	-1.805	0.071
		*Period	-0.095	0.039	-2.444	**0.015**
	Baía	(Intercept)	-0.722	0.093	-7.786	< 0.001
		Env. heterogeneity	0.025	0.072	0.349	0.727
		Water level	-0.022	0.047	-0.457	0.647
		*Period	-0.165	0.124	-1.323	0.186

Regarding the EMS, regardless of a period with extreme flood events or a period of prolonged drought, the most frequent pattern, at both spatial scales was the Clementsian (Figure 7). In this case, species distribution showed significant and positive coherence and species range turnover. The boundary clumping presented a Morisita index higher than 1 and was also significant (Table S3-S6 in Appendix A; Figure 7).

As predicted, at the largest spatial scale species range turnover was always significant and positive. In this case, the Clementsian pattern was the only one found for the zooplankton metacommunity at the largest spatial scale (n = 16; Table S3; Appendix A) (Figure 7). However, when we considered a smaller spatial scale this pattern became more variable, with records of quasi-structures such as quasi-Clementsian (n = 1), quasi-Gleasonian (n = 1), and Gleasonian pattern (n = 5; Table S4-S6 in Appendix A; Figure 7).

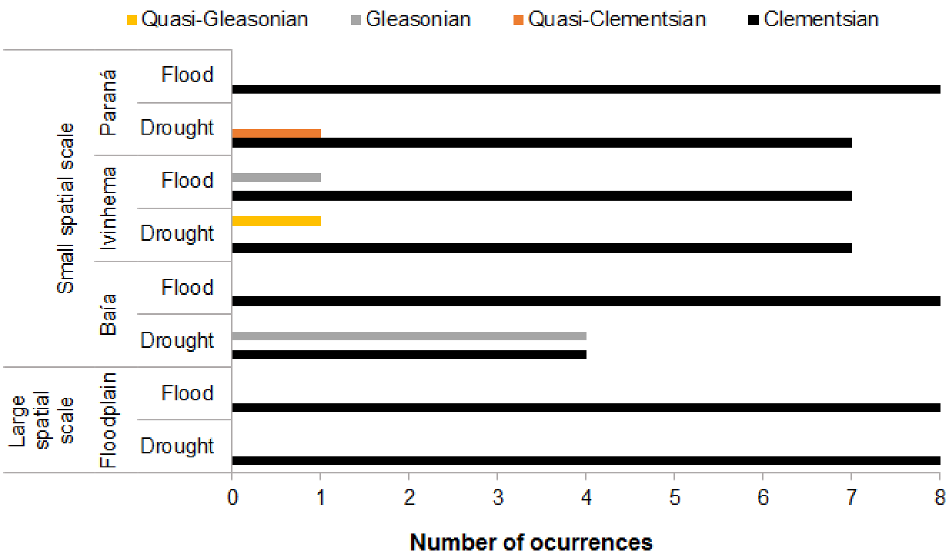

Figure 7 Zooplankton metacommunity patterns according to EMS approach considering the largest spatial scale (floodplain) and smallest spatial scale (Baía, Paraná and Ivinhema sub-basins) of the Upper Paraná River floodplain. The years 2000-2001 were considered to be the period with prolonged droughts, while the years 2010-2011 were periods with extreme flood events. Drought, period of prolonged drought. Flood, period of extreme flood events.

Finally, only water level was an important predictor over time for β diversity at the largest spatial scale, while the hydrological period was important only at the smaller spatial scale for a single sub-basin (i.e. Ivinhema). Environmental heterogeneity did not influence β diversity over time at either spatial scales (Table 1).

2.4 Discussion

The flood peak (> 6 m) observed in the snapshot sampling was responsible for homogenizing the zooplankton metacommunity. However, on a broad temporal scale, the years with extreme flood events (2010-2011) did not show reduced β diversity at any spatial scales (floodplain and sub-basins). Only in a single sub-basin (i.e. the smallest spatial scale) did β diversity increase over the 2-year period with extreme flooding. This shows that when considering a longer period of time, the effect of extreme floods does not negatively affect β diversity, emphasizing the importance of longer-term ecological studies to understand the dynamics of freshwater biota better. The structuring of the zooplanktonic metacommunity (EMS) remained practically constant throughout the four years, with a predominance of species range turnover (Clementsian). Only at the smaller scale (sub-basins) did we observe quasi-structural (quasi-Clementsian and quasi-Gleasonian) and Gleasonian patterns. Even so, the occurrence of quasi-structural patterns was rare, and the Clementsian pattern was more common over time at both spatial scales. This reinforces the understanding that the floodplain zooplankton metacommunity responds to latent environmental gradients, and groups of species have coincident range boundaries in the metacommunity.

Due to low connectivity and the long period of isolation between environments in the prolonged drought years, especially in 2001 (connectivity index = 0.028 e 335 isolation days) (Lansac-Tôha et al., 2009), we expected greater environmental heterogeneity. However, only the Ivinhema sub-basin showed greater heterogeneity in the prolonged drought period. Even though low water levels characterized this period, at times the level of the river varied between 4 and 5m, approximately. This may justify the similar environmental heterogeneity between periods of extreme flood and prolonged drought. Contrary to what we expected, environmental heterogeneity was not selected as a significant predictor for β diversity at any spatial scale. Although a positive relationship between β diversity and environmental heterogeneity is well established in the literature (Maloufi et al., 2016), some authors have also found no relationship between them (Bini et al., 2014; Lopes et al., 2014). In our case, it may be that other factors, not measured, are more critical. For example, dispersal limitation can be an extremely important predictor (Dias et al., 2016; Heino, 2013), mostly when environments are isolated (Lansac-Tôha et al., 2016). However, in our case, we do not believe that dispersal limitation was a determining process. Even in the prolonged drought period, when the lakes are even more isolated, zooplankton composition and variability were similar, even among the geographically more distant sub-basins (Ivinhema and Paraná, which are approximately 45 km apart from each other) which theoretically would be more distinct if limitation was important. Only during the period of extreme flooding, when the lakes were connected, and dispersal does not tend to be a limiting factor (Lansac-Tôha et al., 2016), the variability was different, including between the nearest sub-basins (Paraná and Baía, which are approximately 10 km apart).

β diversity was also not higher in the prolonged drought period (2000-2001). This finding was not expected, since in general, there is an increase in environmental variability during drought (Simões et al., 2013), and the greater heterogeneity allows the occupation of different niches by species, leading to higher species replacement (Maloufi et al., 2016). When drought events occur at high frequency and intensity, they can increase community similarity, reducing diversity and homogenizing the aquatic biota (Angeler et al., 2010). This is because extreme and prolonged droughts, as we observed in 2000-2001, can act as a filter allowing only species tolerant to this environmental stress to occur and, consequently, decreasing β diversity (Bertoncin et al., 2019; Chase, 2007).

We recorded some zooplankton species that, although they occurred at both low and high water, were more common in periods of lower water volume, such as *Moina micrura* Kurz, 1874 and *Brachionus angularis* Gosse, 1851 (Chaparro et al., 2011). Unlike species of the genus *Keratella*, for example, which tended to be more common at high water (Chaparro et al., 2011). Although periods of flooding may also cause biotic and habitat homogenization (Thomaz et al., 2007), the connection between environments can enable a high exchange of species or propagules, which may favor an increase in replacement and β diversity (Gianuca et al., 2017; Grabowska et al., 2014). Only when dispersal is too high can replacement decrease due to the mass effect (Mouquet & Loreau, 2003). For example, Chaparro et al. (2018) observed that the replacement of plankton species can be high during or even after floods. The authors argue that flooding may not have an instantaneous effect on plankton and that it is crucial to consider spatial structure over longer time scales (Chaparro et al., 2018).

An interesting point observed is that when we consider only the level of the river, at discrete moments (single collection), the flood events showed biotic homogenization in the floodplain. However, when we consider the 2 years of prolonged drought (time scale), we observed that this scenario also led to biotic homogenization (at least for one sub-basin). The species are continually changing, and this result indicates the mechanism of cyclical renewal of aquatic biota over time, following environmental conditions (Benincà et al., 2015). Thus, studies of metacommunity or β diversity based on single instants can mask critical ecological processes, which are often only perceived when a more extended period is considered (Fernandes et al., 2014). This shows the importance of both spatial and temporal scales to maximize knowledge of metacommunity dynamics. Nature is exceptionally dynamic, and biodiversity changes over time, at both large and short time scales (Magurran & Dornelas, 2010).

The Clementsian pattern was the most frequently found, regardless of years of drought or extreme flooding, and environmental heterogeneity. This result is similar to Petsch et al., (2017), who studied the benthic metacommunity and observed that the patterns did not change between flood and drought events. The dominance of this pattern indicates that the zooplankton metacommunity in the floodplain is composed of discrete species that show similar responses to environmental gradients and replace in groups across space and time. In this case, species groups respond to the same ecological gradient (here represented by the first RA axis) and have coincident range boundaries (Leibold & Mikkelson, 2002; Presley et al., 2010). Also, it reinforces the role of the environmental filter in structuring the zooplankton metacommunity (Wojciechowski et al., 2017).

Different mechanisms may be responsible for maintaining a metacommunity pattern over time, including the degree of environmental impacts (Brasil et al., 2017). However, in our case, even in the sub-basins with different determinants of hydrodynamics (one river is dammed and another conserved, for example), metacommunity patterns did not differ. Other researchers, studying metacommunity structure in forests, observed that the Clementsian structure had been maintained over 70 years, even though biotic homogenization has been registered throughout this period (Keith et al., 2011; Newton et al., 2012). The stability of the same metacommunity pattern in different environmental scenarios may suggest that EMS may not be sensitive enough and/or indicated to detect more subtle environmental variation. However, as few studies have been carried out on EMS for the zooplankton community, it is challenging to define patterns. In our case, the establishment of the Clementsian pattern over time, especially at the largest spatial scale, indicates the high diversity of the floodplain. The quasi-structural (quasi-Clementsian and quasi-Gleasonian) were recorded overtime only at the smallest spatial scale. Despite having occurred at low frequency, the quasi-structures are probably associated with extended niche breadth extended beyond the range in which species turnover is significant.

Many studies have sought to associate the entire dynamics of the metacommunity with one of the well-known *Big 4* (which refer to the four classic models of metacommunity: species sorting, patch dynamics, mass effects, and neutral dynamics) or have partitioned the variance in the search to establish the importance of environmental filters or spatial processes. However, the effectiveness of these tests has been discussed, and the *Big 4* have often been misinterpreted (Brown et al., 2017; Gilbert & Bennett, 2010). Although many researchers used the mechanistic approach (Big 4) in association with EMS, we were interested in determining only the EMS in this study. That is because we wanted to test multiple ecological patterns of metacommunity (random for periods of extreme flooding and the Clementsian or Gleasonian for periods of prolonged drought) and not the importance of environmental filters or spatial processes, for example. EMS has also received some criticism regarding its consistency in determining certain idealized metacommunity patterns. Some of the criticisms are mainly focused on the fact that a data set can present different patterns depending on the metric used. Also, it is questioned whether the species range turnover can detect nested patterns, since although high species range turnover is related to low nestedness, low species range turnover may not accurately predict possible high nesting (Schmera et al., 2018; Ulrich & Gotelli, 2013). Despite these constraints, the EMS approach is still promising, since it has the advantage of being able to examine the existence of several different patterns along an environmental gradient, while other approaches only can examine a single pattern at a time (Alves et al., 2020; Heino, Melo et al., 2015;

Henriques-Silva et al., 2013; Petsch et al., 2017). Also, cautious use and interpretation of EMS results allows for a better understanding of patterns in metacommunities in space and time.

Although the Clementsian pattern was also the most frequent at the smaller spatial scale (sub-basins), we also recorded the Gleasonian gradient and the appearance of quasi-structures. The occurence of quasi-structures shows that the species niche breadth extended beyond the range in which species turnover is significant, thus affecting the identification of boundaries at small spatial scale. Even if the number of quasi-structure patterns has not been high, this indicates that the metacommunity patterns found for small spatial scales should not be extrapolated to a large spatial scale. Patterns measured at smaller spatial scales are actually less evident since they do not cover all environmental variation (Field et al., 2009). Therefore, studies of β diversity or metacommunity structure can reach different conclusions when only smaller spatial scales are considered (Beck et al., 2013). Thus, although there is no single rule or scale on which ecological studies should be conducted (Levin, 1992), the choice of the scale deserves much attention in the sample designs of ecological studies, as it can lead to different conclusions (Chave, 2013).

On the largest spatial scales (floodplain), only the river level was an important environmental predictor. The importance of the water level in the control of ecological patterns of aquatic communities is already well established in the literature, mainly in dynamic floodplain systems that undergo great fluctuations in their water volume in a single year (Junk et al., 1989; Thomaz et al., 2007). This fact was corroborated by the significance of β diversity when the largest scale was considered. Although the flood peaks (> 6 m) were sporadic events, a negative and significant relationship with β diversity was expected since the higher connectivity between the habitats during the flood increases organisms dispersal, justifying the decline in β diversity in this hydrological phase (Gonzalez, 2009).

Not all environmental predictors influenced β diversity across different spatial scales over time. In our case, the particular characteristics of lakes in each sub-basin (smaller spatial scale) may have had a greater influence on β diversity. This may be related to the fact that the sub-basins have quite different characteristics. The sub-basin of Baía and Ivinhema, for example, retain characteristics of more conserved environments, such as a higher concentration of nutrients (Roberto et al., 2009). The Ivinhema sub-basin is located in a Conservation Unit, with restricted use (Várzeas State Park on the Ivinhema River). There are no dams along its course (Braghin et al., 2015), reducing limnological changes over time. This is the opposite of the sub-basin of Paraná, for example, which has been suffering from the oligotrophication process, due to cascading reservoirs upstream (Agostinho et al., 2008; Oliveira et al., 2018).

Environmental disturbances resulting from human actions, such as the construction of dams, can lead to changes in β diversity. This is because the construction of dams alters the natural dynamics of rivers, leading to a taxonomic and functional simplification of aquatic biota (Oliveira et al., 2018). Other studies in this same floodplain, for example, have already registered a difference in the spatial and temporal patterns of β diversity when comparing the dammed sub-basin (Paraná) with the conserved sub-basin (Ivinhema), showing the negative influence of anthropic actions on aquatic ecosystems (Braghin et al., 2018; Bonecker et al., 2020).

Given the *conservation paradox,* which involves a debate about the choice of conservation priorities (Socolar et al., 2016), studies of β diversity and metacommunities can provide valuable information (Chase et al., 2020). In this context, when turnover is high, conservation incentives should involve as many locations as possible and not only the richest (when nestedness predominates) (Socolar et al., 2016). Although we did not use the nestedness component of β diversity, we observed predominance of a metacommunity pattern when the species range turnover is significant (i.e. Clementsian). This may indicate that conservation measures in the Upper Paraná River floodplain need to consider as many locations as possible. Also, as the environmental predictors selected from spatial scales are different, it suggests that environmental variability between sites is also different, reinforcing the importance of "spatial insurance" for the entire floodplain to maintain ecological stability and provide its ecosystem services (Thompson et al., 2015). This finding also reinforces the importance of considering both smaller and larger spatial scales to cover all heterogeneity and better capture the dynamics of organisms, thus helping to define more consolidated conservation strategies in the floodplain. When considering a 2-year period with extreme flood events, β diversity was not reduced as in the snapshot. Thus, over time organisms can adapt to extreme events without having an associated reduction in β diversity or without differing between periods, showing that zooplankton exhibit cyclical renewal of species following environmental dynamics (Benincà et al., 2015). Since ecological processes are multidimensional and dependent on spatial scale (Chase et al., 2018), considering different spatial scales over time in the floodplain will allow us to better investigate the scale at which each phenomenon occurs (Meynard et al., 2013) and, thus, assist in establishing more accurate environmental conservation measures in Upper Paraná River floodplain.

β diversity fluctuated over time, and although the flood peak (6 m) reduced β diversity (snapshot collections) on a larger time scale, β diversity did not differ between one period with extreme flood events and another with a prolonged drought. This shows the importance of long-term ecological studies to better capture metacommunity dynamics. Zooplankton metacommunity structure was marked predominantly by the Clementsian pattern, regardless of the temporal or spatial scale. Thus, even though the floodplain of the Upper Paraná River is highly dynamic (Agostinho et al., 2004; Lansac-Tôha et al., 2009), the smaller spatial scale (sub-basin) manages to better represent the dynamics of β diversity and the structure of the floodplain zooplankton metacommunity. However, considering that the environmental predictors that influenced β diversity (water level and hydrological period) fluctuated between spatial scales, we suggest that the planning of priority areas for conservation in the Upper Paraná River floodplain should consider both the smaller and larger spatial scale over time. We emphasize the need for further studies to consider different biological groups and larger spatial scales over time to maximize the understanding of aquatic dynamics.

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APPENDIX A - Details of the study area and results.

Table S1 Geographic coordinates, connectivity, and mean depth per period (prolonged drought and extreme floods) of the 29 lakes studied in three subsystems of the Upper Paraná River floodplain, Brazil.

Sub-basins	**Lakes**	**Coordinates**	**Connectivity**	**Depth drought**	**Depth floods**
Ivinhema	Patos	22°49'33.66"S; 53°33"9.9"W	Connected	3.4	4.7
	Boca do Ipoitã	22°50' 7.92"S; 53°33'55.38"W	Connected	3.5	3.9
	Finado Raimundo	22°47' 57.6"S; 53°32'29.16"W	Connected	3.2	2.8
	Peroba	22°54' 30.3"S; 53°38' 24.3"W	Connected	3.2	4.3
	Sumida	22°46'54.78"S; 53°29' 22.2"W	Connected	1.8	3.0
	Capivara	22°47'56.52"S; 53°32"5.4"W	Isolated	3.7	3.2
	Cervo	22°46'29.58"S; 53°29'46.98"W	Isolated	2.0	2.9
	Jacaré	22°47' 2.04"S; 53°29'49.08"W	Isolated	2.3	4.6
	Ventura	22°51' 23.7"S; 53°36' 1.02"W	Isolated	2.3	3.5
	Zé do Paco	22°50' 3.72"S; 53°34" 18"	Isolated	4.0	3.1
Paraná	Ressaco do Pau Véio	22°44'50.76"S; 53°15'11.16"W	Connected	2.2	4.3
	Garças	22°43'27.18"S; 53°13' 4.56"W	Connected	1.5	2.1
	Pombas	22°47'55.92"S; 53°21'32.58"W	Connected	1.5	1.5
	Ressaco do Manezinho	22°46'44.7"S; 53°20'56.76"W	Connected	2.9	4.3
	Ressaco do Bilé	22°45'13.56"S; 53°17' 9.48"W	Connected	1.9	3.1
	Ressaco do Leopoldo	22°45" 24"S; 53°16' 7.98"W	Connected	3.5	4.0
	Osmar	22°46'26.64"S; 53°19'56.16"	Isolated	1.1	2.4
	Clara	22°45’17.52”S; 53°15’28.62”W	Isolated	1.1	1.8
	Genipapo	22°45'33.24”S; 53°16' 5.94"W	Isolated	1.3	1.8
	Pousada	22°44'41.76"S; 53°14' 7.32"W	Isolated	0.6	3.9
Baía	Porcos	22°42' 4.44"S; 53°14'40.08"W	Connected	2.7	2.7
	Gavião	22°40'47.94"S; 53°13'53.46"S	Connected	2.1	3.8
	Guaraná	22°43'16.68"S; 53°18' 9.24"W	Connected	1.8	2.8
	Maria Luiza	22°40'30.18"S; 53°13'11.16"W	Connected	3.0	2.3
	Onça	22°39'48.42"S; 53°12' 1.62"W	Connected	1.9	3.0
	Aurélio	22°41'34.68"S; 53°13'50.58"W	Isolated	2.0	2.9
	Fechada	22°42'37.92"S; 53°16'33.06"W	Isolated	2.5	2.2
	Pousada das Garças	22°42' 1.14"S; 53°15'23.52"W	Isolated	2.1	2.6
	Traíra	22°44' 45.6"S; 53°20'21.66"W	Isolated	2.8	2.1

Table S2 List of zooplankton species recorded between the periods of prolonged drought (2000-2001) and extreme floods (2010-2011) in the Upper Paraná River Floodplain. Brazil.

Species	**Period**	
	Prolonged drought	**Extreme floods**
ROTIFERA		
Lecane aculeata (Jakubski. 1912)		x
Lecane amazonica (Murray. 1913)		x
Lecane boettgeri Koste. 1986	x	
Lecane bulla (Gosse. 1851)	x	x
Lecane closterocerca (Schmarda. 1859)	x	x
Lecane cornuta (Müller. 1786)	x	x
Lecane curvicornis (Murray. 1913)	x	x
Lecane decipiens (Murray. 1913)		
Lecane doryssa Harring. 1914	x	
Lecane elsa Hauer. 1931	x	x
Lecane furcata (Murray. 1913)	x	x
Lecane haliclysta Harring & Myers. 1926	x	x
Lecane hamata (Stokes. 1896)	x	
Lecane hastata (Murray. 1913)	x	
Lecane hornemanni (Ehrenberg. 1834)		x
Lecane inopinata Harring & Myers. 1926	x	
Lecane leontina (Turner. 1892)	x	x
Lecane ludwigii (Eckstein. 1883)	x	x
Lecane luna (Müller. 1776)	x	x
Lecane lunaris (Ehrenberg. 1832)	x	x
Lecane mira (Murray. 1913)		x
Lecane monostyla (Daday. 1897)	x	x
Lecane ohioensis (Herrick. 1885)	x	
Lecane papuana (Murray. 1913)	x	x
Lecane proiecta Hauer. 1956	x	x
Lecane pusilla Harring. 1914		x
Lecane rhytida Harring & Myers. 1926		x
Lecane quadridentata (Ehrenberg. 1830)	x	x
Lecane signifera (Jennings. 1896)	x	x
Lecane scutata (Harring & Myers. 1926)	x	
Lecane stenroosi (Meissner. 1908)	x	
Lecane stichaea Harring. 1913	x	x
Lecane thienemanni (Hauer. 1938)		x
Lecane ungulata (Gosse. 1887)	x	
Lecane sp.	x	
Anuraeopsis fissa (Gosse. 1851)	x	
Anuraeopsis navicula Rousselet. 1911	x	x
Brachionus angularis Gosse. 1851	x	x
Brachionus bidentatus Anderson. 1889	x	x

Species	Period	
	Prolonged drought	**Extreme floods**
Brachionus budapestinensis Daday. 1885	x	
Brachionus calyciflorus Pallas. 1766	x	x
Brachionus caudatus Barrois & Daday. 1894	x	x
Brachionus austrogenitus Ahlstrom. 1940		x
Brachionus caudatus var. *personatus* Ahlstrom. 1940		x
Brachionus dolabratus Harring. 1914	x	x
Brachionus falcatus Zacharias. 1898	x	x
Brachionus forficula Wierzejski. 1891	x	x
Brachionus mirus Daday. 1905	x	x
Brachionus mirus f. *angustus* Koste. 1972	x	
Brachionus quadridentatus Kertész. 1894	x	x
Brachionus urceolaris Müller. 1773	x	x
Kellicottia bostoniensis (Rousselet. 1908)	x	x
Keratella americana Carlin. 1943	x	x
Keratella cochlearis (Gosse. 1851)	x	x
Keratella lenzi Hauer. 1953	x	x
Keratella tropica (Apstein. 1907)	x	x
Plationus patulus macracanthus (Daday. 1905)	x	x
Plationus patulus (Müller. 1786)	x	x
Platyias leloupi Gillard. 1957	x	x
Platyias quadricornis (Ehrenberg. 1832)	x	x
Elosa sp.	x	
Trichocerca bicristata (Gosse. 1887)	x	x
Trichocerca bidens (Lucks. 1912)	x	x
Trichocerca capucina (Wierzejski & Zacharias. 1893)	x	
Trichocerca cylindrica (Imhof. 1891)	x	x
Trichocerca chattoni (Beauchamp. 1907)	x	x
Trichocerca dixonnuttalli (Jennings. 1903)	x	x
Testudinella elongata De Smet. 2009	x	
Trichocerca braziliensis (Murray. 1913)	x	x
Trichocerca flagellata Hauer. 1937	x	
Trichocerca macera (Gosse. 1886)		
Trichocerca gracilis (Tessin. 1890)	x	
Trichocerca heterodactyla (Tschugunoff. 1921)	x	x
Trichocerca iernis (Gosse. 1887)	x	x
Trichocerca inermis (Linder. 1904)	x	x
Trichocerca insignis (Herrick. 1885)	x	x
Trichocerca insulana (Hauer. 1937)	x	
Trichocerca intermedia (Stenroos. 1898)	x	
Trichocerca longiseta (Schrank. 1802)	x	
Trichocerca mus Hauer. 1938	x	
Trichocerca myersi (Hauer. 1931)		x
Trichocerca porcellus (Gosse. 1851)		x

Species	Period	
	Prolonged drought	**Extreme floods**
Lecane pusilla Harring. 1914	x	
Trichocerca rattus (Müller. 1776)	x	x
Trichocerca rousseleti (Voigt. 1902)	x	
Trichocerca ruttneri Donner. 1953	x	x
Trichocerca scipio (Gosse. 1886)	x	
Trichocerca similis (Wierzejski. 1893)	x	x
Trichocerca similis grandis Hauer. 1965	x	x
Trichocerca stylata (Gosse. 1851)	x	x
Trichocerca tenuior (Gosse. 1886)		x
Trichocerca tigris (Müller. 1786)	x	x
Beauchampiella eudactylota (Gosse. 1886)	x	x
Dipleuchlanis propatula (Gosse. 1886)	x	x
Dipleuchlanis propatula f. *macrodactyla* Hauer. 1965	x	
Euchlanis dilatata Ehrenberg. 1830	x	x
Euchlanis dilatata lucksiana Hauer. 1930		x
Euchlanis incisa Carlin. 1939	x	x
Lophocharis salpina (Ehrenberg. 1834)		x
Lophocharis oxysternon (Gosse. 1851)		x
Mytilina acanthophora Hauer. 1938		x
Mytilina bisulcata (Lucks. 1912)	x	x
Mytilina macrocera (Jennings. 1894)	x	x
Mytilina mucronata (Müller. 1773)	x	x
Mytilina ventralis (Ehrenberg. 1830)	x	x
Mytilina ventralis var. *macracantha* (Gosse. 1886)		x
Testudinella ahlstromi Hauer. 1956	x	
Testudinella discoidea Ahlstrom. 1938	x	
Testudinella mucronata (Gosse. 1886)	x	x
Testudinella mucronata haueriensis Gillard. 1967		x
Testudinella ohlei Koste. 1972	x	x
Testudinella patina (Hermann. 1783)	x	x
Testudinella patina dendradena Beauchamp. 1955		x
Testudinella tridentata Smirnov. 1931	x	x
Testudinella truncata (Gosse. 1886)	x	x
Pompholyx complanata Gosse. 1851	x	x
Pompholyx triloba Pejler. 1957	x	x
Pompholyx sulcata Hudson. 1885	x	
Filinia longiseta (Ehrenberg. 1834)	x	x
Filinia opoliensis (Zacharias. 1898)	x	x
Filinia pejleri Hutchinson. 1964	x	
Filinia saltator (Gosse. 1886)	x	
Filinia terminalis (Plate. 1886)	x	x
Ploesoma lenticulare Herrick. 1885	x	x
Ploesoma truncatum (Levander. 1894)		x

Species	Period	
	Prolonged drought	Extreme floods
Polyarthra dolichoptera Idelson. 1925	x	x
Polyarthra vulgaris Carlin. 1943	x	x
Polyarthra remata Skorikov. 1896		x
Synchaeta pectinata Ehrenberg. 1832	x	x
Synchaeta oblonga Ehrenberg. 1832	x	x
Synchaeta stylata Wierzejski. 1893	x	x
Floscularia ringens (Linnæus. 1758)		x
Floscularia sp.	x	x
Octotrocha speciosa Thorpe. 1893	x	
Ptygura libera Myers. 1934	x	
Ptygura sp.	x	x
Sinantherina ariprepes Edmondson. 1939	x	
Sinantherina spinosa (Thorpe. 1893)	x	x
Cephalodella forficula (Ehrenberg. 1838)	x	x
Cephalodella gibba (Ehrenberg. 1830)	x	x
Cephalodella anebodica Bērziņš. 1976	x	
Cephalodella gracilis (Ehrenberg. 1830)	x	
Cephalodella hiulca Myers. 1924		x
Cephalodella mucronata Myers. 1924	x	x
Cephalodella obvia Donner. 1951		x
Cephalodella tenuiseta (Burn. 1890)		x
Enteroplea lacustris Ehrenberg. 1830		x
Eothinia elongata (Ehrenberg. 1832)		x
Eosphora thoides Wulfert. 1935	x	
Monommata dentata Wulfert. 1940	x	x
Monommata maculata Harring & Myers. 1930		x
Monommata actices Myers. 1930	x	x
Monommata grandis Tessin. 1890		x
Monommata pseudophoxa Wulfert. 1960		
Notommata angusta Harring & Myers. 1922	x	
Notommata cerberus (Gosse. 1886)	x	
Notommata copeus Ehrenberg. 1834	x	x
Notommata pachyura (Gosse. 1886)	x	x
Notommata pseudocerberus Beauchamp. 1908	x	
Notommata saccigera Ehrenberg. 1830	x	
Notommata tripus Ehrenberg. 1838	x	
Notommata stitista Myers. 1937	x	
Pleurotrocha robusta (Glascott. 1893)	x	
Taphrocampa selenura Gosse. 1887	x	
Tetrasiphon hydrocora Ehrenberg. 1840	x	
Colurella adriatica Ehrenberg. 1831		
Colurella sp.	x	
Lepadella benjamini Harring. 1916	x	

Species	Period	
	Prolonged drought	**Extreme floods**
Lepadella dactyliseta (Stenroos. 1898)	x	
Lepadella donneri Koste. 1972	x	
Lepadella imbricata Harring. 1914		x
Lepadella ovalis (Müller. 1786)	x	x
Lepadella patella (Müller. 1773)	x	x
Lepadella patella oblonga (Ehrenberg. 1834)		x
Lepadella rhomboides (Gosse. 1886)	x	
Lepadella triptera (Ehrenberg. 1830)		
Conochilus coenobasis (Skorikov. 1914)	x	x
Conochilus dossuarius Hudson. 1885	x	x
Conochilus natans (Seligo. 1900)	x	x
Conochilus unicornis Rousselet. 1892	x	x
Ascomorpha ecaudis Perty. 1850	x	x
Ascomorpha ovalis (Bergendal. 1892)	x	x
Ascomorpha saltans Bartsch. 1870	x	x
Gastropus hyptopus (Ehrenberg. 1838)	x	x
Gastropus stylifer Imhof. 1891	x	
Proales minima (Montet. 1915)	x	
Proales sigmoidea (Skorikov, 1896)	x	
Proales sp.	x	
Aspelta angusta Harring & Myers. 1928		
Dicranophoroides caudatus (Ehrenberg. 1834)		x
Dicranophoroides claviger (Hauer. 1965)	x	
Dicranophorus difflugiarum (Penard. 1914)	x	
Dicranophorus forcipatus (Müller. 1786)	x	x
Dicranophorus luetkeni (Bergendal. 1892)		
Dicranophorus prionacis Harring & Myers. 1928	x	x
Macrochaetus collinsii (Gosse. 1867)	x	x
Macrochaetus longipes Myers. 1934		x
Macrochaetus sericus (Thorpe. 1893)	x	x
Macrochaetus subquadratus Perty. 1850	x	
Trichotria tetractis (Ehrenberg. 1830)	x	x
Trichotria tetractis similis (Stenroos. 1898)	x	
Collotheca ornata (Ehrenberg. 1830)		x
Collotheca sp.	x	x
Hexarthra intermedia (Wiszniewski. 1929)	x	x
Hexarthra intermedia brasiliensis (Hauer. 1953)	x	x
Hexarthra mira (Hudson. 1871)	x	x
Horaella brehmi Donner. 1949	x	
Horaella thomassoni Koste. 1973	x	
Asplanchna sieboldii (Leydig. 1854)	x	x
Epiphanes clavulata (Ehrenberg. 1831)	x	x
Epiphanes macroura (Barrois & Daday. 1894)	x	x

Species	Period	
	Prolonged drought	Extreme floods
Epiphanes senta (Müller. 1773)		x
Mikrocodides robustus (Glascott, 1893)		
Dissotrocha aculeata (Ehrenberg. 1830)	x	
Dissotrocha sp.	x	
Rotaria sp.	x	
Scaridium grande Segers. 1995	x	
Scaridium longicauda (Müller. 1786)	x	
Itura aurita (Ehrenberg. 1830)	x	
Itura deridderae Segers. 1993	x	
Itura myersi Wulfert. 1935	x	
Lindia torulosa Dujardin. 1841	x	
Cupelopagis vorax (Leidy. 1857)		
Bdelloidea	x	x
CLADOCERA		
Moina minuta Hansen, 1899	x	x
Moina micrura Kurz, 1874	x	x
Moina sp.	x	x
Moina reticulata Daday, 1905	x	x
Moinodaphnia macleayi King, 1853	x	x
Bosmina hagmanni Stingelin, 1904	x	x
Bosmina sp.		x
Bosmina frey De Mello & Hebbert 1994	x	x
Bosmina tubicen Brehm, 1939	x	x
Bosminopsis deitersi Richard, 1895	x	x
Ceriodaphnia cornuta Sars, 1886	x	x
Ceriodaphnia reticulata Jurine, 1820	x	
Ceriodaphnia silvestrii Daday, 1903		x
Ceriodaphnia pulchela Sars, 1862		x
Ceriodaphnia richardi Sars, 1901		x
Daphnia gessneri Herbst, 1967	x	x
Daphnia ambigua Scourfield, 1947	x	
Daphnia laevis Birge, 1878	x	
Daphnia lumholtzi Sars, 1885		x
Scapholeberis sp.	x	
Scapholeberis cf. *armata freyi* Herrick, 1882		x
Simocephalus serrulatus Koch, 1841	x	x
Simocephalus semiserratus Sars, 1901		x
Simocephalus latirostris Stingelin, 1906	x	x
Simocephalus vetulus O.F. Muller, 1776		
Simocephalus sp.		x
Diaphanosoma birgei Korineck, 1981	x	x
Diaphanosoma brevireme Sars, 1901		x
Diaphanosoma fluviatile Hansen, 1899	x	x

Species	**Period**	
	Prolonged drought	**Extreme floods**
Diaphanosoma spinulosum Herbst, 1975	x	x
Diaphanosoma polyspina Korovchink, 1982		
Pseudosida ramosa Daday, 1904		x
Acroperus tupinamba Sinev & Elmoor-Loureiro, 2010		x
Magnospina dentifera (Sars. 1901)	x	x
Alona ossiani Sinev. 1998	x	x
Ovalona glabra (Sars. 1901)		
Karualona muelleri (Richard. 1897)		x
Coronatella monocantha (Sars. 1901)	x	x
Lebiris davidi (Richard. 1895)		x
Nicsmirnovius paggii Sousa & Elmoor-Loureiro. 2017	x	x
Alona cf *guttata*	x	x
Alona intermedia Sars. 1862	x	x
Alona yara Sinev & Elmoor-Loureiro. 2010	x	
Coronatella rectangula (Sars. 1861)	x	
Anthalona verrucosa (Sars. 1901)	x	x
Coronatella poppei (Richard. 1897)	x	x
Alona sp.1.	x	x
Alona sp.2.	x	x
Alonella clathratula Sars. 1896	x	x
Alonella dadayi Birge. 1910	x	x
Alonella sp.	x	x
Bergamina lineolata (Sars. 1901)		x
Camptocercus australis Sars. 1896	x	x
Chydorus eurynotus Sars. 1901	x	x
Chydorus parvireticulatus Frey. 1987		x
Chydorus sp.	x	x
Chydorus nitidulus Sars, 1901	x	x
Chydorus pubescens Sars, 1901	x	x
Chydorus cf. *sphaericus*	x	x
Disparalona leptorhyncha Smirnov, 1996		x
Disparalona hamata Birge, 1879		x
Dunhevedia odontoplax Sars, 1901	x	x
Ephemeroporus tridentatus Bergamin, 1932	x	x
Ephemeroporus barroisi Richardi, 1894	x	x
Ephemeroporus hybridus (Daday, 1905)	x	x
Euryalona brasiliensis Brehm & Thomsen, 1936	x	x
Euryalona orientalis Daday, 1908	x	x
Graptoleberis ocidentalis Sars, 1901	x	x
Kurzia polyspina Kurz, 1974	x	x
Kurzia longirostris Daday, 1898		x
Leydigia striata Berabén, 1939	x	x
Leydigia propinqua Sars, 1903		x

Species	**Period**	
	Prolonged drought	**Extreme floods**
Leydigiopsis brevirostris Brehm, 1938	x	
Leydigiopsis curvirostris Sars, 1901		x
Leydigiopsis ornata Daday, 1905		x
Leydigiopsis megalops Sars, 1901		x
Notoalona globulosa Daday, 1898	x	
Notoalona sculpta (Sars, 1901)	x	x
Oxyurella ciliata Bergamin, 1931		x
Oxyurella longicaudis Birge, 1910	x	x
Ilyocryptus spinifer Herrich, 1884	x	x
Guernella raphaelis Richard, 1892	x	x
Grimaldina brazzai Richard, 1892		x
Macrothrix elegans Sars, 1901	x	x
Macrothrix laticornis Jurine, 1820		x
Macrothrix paulensis, Sars, 1888		x
Macrothrix superaculeata Smirnov, 1992	x	x
Macrothrix squamosa Sars, 1901	x	x
Macrothrix sp.	x	x
Streblocerus cf. *pygmaeus* Sars, 1901		
COPEPODA		
Ectocyclops rubescens Brady, 1904		x
Eucyclops ensifer Fischer, 1853	x	
E. solitarius Herbst, 1959	x	
Eucyclops sp.	x	x
Macrocyclops albidus Jurine, 1820		x
Mesocyclops longisetus var. *longisetus* Thiébaud, 1914	x	x
Mesocyclops longisetus var. *curvatus* Dussart, 1987	x	
Mesocyclops ogunnus Onabaniro, 1957	x	x
Mesocyclops aspericornis Daday, 1906		x
Mesocyclops meridianus Kiefer, 1926	x	x
Mesocyclops ellipticus Kiefer, 1936		x
Microcyclops anceps Richard, 1897	x	x
Microcyclops ceibaensis Marsh, 1919	x	x
Microcyclops finitimus Dussart, 1984		x
Microcyclops sp.	x	x
Metacyclops mendocinus Wierzejski, 1892	x	x
Paracyclops fimbriatus Fischer, 1853		x
Paracyclops chiltoni Thomson, 1882	x	x
Paracyclops sp.		x
Thermocyclops decipiens Kiefer, 1929	x	x
Thermocyclops minutus Lowndes, 1934	x	x
Thermocyclops inversus Kiefer, 1936		x
Tropocyclops prasinus Fischer, 1860	x	
Argyrodiaptomus azevedoi Wright, 1935	x	x

Species	**Period**	
	Prolonged drought	**Extreme floods**
Argyrodiaptomus furcatus Sars, 1901	x	
Argyrodiaptomus sp.		x
Notodiaptomus anisitsi (Daday, 1905)		x
Notodiaptomus cearensis Wright, 1936	x	x
Notodiaptomus conifer Sars, 1901	x	
Notodiaptomus deitersi Poppe, 1891		x
Notodiaptomus henseni Dahl, 1894	x	x
Notodiaptomus iheringi Wright, 1935	x	x
Notodiaptomus jatobensis Kiefer, 1956		x
Notodiaptomus incompositus Pesta, 1927	x	x
Notodiaptomus isabelae Wright, 1936	x	x
Notodiaptomus kieferi Brandorff, 1973	x	
Notodiaptomus spiniger Brian 1925	x	x
Notodiaptomus spinuliferus D. & M.T., 1986	x	
Total richness	**266**	**252**

Table S3 Result of the elements of metacommunity structure (EMS), with the respective pattern found, considering the years and periods of the Upper Paraná River floodplain (largest spatial scale). BC = boundary clumping.

Year	Period	Collect	Result	Coherence	Turnover	BC	Patterns
2000	Prolonged drought	1C	z/index	1.42E+01	8.40E+00	2.29E+00	Clementsian
			p	1.81E-45	4.32E-17	0.00E+00	
		2C	z	1.12E+01	6.50E+00	1.84472	Clementsian
			p	5.61E-29	8.23E-11	0.00E+00	
		3C	z	1.14E+01	6.13E+00	1.97E+00	Clementsian
			p	3.83E-30	8.79E-10	0.00E+00	
		4C	z	8.64E+00	6.74E+00	1.65E+00	Clementsian
			p	5.66E-18	1.63E-11	0.00E+00	
2001		5C	z	1.08E+01	7.54E+00	1.66E+00	Clementsian
			p	2.60E-27	4.54E-14	0.00E+00	
		6C	z	1.25E+01	8.72E+00	1.79E+00	Clementsian
			p	4.77E-36	2.76E-18	0.00E+00	
		7C	z	8.42E+00	7.09E+00	1.41E+00	Clementsian
			p	3.69E-17	1.30E-12	1.33E-07	
		8C	z	9.33E+00	9.08E+00	1.52E+00	Clementsian
			p	1.04E-20	1.12E-19	0.00E+00	
2010	Extreme floods	9C	z	1.78E+01	8.75E+00	1.55E+00	Clementsian
			p	6.37E-71	2.14E-18	2.22E-16	
		10C	z	1.56E+01	7.88E+00	2.03E+00	Clementsian
			p	1.17E-54	3.40E-15	0.00E+00	
		11C	z	1.13E+01	6.87E+00	1.46E+00	Clementsian
			p	1.53E-29	6.26E-12	6.27E-12	
		12C	z	1.76E+01	9.47E+00	1.31E+00	Clementsian
			p	4.67E-69	2.88E-21	9.76E-09	
2011		13C	z	1.49E+01	1.09E+01	1.45E+00	Clementsian
			p	6.82E-50	1.52E-27	1.11E-16	
		14C	z	1.04E+01	6.69E+00	1.60E+00	Clementsian
			p	2.09E-25	2.25E-11	0.00E+00	
		15C	z	1.10E+01	6.72E+00	1.83E+00	Clementsian
			p	3.58E-28	1.82E-11	0.00E+00	
		16C	z	1.42E+01	1.05E+01	1.42E+00	Clementsian
			p	1.00E-45	9.21E-26	1.49E-12	

Table S4 Result of the elements of metacommunity structure (EMS), with the respective pattern found, considering the years and periods in the sub-basin of Paraná (smaller spatial scale). BC = boundary clumping.

Year	Period	Collect	Result	Coherence	Turnover	BC	Patterns
2000	Prolonged drought	1C	z/index	1.44E+01	3.01E+00	1.24E+00	Clementsian
			p	5.46E-47	2.63E-03	1.95E-05	
		2C	z	1.17E+01	3.93E+00	1.34E+00	Clementsian
			p	1.32E-31	8.40E-05	1.02E-06	
		3C	z	1.20E+01	3.06E+00	1.27E+00	Clementsian
			p	6.03E-33	2.20E-03	2.77E-06	
		4C	z	1.38E+01	2.42E+00	1.22E+00	Clementsian
			p	3.10E-43	1.55E-02	1.62E-05	
2001		5C	z	9.97E+00	2.95E+00	1.45E+00	Clementsian
			p	1.96E-23	3.15E-03	5.98E-10	
		6C	z	1.43E+01	5.26E+00	1.54E+00	Clementsian
			p	3.45E-46	1.42E-07	4.48E-12	
		7C	z	1.29E+01	2.28E+00	1.09E+00	Clementsian
			p	2.78E-38	2.29E-02	3.21E-02	
		8C	z	1.33E+01	1.98E+00	1.12E+00	Quasi-Clementsian
			p	3.83E-40	4.72E-02	1.88E-03	
2010	Extreme floods	9C	z	1.19E+01	3.33E+00	1.35E+00	Clementsian
			p	7.69E-33	8.78E-04	1.44E-07	
		10C	z	9.39E+00	2.69E+00	1.09E+00	Clementsian
			p	6.01E-21	7.25E-03	3.18E-02	
		11C	z	1.04E+01	2.94E+00	1.14E+00	Clementsian
			p	1.64E-25	3.31E-03	3.42E-03	
		12C	z	1.26E+01	2.90E+00	1.19E+00	Clementsian
			p	1.22E-36	3.70E-03	6.26E-05	
2011		13C	z	1.73E+01	4.34E+00	1.39E+00	Clementsian
			p	4.29E-67	1.45E-05	9.67E-14	
		14C	z	9.94E+00	3.47E+00	1.20E+00	Clementsian
			p	2.68E-23	5.16E-04	7.94E-04	
		15C	z	1.26E+01	2.15E+00	1.33E+00	Clementsian
			p	1.58E-36	3.14E-02	1.15E-07	
		16C	z	8.70E+00	3.75E+00	1.19E+00	Clementsian
			p	3.35E-18	1.78E-04	2.29E-05	

Table S5 Result of the elements of metacommunity structure (EMS), with the respective pattern found, considering the years and periods in the sub-basin of Ivinhema (smaller spatial scale). BC = boundary clumping.

Year	Period	Collect	Result	Coherence	Turnover	BC	Patterns
2000	Prolonged drought	1C	z/index	1.24E+01	1.554747	1.018304	Quasi-Glesonian
			p	3.05E-35	0.120006	0.269178	
		2C	z	7.91E+00	2.50E+00	1.33E+00	Clementsian
			p	2.68E-15	1.25E-02	4.87E-06	
		3C	z	8.52E+00	3.04E+00	1.09127	Clementsian
			p	1.63E-17	2.35E-03	0.078439	
		4C	z	1.20E+01	2.69E+00	1.22447	Clementsian
			p	4.69E-33	7.13E-03	0.000336	
2001		5C	z	1.00E+01	3.88E+00	1.240506	Clementsian
			p	1.34E-23	1.03E-04	0.000504	
		6C	z	9.30E+00	3.03E+00	1.27E+00	Clementsian
			p	1.41E-20	2.48E-03	1.90E-06	
		7C	z	9.57E+00	3.00E+00	1.226923	Clementsian
			p	1.02E-21	2.68E-03	0.003068	
		8C	z	1.14E+01	4.40E+00	1.37E+00	Clementsian
			p	4.87E-30	1.08E-05	1.59E-08	
2010	Extreme floods	9C	z	1.86E+01	4.25E+00	1.37E+00	Clementsian
			p	7.92E-77	2.13E-05	1.77E-09	
		10C	z	1.04E+01	3.20E+00	9.61E-01	Glesonian
			p	2.74E-25	1.37E-03	1.47E-01	
		11C	z	1.03E+01	2.62E+00	1.47E+00	Clementsian
			p	7.58E-25	8.84E-03	1.59E-09	
		12C	z	1.03E+01	3.67E+00	1.19E+00	Clementsian
			p	4.92E-25	2.45E-04	5.02E-04	
2011		13C	z	1.79E+01	4.83E+00	1.07E+00	Clementsian
			p	8.18E-72	1.38E-06	3.80E-02	
		14C	z	1.26E+01	3.84E+00	1.15E+00	Clementsian
			p	2.83E-36	1.21E-04	5.89E-03	
		15C	z	1.04E+01	3.43E+00	1.13E+00	Clementsian
			p	1.62E-25	6.06E-04	9.65E-03	
		16C	z	1.38E+01	3.40E+00	1.26E+00	Clementsian
			p	1.70E-43	6.78E-04	2.99E-08	

Table S6 Result of the elements of metacommunity structure (EMS), with the respective pattern found, considering the years and periods in the sub-basin of Baía (smaller spatial scale). BC = boundary clumping.

Year	**Period**	**Collect**	**Result**	**Coherence**	**Turnover**	**BC**	**Patterns**
2000	Prolonged drought	1C	z/index	1.32E+01	3.11E+00	9.86E-01	Glesonian
			p	1.55E-39	1.90E-03	3.98E-01	
		2C	z	1.32E+01	4.19E+00	1.08E+00	Glesonian
			p	1.14E-39	2.77E-05	6.88E-02	
		3C	z	1.18E+01	2.34E+00	1.04E+00	Glesonian
			p	5.74E-32	1.94E-02	1.19E-01	
		4C	z	8.47E+00	2.30E+00	1.21E+00	Clementsian
			p	2.46E-17	2.13E-02	5.46E-06	
2001		5C	z	1.07E+01	3.82E+00	1.11E+00	Clementsian
			p	7.87E-27	1.33E-04	1.65E-02	
		6C	z	1.07E+01	4.02E+00	1.25E+00	Clementsian
			p	1.58E-26	5.72E-05	3.02E-04	
		7C	z	8.97E+00	3.46E+00	1.02E+00	Glesonian
			p	2.96E-19	5.45E-04	2.97E-01	
		8C	z	1.52E+01	4.34E+00	1.08E+00	Clementsian
			p	5.05E-52	1.45E-05	2.45E-02	
2010	Extreme floods	9C	z	1.31E+01	3.09E+00	1.33E+00	Clementsian
			p	4.21E-39	2.01E-03	1.01E-07	
		10C	z	1.23E+01	2.91E+00	1.13E+00	Clementsian
			p	6.16E-35	3.65E-03	1.02E-03	
		11C	z	1.01E+01	3.13E+00	1.31E+00	Clementsian
			p	5.67E-24	1.75E-03	2.45E-06	
		12C	z	1.68E+01	3.95E+00	1.10E+00	Clementsian
			p	2.61E-63	7.87E-05	4.29E-03	
2011		13C	z	1.65E+01	5.15E+00	1.18E+00	Clementsian
			p	1.63E-61	2.66E-07	3.07E-05	
		14C	z	1.22E+01	2.11E+00	1.07E+00	Clementsian
			p	3.38E-34	3.46E-02	2.40E-02	
		15C	z	1.05E+01	3.03E+00	1.13E+00	Clementsian
			p	7.63E-26	2.44E-03	6.72E-03	
		16C	z	1.19E+01	3.83E+00	1.29E+00	Clementsian
			p	8.03E-33	1.26E-04	5.06E-05	

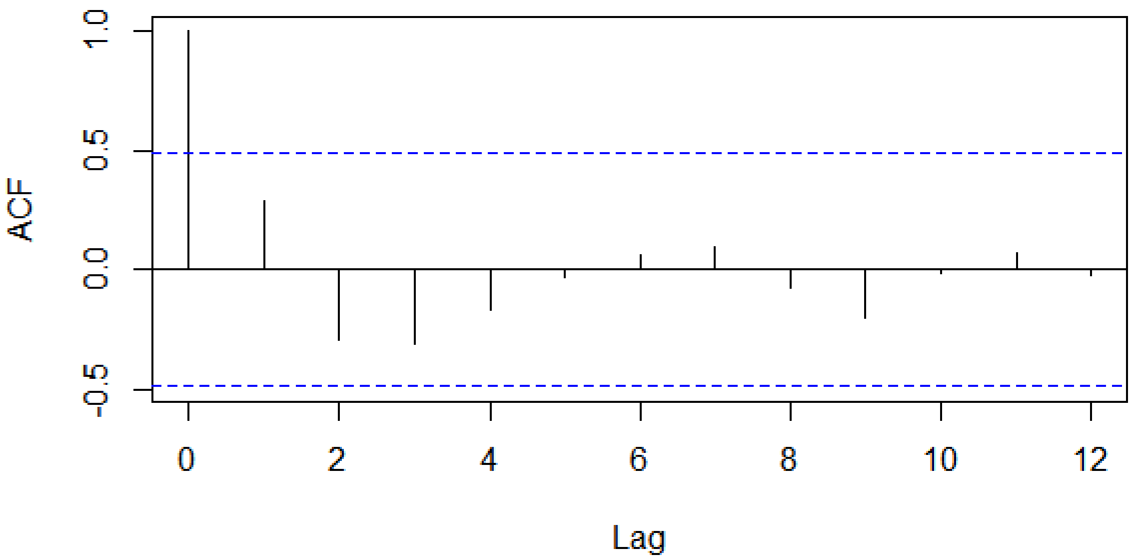

Figure S1 Graph of the ACF function showing the absence of temporal autocorrelation in the zooplankton samples from the lakes of the Upper Paraná River floodplain.

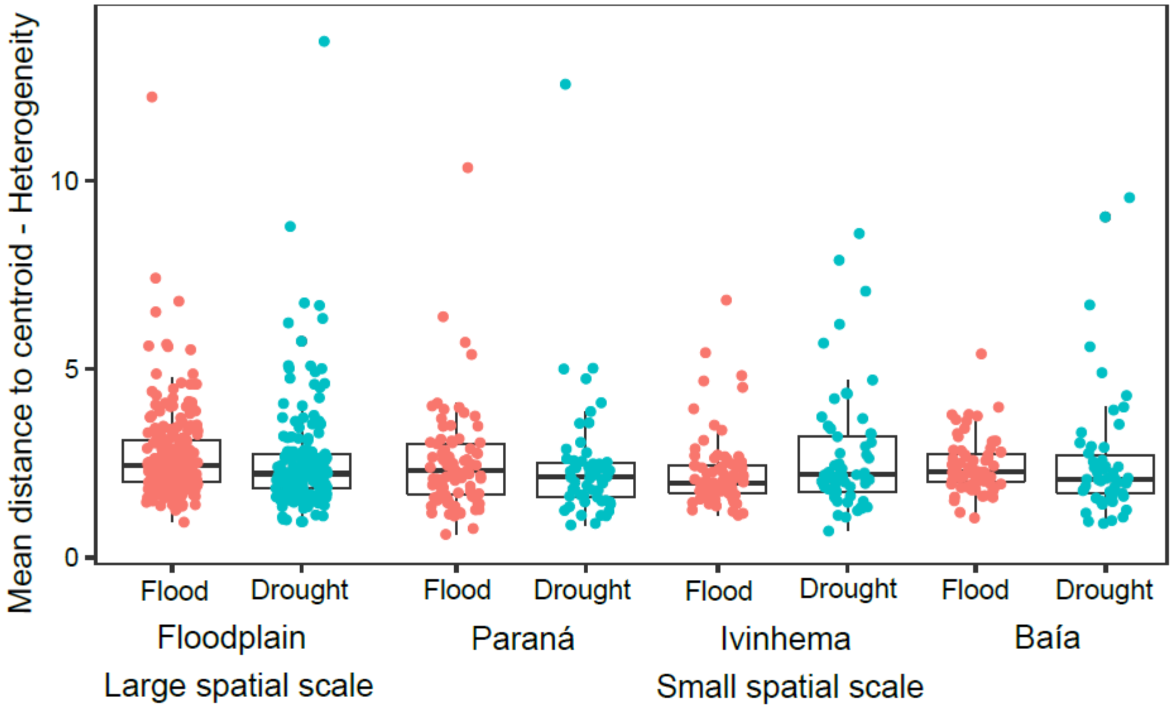

Figure S2 Box-plot representing environmental heterogeneity (though the distance to the centroid) considering the largest spatial scale (floodplain) and the smallest spatial scale (sub-basins) of the Upper Paraná river floodplain. Drought – period of prolonged drought. Flood – period of extreme flood events.

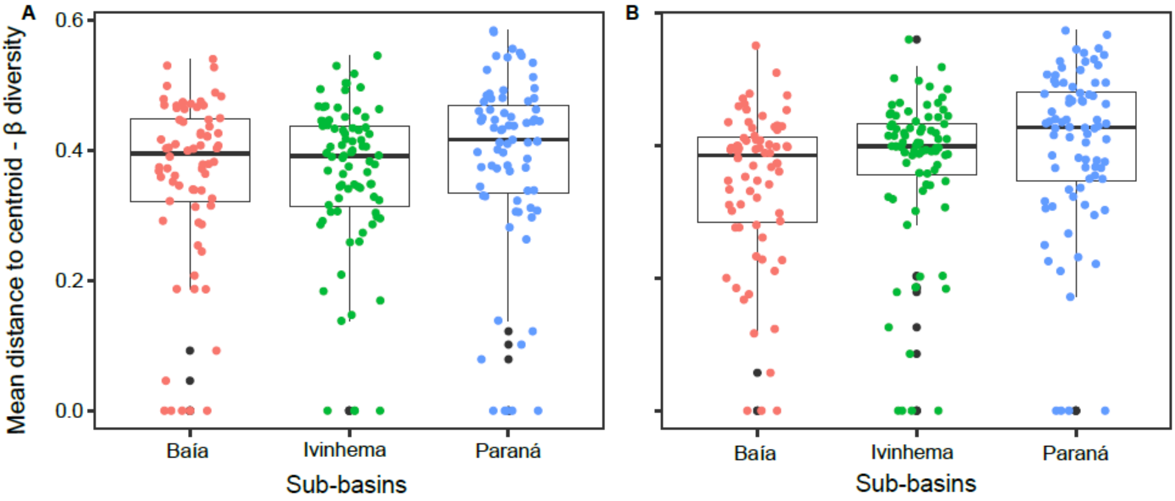

Figure S3 Box-plot representing the similarities recorded (though the distance to the centroid - β diversity) for the Upper Paraná River floodplain sub-basins considering the prolonged drought period (A) and the extreme flooding period (B). For the prolonged drought period the species variability was homogeneous (F = 0.82; $p > 0.05$). While for the period of extreme flooding the variability was different between the three sub-basins (F = 3.87; $p < 0.05$).

Temporal processes drive the taxonomic and functional ecological uniqueness of zooplankton in a Neotropical floodplain*

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*Manuscrito derivado da tese, a ser submetido para revista científica *Science of the Total Environment.*

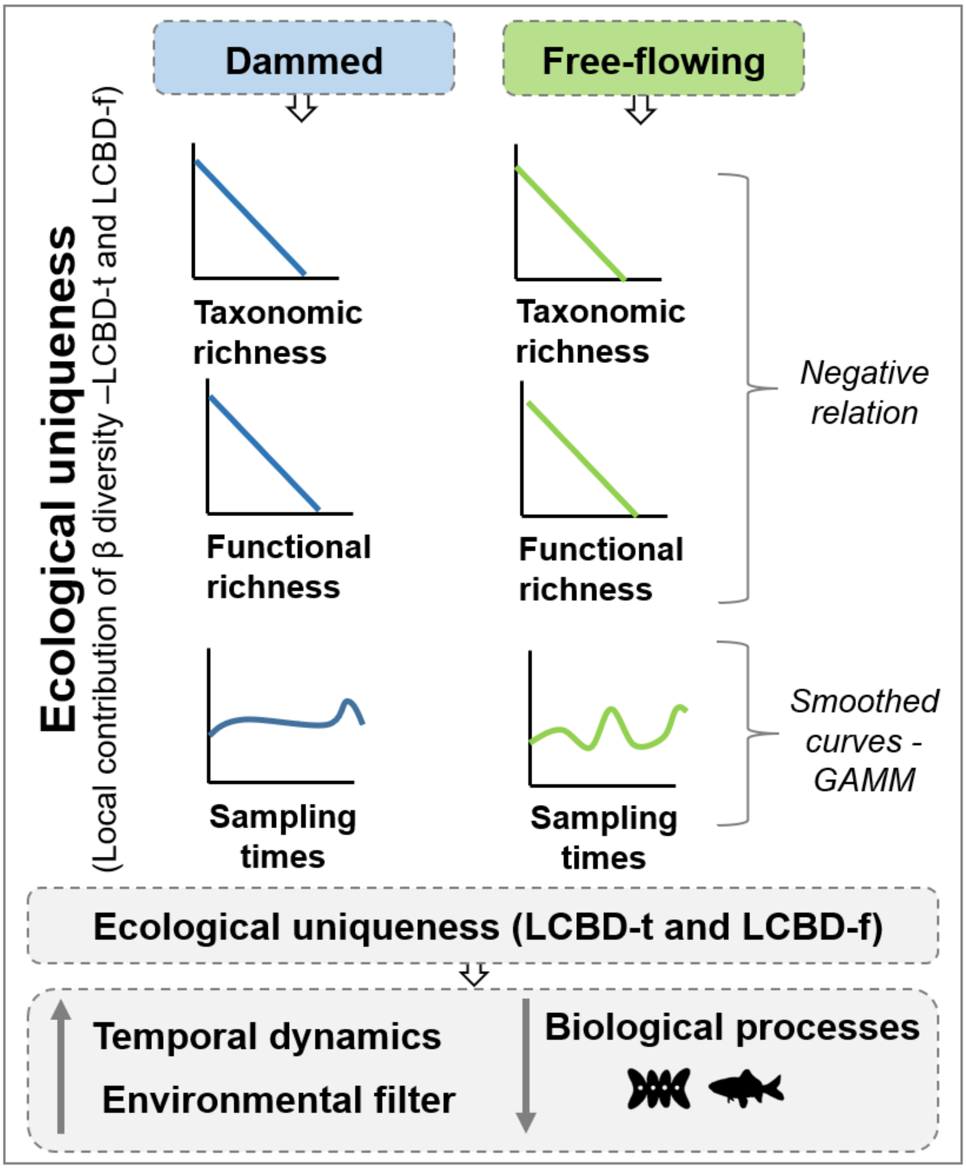
3 TEMPORAL PROCESSES DRIVE THE TAXONOMIC AND FUNCTIONAL ECOLOGICAL UNIQUENESS OF ZOOPLANKTON IN A NEOTROPICAL FLOODPLAIN

Abstract

Although studies on β diversity have increased worldwide, it is still a topic with much to be explored, especially regarding the integration of the contribution site for β diversity in floodplain systems. We investigated which processes (temporal, environmental, and biological) are potentially driving the taxonomic (LCBD-t) and functional (LCBD-f) ecological uniqueness of zooplankton in lakes and rivers of two sub-basins (one dammed and the other free-flowing), over 19 years, in a Neotropical floodplain. Regardless of the sub-basin, the highest LCBD-t and LCBD-f were related to lower species and trait richness, respectively. Although we expected this to occur only in the dammed sub-basin, this result shows that sampling times with lower species and trait richness are those that contribute most to the ecological uniqueness of zooplankton. Taxonomic uniqueness showed to be cyclical over time in the dammed sub-basin, but the ecosystem function of zooplankton did not change significantly. In the free-flowing sub-basin, we recorded cyclical fluctuations between years in taxonomic and functional uniqueness. Over the 19 years, temporal dynamics was the main driver of the ecological uniqueness of zooplankton, and it was more important than the biological processes themselves (phytoplankton biovolume and fish biomass representing food resource and potential predation, respectively). Our findings reinforce the idea that exclusivity is not synonymous with high species richness or functional traits, and that it does not depend on the characteristics of each sub-basin. We also suggest that other studies focus simultaneously on the richness and ecological uniqueness (taxonomic and functional), over time, to better design plans for managing and conserving aquatic biodiversity in floodplains.

Keywords: β diversity, LCBD, Paraná River, fish, phytoplankton, metacommunity.

Graphical abstract



Highlights

1. We investigated the processes driving the LCBD of zooplankton in a dammed sub-basin and in a free-flowing sub-basin.
2. The highest LCBD-t and LCBD-f were related to lower species and trait richness.
3. The LCBD-f did not change over time in the dammed sub-basin.
4. The ecological uniqueness of zooplankton was driven mainly by temporal processes.
5. Conservation studies need to focus on the richness and LCBD-t and LCBD-f.

3.1 Introduction

How and why does biodiversity change over time? How should this change be interpreted? To answer these questions accurately, β diversity studies accompanied by robust data analysis are extremely necessary (Mori et al., 2018). In the Anthropocene, biodiversity is dramatically threatened due to several direct and indirect human actions, and β diversity studies prove to be an important tool for establishing conservation measures (Socolar et al., 2016). Although β diversity studies have increased worldwide, it is still a topic full of uncertainties, especially when considering larger time scales (Dornelas et al., 2013; Lopes et al., 2019; Magurran et al., 2010). That is because most studies on β diversity have been developed in a spatial context (Chaparro et al., 2019), based on community snapshots. Patterns related to temporal dynamics have been neglected in many ecological studies.

β diversity can be defined as the change in the composition of species and/or functional traits over space and/or time. The interest in this subject has increased with recent advances in ecological research (Magurran et al., 2019), and it contributes to new ideas on conservation strategies for communities in the face of countless and constant environmental changes (Gotelli et al., 2017). Over time, several metrics have been suggested to quantify β diversity (Baselga, 2010; Carvalho et al., 2012; Podani and Schmera, 2011). An effective method that allows the contribution of each location (or each observation) to β diversity (Location Contribution to β diversity - LCBD) to be estimated was proposed by Legendre and De Cáceres (2013), which may work as an indicator of the ecological uniqueness among the sampling units over time. The higher the LCBD value, the more exclusive is the species composition in that location. The main advantage of this metric is that it is possible to verify whether the highest values of diversity are related to places of greater or lower species richness. Often the places with the lowest taxonomic richness are those with the most distinct composition, and thus they will have a high LCBD. For this reason, many researchers have found a negative relationship between LCBD and richness (Heino and Grönroos, 2017; Landeiro et al., 2018; Silva et al., 2018). In this context, high LCBD values may also indicate either a favorable place for environmental conservation or even degraded places that need restoration (Legendre and Gauthier, 2014). This is because the high value of LCBD is often associated with the presence of exotic species or the establishment of new species that perform functions that are completely different from the previous ones, changing ecosystem processes and functioning (Dornelas et al., 2014). This metric proves to be highly effective in studies of both conservation and environmental impact assessment (Legendre and De Cáceres, 2013; Legendre and Gauthier, 2014), and many researchers have successfully used it for these purposes (Brito et al., 2020; Landeiro et al., 2018; Legendre and De Cáceres, 2013; Pozzobom et al., 2020).

Most studies with LCBD have had a taxonomic focus (Brito et al., 2020; Landeiro et al., 2018; Pozzobom et al., 2020). However, functional characteristics can also predict important variations in ecological uniqueness (Kruk et al., 2010; Quirino et al., 2021; Silva et al., 2020). This functional approach enables a better understanding of the functioning of the ecosystem, since the loss of species is not always related to the loss of ecosystem functions (Villéger et al., 2012). Moreover, it may be more sensitive for evaluating environmental impacts than the taxonomic approach, making the community's response to a certain environmental disturbance noticeable even before the effective loss of one or more species (Braghin et al., 2018; Mouillot et al., 2013; Oliveira et al., 2018). Therefore, coupling taxonomic (LCBD-t) and functional (LCBD-f) data can generate valuable information in biodiversity conservation studies (Silva et al., 2020).

Several factors may be responsible for the variation in taxonomic and functional uniqueness (Brito et al., 2020; Gomes et al., 2020; Landeiro et al., 2018; Pozzobom et al., 2020; Silva et al., 2020). The construction of dams, for example, is considered one of the main threats to aquatic biodiversity (Chen and Olden, 2017; Winemiller et al., 2016), due, among other factors, to habitat fragmentation in the river channel and reduced connectivity to lateral environments. Dams in floodplain systems regulate the flow downstream, reducing the amplitude and intensity of the flood and decreasing the connectivity among environments (Agostinho et al., 2004; Junk et al., 1989; Neiff, 1990). All these effects result in changes in β diversity (Diniz et al., 2021b; Lansac-Tôha et al., 2019) and threats for overall ecological integrity (Chaparro et al., 2019). This is because the environmental impact filters selected only those that can withstand the new conditions or different variability (Vinebrooke et al., 2004). Dams also alter the transport of sediments and the discharge of water in rivers and floodplains and, consequently, modify the dynamics of most aquatic communities and patterns of β diversity over time. This may result in a homogenization of species or even functional attributes (Oliveira et al., 2018).

In addition to the construction of dams, the biotic factors themselves, involved in the competition, predation, and tolerance to environmental conditions, are also decisive in the patterns of ecological uniqueness. In zooplankton studies, for example, fish (mostly due to predation activity) and phytoplankton (as a potential food resource) are often major drivers of diversity patterns (Ersoy et al., 2019; Striebel et al., 2012). However, environmental variables (i.e., environmental filtering) also tend to be more determinant for LCBD (Heino et al., 2017), especially for smaller organisms (Finlay, 2002). In addition, according to the theory of ecological succession, abiotic and biotic variability tends to change over time, due to natural disturbances including extreme ecological events, or anthropogenic ones, such as the construction of dams (Chang and Turner, 2019). Therefore, temporal variability is also an important mechanism for taxonomic and functional ecological uniqueness, especially for organisms that are more sensitive to environmental variations (Lopes et al., 2017; Wojciechowski et al., 2017). In addition to these deterministic processes, stochastic events, resulting from colonization or random extinction, can also be important in the structuring of aquatic metacommunities (Chase and Myers, 2011).

Zooplankton are considered "sentinels of environmental change" because these organisms can respond quickly to environmental changes (Eggermont and Martens, 2011). Moreover, they comprise phylogenetically distinct groups and large variations in body sizes, performing various functions in aquatic ecosystems (Litchman et al., 2013). The β diversity patterns for these organisms are quite unpredictable for a taxonomic approach, since it can be very difficult to predict the reasons for certain patterns over time (Lopes et al., 2019) and, mainly, for a functional one that is still little studied for this group (but see Braghin et al., 2018; Diniz et al., 2021a).

We aimed to determine the taxonomic (LCBD-t) and functional (LCBD-f) ecological uniqueness of zooplankton over 19 years in lakes and river systems of two sub-basins (one that was dammed a long time ago and the other free-flowing) of a Neotropical floodplain, in addition to investigating which processes (temporal, environmental, and biological) drive the LCBD-t and LCBD-f. The following hypotheses were tested: (i) The dammed sub-basin has a lower richness of species and traits and a greater ecological uniqueness (LCBD-t and LCBD-f), compared to a free-flowing sub-basin. This is expected considering that impacted systems have lower richness, supporting a lower taxonomic and functional β diversity (Braghin et al., 2018; Oliveira et al., 2018; Pineda et al., 2020). Thus, considering the negative relationship constantly recorded between LCBD and richness (Heino and Grönroos, 2017; Landeiro et al., 2018; Silva et al., 2018), we expected that the most unique sites would be those with low richness. (ii) In the dammed sub-basin, taxonomic (LCBD-t) and functional (LCBD-f) uniqueness increase over time. In the free-flowing sub-basin, on the contrary, the taxonomic (LCBD-t) and functional (LCBD-f) uniqueness oscillate cyclically over time. This is expected since systems with more conserved characteristics of their biota can show cyclical renewal of species following hydrological dynamics (Benincà et al., 2015). Finally, we predicted (iii) the taxonomic (LCBD-t) and functional (LCBD-f) ecological uniqueness of the zooplankton to be more related to temporal dynamics (largely led by variations in the hydrological regime) and the environmental filters than biological processes (phytoplankton biovolume and fish biomass representing food resource and potential predation, respectively). This is because zooplankton is sensitive to environmental variations over time, and our study monitored a highly dynamic system for 19 years (Eggermont and Martens, 2011; Junk et al., 1989).

3.2 Material and Methods

3.2.1 Study area

The study was carried out in the Upper Paraná River floodplain (Brazil) and sampling was carried out in six sites: three associated with a free-flowing sub-basin (two lakes and the Ivinhema River), and another three associated with a dammed sub-basin (two lakes and the Paraná River) (Fig. 1). The Porto Primavera Reservoir (upstream, located in São Paulo State) was built in 1998, and the sampling of our study started in 2000. Thus, sampling in the Paraná sub-basin has always been under the effect of the dam. The floodplain, which previously occupied 480 km, now occupies only 230 km after the closure of the Porto Primavera reservoir (Agostinho et al., 2008). Even so, this area has an extremely high aquatic biodiversity (Bonecker et al., 2020; Lansac-Tôha et al., 2009) and a wide variety of ecosystems: rivers, canals, and connected and isolated lakes (Agostinho et al., 2004). Due to this mosaic of environments and high biodiversity, the floodplain has become an Environmental Protection Area.

The free-flowing sub-basin (Ivinhema River) is located in the state of Mato Grosso do Sul (Brazil) and inserted in the State Park Várzeas do Rio Ivinhema. It maintains the characteristics of a conserved system in this region, such as a high concentration of nutrients and organic matter (Roberto et al., 2009). In this sub-basin, we selected a collection point on the river itself and in two other lakes, one permanently connected and another that remains temporarily isolated. The isolated lake of this sub-basin (Ventura lake) (22°51' 23.7"S; 53°36' 1.02"W) is approximately 200m from the Ivinhema River shore, which has an average depth of 2.16 m and a length of 2084.82m. The connected lake (Patos lake) (22°49'33.66"S; 53°33"9.9"W) is approximately 10 m from the Ivinhema River shore, has an average depth of 3.50 m and a length of 2065.6m.

The dammed sub-basin (Paraná River) is impacted by a series of upstream reservoirs, and the water transparency increased and the total phosphorus concentration decreased (Roberto et al., 2009). These factors have led the Paraná River to go through an oligotrophization process, resulting in negative effects for aquatic biota (Braz et al., 2020).

Also, the regulation of water flow, caused by the dam, has reduced the extreme flooding of the plain (> 6 m changes in water level), generating changes in the dynamics of aquatic communities (Braghin et al., 2018; Oliveira et al., 2018; Pineda et al., 2020). In this sub-basin, we also selected three collection points, one on the Paraná River itself and two lakes. The isolated lake of this sub-basin (Osmar lake) (22°46'26.64"S; 53°19'56.16") is temporary, has an area of approximately 0.006ha, an average depth of 1.1 m, and has already dried up completely a few times (Rosa et al., 2020). The connected lake (Garças lake) (22°43'27.18"S; 53°13' 4.56"W) is connected to the Paraná River through a channel approximately 50 m long and has an average depth of approximately 2 m. Also, it has a length of 2128.1m.

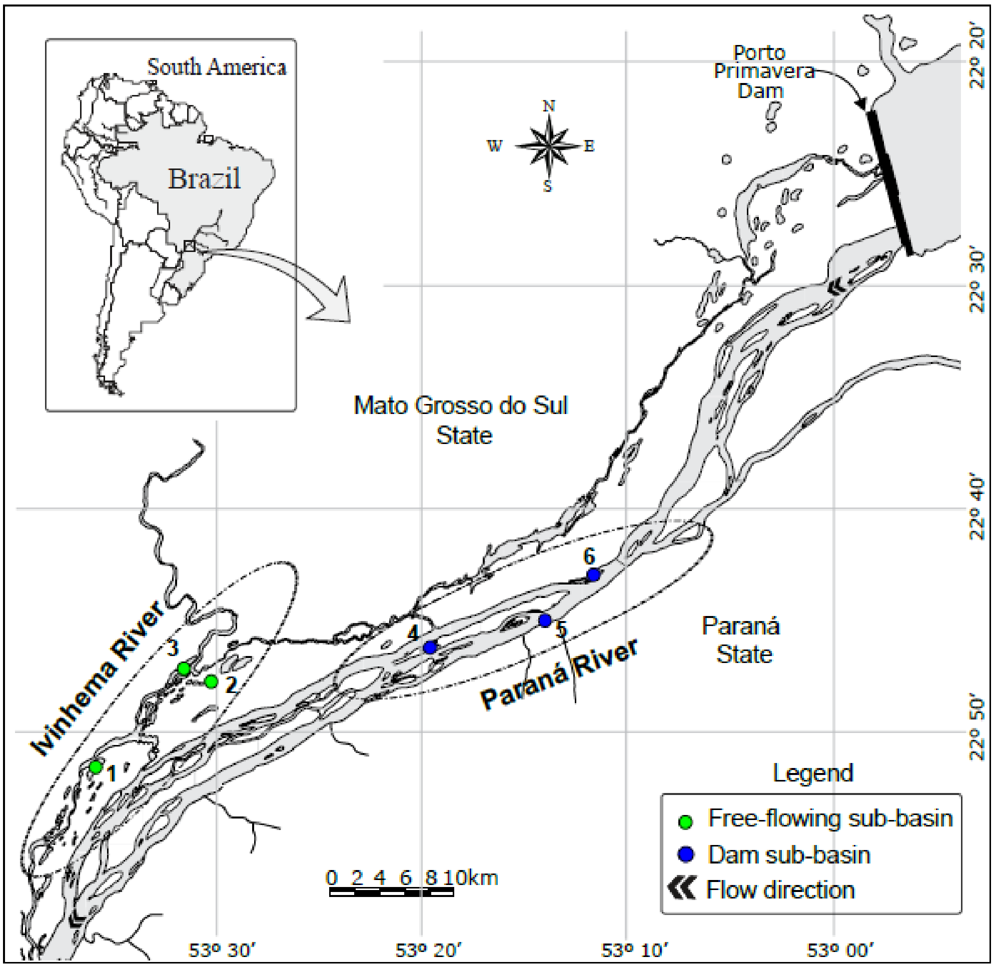


Fig. 1. Study area, including the six sampling systems, in the upper Paraná River floodplain, Brazil. Systems associated with free-flowing sub-basin (Ivinhema): 1 – isolated lake (Ventura), 2 – connected lake (Patos), 3 – lotic (Ivinhema River). Systems associated with dammed sub-basin (Paraná): 4 – isolated lake (Osmar); 5 – lotic (Paraná River); 6 – connected lake (Garças).

3.2.2 Sampling and analysis in the laboratory

Sampling of abiotic variables and biological groups was performed quarterly (in the flooding, flood, ebb, and drought seasons) for 19 years (2000-2018), except in 2003 and 2017, when two samplings occurred (flood and drought seasons). Since the isolated lake of the dammed sub-basin dried up completely, there was no sampling at some times (May, August and November 2001, September 2014, June and September 2015). Also, for the analysis of the functional uniqueness (LCBD-f), each sample must have more than three species (Villéger et al., 2013). Two samples in the Paraná River and one sample in the Ivinhema River showed less than three species. The current of the water in lotic systems can hinder the establishment and development of zooplankton (Paggi and José de Paggi, 1990). Therefore, when the richness was less than three species or when one of the lakes dried up, we excluded all data of the system to standardize the number of samplings, totaling 63 samplings over 19 years.

The abiotic variables were measured simultaneously with the sampling of biological communities: depth (m), water temperature (°C; YSI digital), pH (digital pH-meter Digimed), dissolved oxygen (mg L^{-1}; YSI digital), electric conductivity (µS cm^{-1}; conductivimeter Digimed), turbidity (NTU; portable turbidimeter LaMotte 2008), alkalinity (µEq L^{-1}; Carmouze, 1994); nitrate (µg L^{-1}; Giné et al., 1980), ammonia (µg L^{-1}; Koroleff, 1976), and phosphate (µg L^{-1}; Golterman et al., 1978).

Zooplankton sampling was taken always from the sub-surface in the pelagic region of each site and during the day. The samples were obtained using a motor-pump, filtering 600 L in a plankton net (68 µm), and preserved with 4% formaldehyde solution buffered with calcium carbonate. Phytoplankton samples were obtained on the sub-surface of each site using glass pots (100mL) and preserved with 1% acetic Lugol (Utermöhl, 1958). We also collected fish in each site by gillnets (4, 5, 6, 7, 8, 10, 12, 14, and 16 cm between opposite knots, 20 m in total length, and 1.45–1.70 m in height). In each site, the net was exposed for 24 hours, with the fish being removed every 8 hours. The fish were anesthetized with 5% benzocaine and killed. The methodology for the fish sampling was according to the National Council for Control of Animal Experimentation (CONCEA - #1420221018$_{(ID\ 001974)}$) and was approved by the Ethics Committee on Animal Use of the State University of Maringá (CEUA/UEM). In the isolated lake of the dammed sub-basin, it was not possible to collect fish by gillnets due to its reduced water volume.

Zooplankton individuals (rotifers, cladocerans, and copepods) were counted under an optical microscope and identified using specialized bibliography (Elmoor-Loureiro, 1997; Koste, 1978; Matsumura-Tundisi, 1986; Reid, 1985; Segers, 1995). For each sample, quantification was performed by subsampling with a Hensen-Stempell pipette, with at least 10% of the sample being counted in Sedgwick-Rafter chambers (Bottrell et al., 1976). Richness was expressed by the species occurrence in each sample until the species stabilization curve.

Phytoplankton counting and identification were performed using an inverted microscope (Utermöhl, 1958). After that, the phytoplankton biovolume was calculated by multiplying the density of each species by its respective volume (mm^3 L^{-}). The volume of each phytoplankton cell was obtained from the approximate geometric shape (Sun and Liu, 2003). Due to differential sensitivity to grazing, we classified phytoplankton biovolume in three size classes: picoplankton (< 2 µm), nanoplankton (2 – 63 µm), and microplankton (60 – 500 µm). The total biovolume of each phytoplankton size class was used as a proxy of food resources for zooplankton.

The biomass of the fish species was obtained through CPUE (numbers of individuals captured per unit of effort; individuals/1,000 m^2 gillnets for 24 h) multiplied by the fresh weight for each individual fish. We categorized the fish species into seven trophic guilds to facilitate the interpretation of the results: herbivores, detritivores, invertivores, insectivores, piscivores, omnivores, and planktivores, according to Oliveira et al. (2018) (see Table S1 in Appendix B). The biomass of each of the guilds, in each site, was used as a proxy for predation in zooplankton. Although some guilds do not feed directly on zooplankton, such as the piscivores, all can have an indirect influence through the top-down effect (Sinistro, 2010).

3.2.3 Functional traits

The functional uniqueness of zooplankton (LCBD-f) (336 species: 218 rotifers, 78 cladocerans, and 40 copepods; see Table S3) was estimated following the features: body size (mm), type of reproduction (asexual and sexual), feeding type (filterer, sucking, scraper, raptorial and predator) and predation avoidance behavior (absent, low, intermediate, and efficient escape behavior) (see Braghin et al., 2021; Diniz et al., 2021a) (see Table S2 in Appendix B for details). Since the filtration rate may fluctuate depending on the size of the species, the species that feed on filtration were classified as small, intermediate, and large filter species (based on Bonecker et al., 2011) (Table S3; Appendix B). For 4% of the species, the length values were obtained from the literature (see Table S3 in Appendix B). For the other species, the average body sizes were obtained from the Upper Paraná River floodplain measurements (see Table S3).

3.2.4 Data analysis

The β diversity was estimated followed the methodology proposed by Legendre and De Cáceres (2013), which consists of the contribution of each sample unit to β diversity. We calculated the LCBD from a site-by-species dissimilarity matrix based on presence-absence data using the Sørensen distance (function “beta.pair” from the R-package *betapart;* Baselga et al., 2018) (Fig. 2). For the functional facet, we calculated the between-species distances based on the Gower index from the species-by-traits matrix (function “gowdis” from the R-package *FD*; Gower, 1971; Villéger et al., 2008). Gower distance was used because it can handle different types of variables (e.g., continuous and categorical variables). At this stage, weights were assigned to the traits of the species. This was done to make traits comparable and with the same weight, since each trait had categories with different quantities. For example, the trait "predation avoidance behavior" was composed of four traits (absent, low, intermediate, and efficient escape behavior). Subsequently, this matrix was subjected to a Principal Coordinates Analysis (PCoA) using the function “cmdscale” from the R-package *stats*. We extracted the PCoA axes to calculate the functional dissimilarity (function “functional.beta.pair” from the R-package *betapart*; Baselga et al., 2018), also through the Sørensen method. Using the generated dissimilarity matrices, we calculated taxonomic uniqueness (LCBD-t) and functional uniqueness (LCBD-f) by dividing the sum of the corresponding squares of each site by the total sum of squares (function “LCBD.comp” from the R-package *adespatial*; Legendre and De Cáceres, 2013) (Fig. 2). To verify whether the locations with the lowest taxonomic and functional richness were the ones that most contributed to LCBD-t and LCBD-f, respectively (hypothesis i), a Pearson correlation (function “cor.test”) was performed between the LCBD and richness values. Functional richness (FRic) represents the volume of multidimensional space filled by the species of the community, increasing with the presence of extreme traits (function “dbFD” from the R-package *FD*; Villéger et al., 2008).

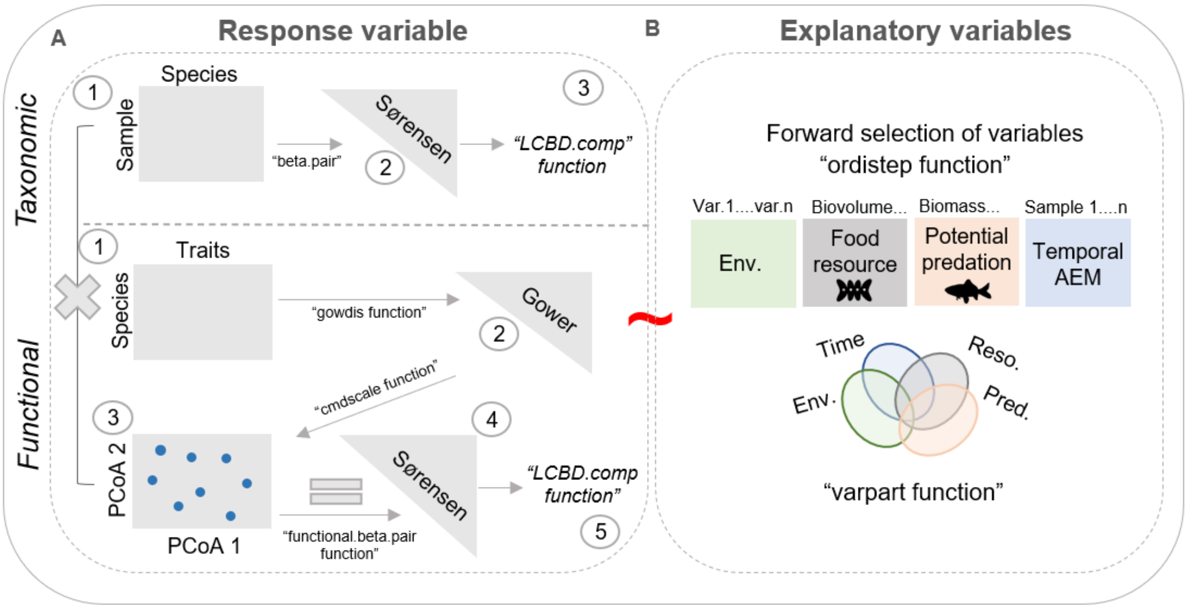


Fig. 2. A flow-chart representing (A) the steps for analyzing the taxonomic uniqueness (LCBD-t) and functional uniqueness (LCBD-f) and (B) the partial Redundancy Analysis (pRDA). The numbers represent the order of each step of the analysis.

The temporal trends in the taxonomic and functional ecological uniqueness throughout the 19 years studied (hypothesis ii) were tested using additive models of generalized mixed-effects (GAMM; function "gamm4" from the R-package *gamm4*; Wood and Scheipl, 2020), considering the system as a random factor in the model. The inclusion of systems as a random factor solves the question of having different systems (lakes and rivers, for example), which also have different hydrodynamic and limnological features. The normal (Gaussian) distribution was the one that best fitted the data. To test the possible temporal autocorrelation in the data, an "acf" function was calculated. The GAMM model was adjusted separately for the dammed and free-flowing sub-basins. The curve with the time trend was obtained by the smoothing method LOESS (Locally-Weighted Scatterplot Smoother) (function "plotGAMM" from the R-package *voxel*; Garza et al., 2018).

We used a partial Redundancy Analysis (pRDA) to test the last hypothesis (iii) that the taxonomic (LCBD-t) and functional (LCBD-f) uniqueness of zooplankton (response variable) is more influenced by environmental filtering (abiotic variables) and the temporal processes than the biological processes (food resource and potential predation) (explanatory variables). The abiotic variables, phytoplankton biovolume, and biomass of the fish trophic guilds' datasets were standardized before the analysis. To set up a temporal matrix, we used the asymmetric eigenvector map (AEM, function "aem.time" from R-package *adespatial*), where the eigenvector acts as a proxy for temporal processes (Legendre and Gauthier, 2014). The AEM is indicated for temporal data since it considers that the temporal processes are directional (Legendre and Gauthier, 2014). For the calculation of temporal AEM, we considered the 63 sampling times carried out over time. Only the positive eigenvalues generated were considered (31 temporal eigenvalues, in our case), since they are more suitable for determining the temporal influence on the response variable (Blanchet et al., 2011). To test for possible multicollinearity between temporal and abiotic variables, variance inflation factors (VIF) were used. Following this method, variables in which the variance of regression coefficient is inflated in the presence of other explanatory variables (i.e. VIF > 5) must be removed (Oksanen et al., 2019). However, in our case, all variables had VIF of less than five. RDA was built using the function "rda", and variation partitioning was run using the function "varpart" from the R-package *vegan* (Oksanen et al., 2019). The significance of each component of the pRDA was tested with ANOVA (p <0.05). We used the forward selection procedure on the environmental, biological (i.e, resources and potential predation), and temporal factors to identify the main variables associated with an LCBD-t and LCBD-f of the zooplankton that would be included in the analysis (Blanchet et al., 2008) (Fig. 2).

All analyses were run separately for each system to detect coherence (or not) in the temporal variation of ecological uniqueness and to avoid the potential masking of some important results. All data handling and statistical analyses were performed in the R environment (R Core Team, 2019), and each procedure and package used were described above.

3.3 Results

The ecological uniqueness of zooplankton varied over time, making it possible to observe a tendency for the sites with less richness to be those that contribute the most to LCBD-t and LCBD-f (Fig. 3 and Fig. 4). Although ecological uniqueness varied over time, it did not vary much among the systems studied (Fig. S1; Appendix B).

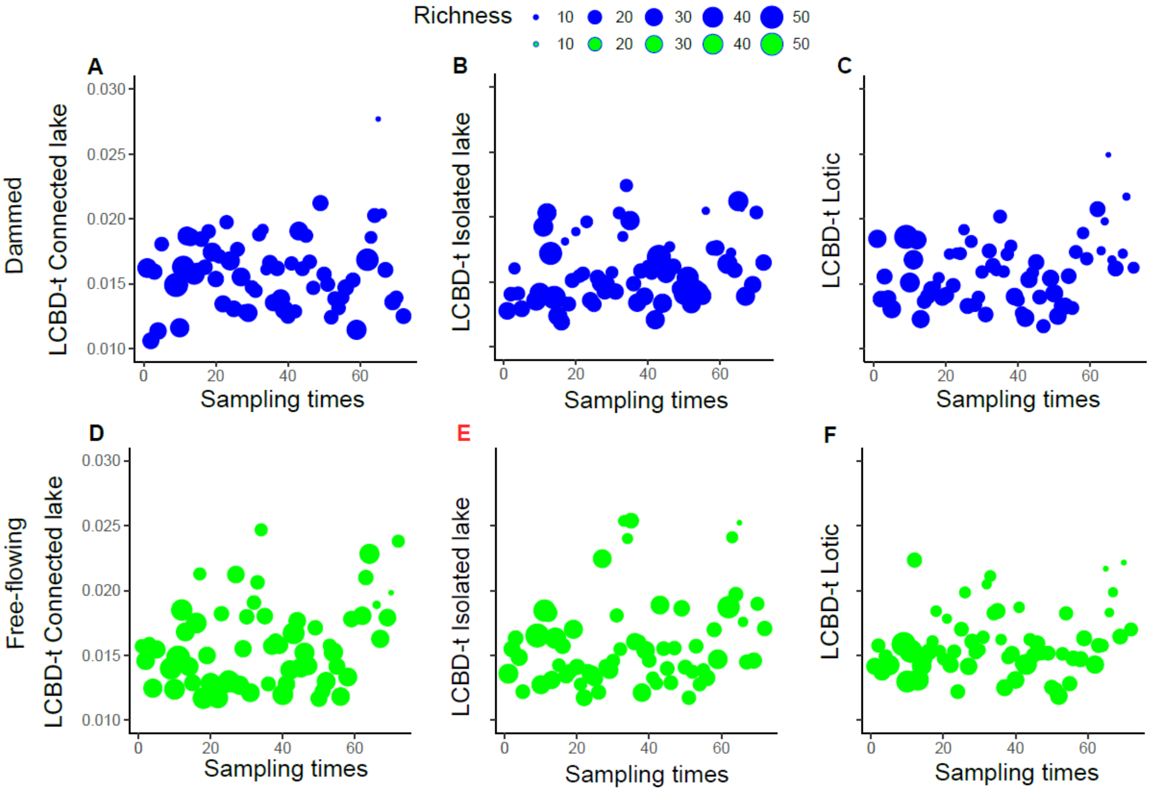


Fig. 3. Taxonomic uniqueness (LCBD-t) of zooplankton in the Upper Paraná River floodplain. – The lotic system and lakes belonging to the dammed sub-basin (A, B, C), and the lotic system and lakes in free-flowing sub-basin (D, E, F). The size of each circle is proportional to the species richness at each of the 63 sampling times. In red (E) the system in which LCBD and richness were not significant.

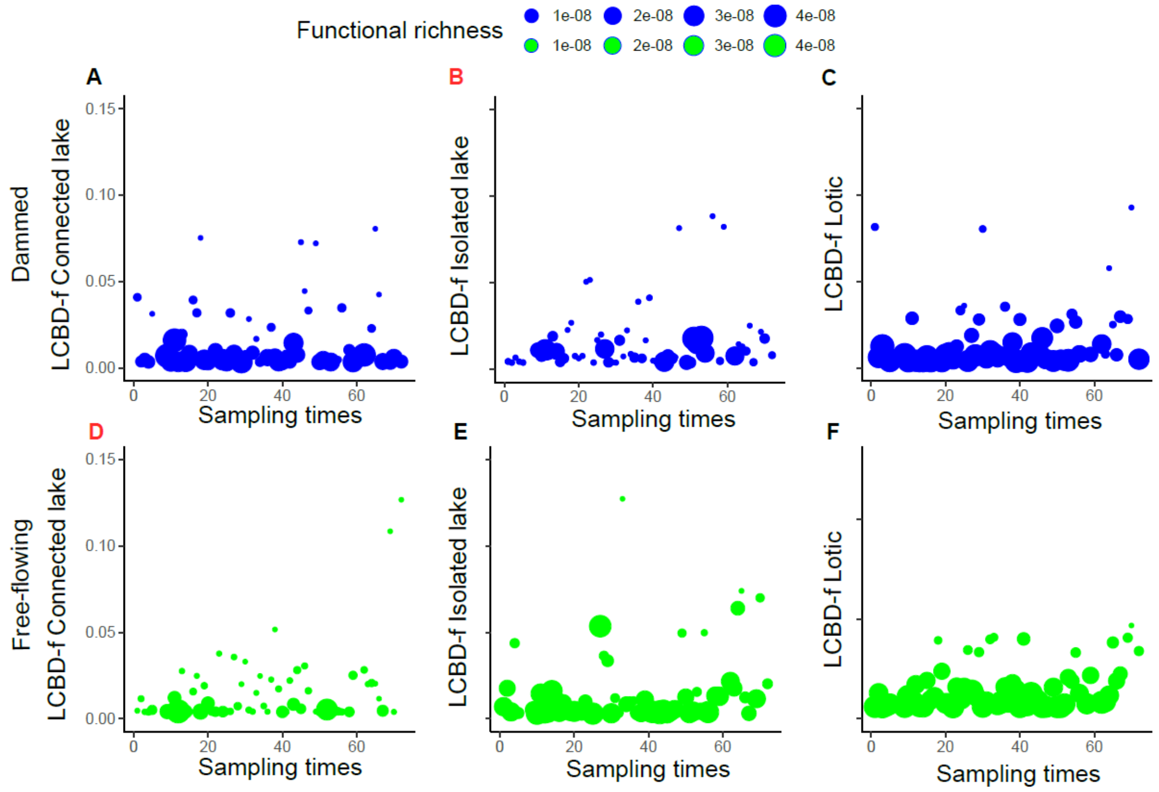


Fig. 4. Functional uniqueness (LCBD-f) of zooplankton in the Upper Paraná River floodplain. – The lotic system and lakes belonging to the dammed sub-basin (A, B, C), and the lotic system and lakes in free-flowing sub-basin (D, E, F). The size of each circle is proportional to the functional richness (FRic) at each of the 63 sampling times. In red (B and D) the systems in which LCBD and richness were not significant.

Contrary to what we expected (hypothesis i), for the three systems in the dammed and free-flowing sub-basins, ecological uniqueness (LCBD-t) was negatively related to species richness. In that case, the moments with the lowest species richness were the ones that most contributed to uniqueness, except in the isolated lake in the free-flowing sub-basin (Pearson's correlation; correlation coefficient = -0.09; df = 61; p = 0.48) (Table 1) (Fig. S2; Appendix B).

Table 1. Pearson's correlation (r) between ecological uniqueness and richness for the systems of the dammed and free-flowing sub-basin, considering the taxonomic and functional approach. In bold, correlation coefficients that were significant.

	Taxonomic			Functional		
Sub-basin	r	t	p	r	t	p
Dammed						
Connected	**-0.27**	-2.19	**0.033**	**-0.41**	-3.52	**<0.01**
Isolated	**-0.33**	-2.68	**0.009**	-0.11	-0.89	0.38
Lotic	**-0.31**	-2.50	**0.015**	**-0.64**	-6.46	**<0.01**
Free-flowing						
Connected	**-0.51**	-4.60	**<0.001**	-0.20	-1.58	0.12
Isolated	-0.09	-0.70	0.484	**-0.44**	-3.82	**<0.01**
Lotic	**-0.49**	-4.44	**<0.001**	**-0.92**	-18.60	**<0.01**

For functional uniqueness (LCBD-f), the ecological uniqueness was not related to functional richness only in the isolated lake in the dammed sub-basin. In the same sub-basin, both the connected lake (Pearson's correlation; correlation coefficient = -0.41; df = 61; p <0.01) and the lotic environment (Pearson's correlation; correlation coefficient = -0.64; df = 61; p <0.01) showed the greatest ecological uniqueness and the lowest functional richness (Table 1). In the free-flowing sub-basin, the connected lake was the only one that showed no relationship between LCBD and functional richness. Both the isolated lake (Pearson's correlation; correlation coefficient = -0.44; df = 61; p <0.01) and the lotic environment (Pearson's correlation; correlation coefficient = -0.92; df = 61; p <0.01) showed greater ecological uniqueness in the sampling times of lower functional richness (Table 1) (Fig. S3; Appendix B).

In the dammed sub-basin, although the taxonomic uniqueness (LCBD-t) did not show such a large upward trend as expected (hypothesis ii), a small increase occurred (Fig. 5A). In the first 10 years, taxonomic uniqueness varied little, showing a peak, followed by a decline, in the last years of sampling (edf = 6.37; F = 4.97; p = 0.0003) (Fig. 5A). For the functional uniqueness, the variation was not significant (edf = 1; F = 3.41; p = 0.07) (Fig. 5C). In the free-flowing sub-basin, both taxonomic and functional uniqueness showed cyclical fluctuations over time, confirming our hypothesis (Fig. 5B and 5D). Even with cyclical fluctuations, taxonomic uniqueness (edf = 7.63; F = 8.75; p < 0.01) (Figure 5B) and, mainly, functional uniqueness (edf

= 4.76; F = 8.84; p < 0.01) (Fig. 5D) showed a slight increase in the last four years of the sampling times.

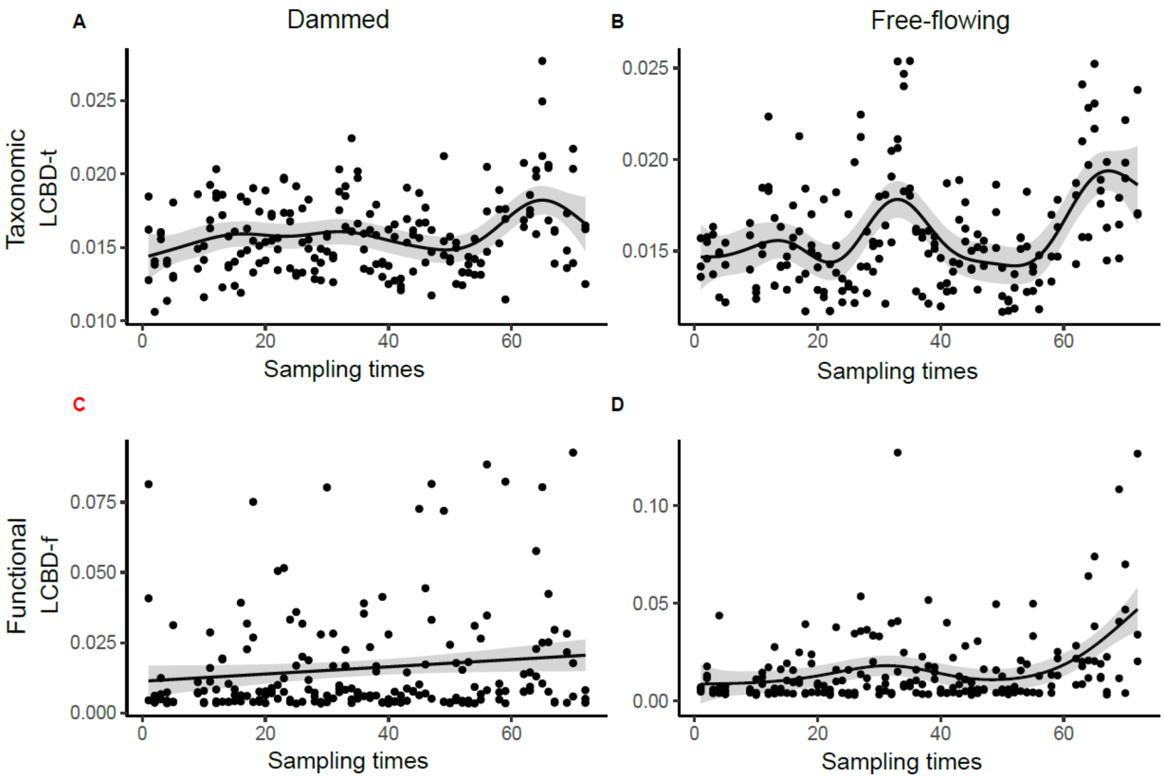


Fig. 5. Smoothed curves showing temporal fluctuations in taxonomic (LCBD-t) and functional (LCBD-f) uniqueness in the three dammed (A and C) and three free-flowing (B and D) systems of the upper Paraná River floodplain. The continuous line is the regression line adjusted by GAMM. The shaded lines indicate the confidence interval of the data ± 95%. In red (C) the only model that was not significant.

The taxonomic and functional uniqueness was strongly explained by the environmental filtering and mainly by the temporal component, in most systems and sub-basins, confirming our hypothesis (iii). The food resource did not appear as the driver for any significant variation in the zooplankton metacommunity, whereas predation pressure significantly influenced the functional uniqueness only in the lotic environment in the dammed sub-basin (11%). The temporal component was important for all sub-basins and systems, with an explanation ranging between 10% and 33%, except for two systems in the dammed sub-basin (lotic and isolated lake), where the influence of time was not significant (Fig. 6).

The environmental filter was only significant in three situations: for LCBD-t in the isolated lake (5%) in the dammed sub-basin, and LCBD-t of the lotic system (12%) and LCBD-f of the connected lake (11%) in the free-flowing sub-basin. The isolated lake of the dammed sub-basin was the only site where the LCBD-f of the zooplankton metacommunity was not explained by any of the components. In general, considering the two sub-basins studied, the predictive power of explanatory variables was greater for the LCBD-t than for the LCBD-f (Fig. 6).

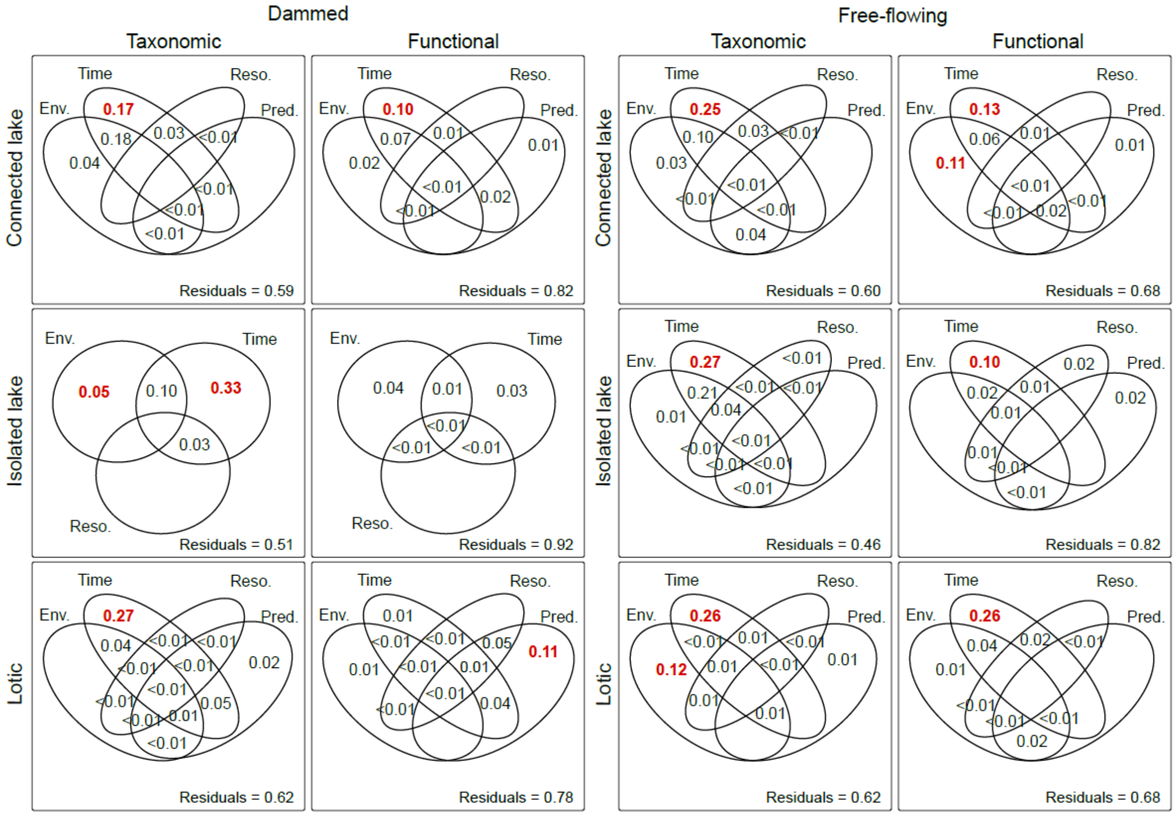


Fig. 6. Venn diagrams, based on the variance partitioning, showing the relative importance of the environment (env.), time (temporal AEM eigenvectors), resource (reso.), and potential predation (pred.) for taxonomic and functional uniqueness (LCBD) of zooplankton in systems associated with the dammed and free-flowing sub-basins of the Upper Paraná River Floodplain, Brazil. Red values indicate significant relationships.

The selected variables (forward selection) varied between the two sub-basins and between the taxonomic and functional uniqueness of zooplankton. Overall, the taxonomic approach selected more explanatory variables than the functional. Among the abiotic variables, turbidity and dissolved oxygen concentration were the most selected variables in both sub-basins. The main size class of the food resource was nanoplankton. As for fish, detritivores, invertivores, and omnivores were selected, with invertivores and omnivores the most frequently selected guilds. Of the 31 temporal vectors with positive autocorrelation generated (AEM), 17 were selected to build the pRDA (Table 2).

Table 2. Environmental, temporal (temporal vector), and biological factors (i.e., phytoplankton/food resource and fish/predation) selected by the forward selection method and used to partition the variance (pRDA) of the taxonomic (Tax.) and functional (Fun.) uniqueness of zooplankton in the systems of the dammed and free-flowing sub-basin. Turb – turbidity (NTU), Alka – alkalinity (µEq l^{-1}), DO - dissolved oxygen (mg l^{-1}), EC – electric conductivity (µS cm^{-1}), Temp. - water temperature (°C), NH_4 – ammonia (µg l^{-1}), PO_4 – phosphate (µg l^{-1}), NO_3 – nitrate (µg l^{-1}), nano – nanoplankton, micro – microplankton, pico – picoplankton, Detrit. - detritivores (g $m^{-2}net^{-1}$ $24hs^{-1}$), Inver. – invertivores (g $m^{-2}net^{-1}$ $24hs^{-1}$), Oniv. – omnivores (g $m^{-2}net^{-1}$ $24hs^{-1}$).

	Environmental		Temporal		Food Resource		Predation	
Sub-basin	Tax.	Fun.	Tax.	Fun.	Tax.	Fun.	Tax.	Fun.
Dammed								
Connected	Turb., Alka.	Alka.	5,9,10,13,21	9	Nano	Pico	Detrit.	Inver.
Isolated	DO, PO_4	NH_4	1,3,6,10,11,17,19,23	30	Nano	Micro	-	-
Lotic	EC.	Temp.	1,2,3,4,7,10	4	Pico	Nano	Inver.	Inver.
Free-flowing								
Connected	DO, Alka., NH_4	DO	1,3,4,9,23	1,3,4,5	Nano	Nano	Inver.	Inver.
Isolated	Turb., Alka., PO_4, EC.	Turb.	1,4,6,9,10,16,19,30	19,23	Nano	Nano	Inver.	Oniv.
Lotic	Turb., NO_3	Turb.	3,4,17	1,3,10,1,7	Micro	Micro	Oniv.	Oniv.

3.4 Discussion

In general, the sampling times with the lowest richness were those that had the greatest ecological uniqueness, in both taxonomic and functional approaches. These results reinforce the idea that exclusivity of taxa is not synonymous with high species richness or functional traits and that it does not depend on the characteristics of each sub-basin. The changes in taxonomic uniqueness observed in the dammed sub-basin, but not changes in the functional uniqueness, over time, show that the changes in temporal diversity do not favor changes in zooplankton function in the ecosystem. The opposite relationship was observed in the free-flowing sub-basin, which exhibits cyclical fluctuations for both LCBD-t and LCBD-f, suggesting a lower redundancy function in the diversity of zooplankton. Furthermore, biological processors (food resource and potential predation) were not important drivers of the ecological uniqueness of zooplankton. The temporal processors stood out, probably because a floodplain is a highly dynamic system, presenting large temporal fluctuations in a single year.

For most systems in the dammed and free-flowing sub-basins, the periods with the most exclusive species were those with the lowest taxonomic richness. Although a negative relationship between ecological uniqueness and richness is a fairly common pattern in the literature (Legendre and De Cáceres, 2013; Quirino et al., 2021; Silva and Hernández, 2014), we expected that this result would be found only for the dammed sub-basin. This was because other studies in the same sub-basin had already registered a temporal homogenization in zooplankton taxonomic richness (Bonecker et al., 2020) and, at the same time, high β diversity values compared to free-flowing sub-basin (Bonecker et al., 2013; Simões et al., 2020). However, we emphasize that for impacted systems, the increase in ecological uniqueness may be associated with the appearance of species that will play an ecosystem function different from the previous ones, resulting in changes in the food web and all aquatic dynamics (Hobbs et al., 2006). Therefore, an increase in ecological uniqueness or species turnover should not always be interpreted as positive, as this increase may indicate various major ecosystem changes (Hobbs et al., 2006).

We expected that the traits would be altered over time as a result of the impact of the damming. However, in our case, although the taxonomic uniqueness oscillated over time, the functional uniqueness was not altered. Thus, greater variation in the species composition in a system will not always indicate greater ecosystem functionality (Simões et al., 2020). Porto Primavera Reservoir was built in 1998, and over the 19 years of monitoring of our study (2000-2018), species may have developed different strategies to cope with the impacts of the dam. Zooplankton organisms are known to respond quickly to environmental changes (Eggermont and Martens, 2011) and, because of their short life cycle, they can produce several generations in a short time. Thus, genetic adaptation and phenotypic plasticity in zooplankton species can occur more quickly (Brans and De Meester, 2018; Dam, 2013; Stoks et al., 2016) from unfavorable environmental conditions. In addition, anthropic impacts do not always cause changes in the functionality of species (Iserhard et al., 2019), especially in floodplains that present high temporal variability and biodiversity that allow buffering of many environmental impacts (Simões et al., 2020, 2013). The resilience of zooplankton in a floodplain, as well as other biological groups, where the species constantly experiences drought and flood events, makes them respond better to changing dynamics or environmental damage, managing to recover more effectively (Shilpakar et al., 2021).

In contrast, the cyclical taxonomic and functional uniqueness in the free-flowing sub-basin over the years was to be expected. In conserved systems, the aquatic biota can show cyclical renewal of species following environmental dynamics (Benincà et al., 2015). Another study carried out in that same sub-basin (Ivinhema River) also showed cyclic fluctuations in the phytoplankton β diversity (Pineda et al., 2020). The Ivinhema sub-basin is located in a Conservation Unit (State Park Várzeas do Rio Ivinhema), with restricted anthropic use. There are no dams along its course (Braghin et al., 2015) and natural and free-flowing environments can maintain high levels of taxonomic and functional β diversity (Braghin et al., 2018).

Although the environmental filter was also important, the temporal processes were more prominent and explained most of the taxonomic and functional uniqueness of zooplankton. Even so, the shared fraction between temporal and environmental processes reached 21% in some cases, indicating that the environmental variables are most likely being structured over time, and influence the ecological uniqueness of zooplankton. The importance of temporal processes could have been expected, since our study considered a long time period (19 years), and because the floodplain is a highly dynamic system, characterized by flood and drought events. During the time period of our study, for example, we recorded some extreme climatic events, such as a prolonged period of drought (2000-2001) and a prolonged period of atypical floods (2010-2011) (Diniz et al., 2021b). The diversity of invertebrates is influenced by extreme climatic events that occur on long time scales in the floodplain, such as *El Niño* and *La Niña* (Bomfim et al., 2021; Pineda et al., 2019).

For functional uniqueness in the dammed sub-basin, the temporal dynamic did not significantly affect the major systems (isolated lake and lotic system). This may explain the absence of a significant temporal trend for LCBD-f in this sub-basin. For the isolated lake, we expected an even more pronounced effect of the temporal processes since it is a temporary environment, even drying up completely in some periods of the year. However, the temporal component was only important in the taxonomic approach. Bertoncin et al. (2019) studied the same lake and observed a biotic homogenization of the macroinvertebrate community based on taxonomic data; they emphasized that the resilience of this lake can be compromised due to extreme droughts. The dynamics of temporal processes to structure the invertebrate and vertebrate communities also proved to be important in another study in the same isolated lake (Moi et al., 2020). However, we emphasize that those studies considered taxonomic data. The importance of temporal processes in the functional uniqueness of zooplankton had not yet been considered in this temporary lake. In addition, none of the other evaluated processes (environment, resource, and predation) were responsible for driving functional uniqueness, suggesting that stochastic processes may be driving LCBD-f or possibly some influential variable for the structure of the zooplankton metacommunity not included in the set of analyzed variables.

The fish influenced the functional uniqueness of zooplankton only in the lotic system in the dammed sub-basin. This may be related to a sampling effect. The collection method used (gillnets) selects larger species and, therefore, collects a greater number of fish in rivers than in lakes. Also, planktonic organisms in this system suffers most directly from the effects of water flow control (Agostinho et al., 2008) and, due to the greater current velocity, the communities tend to be random, making it difficult to establish and develop plankton populations (Lansac-Tôha et al., 2019). Perhaps this is why it was only in this system that the fish of the invertivore guild played an important role in the functional uniqueness of zooplankton. These fish are known to feed predominantly (> 50%) on aquatic invertebrates (Delariva et al., 2013), including planktonic organisms as a major component of their diet (Carniatto et al., 2017). The invertivore species *Moenkhausia gracilima* Eigenmann, 1908, for example, recorded in the same dammed sub-basin, predominantly included Cladocera in its diet (up to 99%) (Carniatto et al., 2017). In addition, we emphasize that this lotic system was the only one in which the temporal processes were not significant. The predation of invertivore fish over zooplankton may have masked the effect of temporal processes on this system.

Food resources did not influence singularity (LCBD-t and LCBD-f) over time in either of the sub-basins. Since most zooplankton species are filterers and feed on phytoplankton (Goldyn and Kowalczewska-Madura, 2008), we expected an important role in food resources. In addition, another study carried out in the same floodplain observed that food availability (estimated as the concentration of chlorophyll *a*) is a driver for the functional diversity of zooplankton over time (Braghin et al., 2021). However, zooplankton can also feed on other organisms not measured in our studies, such as bacteria and ciliates (Oliveira et al., 2019; Segovia et al., 2018). In addition, food resources may also be influenced by temporal processes (Pineda et al., 2020). Thus, since we found the significant importance of time, the temporal oscillations in the food resource may have indirectly influenced the ecological singularity of zooplankton through time dynamics over 19 years.

LCBD allows sites with high conservation value or that need ecological restoration (Legendre and De Cáceres, 2013) to be detected. Therefore, it is a fundamental approach in conservation biology (Heino and Grönroos, 2017). Many conservation strategies involve considering the taxonomically richest sites. However, high temporal uniqueness is not synonymous with high species and trait richness, but rather an indicator of unusual biota in other times (Legendre and De Cáceres, 2013; Silva and Hernández, 2014). Therefore, in these cases, the ideal would be to conserve a combined set of ecologically unique sites that are at the same time taxonomically or functionally rich (Heino and Grönroos, 2017). In our case, for example, only three lakes had high uniqueness and showed no negative relationship with richness: the isolated lake from the dammed sub-basin (for LCBD-t) and the isolated and connected lakes from the free-flowing sub-basin (for LCBD-t and LCBD-f, respectively). Thus, these lakes, in particular, have a high potential for conservation, since they have sampling points over time that are ecologically unique and with high taxonomic and/or functional richness.

3.5 Conclusions

Our study showed that, regardless of whether some systems belong to a dammed or a free-flowing sub-basin, it is the exclusive biota at sampling times with low species richness and functional traits that contributes strongly to β diversity in the Upper Paraná River floodplain. This greater taxonomic and functional uniqueness at times of comparatively low richness provides useful ecological information that can be used to support the restoration of dammed systems or even reinforce the importance of maintaining free-flowing areas. This indicates that the high β diversity in this sub-basin is formed by species with similar ecosystem functions. In addition, as the zooplankton LCBD-t and LCBD-f are being driven primarily by temporal processes, we reinforce the importance of long-term ecological studies to better monitor the dynamics of aquatic biota and establish more robust ecological standards. We propose that ecological and/or biodiversity conservation studies focus simultaneously on the richness and ecological uniqueness, both taxonomic and functional, to design better plans for managing and conserving aquatic biodiversity in floodplains. From our appraisal, it is hoped that the results found here will provide an interesting tool in a conservation context, showing the need to consider longer time scales in ecological studies and planning priority areas.

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APPENDIX B - Trophic guild of fish species, list of species and functional traits of zooplankton, and details of some results.

Table S1. Trophic guild of fish species from the upper Paraná River floodplain. Pisc = Piscivores, Ins = Insectivores, Inv = Invertivores, Herb = Herbivores, Omn = Omnivores, Plan = Planktivores, Det = Detritivores.

Fish species	**Guild**
Astyanax aff. *fasciatus* (Cuvier, 1819)	Detritivores
Apareiodon affinis (Steindachner, 1879)	Detritivores
Astronotus crassipinnis (Heckel, 1840)	Piscivores
Acestrorhynchus lacustris (Lütken, 1875)	Piscivores
Ageneiosus militaris Valenciennes, 1835	Piscivores
Auchenipterus osteomystax (Miranda Ribeiro, 1918)	Insectivores
Acestrorhynchus pantaneiro Menezes, 1992	Piscivores
Ageneiosus ucayalensis Castelnau, 1855	Piscivores
Astyanax lacustris (Lütken, 1875)	Insectivores
Apteronotus cf. *caudimaculosus* de Santana, 2003	Invertivores
Ageneiosus inermis (Linnaeus, 1766)	Piscivores
Astyanax aff. *paranae* Eigenmann, 1914	Insectivores
Apteronotus ellisi (Alonso de Arámburu, 1957)	Omnivores
Astyanax schubarti Britski, 1964	Herbivores
Brachyhypopomus gauderio Giora, Malabarba, 2009	Insectivores
Brycon orbignyanus (Valenciennes, 1850)	Herbivores
Brycon hilarii (Valenciennes, 1850)	Herbivores
Bryconamericus stramineus Eigenmann, 1908	Herbivores
Crenicichla britskii Kullander, 1982	Insectivores
Crenicichla jaguarensis Haseman, 1911	Piscivores
Cichla kelberi Kullander & Ferreira, 2006	Piscivores
Cyphocharax modestus (Fernández-Yépez, 1948)	Detritivores
Cyphocharax nagelii (Steindachner, 1881)	Detritivores
Cichlasoma paranaense Kullander, 1983	Piscivores
Cichla piquiti Kullander & Ferreira, 2006	Piscivores
Cichla sp.	Invertivores
Callichthys callichthys (Linnaeus, 1758)	Invertivores
Clarias gariepinus (Burchell, 1822)	Omnivores
Catathyridium jenynsii (Günther, 1862)	Piscivores
Colossoma macropomum (Cuvier, 1816)	Omnivores
Cyphocharax sp.	Detritivores
Crenicichla haroldoi Luengo & Britski, 1974	Insectivores
Crenicichla niederleinii (Holmberg, 1891)	Insectivores
Crenicichla sp.	Insectivores
Eigenmannia trilineata López & Castello, 1966	Insectivores
Eigenmannia virescens (Valenciennes, 1836)	Insectivores
Erythrinus erythrinus (Bloch & Schneider, 1801)	Piscivores

Fish species	**Guild**
Gymnotus inaequilabiatus (Valenciennes, 1839)	Insectivores
Geophagus cf. *sveni* Lucinda, Lucena & Assis, 2010	Detritivores
Gymnotus sylvius Albert & Fernandes-Matioli, 1999	Insectivores
Galeocharax gulo (Cope, 1864)	Piscivores
Gymnotus pantanal Fernandes, Albert, Daniel-Silva,	Insectivores
Gymnotus paraguensis Albert & Crampton, 2003	Insectivores
Gymnotus sp.	Insectivores
Hypostomus ancistroides (Ihering, 1911)	Detritivores
Hypostomus iheringii (Regan,1908)	Detritivores
Hypostomus cochliodon Kner, 1854	Detritivores
Hoplosternum littorale (Hancock, 1828)	Invertivores
Hoplias mbigua Azpelicueta, Benítez, Aichino, Mendez, Damián, 2015	Piscivores
Hypophthalmus oremaculatus Nani, Fuster, 1947	Planktivores
Hemiodus orthonops Eigenmann & Kennedy, 1903	Herbivores
Hypostomus regani (Ihering, 1905)	Detritivores
Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)	Piscivores
Hoplias sp.2	Piscivores
Hoplias sp.3	Piscivores
Hoplias argentinensis Rosso, Mabragaña, González-Castro, Bogan, Cardoso, Mabragaña, Delpiani & Díaz de Astarloa, 2018	Piscivores
Hemisorubim platyrhynchos (Valenciennes, 1840)	Piscivores
Hoplias sp.4	Piscivores
Hypostomus albopunctatus (Regan, 1908)	Detritivores
Hypostomus cf. *strigaticeps* (Regan, 1908)	Detritivores
Hypostomus sp.	Detritivores
Hypostomus hermanni (Ihering, 1905)	Detritivores
Hypostomus commersoni Valenciennes, 1836	Detritivores
Hypostomus hermanni (Ihering, 1905)	Detritivores
Hypostomus microstomus Weber, 1987	Detritivores
Hypostomus ternetzi (Boulenger, 1895)	Detritivores
Iheringichthys labrosus (Lütken, 1874)	Invertivores
Leporinus friderici (Bloch, 1794)	Omnivores
Leporinus lacustris Campos, 1945	Omnivores
Lepthoplosternum pectorale (Boulenger, 1895)	Omnivores
Loricariichthys platymetopon Isbrücker & Nijssen, 1979	Detritivores
Loricaria prolixa (Isbrücker & Nijssen, 1978)	Herbivores
Loricariichthys rostratus Reis & Pereira, 2000	Detritivores
Loricariichthys sp.	Detritivores
Loricaria cataphracta Linnaeus 1758	Detritivores
Laetacara araguaiae Ottoni & Costa, 2009	Invertivores
Leporinus octofasciatus Steindachner 1915	Omnivores
Leporinus striatus Kner, 1858	Omnivores
Leporellus vittatus (Valenciennes, 1850)	Insectivores
Leporinus sp.	Omnivores
Moenkhausia aff. *intermedia* Eigenmann, 1908	Omnivores

Fish species	**Guild**
Metynnis lippincottianus (Cope, 1870)	Omnivores
Megaleporinus macrocephalus (Garavello & Britski, 1988)	Omnivores
Megaleporinus obtusidens (Valenciennes, 1836)	Omnivores
Megaleporinus piavussu (Britski, Birindelli, Garavello, 2012)	Herbivores
Myloplus tiete (Eigenmann & Norris, 1900)	Herbivores
Megalancistrus parananus (Peters, 1881)	Detritivores
Moenkhausia bonita Benine, Castro & Sabino, 2004	Invertivores
Moenkhausia gracilima Eigenmann, 1908	Invertivores
Megalonema platanum (Günther, 1880)	Piscivores
Ossancora eigenmanni (Boulenger, 1895)	Invertivores
Pterygoplichthys ambrosettii (Holmberg, 1893)	Detritivores
Platydoras armatulus (Valenciennes, 1840)	Omnivores
Pseudoplatystoma corruscans (Spix & Agassiz, 1829)	Piscivores
Parauchenipterus galeatus (Linnaeus, 1766)	Omnivores
Prochilodus lineatus (Valenciennes, 1837)	Detritivores
Pimelodus maculatus Lacepède, 1803	Omnivores
Potamotrygon amandae Loboda, Carvalho, 2013	Invertivores
Pimelodella avanhandavae Eigenmann, 1917	Insectivores
Pimelodella gracilis (Valenciennes, 1835)	Insectivores
Pterodoras granulosus (Valenciennes, 1821)	Omnivores
Psellogrammus kennedyi (Eigenmann, 1903)	Omnivores
Piaractus mesopotamicus (Holmberg, 1887)	Herbivores
Pimelodus microstoma Steindachner, 1877	Piscivores
Pimelodus mysteriosus Azpelicueta, 1998	Omnivores
Pimelodus ornatus Kner, 1858	Omnivores
Pinirampus pirinampu (Agassiz, 1829)	Piscivores
Plagioscion squamosissimus (Heckel, 1840)	Piscivores
Pimelodella sp.	Insectivores
Piaractus mesopotamicus (Holmberg, 1887)	Herbivores
Parodon nasus Kner, 1859	Detritivores
Pseudoplatystoma sp.	Piscivores
Potamotrygon cf. *falkneri* Castex & Maciel, 1963	Piscivores
Pimelodella taenioptera Miranda-Ribeiro, 1914	Omnivores
Rhinelepis aspera Spix & Agassiz,1829	Detritivores
Roeboides descalvadensis Fowler, 1932	Insectivores
Rhamphichthys hahni (Meinken, 1937)	Insectivores
Rhaphiodon vulpinus Spix & Agassiz, 1829	Piscivores
Rhinodoras dorbignyi (Kner,1855)	Detritivores
Rhamdia quelen (Quoy & Gaimard, 1824)	Piscivores
Schizodon borellii (Boulenger, 1900)	Herbivores
Salminus brasiliensis (Cuvier, 1816)	Piscivores
Steindachnerina brevipinna (Eigenmann & Eigenmann, 1889)	Detritivores
Steindachnerina insculpta (Fernández-Yépez, 1948)	Detritivores
Sorubim lima (Bloch & Schneider,1801)	Piscivores
Serrasalmus maculatus Kner, 1858	Piscivores

Fish species	Guild
Serrasalmus marginatus Valenciennes, 1837	Piscivores
Schizodon nasutus (Kner, 1858)	Herbivores
Satanoperca sp.	Detritivores
Schizodon altoparanae Garavello & Britski, 1990	Herbivores
Steindachnerina sp.	Detritivores
Salminus hilarii Valenciennes, 1850	Piscivores
Sternopygus macrurus (Bloch & Schneider, 1801)	Invertivores
Schizodon sp.	Herbivores
Synbranchus marmoratus Bloch, 1795	Piscivores
Trachydoras paraguayensis (Eigenmann & Ward,1907)	Invertivores
Triportheus nematurus (Kner, 1858)	Omnivores
Trachydoras sp.	Invertivores
Zungaro jahu (Ihering, 1898)	Piscivores

REFERENCES USED TO CHARACTERIZE FISH TROPHIC GUILDS

Dias, J.D., Simões, N.R., Meerhoff, M., Lansac-Tôha, F.A., Velho, L.F.M., Bonecker, C.C., 2016. Hydrological dynamics drives zooplankton metacommunity structure in a Neotropical floodplain. Hydrobiologia 781, 109–125. https://doi.org/10.1007/s10750-016-2827-2

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Table S2. Functional traits of zooplanktonic species, including the categories and the importance of each one. The list of species with the corresponding traits is available in Table S3.

Traits	Categories (%)	Importance
Mean body size	Average length (mm)	Body size influences from metabolism to zooplankton feeding and dispersion rates (Dias et al., 2016; Litchman et al., 2013). Also, it is responsible for determining many biological processes, such as top-down control over algae, for example (Pinheiro-Silva et al., 2020; Ye et al., 2013).
Reproduction	Asexual Sexual	The type of reproduction can be considered an indication of environmental conditions since in the face of stressful conditions some zooplanktonic organisms invest in sexual reproduction for the production of resistance eggs.
Predatory escape response	Absent Low Intermediate Efficient	This trait is important because depending on the escape response of each species, it can minimize capture rates or encounter predators (Ohman, 1988).
Feeding type	Filtration Sucking Predator Raptorial Scraper	Each type of food has associated costs and benefits and, like other traits, can affect secondary productivity and other trophic levels (Litchman et al., 2013).

REFERENCES USED TO DESCRIBE THE IMPORTANCE OF EACH TRAIT USED

Dias, J.D., Simões, N.R., Meerhoff, M., Lansac-Tôha, F.A., Velho, L.F.M., Bonecker, C.C., 2016. Hydrological dynamics drives zooplankton metacommunity structure in a Neotropical floodplain. Hydrobiologia 781, 109–125. https://doi.org/10.1007/s10750-016-2827-2

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Ye, L., Chang, C.Y., García-Comas, C., Gong, G.C., Hsieh, C. hao, 2013. Increasing zooplankton size diversity enhances the strength of top-down control on phytoplankton through diet niche partitioning. J. Anim. Ecol. 82, 1052–1061. https://doi.org/10.1111/1365-2656.12067

Table S3. List of zooplankton species, the functional traits of each, and their respective references. S – small filter (< 300 µm), I – intermediate filter (301 – 600 µm), and L – large filter (> 601 µm).

Species	**Body size (µm)**	**Feeding type**	**Reproduction**	**Predatory escape response**
Rotifera				
Lecane aculeata (Jakubski, 1912)	74	Filtration-S	Asexual	absent
Lecane amazonica (Murray, 1913)	115	Filtration-S	Asexual	absent
Lecane braumi Koste, 1988	162	Filtration-S	Asexual	absent
Lecane bulla (Gosse, 1851)	114.61	Filtration-S	Asexual	absent
Lecane closterocerca (Schmarda, 1859)	85	Filtration-S	Asexual	absent
Lecane cornuta (Müller, 1786)	109	Filtration-S	Asexual	absent
Lecane crenata (Harring, 1913)	119.5	Filtration-S	Asexual	absent
Lecane curvicornis (Murray, 1913)	131.25	Filtration-S	Asexual	absent
Lecane unguitata (Fadeev, 1925)	107.5	Filtration-S	Asexual	absent
Lecane doryssa Harring, 1914	66	Filtration-S	Asexual	absent
Lecane elsa Hauer, 1931	150	Filtration-S	Asexual	absent
Lecane furcata (Murray, 1913)	65.5	Filtration-S	Asexual	absent
Lecane haliclysta Harring & Myers, 1926	92	Filtration-S	Asexual	absent
Lecane hornemanni (Ehrenberg, 1834)	94	Filtration-S	Asexual	absent
Lecane inermis (Bryce, 1892)	88.5	Filtration-S	Asexual	absent
Lecane inopinata Harring & Myers, 1926	75	Filtration-S	Asexual	absent
Lecane leontina (Turner, 1892)	175	Filtration-S	Asexual	absent
Lecane ludwigii (Eckstein, 1883)	134.38	Filtration-S	Asexual	absent
Lecane luna (Müller, 1776)	126.95	Filtration-S	Asexual	absent
Lecane lunaris (Ehrenberg, 1832)	101.94	Filtration-S	Asexual	absent
Lecane mira (Murray, 1913)	145	Filtration-S	Asexual	absent
Lecane monostyla (Daday, 1897)	69	Filtration-S	Asexual	absent
Lecane ohioensis (Herrick, 1885)	119.5	Filtration-S	Asexual	absent
Lecane papuana (Murray, 1913)	107.7	Filtration-S	Asexual	absent
Lecane proiecta Hauer, 1956	113	Filtration-S	Asexual	absent
Lecane pusilla Harring, 1914	60	Filtration-S	Asexual	absent
Lecane rhytida Harring & Myers, 1926	81	Filtration-S	Asexual	absent
Lecane robertsonae Segers, 1993	119.5	Filtration-S	Asexual	absent
Lecane quadridentata (Ehrenberg, 1830)	162.5	Filtration-S	Asexual	absent
Lecane signifera (Jennings, 1896)	113	Filtration-S	Asexual	absent
Lecane scutata (Harring & Myers, 1926)	74	Filtration-S	Asexual	absent
Lecane stenroosi (Meissner, 1908)	118.5	Filtration-S	Asexual	absent
Lecane stichaea Harring, 1913	173	Filtration-S	Asexual	absent
Lecane ungulata (Gosse, 1887)	157.5	Filtration-S	Asexual	absent
Lecane obtusa (Murray, 1913)	102*[2]	Filtration-S	Asexual	absent
Anuraeopsis navicula Rousselet, 1911	72.5	Filtration-S	Asexual	absent
Anuraeopsis quadriantennata (Koste, 1974)	73	Filtration-S	Asexual	absent
Brachionus angularis Gosse, 1851	107.5	Filtration-S	Asexual	absent

Species	**Body size (µm)**	**Feeding type**	**Reproduction**	**Predatory escape response**
Brachionus bidentatus Anderson, 1889	368	Filtration-I	Asexual	absent
Brachionus budapestinensis Daday, 1885	100	Filtration-S	Asexual	absent
Brachionus calyciflorus Pallas, 1766	201.19	Filtration-S	Asexual	absent
Brachionus caudatus Barrois & Daday, 1894	270	Filtration-S	Asexual	absent
Brachionus dolabratus Harring, 1914	167	Filtration-S	Asexual	absent
Brachionus falcatus Zacharias, 1898	430	Filtration-I	Asexual	absent
Brachionus forficula Wierzejski, 1891	145	Filtration-S	Asexual	absent
Brachionus havanaensis Rousselet, 1911	135	Filtration-S	Asexual	absent
Brachionus mirus Daday, 1905	138.8	Filtration-S	Asexual	absent
Brachionus quadridentatus Kertész, 1894	143.75	Filtration-S	Asexual	absent
Brachionus urceolaris Müller, 1773	187.5	Filtration-S	Asexual	absent
Brachionus satanicus Rousselet, 1911	325	Filtration-S	Asexual	absent
Kellicottia bostoniensis (Rousselet, 1908)	113.85	Filtration-S	Asexual	absent
Keratella americana Carlin, 1943	159.74	Filtration-S	Asexual	absent
Keratella cochlearis (Gosse, 1851)	107.16	Filtration-S	Asexual	absent
Keratella lenzi Hauer, 1953	112.5	Filtration-S	Asexual	absent
Keratella tropica (Apstein, 1907)	115.42	Filtration-S	Asexual	absent
Plationus patulus (Müller, 1786)	122.5	Filtration-S	Asexual	absent
Platyias leloupi Gillard, 1957	218.75	Filtration-S	Asexual	absent
Platyias quadricornis (Ehrenberg, 1832)	141.67	Filtration-S	Asexual	absent
Notholca caudata Carlin, 1943	200	Filtration-S	Asexual	absent
Trichocerca bicristata (Gosse, 1887)	660	Sucking	Asexual	absent
Trichocerca agnata Wulfert, 1939	134.5	Sucking	Asexual	absent
Trichocerca bidens (Lucks, 1912)	133.33	Sucking	Asexual	absent
Trichocerca capucina (Wierzejski & Zacharias, 1893)	325	Sucking	Asexual	absent
Trichocerca collaris (Rousselet, 1896)	119	Sucking	Asexual	absent
Trichocerca cylindrica (Imhof, 1891)	325	Sucking	Asexual	absent
Trichocerca chattoni (Beauchamp, 1907)	177*[2]	Sucking	Asexual	absent
Trichocerca dixonnuttalli (Jennings, 1903)	117	Sucking	Asexual	absent
Testudinella elongata De Smet, 2009	237.5	Sucking	Asexual	absent
Trichocerca braziliensis (Murray, 1913)	138*[2]	Sucking	Asexual	absent
Trichocerca flagellata Hauer, 1937	112.5	Sucking	Asexual	absent
Trichocerca macera (Gosse, 1886)	294.5	Sucking	Asexual	absent
Trichocerca gracilis (Tessin, 1890)	209.9	Sucking	Asexual	absent
Trichocerca heterodactyla (Tschugunoff, 1921)	225	Sucking	Asexual	absent
Trichocerca iernis (Gosse, 1887)	135	Sucking	Asexual	absent
Trichocerca inermis (Linder, 1904)	88.5	Sucking	Asexual	absent
Trichocerca insignis (Herrick, 1885)	376	Sucking	Asexual	absent
Trichocerca insulana (Hauer, 1937)	100.5	Sucking	Asexual	absent
Trichocerca longiseta (Schrank, 1802)	222	Sucking	Asexual	absent
Trichocerca mus Hauer, 1938	59.5	Sucking	Asexual	absent
Trichocerca myersi (Hauer, 1931)	175	Sucking	Asexual	absent
Trichocerca porcellus (Gosse, 1851)	162	Sucking	Asexual	absent

Species	**Body size (µm)**	**Feeding type**	**Reproduction**	**Predatory escape response**
Trichocerca pusilla (Jennings, 1903)	175	Sucking	Asexual	absent
Trichocerca rattus (Müller, 1776)	168	Sucking	Asexual	absent
Trichocerca rousseleti (Voigt, 1902)	102.5	Sucking	Asexual	absent
Trichocerca ruttneri Donner, 1953	85.5	Sucking	Asexual	absent
Trichocerca scipio (Gosse, 1886)	408	Sucking	Asexual	absent
Trichocerca similis (Wierzejski, 1893)	300	Sucking	Asexual	absent
Trichocerca stylata (Gosse, 1851)	167	Sucking	Asexual	absent
Trichocerca tigris (Müller, 1786)	260	Sucking	Asexual	absent
Trichocerca sulcata (Jennings, 1894)	54*^{2}	Sucking	Asexual	absent
Beauchampiella eudactylota (Gosse, 1886)	760	Filtration-L	Asexual	absent
Dipleuchlanis propatula (Gosse, 1886)	508	Filtration-L	Asexual	absent
Euchlanis deflexa Gosse, 1851	275	Filtration-S	Asexual	absent
Euchlanis dilatata Ehrenberg, 1830	187.8	Filtration-S	Asexual	absent
Euchlanis incisa Carlin, 1939	229.3	Filtration-S	Asexual	absent
Euchlanis meneta Myers, 1930	136.5	Filtration-S	Asexual	absent
Euchlanis oropha Gosse, 1887	174	Filtration-S	Asexual	absent
Tripleuchlanis plicata (Levander, 1894)	115	Filtration-S	Asexual	absent
Lophocharis salpina (Ehrenberg, 1834)	102.5	Filtration-S	Asexual	absent
Lophocharis oxysternon (Gosse, 1851)	84	Filtration-S	Asexual	absent
Mytilina acanthophora Hauer, 1938	216.6	Filtration-S	Asexual	absent
Mytilina bisulcata (Lucks, 1912)	159	Filtration-S	Asexual	absent
Mytilina macrocera (Jennings, 1894)	320	Filtration-I	Asexual	absent
Mytilina mucronata (Müller, 1773)	212.5	Filtration-S	Asexual	absent
Mytilina ventralis (Ehrenberg, 1830)	175	Filtration-S	Asexual	absent
Testudinella ahlstromi Hauer, 1956	235	Filtration-S	Asexual	absent
Testudinella discoidea Ahlstrom, 1938	209	Filtration-S	Asexual	absent
Testudinella mucronata (Gosse, 1886)	181.5	Filtration-S	Asexual	absent
Testudinella ohlei Koste, 1972	140	Filtration-S	Asexual	absent
Testudinella patina (Hermann, 1783)	350	Filtration-I	Asexual	absent
Testudinella tridentata Smirnov, 1931	185	Filtration-S	Asexual	absent
Pompholyx complanata Gosse, 1851	90	Filtration-S	Asexual	absent
Pompholyx triloba Pejler, 1957	83.5	Filtration-S	Asexual	absent
Pompholyx sulcata Hudson, 1885	110	Filtration-S	Asexual	absent
Filinia longiseta (Ehrenberg, 1834)	140.6	Filtration-S	Asexual	absent
Filinia opoliensis (Zacharias, 1898)	220.2	Filtration-S	Asexual	absent
Filinia pejleri Hutchinson, 1964	179	Filtration-S	Asexual	absent
Filinia saltator (Gosse, 1886)	149	Filtration-S	Asexual	absent
Filinia terminalis (Plate, 1886)	138.3	Filtration-S	Asexual	absent
Ploesoma lenticulare Herrick, 1885	254.5	Filtration-S	Asexual	absent
Ploesoma truncatum (Levander, 1894)	131.5	Filtration-S	Asexual	absent
Polyarthra dolichoptera Idelson, 1925	94	Filtration-S	Asexual	absent
Polyarthra vulgaris Carlin, 1943	115.3	Filtration-S	Asexual	absent
Polyarthra remata Skorikov, 1896	92.5	Filtration-S	Asexual	absent
Synchaeta longipes Gosse, 1887	204	Filtration-S	Asexual	absent

Species	**Body size (µm)**	**Feeding type**	**Reproduction**	**Predatory escape response**
Synchaeta pectinata Ehrenberg, 1832	86.03	Filtration-S	Asexual	absent
Synchaeta oblonga Ehrenberg, 1832	110.4	Filtration-S	Asexual	absent
Synchaeta stylata Wierzejski, 1893	238.5	Filtration-S	Asexual	absent
Floscularia melicerta (Ehrenberg, 1832)	800	Filtration-L	Asexual	absent
Floscularia ringens (Linnæus, 1758)	900	Filtration-L	Asexual	absent
Octotrocha speciosa Thorpe, 1893	200	Filtration-S	Asexual	absent
Limnias ceratophylli Schrank, 1803	750*[2]	Filtration-L	Asexual	absent
Limnias melicerta Weisse, 1848	190*[2]	Filtration-S	Asexual	absent
Ptygura melicerta Ehrenberg, 1832	200*[2]	Filtration-S	Asexual	absent
Sinantherina ariprepes Edmondson, 1939	680	Filtration-L	Asexual	absent
Sinantherina procera (Thorpe, 1893)	540	Filtration-I	Asexual	absent
Sinantherina spinosa (Thorpe, 1893)	1050	Filtration-L	Asexual	absent
Cephalodella forficula (Ehrenberg, 1838)	243	Sucking	Asexual	absent
Cephalodella sterea (Gosse, 1887)	144	Sucking	Asexual	absent
Cephalodella gibba (Ehrenberg, 1830)	114	Sucking	Asexual	absent
Cephalodella anebodica Bērziņš, 1976	260	Sucking	Asexual	absent
Cephalodella hiulca Myers, 1924	91	Sucking	Asexual	absent
Cephalodella mucronata Myers, 1924	209	Sucking	Asexual	absent
Cephalodella obvia Donner, 1951	143	Sucking	Asexual	absent
Cephalodella tenuiseta (Burn, 1890)	143	Sucking	Asexual	absent
Enteroplea lacustris Ehrenberg, 1830	431.5	Sucking	Asexual	absent
Eothinia elongata (Ehrenberg, 1832)	410	Sucking	Asexual	absent
Eosphora anthadis Harring & Myers, 1922	312	Sucking	Asexual	absent
Eosphora thoides Wulfert, 1935	345	Sucking	Asexual	absent
Monommata dentata Wulfert, 1940	400	Sucking	Asexual	absent
Monommata maculata Harring & Myers, 1930	271.5	Sucking	Asexual	absent
Monommata actices Myers, 1930	178.5	Sucking	Asexual	absent
Monommata arndti Remane, 1933	283.3	Sucking	Asexual	absent
Monommata caeca Myers, 1930	150.5	Sucking	Asexual	absent
Monommata grandis Tessin, 1890	183.5	Sucking	Asexual	absent
Notommata cerberus (Gosse, 1886)	355	Sucking	Asexual	absent
Notommata copeus Ehrenberg, 1834	544.5	Sucking	Asexual	absent
Notommata falcinella Harring & Myers, 1922	547	Sucking	Asexual	absent
Notommata haueri Wulfert, 1939	384.4	Sucking	Asexual	absent
Notommata pachyura (Gosse, 1886)	325	Sucking	Asexual	absent
Notommata pseudocerberus Beauchamp, 1908	493	Sucking	Asexual	absent
Notommata saccigera Ehrenberg, 1830	271.5	Sucking	Asexual	absent
Pleurotrocha robusta (Glascott, 1893)	221	Sugador	Asexual	absent
Taphrocampa selenura Gosse, 1887	135	Sucking	Asexual	absent
Tetrasiphon hydrocora Ehrenberg, 1840	450	Sucking	Asexual	absent
Colurella adriatica Ehrenberg, 1831	101.5	Filtration-S	Asexual	absent
Colurella obtusa (Gosse, 1886)	55	Filtration-S	Asexual	absent
Lepadella benjamini Harring, 1916	87.5	Filtration-S	Asexual	absent
Lepadella dactyliseta (Stenroos, 1898)	66	Filtration-S	Asexual	absent

Species	**Body size (µm)**	**Feeding type**	**Reproduction**	**Predatory escape response**
Lepadella cristata (Rousselet, 1893)	66	Filtration-S	Asexual	absent
Lepadella donneri Koste, 1972	97	Filtration-S	Asexual	absent
Lepadella imbricata Harring, 1914	97	Filtration-S	Asexual	absent
Lepadella ovalis (Müller, 1786)	150	Filtration-S	Asexual	absent
Lepadella patella (Müller, 1773)	145	Filtration-S	Asexual	absent
Lepadella rhomboides (Gosse, 1886)	119	Filtration-S	Asexual	absent
Lepadella triptera (Ehrenberg, 1830)	61	Filtration-S	Asexual	absent
Conochilus coenobasis (Skorikov, 1914)	112.5	Filtration-S	Asexual	absent
Conochilus dossuarius Hudson, 1885	120.8	Filtration-S	Asexual	absent
Conochilus natans (Seligo, 1900)	75	Filtration-S	Asexual	absent
Conochilus unicornis Rousselet, 1892	175	Filtration-S	Asexual	absent
Ascomorpha ecaudis Perty, 1850	170	Sucking	Asexual	absent
Ascomorpha agilis Zacharias, 1893	150	Sucking	Asexual	absent
Ascomorpha ovalis (Bergendal, 1892)	176	Sucking	Asexual	absent
Ascomorpha saltans Bartsch, 1870	165	Sucking	Asexual	absent
Gastropus hyptopus (Ehrenberg, 1838)	96.9	Sucking	Asexual	absent
Gastropus minor (Rousselet, 1892)	138.5	Sucking	Asexual	absent
Gastropus stylifer Imhof, 1891	180	Sucking	Asexual	absent
Proales sp.	95	Filtration-S	Asexual	absent
Dicranophoroides caudatus (Ehrenberg, 1834)	310	Predator	Asexual	absent
Dicranophoroides claviger (Hauer, 1965)	187	Predator	Asexual	absent
Dicranophorus epicharis Harring & Myers, 1928	238	Predator	Asexual	absent
Dicranophorus forcipatus (Müller, 1786)	296	Predator	Asexual	absent
Dicranophorus luetkeni (Bergendal, 1892)	167	Predator	Asexual	absent
Dicranophorus prionacis Harring & Myers, 1928	271	Predator	Asexual	absent
Dicranophorus hauerianus Wiszniewski, 1939	325	Predator	Asexual	absent
Macrochaetus collinsii (Gosse, 1867)	250	Filtration-S	Asexual	absent
Macrochaetus longipes Myers, 1934	87	Filtration-S	Asexual	absent
Macrochaetus sericus (Thorpe, 1893)	112	Filtration-S	Asexual	absent
Macrochaetus subquadratus Perty, 1850	157	Filtration-S	Asexual	absent
Trichotria tetractis (Ehrenberg, 1830)	295	Filtration-S	Asexual	absent
Collotheca ornata (Ehrenberg, 1830)	1200	Filtration-L	Asexual	absent
Hexarthra intermedia (Wiszniewski, 1929)	234	Filtration-S	Asexual	absent
Hexarthra mira (Hudson, 1871)	151.93	Filtration-S	Asexual	absent
Trochosphaera aequatorialis Semper, 1872	1100	Filtration-L	Asexual	absent
Asplanchnopus hyalinus Harring, 1913	700*[2]	Predator	Asexual	absent
Asplanchna priodonta Gosse, 1850	323	Predator	Asexual	absent
Asplanchna sieboldii (Leydig, 1854)	1500	Predator	Asexual	absent
Harringia rousseleti Beauchamp, 1911	383.5	Predator	Asexual	absent
Epiphanes clavulata (Ehrenberg, 1831)	125	Filtration-S	Asexual	absent
Epiphanes macroura (Barrois & Daday, 1894)	187.5	Filtration-S	Asexual	absent
Epiphanes senta (Müller, 1773)	200	Filtration-S	Asexual	absent
Scaridium grande Segers, 1995	400	Predator	Asexual	absent
Scaridium longicauda (Müller, 1786)	400	Predator	Asexual	absent

Species	**Body size (µm)**	**Feeding type**	**Reproduction**	**Predatory escape response**
Itura chamadis Harring & Myers, 1928	263.5	Predator	Asexual	absent
Itura deridderae Segers, 1993	305	Predator	Asexual	absent
Itura myersi Wulfert, 1935	112	Predator	Asexual	absent
Lindia torulosa Dujardin, 1841	293	Predator	Asexual	absent
Bdelloidea	625	Filtration-L	Asexual	absent
Cladocera				
Moina minuta Hansen, 1899	612	Filtration-L	Asexual	low
Moina micrura Kurz, 1874	440	Filtration-I	Asexual	low
Moina reticulata (Daday, 1905)	750	Filtration-L	Asexual	low
Moina rostrata McNair, 1980	640	Filtration-L	Asexual	low
Moinodaphnia macleayi (King, 1853)	580	Filtration-I	Asexual	low
Bosmina hagmanni Stingelin, 1904	301.18	Filtration-I	Asexual	low
Bosmina freyi De Melo & Hebert, 1994	314*[1]	Filtration-I	Asexual	low
Bosmina tubicen Brehm, 1953	294.54	Filtration-S	Asexual	low
Bosminopsis deitersi Richard, 1895	227.13	Filtration-S	Asexual	low
Ceriodaphnia cornuta G.O. Sars, 1885.	289.11	Filtration-S	Asexual	low
Ceriodaphnia reticulata (Jurine, 1820)	1000	Filtration-L	Asexual	low
Ceriodaphnia laticaudata P.E.Müller, 1867	950	Filtration-L	Asexual	low
Ceriodaphnia silvestrii Daday, 1902	450	Filtration-I	Asexual	low
Ceriodaphnia richardi Sars, 1901	647	Filtration-L	Asexual	low
Daphnia gessneri (Herbst, 1967)	812.5	Filtration-L	Asexual	low
Daphnia ambigua Scourfield, 1947	1112*[1]	Filtration-L	Asexual	low
Daphnia laevis (Birge, 1878)	1500	Filtration-L	Asexual	low
Daphnia lumholtzi Sars, 1885	842	Filtration-L	Asexual	low
Scapholeberis armata freyi Dumont & Pensaert, *1983*	700	Filtration-L	Asexual	low
Simocephalus iheringi Richard, 1897	1761.3	Filtration-L	Asexual	low
Simocephalus serrulatus (Koch 1841)	2005	Filtration-L	Asexual	low
Simocephalus latirostris Stingelin, 1906	1600	Filtration-L	Asexual	low
Simocephalus punctatus Orlova-Bienkowskaja, 1998	1701	Filtration-L	Asexual	low
Simocephalus vetulus (Müller, 1776)	1850	Filtration-L	Asexual	low
Simocephalus sp.	1650.5	Filtration-L	Asexual	low
Diaphanosoma birgei Korineck, 1981	506.42	Filtration-I	Asexual	low
Diaphanosoma brevireme Sars, 1901	612.5	Filtration-L	Asexual	low
Diaphanosoma fluviatile Hansen, 1899	538.28	Filtration-I	Asexual	low
Diaphanosoma spinulosum Herbst, 1967	550.31	Filtration-I	Asexual	low
Diaphanosoma polyspina Korovchinsky, 1982	630	Filtration-L	Asexual	low
Latonopsis australis Sars, 1888	700	Filtration-L	Asexual	low
Sarsilatona serricauda Sars, 1901	1920	Filtration-L	Asexual	low
Acroperus tupinamba Sinev & Elmoor-Loureiro, 2010	900	Scraper	Asexual	absent
Magnospina dentifera (Sars, 1901)	480	Scraper	Asexual	absent
Alona ossiani Sinev, 1998	800	Scraper	Asexual	absent
Ovalona glabra (Sars, 1901)	325	Scraper	Asexual	absent

Species	Body size (µm)	Feeding type	Reproduction	Predatory escape response
Karualona muelleri (Richard, 1897)	462	Scraper	Asexual	absent
Coronatella monacantha (Sars, 1901)	264	Scraper	Asexual	absent
Leberis davidi (Richard, 1895)	670	Scraper	Asexual	absent
Nicsmirnovius paggii Sousa & Elmoor-Loureiro, 2017	325	Scraper	Asexual	absent
Alona cf *guttata*	250	Scraper	Asexual	absent
Alona intermedia Sars, 1862	425	Scraper	Asexual	absent
Nicsmirnovius incredibilis (Smirnov, 1984)	440	Scraper	Asexual	absent
Alona yara Sinev & Elmoor-Loureiro, 2010	580	Scraper	Asexual	absent
Coronatella rectangula (Sars, 1861)	434*[5]	Scraper	Asexual	absent
Anthalona verrucosa (Sars, 1901)	300	Scraper	Asexual	absent
Coronatella poppei (Richard, 1897)	393.5	Scraper	Asexual	absent
Flavalona iheringula (Kotov & Sinev, 2004)	300	Scraper	Asexual	absent
Alonella clathratula Sars, 1896	450	Scraper	Asexual	absent
Alonella dadayi Birge, 1910	213.95	Scraper	Asexual	absent
Camptocercus australis Sars, 1896	680	Scraper	Asexual	absent
Chydorus eurynotus Sars, 1901	241.67	Scraper	Asexual	absent
Chydorus parvireticulatus Frey, 1987	300	Scraper	Asexual	absent
Chydorus nitidulus (Sars, 1901)	260	Scraper	Asexual	absent
Chydorus pubescens Sars, 1901	287.5	Scraper	Asexual	absent
Chydorus cf. *sphaericus*	500	Scraper	Asexual	absent
Disparalona hamata (Birge, 1879)	510	Scraper	Asexual	absent
Dadaya macrops (Daday, 1898)	310	Scraper	Asexual	absent
Dunhevedia odontoplax Sars, 1901	460	Scraper	Asexual	absent
Ephemeroporus tridentatus (Bergamin, 1931)	310	Scraper	Asexual	absent
Ephemeroporus barroisi (Richard, 1894)	270	Scraper	Asexual	absent
Ephemeroporus hybridus (Daday, 1905)	260	Scraper	Asexual	absent
Euryalona brasiliensis Brehm & Thomsen, 1936	362.5	Scraper	Asexual	absent
Euryalona orientalis (Daday, 1898)	450	Scraper	Asexual	absent
Graptoleberis occidentalis Sars, 1901	391	Scraper	Asexual	absent
Kurzia polyspina Hudec, 2000	600	Scraper	Asexual	absent
Kurzia longirostris (Daday, 1898)	420	Scraper	Asexual	absent
Leydigiopsis curvirostris Sars, 1901	850	Scraper	Asexual	absent
Leydigiopsis megalops Sars, 1901	800	Scraper	Asexual	absent
Notoalona sculpta (Sars, 1901)	430	Scraper	Asexual	absent
Oxyurella ciliata Bergamin, 1939	440	Scraper	Asexual	absent
Oxyurella longicaudis (Birge, 1910)	635	Scraper	Asexual	absent
Guernella raphaelis Richard, 1892	415	Scraper	Asexual	absent
Macrothrix elegans Sars, 1901	300	Scraper	Asexual	absent
Macrothrix laticornis (Jurine, 1820)	375	Scraper	Asexual	absent
Macrothrix superaculeata (Smirnov, 1982)	350	Scraper	Asexual	absent
Macrothrix squamosa Sars, 1901	400	Scraper	Asexual	absent
Streblocercus pygmaeus Sars, 1901	225	Scraper	Asexual	absent
Copepoda				

Species	**Body size (µm)**	**Feeding type**	**Reproduction**	**Predatory escape response**
Acanthocyclops robustus (Sars GO, 1863)	1005	Raptorial	Sexual	efficient
Ectocyclops rubescens (Brady 1904)	944	Raptorial	Sexual	efficient
Eucyclops ensifer Kiefer, 1936	962	Raptorial	Sexual	efficient
Eucyclops elegans (Herrick, 1884)	945	Raptorial	Sexual	efficient
Eucyclops prionophorus Kiefer, 1931	770*[4]	Raptorial	Sexual	efficient
Eucyclops solitarius Herbst, 1959	1170	Raptorial	Sexual	efficient
Macrocyclops albidus (Jurine, 1920)	1285	Raptorial	Sexual	efficient
Mesocyclops longisetus (Thiébaud, 1912)	1597	Raptorial	Sexual	efficient
Mesocyclops ogunnus Onabamiro 1957	1185	Raptorial	Sexual	efficient
Mesocyclops aspericornis (Daday, 1906)	1302	Raptorial	Sexual	efficient
Mesocyclops meridianus (Kiefer, 1926)	767.4	Raptorial	Sexual	efficient
Mesocyclops ellipticus Kiefer, 1936	965	Raptorial	Sexual	efficient
Microcyclops anceps (Richard, 1897)	750	Raptorial	Sexual	efficient
Microcyclops alius (Kiefer, 1935)	575	Raptorial	Sexual	efficient
Microcyclops ceibaensis (March, 1929)	650	Raptorial	Sexual	efficient
Microcyclops finitimus Dussart, 1984	578	Raptorial	Sexual	efficient
Metacyclops laticornis (Lowndes, 1934)	772	Raptorial	Sexual	efficient
Metacyclops mendocinus (Wierzejski, 1892)	1145	Raptorial	Sexual	efficient
Paracyclops fimbriatus (Fischer, 1853)	900	Raptorial	Sexual	efficient
Paracyclops chiltoni (Thomson, 1882)	739	Raptorial	Sexual	efficient
Thermocyclops decipiens (Kiefer, 1929)	691.1	Raptorial	Sexual	efficient
Thermocyclops minutus (Lowndes, 1934)	523.1	Raptorial	Sexual	efficient
Thermocyclops inversus Kiefer, 1936	527	Raptorial	Sexual	efficient
Tropocyclops prasinus (Fischer, 1860)	500	Raptorial	Sexual	efficient
Argyrodiaptomus azevedoi (Wright, 1935)	1704	Filtration-L	Sexual	intermediate
Argyrodiaptomus denticulatus (Pesta, 1927)	1753*[3]	Filtration-L	Sexual	intermediate
Argyrodiaptomus furcatus (Sars GO, 1901)	1354	Filtration-L	Sexual	intermediate
Notodiaptomus anisitsi (Daday, 1905)	1144	Filtration-L	Sexual	intermediate
Notodiaptomus cearensis (Wright, 1936)	1100	Filtration-L	Sexual	intermediate
Notodiaptomus conifer (Sars GO, 1901)	1548	Filtration-L	Sexual	intermediate
Notodiaptomus deitersi (Poppe, 1891)	1240	Filtration-L	Sexual	intermediate
Notodiaptomus henseni (Dahl, 1894)	1208.1	Filtration-L	Sexual	intermediate
Notodiaptomus iheringi (Wright, 1935)	922	Filtration-L	Sexual	intermediate
Notodiaptomus jatobensis (S. Wright, 1936)	1073	Filtration-L	Sexual	intermediate
Notodiaptomus incompositus (Brian, 1925)	1029	Filtration-L	Sexual	intermediate
Notodiaptomus isabelae (Wright, 1936)	1058.5	Filtration-L	Sexual	intermediate
Notodiaptomus kieferi Brandorff 1973	1154	Filtration-L	Sexual	intermediate
Notodiaptomus spiniger (Brian, 1925)	952	Filtration-L	Sexual	intermediate
Notodiaptomus spinulifera Dussart & Matsumura-Tundisi, 1986	1466	Filtration-L	Sexual	intermediate
Odontodiaptomus paulistanus (Wright, 1936)	959	Filtration-L	Sexual	intermediate

*Average body size of zooplankton organisms obtained from the literature.

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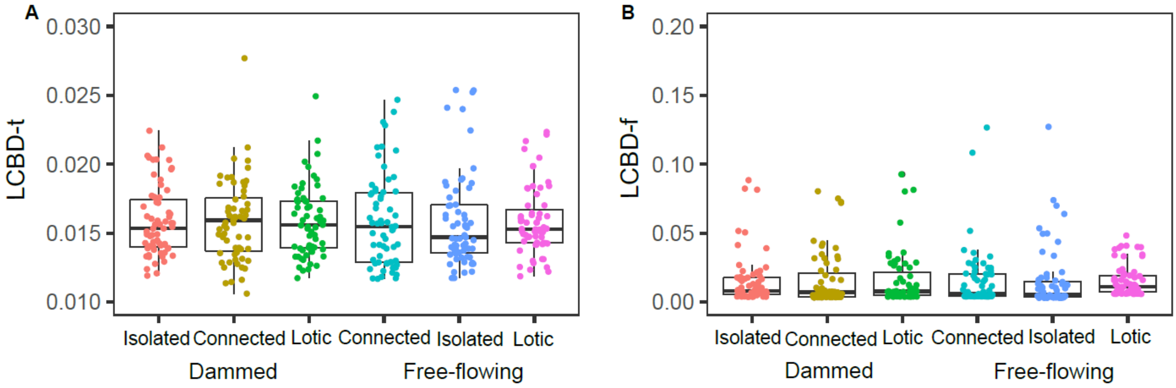

Fig. S1. Box-plot representing the variation over 19 years of study in taxonomic uniqueness (LCBD-t, A) and functional (LCBD-f, B) of zooplankton in the Upper Paraná River floodplain.

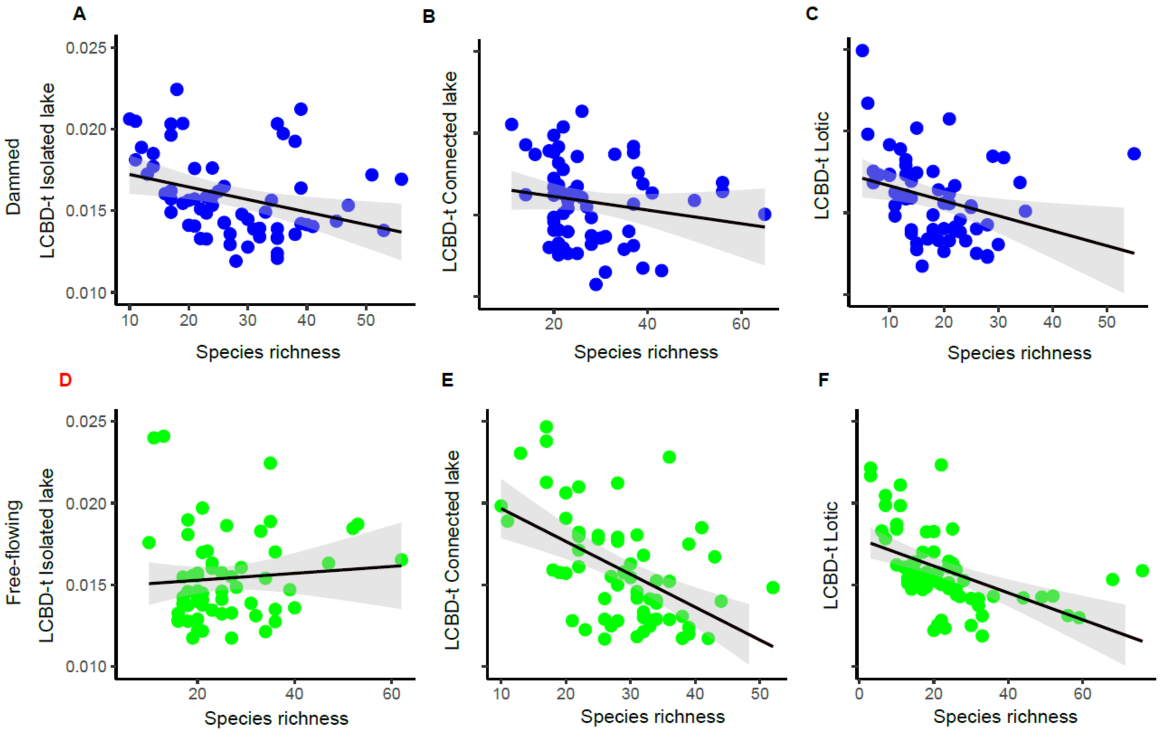

Fig. S2. Relationship between zooplankton ecological uniqueness and richness in dammed and free-flowing sub-basin, considering the taxonomic approach (LCBD-t), in the Upper Paraná River floodplain. In red, the lakes where correlation coefficients were not significant.

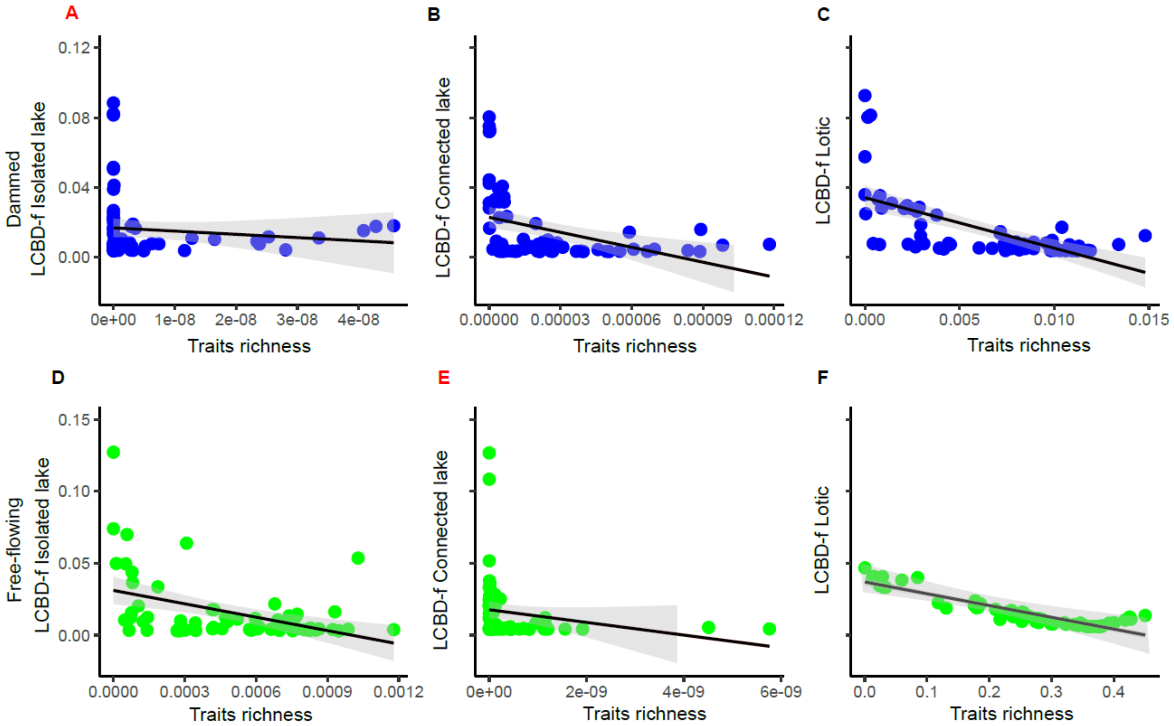

Fig. S3. Relationship between zooplankton ecological uniqueness and richness in dammed and free-flowing sub-basin, considering the functional approach (LCBD-f), in the Upper Paraná River floodplain. In red, the lakes where correlation coefficients were not significant.

A prolonged drought period reduced temporal β diversity of zooplankton, but not phytoplankton and fish metacommunities in a Neotropical floodplain*

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*Manuscrito derivado da tese, a ser submetido para revista científica *Aquatic Sciences*.

4 A PROLONGED DROUGHT PERIOD REDUCED TEMPORAL β DIVERSITY OF ZOOPLANKTON, BUT NOT PHYTOPLANKTON AND FISH METACOMMUNITIES IN A NEOTROPICAL FLOODPLAIN

Abstract

The natural dynamics of floodplains are marked by drought and flood events. However, extreme climate events or even the damming of natural rivers can intensify the effects of droughts and floods and modify aquatic biota. We investigate whether a prolonged drought period makes aquatic metacommunities more similar over time than a period with extreme flood events in 10 neotropical floodplain lakes. Our expectation was to find: (i) lower environmental heterogeneity and lower β diversity in the prolonged drought period (i.e., biotic homogenization), and (ii) a more pronounced decrease of β diversity in the period of prolonged drought for aquatic organisms of active dispersal (fish) than for small passive dispersal organisms (phytoplankton and zooplankton). We estimated the β diversity among sampling occasions using the Sørensen and Bray-Curtis dissimilarity separately for each lake and each period (i.e., prolonged drought and intense floods period). Even though the prolonged drought period had reduced the environmental heterogeneity, only the zooplankton metacommunity underwent homogenization during this period. The β diversity of phytoplankton and fish did not change between different hydrological periods, indicating that the dispersion type does not interfere with drought homogenization. In addition, we warn that in the face of climate change and, consequently, an increase in prolonged droughts, the variability of zooplankton can reduce over time and, thus, change the entire dynamics of the aquatic ecosystem. We emphasize the importance of natural flood events for maintaining aquatic heterogeneity and ecosystem functioning.

Keywords: β diversity, climatic events, flood pulse, Paraná River

4.1 Introduction

Biodiversity has decreased rapidly, resulting mainly from environmental degradation or extreme climate events (Cardinale et al. 2012; Tickner et al. 2020). This scenario motivated and still has encouraged researchers worldwide to understand the variation of biodiversity and establish increasingly accurate conservation measures (Olden 2006; Naeem et al. 2012). β diversity is a component of biodiversity that has been extensively studied due to increased similarity of metacommunities over time. Biotic homogenization is defined as an increase in similarity or a decrease in β diversity over time (taxonomic, functional or phylogenetic diversity). It can occur by anthropic action, such as damming rivers or introducing exotic species, or naturally, involving drought and flood events (Olden et al. 2004; Olden et al. 2018; Petsch 2016). Even so, in many cases, the anthropic action ends up intensifying or changing these natural events and bringing negative consequences for biodiversity (Talbot et al. 2018).

Hydrological variations, as observed in the floodplains, govern the dynamics of β diversity (i.e., variability among communities; Petsch et al. 2021) in different aquatic biological groups, and several studies have been proposed to explain how hydrology affects ecological patterns (Padial et al. 2009; Bortolini et al. 2016; Pinha et al. 2016; Conceição et al. 2017; Aspin et al. 2018; Abrial et al. 2019; Petsch et al. 2021). The natural dynamics of floodplains, marked by drought and flood events every year, drive the biodiversity and functioning of these systems (Junk et al. 1989; Neiff 1990). However, climate change can affect the floodplain dynamic and make drought events more severe (such as the climate event *La Niña* in southern Brazil, for example) or floods more frequent and intense (climate event *El Niño* in southern Brazil, for example), consequently, affecting aquatic biota (Pineda et al. 2019; Alves et al., 2021; Andreotti et al., 2021; Bomfim et al. 2021). In addition, the reservoir buildings in floodplains have increased significantly. In the Upper Paraná River Floodplain, in Brazil, for example, a series of reservoirs upstream has reduced aquatic biodiversity (Oliveira et al. 2018; Braghin et al. 2018). Over time, the damming of the natural course of rivers has intensified prolonged drought and made extreme flood peaks increasingly rare, causing loss of aquatic biodiversity (Agostinho et al. 2004b; Chaparro et al. 2019; Moi et al. 2020).

An extreme or prolonged drought period can homogenize the aquatic biota due to the persistence of only a few dominant species (Bertoncin et al. 2019). This occurs because imposing a prolonged period of drought in the dynamics of the hydrological regime can generate stressful conditions and, thus, reduce the local diversity. In this case, a prolonged disturbance may act as a filter selecting only those species that manage to survive under those conditions (Bonecker et al. 2009), replacing specialist or even rare species with the dominance of generalist species. Although highly dynamic ecosystems, such as floodplains, have high resistance and resilience, the more extended and frequent the drought period, the slower the recovery process (Bond et al. 2008). In addition, the reduction in the volume of water also decreases the quality of the water, increasing the proliferation of toxic cyanobacteria and decreasing the concentration of dissolved oxygen (Mosley 2015). This reduction in water quality affects all aquatic biota, reducing β diversity and affecting the functioning of the ecosystem during drought (Bertoncin et al. 2019).

Flood pulses are also known to homogenize aquatic biota, decreasing environmental variability between sites and increasing connectivity (Thomaz et al. 2007). Even though it is well established in the literature (Thomaz et al. 2007; Lopes et al. 2014; Bozelli et al. 2015), there is still a debate about its homogenizing effect (Mayora et al. 2013). If we consider a larger time scale, covering all phases of the natural dynamics of a floodplain (flood and drought events), the different temporal gradients drive environmental heterogeneity and β diversity over time (Simões et al. 2013a). For example, a floodplain lake has a higher water level during the flood period, with more organic matter and larger inflows of water from different regions and with different environmental characteristics (Mayora et al. 2020). While during the drought period, the lake is shallower and water exchange between sites is reduced (Junk et al. 1989; Simões et al. 2012). Consequently, over time, a period including both drought and flood events is probably more environmentally heterogeneous than a period without floods. Thus, over time the natural dynamics of the flooding drive the maintenance of ecological processes and biodiversity (Junk et al. 1989; Neiff 1990). In addition, the occurrence of flood events over time allows higher stochastic dispersal of species, increasing the turnover of species, consequently increasing temporal β diversity (Bortolini et al. 2016). Therefore, it is important to note that the homogenizing effect of the flood pulse is dependent on the scale (e.g., snapshots or larger time scales) and approach (e.g. similarity among sites or months) considered. This is because the same event can lead to different spatial and temporal patterns in the aquatic metacommunities, especially in highly dynamic environments such as floodplains (Sarremejane et al. 2017; Petsch et al. 2021; Diniz et al. 2021). Therefore, studies that consider different types of scales are essential, especially those that consider a more extended period since many studies have been developed only in a short term (Magurran et al. 2010, 2019; Dornelas et al. 2013; Gotelli et al. 2017).

The prolonged and extreme drought tends to spatially homogenize all aquatic biota (e.g., Magalhães et al. 2007; Bertoncin et al. 2019). However, depending on some biological group dynamic and dispersion capacity, the homogenization process can be intensified (Padial et al.

2014; Dias et al. 2016; Petsch et al. 2017; Landeiro et al. 2018). Fish, for example, have active dispersal and depends even more on watercourses and flood periods to disperse (Padial et al. 2014). Drought periods limit fish movements, spawning and larvae dispersion across the floodplain, resulting in failures in the recruitment of migratory fish (Oliveira et al. 2015). On the other hand, planktonic groups, have passive dispersal and, therefore, they can disperse independently of the watercourse, through biological vectors or by the wind (Pinceel et al. 2016; Morais-Junior et al. 2019a, b). Phytoplanktonic algae have resting stages and/or the presence of mucilage that can act to assist in resistance against desiccation to remain viable even after long distances (Chrisostomou et al. 2009). Zooplankton can produce resting forms (eggs and diapause forms) that remain viable even after passing through the digestive tract of a migratory waterbird (Figuerola and Green 2002). Because fishes have active dispersion over watercourses, their distribution among the lakes is even more limited than the passive dispersion organisms during prolonged drought. Therefore, although the three biological groups (phytoplankton, zooplankton and fish) may homogenize during a prolonged drought, this process can be further intensified for fish, resulting in local extinctions of the most sensitive species (Magalhães et al. 2007).

We investigated whether a prolonged drought makes aquatic metacommunities more similar over time than a period that includes extreme flood events. If our hypothesis is confirmed, we expect to find: (i) lower environmental heterogeneity and (ii) lower β diversity during the prolonged drought compared to the period with extreme flood events. Finally, (iii) we expect a more pronounced decrease of β diversity in the period of prolonged drought for aquatic organisms of active dispersal via watercourse (fish) than for small passive dispersal organisms (phytoplankton and zooplankton) (Fig. 1). We designed our study by analyzing each floodplain lake and aquatic metacommunity separately over four years: two years of extreme drought and two years with extreme flood events.

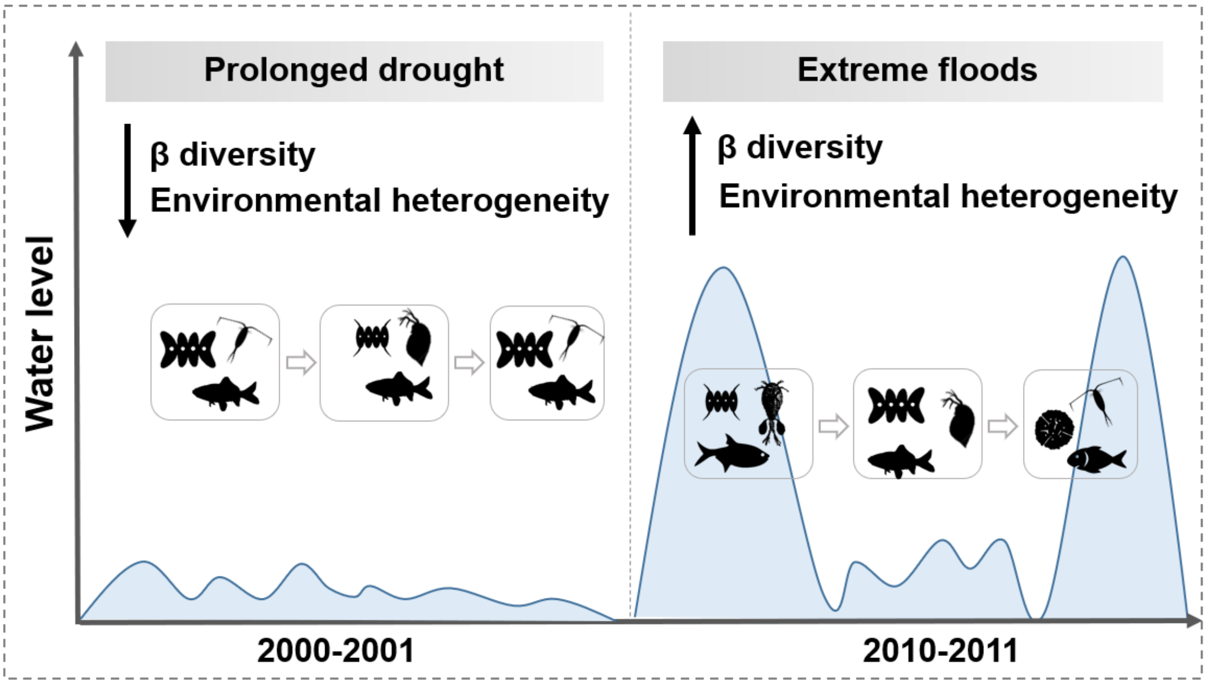

Fig. 1. Conceptual model illustrating our hypotheses comparing the environmental heterogeneity and β diversity of three aquatic metacommunities (phytoplankton, zooplankton and fish) in a period of prolonged drought (2000-2001) and another with extreme flood events (2010-2011) in a single habitat.

4.2 Methods

4.2.1 Study area

We studied shallow lakes in the Upper Paraná River Floodplain (22°40′-22°50′S and 53°10′-53°40′W), located between the states of Paraná and Mato Grosso do Sul, Brazil (Fig. 2). The hydrological regime of this floodplain is regulated by 26 large dams upstream, suffering an even stronger impact from the Porto Primavera dam, which is located only 30 km upstream (Agostinho et al. 2009). Due to regulation by dams, this basin stretch suffers directly from variations in the river level and has been going through an oligotrophization process, as a result of nutrients and sediments retention upstream, increasing transparency and reducing phosphorus in water over time, leading to a reduction in ecosystem services, such as fishing (Agostinho et al. 2009; Roberto et al. 2009; Braz et al. 2020). Even so, this floodplain is a highly dynamic system that supports high biodiversity, attributed mainly to its high spatial and temporal variability (Junk et al. 1989; Agostinho et al. 2004b; Lansac-Tôha et al. 2009; Bonecker et al. 2020).

The 10 shallow lakes studied are associated with the Paraná sub-basin of the Upper Paraná River Floodplain (Fig. 2). In the period of prolonged drought (2000-2001), the depth of the lakes varied from 0.6 to 3.5 m, while in the period with extreme flood events (2010-2011), the depth varied from 1.5 to 4.3 m (see Table S1 in Appendix C). The flood period begins, usually from October to March, when the river reaches a value above 3.5 m (Thomaz et al. 2004; Souza Filho 2009; Moi et al. 2020). The monitoring of our study, carried out for four years, comes from Long-Term Ecological Research in Upper Paraná River Floodplain, Brazil (LTER, site 6 [http://www.peld.uem.br/]).

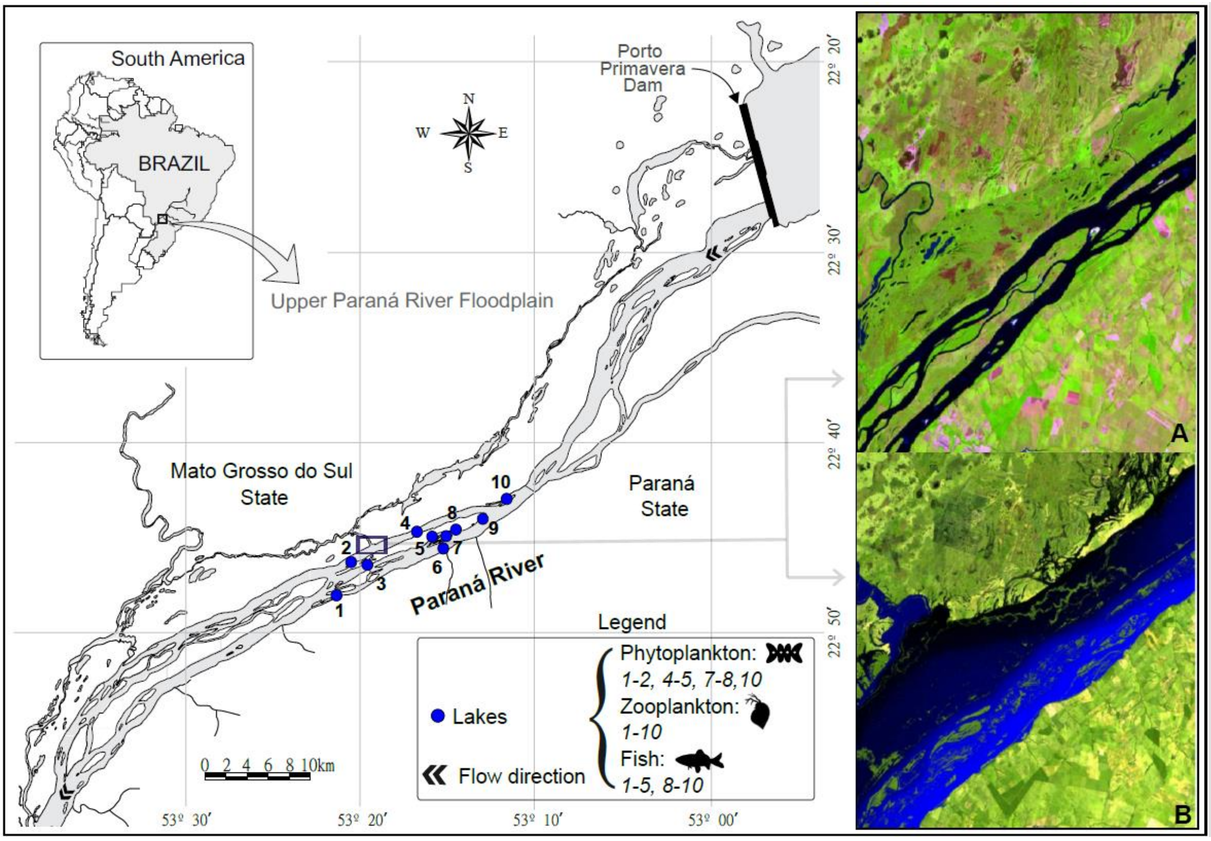

Fig. 2. Study area showing the location of the 10 lakes studied in the Upper Paraná River Floodplain, Brazil. A - drought period (photo taken in October 1996) and B - flood period in the floodplain (photo taken in January 1990). Photos: TM Landsat RGB 345 (Rocha 2010). The numbers in the legend represent the lakes studied for each biological group: 1 - Pombas; 2 - Manezinho; 3 - Osmar; 4 - Bilé; 5 - Leopoldo; 6 - Genipapo; 7 - Clara; 8 - Pau Véio; 9 - Pousada; 10 – Garças.

4.2.2 Sampling and analysis in the laboratory

We compared two distinct hydrological periods: a period of prolonged drought (2000-2001), marked by the climatic event *La Niña*, and a period with extreme floods (2010 and 2011), when above-average rainfall occurs due to *El Niño* (Borges and Train 2009; Moi et al. 2020)

(Fig. 3). The sampling was carried out quarterly during the four years, totaling 16 sampling occasions (eight in each period).

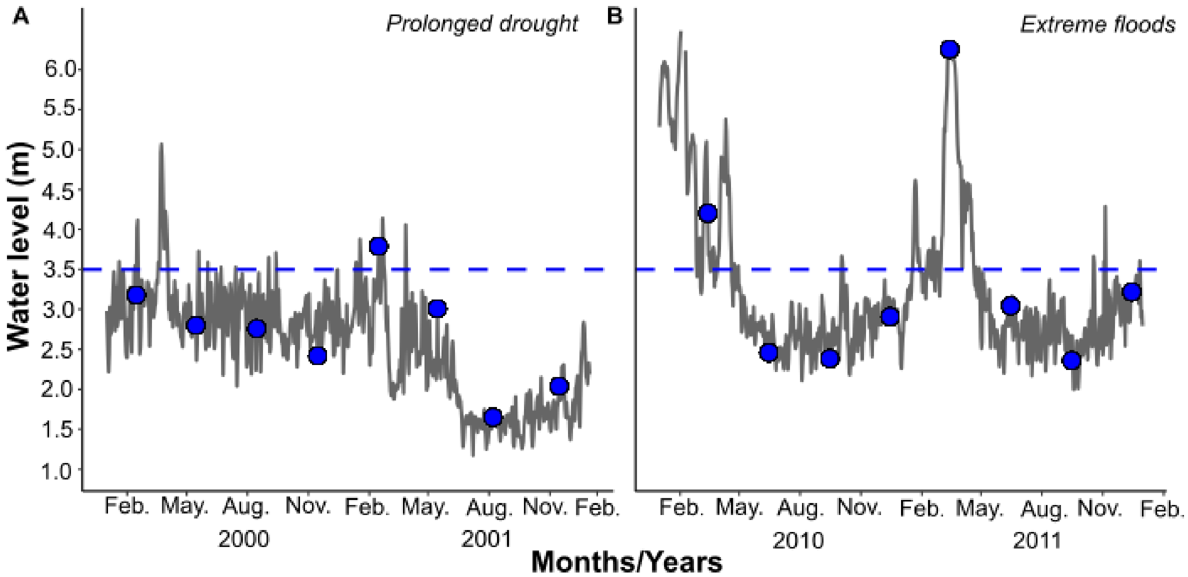

Fig. 3. Variation in water level during the period of prolonged drought (2000-2001) and the period with extreme floods (2010-2011). The blue circles indicate each sampling. The blue line represents the reference value for the overflow and the beginning of the flood in the floodplain. The water level was obtained using a meter at the Nupelia field station (Núcleo de Pesquisa em Limnologia, Ictiologia e Aquicultura), on the left bank of the Paraná river, Brazil.

Each lake was characterized through the following variables: depth (m; portable depth sounder), water temperature (°C; YSI digital portable), pH (digimed digital potentiometer), turbidity (NTU; portable turbidimeter), dissolved oxygen (mg L^{-1}; YSI digital portable), electric conductivity (μS cm^{-1}; digimed digital potentiometer), phosphate (μg L^{-1}; Golterman et al. 1978), and nitrate (μg L^{-1}; Giné et al. 1980). All variables were collected on the sub-surface of each lake, concomitantly to biological groups samplings (phytoplankton, zooplankton and fish).

For the phytoplankton, the samplings were carried out in seven lakes. For the zooplankton, sampling was performed in 10 lakes and for fish, sampling was performed in eight lakes (Table S1 in Appendix C) (Fig. 2). This difference in the number of lakes sampled was due to field problems for phytoplankton and fish. However, as we intended to verify the β diversity pattern for each group separately, this difference in the number of lakes sampled did not strongly interfere with our analyzes.

Phytoplankton and zooplankton were collected in the pelagic region during the day from a single sampling point. Phytoplankton samples were obtained on the sub-surface of each lake directly taken using bottles and preserved with 1% acetic Lugol. Also, additional samples were taken using a 15 µm net, and preserved with *Transeau* solution, to assist in the phytoplankton identification stage. Zooplankton samples were obtained from the sub-surface of each lake, with the aid of a motor-pump and a 68 µm plankton net, being filtered 600 L of water per sample. Samples were preserved with 4% formaldehyde. As for fish, for most lakes, they were collected through trawls. Only for two lakes, slightly deeper, gillnets were employed during the study period. Collection methods can interfere with the interpretation of ichthyofauna data (Oliveira et al. 2014), however, in our study, we estimated β diversity separately for each lake. So, we believe this does not interfere with the interpretation of our results. The trawls were 20 m (20 m × 1.5 m), and the standardized effort of three drags per lake was established. In the two deepest lakes, fish was sampled through gillnets of different mesh sizes (4, 5, 6, 7, 8, 10, 12, 14, and 16 cm between opposite knots). The net was implemented for 24 hours in each lake, removing the fish every 8 hours. Fishes were anesthetized with 5% benzocaine, euthanized and fixed in 10% formalin. Fish collection, following this methodology, was approved by the Ethic Committee on Animal Use of the State University of Maringá (CEUA/UEM) and by the National Council for Control of Animal Experimentation (CONCEA - #1420221018$_{\text{(ID 001974)}}$).

In the laboratory, the phytoplankton was identified using an inverted microscope following the Utermöhl (1958) method and specialized literature (Bicudo and Menezes 2006). Counting was carried randomly per field until the stabilization of the increment of individuals. Zooplankton were counted under an optical microscope and identified using specialized bibliography (Koste 1978; Reid 1985; Matsumura-Tundisi 1986; Segers 1995; Elmoor-Loureiro 1997). For each sample, quantification was performed by subsampling, in Sedgwick-Rafter chambers and with Hensen-Stempell pipette, with at least 10% of each quantified (Bottrell et al. 1976). The fish were identified based on specialized literature (Graça and Pavanelli 2007; Ota et al. 2018) and quantified in their entirety. In addition to measuring the total weight of each fish.

4.2.3 Data analysis

To test the hypothesis that during the prolonged drought period we find lower environmental heterogeneity (hypothesis i) and lower β diversity over time (hypothesis ii), we measure environmental heterogeneity and β diversity separately for each lake, among the samplings of period of prolonged drought (2000-2001) and period with extreme flood events

(2010-2011). β diversity was also calculated separately for each biological group (phytoplankton, zooplankton, and fish). We designed our analysis in this way because we intended to investigate environmental heterogeneity and β diversity in a single site over time (i.e., among sampling occasions), and not the β diversity among sites as usually is done (see more details in Fig. 4).

In addition to temporary ones, three lakses dried up completely in the period of prolonged drought (2000-2001). Therefore, for some lakes the number of samples in each period was not the same: we had six sampling occasions during the period of prolonged drought and eight during the period with extreme flood events (see in Table S1 the name of the lakes and the biological group that this occurred). However, in these cases, in addition to carrying out the analyzes with this uneven number, we performed a standardization by removing the corresponding samplings during the flood period. Even so, the result did not differ (see Fig. S1 in Appendix C).

Environmental heterogeneity and β diversity, for each lake in each period (i.e., prolonged drought and period with extreme floods), were obtained through the permutational analysis of multivariate dispersions (PERMDISP, “betadisper” function; Anderson et al. 2006). This test is based on the average dissimilarity of each sample unit to the centroid of that group in the multivariate space, using an index of a distance matrix (Anderson et al. 2006). In this case, greater average distance to the centroid indicated greater heterogeneity or β diversity. We obtained environmental heterogeneity from Euclidean distances of environmental variables (depth, water temperature, pH, dissolved oxygen, electrical conductivity, turbidity, nitrate, and phosphate). All variables were standardized for z-scores. We calculated β diversity using Sørensen (incidence data) and Bray-Curtis (abundance data log-transformed) dissimilarities separately for phytoplankton, zooplankton, and fish. The approach followed to calculate β diversity was to Podani and Schmera (2011) and Carvalho et al. (2012), where total *β* diversity (Btotal) is partitioned into the replacement (Brepl) and richness difference (Brich) components. In our case, as we were interested in analyzing the total variation of β diversity, we used only the “Btotal” dissimilarity matrix. For each lake over the years, these analyzes generated two values of environmental heterogeneity and β diversity, one corresponding to the period of prolonged drought (2000-2001) and the other corresponding to the period with extreme flood events (2010-2011) (Fig. 4).

After calculating environmental heterogeneity and β diversity for each lake, period and biological group, we used a paired t-test to verify if environmental heterogeneity and β diversity differed significantly between the period of prolonged drought and the period with extreme floods (Fig. 4). The pair was the period of prolonged drought and period with flood periods from each lake. We chose this test because it is appropriate for comparing averages between groups of related samples, as was our case.

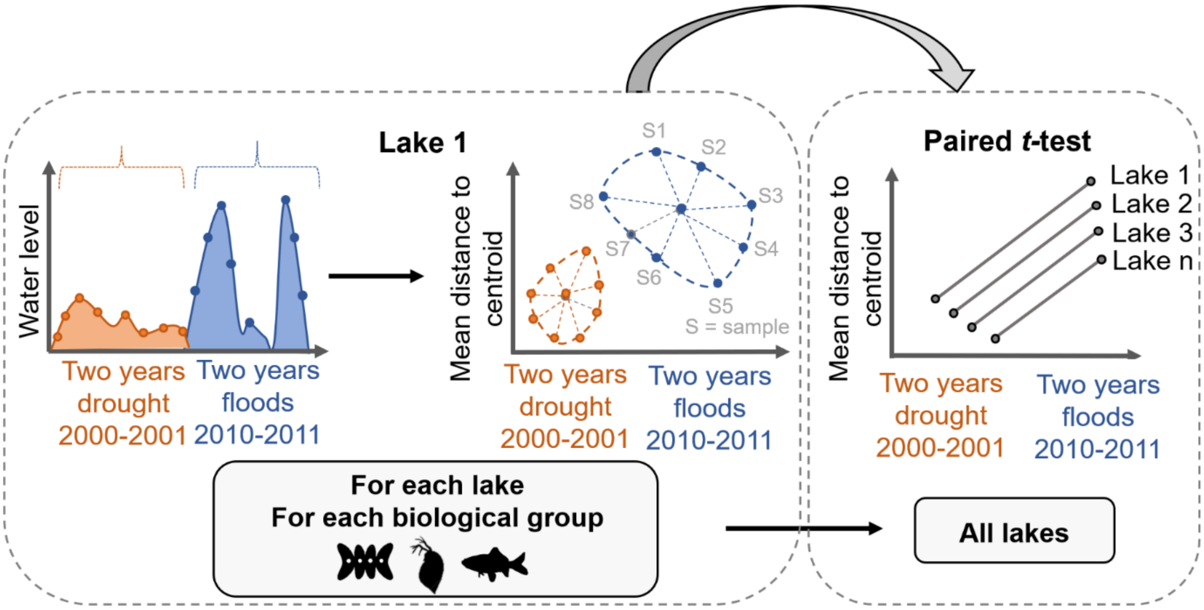

Fig. 4. Steps to calculate environmental heterogeneity and β diversity considering the two different periods and biological groups. Two years drought: prolonged drought period (2000-2001); Two years floods: period with extreme flood events (2010-2011).

All analyses were performed in R (R Core Team 2019), using the following packages: *vegan* (Oksanen et al. 2019), *BAT* (Cardoso et al. 2018), *and ggplot2* (Wickham 2016).

4.3 Results

According to our expectations, environmental heterogeneity was lower during the period of prolonged drought (2000-2001; mean distance to centroid = 2.08) compared to the period of extreme flooding (2010-2011; mean distance to centroid = 2.42) ($t_{(1,9)}$ = -2.87; p = 0.018) (Fig. 5).

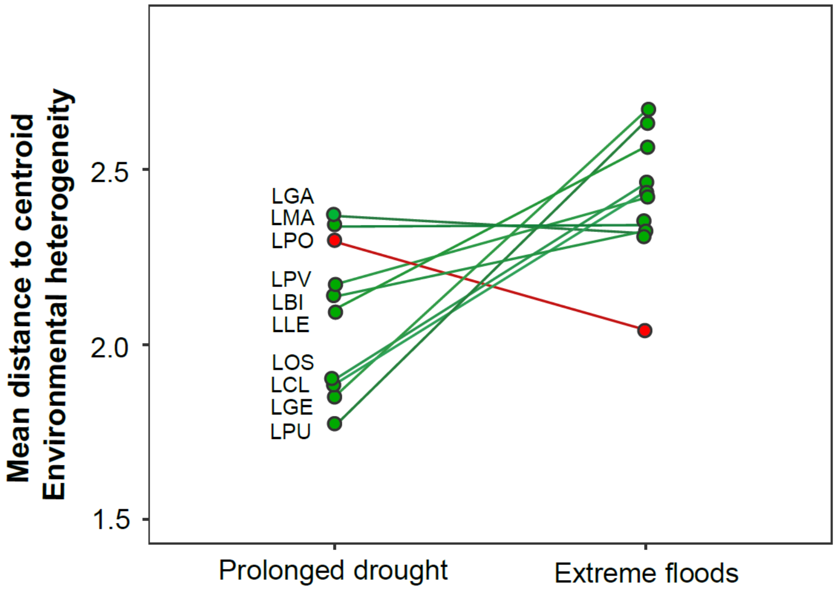

Fig. 5. Environmental heterogeneity represented by the mean distance to the centroid calculated among sampling occasions considering the period of prolonged drought (2000-2001) and the period with extreme flood events (2010-2011) in the Upper Paraná River floodplain, Brazil. Each line represents a different lake. In green, the lakes showed lower heterogeneity in the prolonged drought period (as expected), and in red, those that showed the opposite pattern. LGA – Garças; LMA – Manezinho; LPO – Pombas; LPV – Pau Véio; LBI – Bilé; LLE – Leopoldo; LOS – Osmar; LCL – Clara; LGE – Genipapo; LPU – Pousada.

We recorded 348 phytoplankton species, 287 zooplankton species, and 96 fish species (Table S2, S3, and S4, respectively). Contrarily to expected, using Sørensen dissimilarity, the β diversity did not differ between the prolonged drought period (mean distance to centroid = 0.44) and period of extreme flooding for phytoplankton (mean distance to centroid = 0.46) ($t_{(1,6)}$ = -0.70; p = 0.51; Fig. 6A). The β diversity of fish also did not differ between the prolonged drought period (mean distance to centroid = 0.35) and the period of extreme flooding (mean distance to centroid = 0.39) ($t_{(1,7)}$ = -1.85; p = 0.12; Fig. 6C). Only the zooplankton showed lower β diversity in the prolonged drought period (mean distance to centroid = 0.39) than in the period of extreme flooding (mean distance to centroid = 0.43) ($t_{(1,9)}$ = -2.57; p = 0.03; Fig. 6B). We found the same pattern using Bray-Curtis dissimilarity (see Fig. S2 in Appendix C).

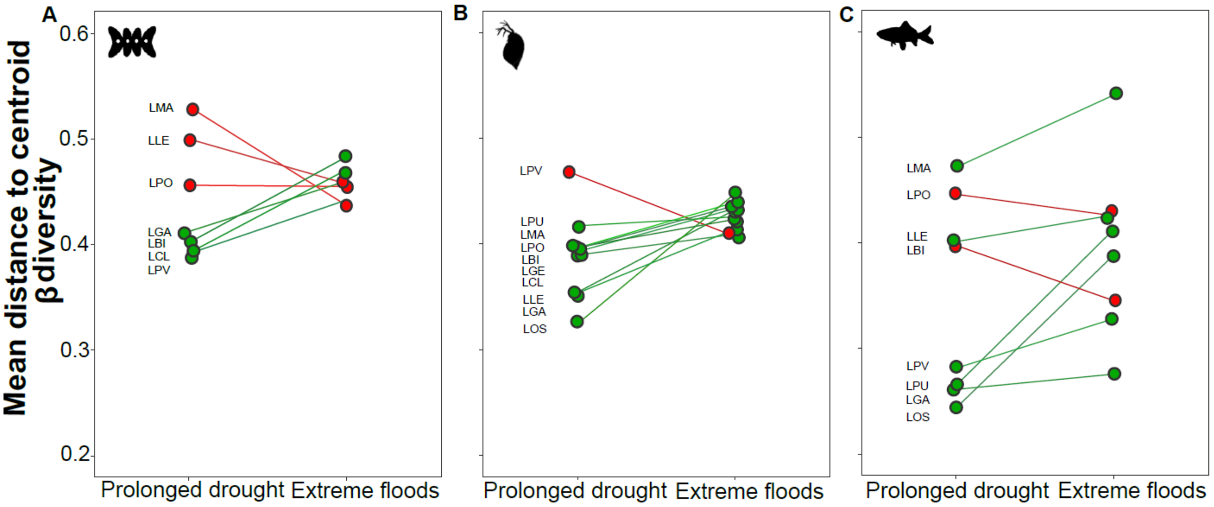

Fig. 6. β diversity (mean distance to the centroid) considering the period of prolonged drought (2000-2001) and the period with extreme flood events (2010-2011) in the Upper Paraná River floodplain, Brazil. A - phytoplankton; B - zooplankton; C - fish. Each line represents a different lake. In green, the lakes showed lower β diversity in the prolonged drought period (as expected), and in red, those lakes that showed the opposite pattern. LGA – Garças; LMA – Manezinho; LPO – Pombas; LPV – Pau Véio; LBI – Bilé; LLE – Leopoldo; LOS – Osmar; LCL – Clara; LGE – Genipapo; LPU – Pousada.

4.4 Discussion

We corroborate our hypothesis that prolonged drought (2000-2001) showed less environmental heterogeneity than the period with extreme floods (2010-2011). Given the forecast of an increase in extreme events occurrence and drought years in some regions of the world (Milly et al. 2005), this result is worrisome and it reinforces the importance of maintaining the natural dynamics of the flood pulse to maintain environmental heterogeneity in floodplains. Although that, only the zooplankton had reduced β diversity during this prolonged drought period. The β diversity of phytoplankton and fish did not change between different hydrological periods, indicating, possibly, the high persistence of these biological groups in the face of different and extreme hydrological conditions over time.

The prolonged drought period reduced the environmental heterogeneity because, in addition to the extreme climatic event *La Niña*, this stretch of the Paraná river basin suffers the effects of hydrological regulation by the upstream reservoirs. After the construction of the Porto Primavera dam in 1998, the frequency and intensity of flood events were changed, causing negative consequences for aquatic biota in the Upper Paraná River floodplain (Agostinho et al. 2008; Oliveira et al. 2018; Braghin et al. 2018). In fact, dams control the flood pulses attributes, such as their amplitude and duration, extending the drought period (Agostinho et al. 2008, 2016; Moi et al. 2020). This interference of dams on the seasonality of aquatic ecosystems becomes even more worrying with the forecast of an increase in the building of hydroelectric in large Brazilian rivers and globally (Zarfl et al. 2015), besides the global warming effects. Thus, although floodplain ecosystems are highly dynamic, the increased frequency of extreme droughts can alter the stability of the ecosystem and impair its resilience (Scheffer et al. 2001).

Each flood event acts as a system reset and can increase environmental and biological heterogeneity over time. In addition, the flood pulse is part of the natural dynamics of the floodplains and acts in the maintenance of ecological processes and biodiversity (Junk et al. 1989; Neiff 1990; Petsch 2016). Some previous studies have found a pattern contrary to ours, showing that the flood events are homogenizing environmental conditions (Thomaz et al. 2007; Padial et al. 2009; Bozelli et al. 2015). However, most of the studies investigated a different question, i.e., if flood pulse increases similarity among sites, typically performing a sampling during the drought and another sampling during flood periods across many sites (Mayora et al. 2020). Our study was designed to estimate the environmental heterogeneity and β diversity over time (i.e., among months), separately for each lake and period. As far as we know, this study was one of the first to test the effect of a prolonged drought period in β diversity estimated among sampling occasions (and not among sites) for different biological groups. In this way, our findings, along with other studies, indicate that flood periods can decrease environmental heterogeneity across sites in a snapshot (Thomaz et al. 2007; Bozelli et al. 2015; Diniz et al., 2021), but increase environmental heterogeneity over time in a single habitat (our findings). Also, it is important to highlight that the period of extreme flood events (2010-2011) was also marked by drought events. Thus, a period with drought and flood events tends to show greater environmental heterogeneity than one without floods. Furthermore, a larger time scale allowed us to capture the alternating phases of the lowland dynamics, which generate different environmental gradients, driving environmental heterogeneity over time.

A drought period can increase diversity over time (Aspin et al. 2018), since habitats are isolated from each other, limiting the dispersal of many organisms and, with this, increasing dissimilarity among sites (Simões et al. 2013b; Campos et al. 2019). However, in these cases the β diversity is calculated between the lakes and not in each lake alone over time, as in our case. In addition, when the drought is prolonged, an opposite effect can occur. Therefore, we expected the biotic homogenization for the three biological groups during the prolonged droughts, as extreme drought conditions make the floodplains more fragmented and can reduce biodiversity (Simões et al. 2012; Bortolini et al. 2016), but only zooplankton showed a reduction in the β diversity in this period. The prolonged drought period may drive the production of dormancy forms in zooplankton, since in the face of unfavorable environmental conditions, this group invests in the production of resting eggs (Figuerola and Green 2002; Morais-Junior et al. 2019a). In this case, the stress caused by the prolonged drought period may drive the production of resistance eggs, increasing the species richness in the sediment but homogenizing the active community in that period (Golec-Fialek et al. 2021). We believe that the highest diversity in the period with extreme floods is related to the hatching of the resistance eggs that had been insisted during the prolonged drought. The environmental filter during the drought may have selected only the zooplankton species that have a high production of resistance eggs, decreasing the β diversity (Lopes et al. 2014). In addition, when the drought is extreme, it is common to have a proliferation of cyanobacteria that negatively affect many zooplankton species (Bouvy et al. 2001; Chaparro et al. 2011), which may favor the homogenization of zooplankton in the years of prolonged drought.

Since the flood pulses that transport different species or propagules (Bortolini et al. 2016), allowing the change of fauna between different environments (lakes and rivers) we expected that the three biological groups would show greater β diversity in the period with extreme floods. However, despite extreme floods increasing dispersion, they also intensify environmental filters (Simões et al. 2013a). Thus, when an organism arrives at a particular site, the environmental filter of that location or even the biotic interactions (such as competition) will act by selecting only those species that manage to survive under those conditions (Bonecker et al. 2009; Cadotte and Tucker 2017). Perhaps the environmental filters favored zooplankton in the period with extreme flood events than the other biological groups studied. Simões et al. (2013a) had already observed that the driving force of the flooding of the Upper Paraná River is determinant for zooplankton β diversity due to its effect on environmental filters. In addition, this period showed the most remarkable environmental heterogeneity, which may have driven the greater diversity of zooplankton. Since more heterogeneous environments allow the occupation of different niches, tending to increase β diversity (Maloufi et al. 2016). We also believe that the greatest diversity in the years with extreme flood events resulted from the mixture of zooplankton from the littoral and pelagic regions in the lakes, contributing to high β diversity (Petsch et al. 2021). The littoral region is known to support a greater diversity of species than the pelagic region (Diniz et al. 2013; Choi et al. 2014; Cabral et al. 2020; Deosti et al. 2021). Although all of the samples in our study were carried out in the pelagic region, the studied lakes are shallow and sometimes the macrophyte banks can significantly influence the pelagic organisms, increasing the β diversity of zooplankton in this region (Braghin et al. 2016).

Phytoplankton did not undergo biotic homogenization with the prolonged drought period, even Bortolini et al. (2016) having already found that the prolonged drought period negatively affected the species richness of this group in the sub-basin of the Baía, in the studied floodplain. Metacommunity distribution patterns can be stochastic due to random colonization and extinction events (Hubbell 2001). In addition, in highly dynamic ecosystems, such as a floodplain, stochasticity events become even more commonly associated with temporal instability, hydrological cycles and high water flow (Rodrigues et al. 2018). For phytoplankton, determining diversity patterns can be difficult since their distribution is influenced by the dispersion stochasticity (Nabout et al. 2009; Rodrigues et al. 2018; Lansac-Tôha et al. 2019). As the β diversity did not differ between the different hydrological periods, we believe that the stochasticity in the dispersion can explain the similar β diversity between two such different hydrological periods. In addition, phytoplankton have passive dispersion and can be transported by the wind. For this reason, the flood effect for this group may not be so intense, and, thus, justify the absence of difference between the periods (Chrisostomou et al. 2009). Finally, we cannot exclude that phytoplankton has a short life cycle and, therefore, its predictability becomes more robust in time scales of days or hours than years, for example.

As the fish have active dispersion, we expected that years with prolonged drought should homogenize, mainly, this biological group (Padial et al. 2014). However, the β diversity of the fish did not differ between periods, suggesting species resistance of this biological group that has been replaced similarly, even in the face of different hydrological periods. In addition, this result may be related to the fact that of the 96 species of fish that we recorded in our study, 83.3% had a sedentary habit, and only 16.7% were truly migratory (see Table S4 in Appendix C). Sedentary fish with parental care depends less on flood events than migratory species. In fact, migratory species spawn in headwaters rivers, above the floodplain and use the flooded areas as nurseries (Agostinho et al. 2004a). This predominance of sedentary species, over four years of study, may justify the similar β diversity between different hydrological periods. The vast majority of freshwater fish can deal with the effects of extreme droughts (Lennox et al. 2019) since they have evolved in highly unstable environments and are already adapted to this (Douglas et al. 2003; Abrial et al. 2019). In addition, we recorded 10 species belonging to the Cichlid family in our study (Table S4 in Appendix C). Lourenço et al. (2012) observed that cichlid fish exhibit high persistence and temporal stability in floodplain lakes, having a balance point at the beginning of the drought and another at the beginning of the flood.

With climate change and rising global temperatures, extreme climatic events may become even more constant (Milly et al. 2005; Jeppesen et al. 2014). This prediction is worrisome, especially for zooplankton that can undergo taxonomic homogenization, as observed in this study, or even functional homogenization in the face of extreme droughts (Bomfim et al. 2021). Although phytoplankton and fish did not show a distinguished response between different hydrological periods, the homogenization of zooplankton can have consequences for all aquatic biota. This is because removing a single trophic group or its simplification can compromise the multifunctionality of the entire ecosystem (Moi et al. 2021). Also, the homogenization of the dynamics of rivers regulated by dams is a global trend (Poff et al. 2007). With the predicted construction of more dams and global warming, a series of negative impacts for these biological groups are also likely (Granzotti et al. 2018; Oliveira et al. 2018; Pineda et al. 2020). Thus, in addition to the damage to biodiversity itself, biotic homogenization will also have consequences for ecosystem services provided to human beings (Olden et al. 2005; Naeem et al. 2012). The high β diversity found during droughts and floods reinforces, at least for zooplankton, the crucial role of flood pulses and the temporal heterogeneity induced by extreme rains, reducing the negative effects of anthropic action on the floodplain. Based on this, we emphasize that conservation and management of biological biodiversity in floodplains must seek the maintenance of the multifunctionality of these systems, avoiding new dams or minimizing their impacts, and threfore prolonged droughts and environmental heterogeneity reduction.

We conclude that the prolonged drought period have less environmental heterogeneity than periods with extreme floods, while years with regular or even extreme flood pulses increase the temporal heterogeneity of the floodplain lakes. Even so, only zooplankton underwent biotic homogenization in the face of prolonged drought. The floodplain is an ecosystem that has temporal instability, but its biota, especially phytoplankton and fish, seems to be highly resistant to its hydrological dynamics. In addition to showing the distinct dispersion capacity between the biological groups, it did not interfere in the potentiation of homogenization. As the response between the biological groups was different, we reinforce the same thinking of others surveyed that the groups are not surrogates of each other and, therefore, the ecological patterns registered for one group cannot be extrapolated to the rest of the ecosystem (Morais et al. 2018; Landeiro et al. 2018; Lansac-Tôha et al. 2019). Not even within for planktonic organisms, since the responses of phytoplankton and zooplankton were different. Finally, we emphasize that in this study we evaluate only the taxonomic aspects of diversity. The interesting point is that future studies consider the functional or even phylogenetic characteristics of aquatic metacommunities in the face of different hydrological periods to maximize the understanding of ecological patterns.

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APPENDIX C - Details of the study area, list of phytoplankton, zooplankton and fish species, and details of some results.

Table S1 Geographic coordinates, connectivity, mean depth per period (prolonged drought and extreme floods) and the biological group studied in each lake in Paraná sub-basin of the Upper Paraná River floodplain, Brazil. P - phytoplankton, Z – zooplankton, and F – fish. *Temporary lakes that came to dry completely for a few moments in the period of prolonged drought.

Lakes	**Coordinates**	**Connectivity**	**Depth drought**	**Depth floods**	**Biological group**
Ressaco do Pau Véio	22°44'50.76"S; 53°15'11.16"W	Connected	2.2	4.3	P,Z,F
Garças	22°43'27.18"S; 53°13' 4.56"W	Connected	1.5	2.1	P,Z,F
Pombas	22°47'55.92"S; 53°21'32.58"W	Connected	1.5	1.5	P, Z,F
Ressaco do Manezinho	22°46'44.7"S; 53°20'56.76"W	Connected	2.9	4.3	P, Z,F
Ressaco do Bilé	22°45'13.56"S; 53°17' 9.48"W	Connected	1.9	3.1	P,Z,F
Ressaco do Leopoldo	22°45" 24"S; 53°16' 7.98"W	Connected	3.5	4.0	P,Z,F
Osmar*	22°46'26.64"S; 53°19'56.16"	Isolated	1.1	2.4	Z,F
Clara*	22°45’17.52”S; 53°15’28.62”W	Isolated	1.1	1.8	P,Z
Genipapo	22°45'33.24”S; 53°16' 5.94"W	Isolated	1.3	1.8	Z
Pousada*	22°44'41.76"S; 53°14' 7.32"W	Isolated	0.6	3.9	Z,F

Table S2 List of phytoplankton species recorded between the periods of prolonged drought (2000-2001) and extreme floods (2010-2011) of the 7 lakes studied in Paraná sub-basin of the Upper Paraná River floodplain, Brazil.

	Period	
Taxa	**Prolonged drought**	**Extreme floods**
Class Bacillariophyceae		
Order Bacillariales		
Family Bacillariaceae		
Nitzschia gracilis Hantzsch 1860	x	
Nitzschia palea (Kützing) W.Smith 1856	x	
Nitzschia sigmoidea (Nitzsch) W.Smith 1853	x	x
Nitzschia sp.		x
Nitzschia sp.1	x	x
Nitzschia tubicola Grunow 1880		x
Order Cocconeidales		
Family Achnanthidiaceae		
Achnanthidium minutissimum (Kützing) Czarnecki 1994		x
Order Cymbellales		
Family Cocconeidaceae		
Cocconeis sp.	x	
Family Cymbellaceae		
Cymbella microcephala Grunow 1885		x
Cymbella tumida (Brébisson) Van Heurck 1880	x	x
Family Gomphonemataceae		
Encyonema sp.		x
Gomphonema augur Ehrenberg 1841	x	
Gomphonema brasiliense Grunow 1878		x
Gomphonema gracile Ehrenberg 1838		x
Gomphonema olivaceum (Hornemann) Ehrenberg 1838	x	x
Gomphonema sp.	x	x
Gomphonema truncatum Ehrenberg 1832	x	x
Order Fragilariales		
Family Fragilariaceae		
Fragilaria aquaplus Lange-Bertalot & S.Ulrich 2014	x	x
Fragilaria crotonensis Kitton 1869		x
Fragilaria longifusiformis (Hains & Sebring) Siver et al.		x
Fragilaria sp.		x
Synedra sp.		x
Order Licmophorales		
Family Ulnariaceae		
Ulnaria ulna (Nitzsch) Compère 2001	x	
Order Naviculales		
Family Amphipleuraceae		
Amphipleura lindheimeri Grunow 1862	x	x
Amphipleura sp.		x
Craticula sp.		x
Frustulia sp.		x
Family Naviculaceae		
Navicula sp.1	x	x
Navicula sp.2	x	
Family Pinnulariaceae		

Taxa	Period Prolonged drought	 Extreme floods
Pinnularia graciloides Hustedt 1937		x
Pinnularia sp.1	x	x
Pinnularia sp.2	x	
Order Surirellales		
Family Surirellaceae		
Surirella tenera W.Gregory 1856	x	x
Order Eunotiales		
Family Catenulaceae		
Anomoeoneis sp	x	x
Order Eunotiales		
Family Eunotiaceae		
Eunotia sp.	x	x
Class Chlorophyceae		
Family Chlorococcales		
Tetranephis sp.	x	
Order Sphaeropleales		
Family Sphaeropleales incertae sedis		
Polyedriopsis spinulosa (Schmidle) Schmidle 1899		x
Family Scenedesmaceae		
Acutodesmus acuminatus (Lagerheim) P.M.Tsarenko 2000	x	
Coelastrum indicum W.B.Turner 1892		x
Coelastrum pseudomicroporum Korshikov 1953	x	
Coelastrum pulchrum Schmidle 1892	x	x
Coenochloris mucolamellata A.Comas 1953	x	
Coenochloris planoconvexa Hindák 1977	x	x
Coenochloris sp.		x
Desmodesmus armatus var. bicaudatus (Guglielmetti) E.H.Hegewald 200	x	x
Desmodesmus brasiliensis (Bohlin) E.Hegewald 2000	x	x
Desmodesmus cf. lefevrei (Deflandre) S.S.An, T.Friedl & E.H.Hegewald 1924	x	x
Desmodesmus communis (Hegew.) Hegew 2000	x	
Desmodesmus denticulatus var. denticulatus (Lag.) Am., Friedl e Hegew 1999		x
Desmodesmus denticulatus var. *linearis* (Hansg.) Hegew 2000		x
Desmodesmus opoliensis (P.G.Richter) E.Hegewald 2000	x	
Desmodesmus perforatus(Lemmerm.) E. Hegew 2000	x	x
Desmodesmus protuberans (F.E.Fritsch & M.F.Rich) E. Hegewald 2000		x
Desmodesmus serratus (Corda) S.S.An, Friedl & E. Hegew 1999	x	
Desmodesmus spinosus (Chodat) E.Hegewald 2000	x	x
Scenedesmus acunae Comas Gonzáles 1980	x	
Scenedesmus ecornis (Ehrenberg) Chodat 1926	x	
Scenedesmus ecornis var. *polymorphus* Chodat 1926	x	x
Scenedesmus indicus Philipose ex Hegewald, Engelberg & Paschma 1988	x	
Scenedesmus linearis Komárek 1974	x	
Scenedesmus microspina Chodat 1926		x
Scenedesmus obliquus (Turpin) Kützing 1833	x	
Scenedesmus ovalternus Brébisson, nom. ined. 1855	x	x

	Period	
Taxa	**Prolonged drought**	**Extreme floods**
Scenedesmus sp.1		x
Scenedesmus sp.2	x	x
Scenedesmus verrucosus Y.V.Roll 1925	x	
Tetrastrum heteracanthum (Nordstedt) Chodat 1895		x
Tetrastrum homoiacanthum (Huber-Pestalozzi*)* Hindák 1984	x	x
Thorakochloris nygardii Komarek 1979		x
Willea komarekii Comas Gonzáles 1984	x	x
Family Schroederiaceae		x
Schroederia setigera (Schröder) Lemmermann 1898	x	
Schroederia sp.	x	x
Schroederia spiralis (Printz) Korshikov 1953	x	
Order Chlamydomonadales		
Family Chlamydomonadaceae		
Chlamydomonas sp.		x
Chlamydomonas sp.1	x	x
Chloromonas sp.	x	x
Family Goniaceae		
Gonium pectorale O.F.Müller 1773		x
Gonium sp.		x
Family Sphaerocystidaceae		
Sphaerellopsis sp.		x
Family Spondylomoraceae		
Pyrobotrys sp.	x	
Family Volvocaceae		
Eudorina sp.	x	x
Pandorina morum (O.F.Müller) Bory 1826		x
Pandorina sp.	x	x
Volvox aureus Ehrenberg 1832		x
Family Tetrabaenaceae		
Basichlamys sp.	x	
Order Sphaeropleales		
Family Cylindrocapsaceae		
Fusola viridis J.W.Snow 1903	x	
Family Hydrodictyaceae		
Pediastrum simplex var. *simplex* Mey 1829	x	x
Pediastrum duplex Meyen 1829	x	
Pediastrum duplex var. *subgranulatum* Raciborski 1889	x	x
Monoraphidium arcuatum (Korshikov) Hindák 1970	x	x
Monoraphidium caribeum Hindák 1970	x	x
Monoraphidium circinale (Nygaard) Nygaard 1979	x	
Monoraphidium contortum (Thuret) Komárková-Legnerová 1969	x	
Monoraphidium convolutum (Corda) Komárková-Legnerová 1969	x	x
Monoraphidium irregulare (G.M.Smith) Komárková-Legnerová 1969	x	x
Monoraphidium komarkovae Nygaard 1979	x	
Monoraphidium minutum (Nägeli) Komárková-Legnerová 1969	x	x

Taxa	Period Prolonged drought	 Extreme floods
Monoraphidium pusillum (Printz) Komárková-Legnorová 1969	x	x
Monoraphidium sp.	x	
Monoraphidium tortile (West & G.S.West) Komárková-Legnerová 1969	x	x
Tetraëdron regulare Kützing 1845	x	x
Tetraëdron sp.	x	
Family Neochloridaceae		
Neochloris sp.	x	x
Golenkinia radiata Chodat 1894	x	
Family Radiococcaceae		
Eutetramorus sp.	x	x
Hindakochloris insularis A.Comas 1992	x	x
Family Scenedesmaceae		
Asterarcys quadricellularis (K.Behre) E.Hegewald & A.W.F.Schmidt 1992		x
Family Selenastraceae		
Ankistrodesmus bernardii Komárek 1983	x	x
Ankistrodesmus fusiformss Corda 1838	x	
Ankistrodesmus gracilis (Reins.) Kors.1953	x	
Ankistrodesmus sp.	x	x
Ankyra judayi (G.W. Sm.) Fott 1986	x	
Ankyra ocellata (Kors.) Fott 1957	x	x
Ankyra sp.	x	
Kirchneriella contorta (Schmidle) Bohlin 1893	x	
Kirchneriella contorta var. *elongata* (G. M. Sm.) Kom. 1897	x	
Kirchneriella irregularis (G. M. Schm.) Kors. 1953	x	x
Kirchneriella obesa (West) West & G.S.West 1894	x	
Class Chrysophyceae		
Chrysophyceae sp**.**	x	x
Order Chromulinales		
Family Dinobryaceae		
Dinobryon bavaricum Imhof 1890		x
Dinobryon divergens O.E.Imhof 1887	x	x
Dinobryon sertularia Ehrenberg 1834	x	x
Dinobryon sp.	x	x
Kephyrion littorale J.W.G.Lund 1942		x
Order Cryptomonadales		
Family Cryptomonadaceae		
Cryptomonas brasiliensis A.Castro, C.E.M.Bicudo & D.Bicudo 1992	x	x
Cryptomonas curvata Ehrenberg 1832	x	x
Cryptomonas marssonii Skuja 1948	x	x
Cryptomonas sp.	x	x
Cryptomonas sp1	x	x
Family Hemiselmidaceae	x	x
Chroomonas sp.	x	x
Class Coscinodiscophyceae		
Order Aulacoseirales		
Family Aulacoseiraceae		
Aulacoseira alpigena (Grunow) Krammer 1991		x

	Period	
Taxa	**Prolonged drought**	**Extreme floods**
Aulacoseira ambigua (Grunow) Simonsen 1979	x	
Aulacoseira ambigua var. *ambigua* f. *spiralis* Ludwig 1979	x	x
Aulacoseira distans (Ehrenberg) Simonsen 1979	x	x
Aulacoseira granulata var. *angustissima* (Otto Müller) Simonsen 1979	x	x
Aulacoseira granulata (Ehrenberg) *Simonsen var. granulata* 1979	x	
Aulacoseira granulata (Ehr.) Sim. var. *angustissima* (O. Mül.) Sim. f. curvata Grunow 1956	x	x
Aulacoseira herzogii (Lemmermann) Simonsen 1979	x	x
Aulacoseira muzzanensis (F.Meister) Krammer 1991	x	x
Aulacoseira sp.		x
Order Melosirales		
Family Melosiraceae		
Melosira sp.	x	x
Order Rhizosoleniales		
Family Rhizosoleniaceae		
Urosolenia eriensis (H.L.Smith) Round & R.M.Crawford 1990		x
Urosolenia longiseta (O.Zacharias) Edlund & Stoermer 1993		x
Urosolenia sp.		x
Class Cyanophyceae		
Order Chroococcales		
Family Aphanothecaceae		
Aphanothece cf. *minutissima* (West) J.Komárková-Legnerová & G.Cronberg 1994	x	
Family Chroococcaceae		
Chroococcus aphanocapsoides Skuja 1964	x	x
Chroococcus microscopicus Komárková-Legnerová & G.Cronberg 1994		x
Chroococcus minor (Kützing) Nägeli 1849		x
Chroococcus turgidus (Kützing*)* Nägeli 1849	x	
Family Microcystaceae		
Microcystis aeruginosa (Kützing) Kützing 1846	x	x
Microcystis novacekii (Komárek) Compère 1974	x	x
Microcystis sp.	x	
Microcystis wesenbergii (Komárek) Komárek ex Komárek 2006	x	x
Gloeocapsa fuscolutea Kirchner 1878	x	x
Gloeocapsa gelatinosa Kützing 1843		x
Family Gomphosphaeriaceae		
Gomphosphaeria natans Komárek & Hindák 1988		x
Order Nostocales		
Family Aphanizomenonaceae		
Cylindrospermopsis raciborskii (Woloszynska) Seenayya & Subba Raju 1972		x
Cylindrospermopsis sp.	x	
Dolichospermum circinale (Rabenhorst ex Bornet & Flahault) P.Wacklin, L.Hoffmann & J.Komárek 2009	x	
Dolichospermum planctonicum (Brunnthaler) Wacklin, L.Hoffmann & Komárek 2009	x	x

	Period	
Taxa	**Prolonged drought**	**Extreme floods**
Dolichospermum solitarium (Klebahn) Wacklin, L.Hoffmann & Komárek 2009	x	
Family Nostocaceae		
Anabaena ambigua C.B.Rao 1937	x	
Anabaena macrospora Klebahn 1895	x	
Aphanizomenon sp.	x	
Order Synechococcales		
Family Coelosphaeriaceae		
Snowella lacustris (Chodat) Komárek & Hindák 1988		x
Family Merismopediaceae		
Aphanocapsa elachista West & G.S.West 1894	x	x
Aphanocapsa holsatica (Lemmermann) G.Cronberg & Komárek 1994	x	
Aphanocapsa incerta (Lemmermann) G.Cronberg & Komárek 1994	x	X
Aphanocapsa parasitica (Kützing) Komárek & Anagnostidis 1995	x	x
Merismopedia sp.	x	x
Order Oscillatoriales		
Family Coleofasciculaceae		
Geitlerinema splendidum (Greville ex Gomont) Anagnostidis 1989	x	x
Family Microcoleaceae		
Planktothrix agardhii (Gomont) Anagnostidis & Komárek 1988	x	x
Planktothrix mougeotii Anagnostidis & Komárek 1988	x	x
Family Oscillatoriaceae		
Oscillatoria princeps Vaucher ex Gomont 1892		x
Phormidium sp.	x	
Family Pseudanabaenaceae		
Pseudanabaena limnetica (Lemmermann) Komárek 1974	x	
Pseudanabaena moniliformis Komárek & Kling 1991	x	x
Pseudanabaena mucicola (Naumann & Huber-Pestalozzi) Schwabe 1964	x	
Pseudanabaena sp.	x	x
Family Synechococcaceae		
Anathece minutissima (West) Komárek, Kastovsky & Jezberová 2011	x	
Cyanodictyon planctonicum Meyer 1994		x
Lemmermanniella flexa Hindák 1985		x
Rhabdogloea smithii (Chodat & F.Chodat) Komárek 1983	x	
Romeria sp.		x
Order Peridiniales		
Family Peridiniaceae		
Peridinium gatunense Nygaard 1925		x
Peridinium sp.1	x	x
Peridinium sp.2		x
Peridinium sp.3		x
Class Euglenophyceae		
Order Euglenida		
Family Euglenidae		
Euglena communis Gojdics 1953	x	x

Taxa	Period Prolonged drought	 Extreme floods
Euglena gibbosa J.Schiller 1955	x	
Euglena sp.		x
Euglena viridis (O.F.Müller) Ehrenberg 1830	x	x
Monomorphina pyrum (Ehrenberg) Mereschkowsky 1877	x	
Strombomonas urceolata (A.Stokes) Deflandre 1930	x	x
Strombomonas costata Deflandre 1930	x	
Strombomonas gibberosa (Playfair) Deflandre 1930	x	x
Strombomonas girardiana var. *glabra* (Playfair) Deflandre 1930	x	x
Strombomonas jaculata (T.C.Palmer) Deflandre 1952		x
Strombomonas rotunda (Playfair) Deflandre 1930	x	x
Strombomonas sp.	x	x
Strombomonas subcurvata (Proskina-Lavrenko) Deflandre 1930	x	x
Trachelomonas abrupta Svirenko 1914	x	x
Trachelomonas allia Drezepolski 1925	x	x
Trachelomonas armata var. *nana* Balech 1944	x	x
Trachelomonas conica Playfair 1915	x	
Trachelomonas cylindrica Ehrenberg 1834	x	
Trachelomonas dastuguei Balech 1944	x	
Trachelomonas hemisphaerica Emiliani 1983	x	
Trachelomonas hirta A.M.Cunha 1914	x	
Trachelomonas hispida (Perty) *F.Stein 1878*		x
Trachelomonas hispida var. *duplex* Deflandre 1926	x	
Trachelomonas hispida var. *hispida* (Perty) Stein 1878	x	x
Trachelomonas intermedia P.A.Dangeard 1902	x	
Trachelomonas irregularis Svirenko 1914	x	
Trachelomonas lacustris var. *ovalis* Drezepolski 1925	x	x
Trachelomonas lemmermannii Wolozynska 1912		x
Trachelomonas levefrei Deflandre 1976	x	
Trachelomonas megalacantha A.M.Cunha 1914	x	
Trachelomonas naviculiformis Deflandre 1926	x	
*Trachelomonas obovata A.*Stokes 1890	x	
Trachelomonas parvicollis Deflandre 1926	x	
Trachelomonas pseudobulla Svirenko 1914	x	
Trachelomonas robusta Svirenko 1914	x	
Trachelomonas rotunda Svirenko 1914	x	
Trachelomonas rugulosa F.Stein 1878	x	x
Trachelomonas sculpta Balech 1944	x	x
Trachelomonas similis A.Stokes 1890	x	x
Trachelomonas spinosa A.Stokes 1890	x	x
Trachelomonas sp.1		x
Trachelomonas sp.2		x
Trachelomonas sp.3		x
Trachelomonas superba Svirenko 1914		x
Trachelomonas volvocina (Ehrenberg) Ehrenberg 1834		x
Trachelomonas volvocinopsis Svirenko 1914	x	x
Trachelomonas woycickii Koczwara 1915	x	x
Trachelomonas bernardii f. *maior* Woloszynska 1912	x	x
Family Phacaceae		
Lepocinclis caudata (A.M.Cunha) Pascher 1927	x	x

Taxa	Period Prolonged drought	 Extreme floods
Lepocinclis oxyuris (Schmarda) B.Marin & Melkonian 2003	x	x
Lepocinclis salina F.E.Fritsch 1914	x	
Lepocinclis spirogyroides B.Marin & Melkonian 2003	x	x
Phacus acuminatus A.Stokes 1885		x
Phacus acutus Pochmann 1942	x	
Phacus hamatus Pochmann 1942	x	
Phacus longicauda var. *attenuatus* (Pochmann) Huber-Pestalozzi 1955	x	
Phacus margaritatus Pochmann 1942	x	x
Phacus plataleus Hortobágyi 1841	x	x
Phacus sp.1		x
Phacus sp.2	x	x
Phacus sp.3	x	
Phacus suecicus Lemmermann 1913		x
Class Eustigmatophyceae		
Order Goniochloridales		
Family Goniochloridaceae		
Goniochloris sculpta Geitler 1928	x	x
Goniochloris contorta (Bourrelly) H.Ettl 1977	x	
Goniochloris fallax Fott 1957		x
Pseudostaurastrum enorme (Ralfs) Chodat 1921		x
Pseudostaurastrum limneticum (Borge) Couté & Rousselin, nom. inval. 1975	x	
Tetraëdriella limbata Pascher 1938	x	
Tetrakentron acuminatum Pascher 1938	x	x
Tetraplektron tribulus (Pascher) Lobelich, III 1967	x	x
Class Mediophyceae		
Order Chaetocerotales		
Family Chaetocerotaceae		
Acanthoceras magdeburgensis Honig. 1963	x	x
Order Stephanodiscales		
Family Stephanodiscaceae		
Cyclotella pseudostelligera Hustedt 1939		x
Discostella sp.	x	x
Discostella stelligera (Cleve & Grunow) Houk & Klee 2004	x	x
Order Thalassiosirales		
Family Thalassiosiraceae		
Thalassiosira sp.	x	x
Class Synurophyceae		
Order Synurales		
Family Mallomonadaceae		
Mallomonas akrokomos Ruttner 1913		x
Mallomonas sp.		x
Mallomonas sp.1	x	x
Mallomonas sp.2	x	x
Class Trebouxiophyceae		
Order Trebouxiophyceae ordo incertae sedis		
Family Trebouxiophyceae incertae sedis		
Crucigenia fenestrata (Schmidle) Schmidle 1900	x	x

	Period	
Taxa	**Prolonged drought**	**Extreme floods**
Crucigeniella irregularis (Wille) P.M.Tsarenko & D.M.John 2002	x	
Crucigeniella rectangularis (Nägeli) Komárek 1974	x	
Crucigeniella saguei Komárek 1975	x	
Lemmermannia tetrapedia (Kirchner) Lemmermann 1904	x	
Order Chlorellales		
Family Chlorellaceae		
Chlorella sp.	x	
Closteriopsis acicularis (Chodat) J.H.Belcher & Swale 1962	x	
Closteriopsis sp.	x	x
Dictyosphaerium elegans Bachmann 1913	x	
Dictyosphaerium pulchellum H.C.Wood 1873	x	x
Dictyosphaerium sp.	x	x
Dictyosphaerium tetrachotomum Printz 1914		x
Diacanthos belenophorus Korshikov 1953	x	x
Family Oocystaceae		
Nephroclamys sp.	x	x
Nephrocytium schilleri (Kammerer) Comas González 1980	x	
Oocystis lacustris Chodat 1897	x	
Oocystis solitaria Wittrock 1879	x	x
Oocystis sp.	x	
Pachycladella komarekii (Fott & Kovácik) Reymond 1980		x
Rhombocystis complanata Komárek 1983		x
Rhombocystis sp.	x	
Trebouxiales		
Family Botryococcaceae		
Botryococcus braunii Kützing 1849	x	x
Class Xanthophyceae		
Order Mischococcales		
Family Centritractaceae		
Brachiogonium ophiaster Pascher & Ettl 1965		x
Xanthophyceae sp.		x
Family Pleurochloridaceae		
Isthmochloron neustonica Zalocar & Pizarro 1954	x	
Class Ulvophyceae		
Order Ulotrichales		
Family Ulotrichaceae		
Ulothrix sp.	x	
Class Zygnematophyceae		
Order Desmidiales		
Family Closteriaceae		
Closterium kuetzingii Brébisson 1856		x
Closterium praelongum Brébisson 1856	x	
Closterium sp.	x	
Closterium sp.1	x	x
Family Desmidiaceae		
Actinotaenium perminutum (G.S.West) Teiling 1954		x
Cosmarium contractum O.Kirchner 1878	x	
Cosmarium decoratum West & G.S.West 1895	x	
Cosmarium lagoense (Nordstedt) Nordstedt 1877	x	
Cosmarium granatum Brébisson ex Ralfs 1848	x	

Taxa	Period Prolonged drought	 Extreme floods
Cosmarium margaritatum (P.Lundell) J.Roy & Bisset 1886	x	
Cosmarium quadrum P.Lundell 1871	x	
Cosmarium rectangulare Grunow 1868	x	
Cosmarium undulatum Corda ex Ralfs 1848	x	
Cosmarium sp.	x	x
Cosmarium sp.1	x	x
Cosmarium sp.2	x	x
Cosmarium sp.3	x	
Cosmarium sphagnicola West & G.S.West 1897	x	
Desmidium sp.	x	
Euastrum abruptum Nordstedt 1870	x	
Euastrum brasiliense O.Borge 1903	x	
Euastrum sp.	x	
Euastrum turneri West 1892	x	x
Hyalotheca mucosa Ralfs 1848	x	
Micrasterias mahabuleshwarensis J.Hobson 1863	x	
Mougeotia sp.	x	
Spondylosium desmidiiforme (Borge) G.S.West 1904	x	x
Spondylosium panduriforme (Heimerl) Teiling 1957	x	
Spondylosium planum (Wolle) West & G.S.West 1912	x	
Spondylosium pulchrum (Bailey) W.Archer 1861	x	
Spondylosium sp.	x	
Staurodesmus connatus (P.Lundell) Thomasson 1960	x	
Staurastrum leptocladum var. *cornutum* Wille 1884	x	
Staurastrum longebrachiatum (O.Borge) Gutwinski 1902	x	
Staurastrum margaritaceum Meneghini ex Ralfs 1848	x	
Staurastrum minesotense Wolle	x	
Staurastrum nudibranchiatum Borge	x	
Staurastrum polymorphum Brébisson 1848	x	
Staurastrum pseudosebaldi Wille 1880	x	
Staurastrum rotula Nordstedt 1869	x	
Staurastrum sebaldi Reinsch 1866	x	
Staurastrum trifidum Nordsted 1870	x	x
Staurastrum sp.1	x	
Staurastrum sp.2	x	x
Staurastrum sp.3	x	
Staurodesmus dejectus (Brébisson) Teiling 1954	x	
Staurodesmus dickiei (Thén- Marc.) Teil 1950	x	
Staurodesmus extensus (O.F.Andersson) Teiling 1948	x	
Staurodesmus glaber (Ralfs) Teiling 1948	x	
Staurodesmus sp.	x	
Xanthidium sp.	x	
Oedogoniales		
Oedogoniaceae		
Oedogonium sp.		x
Order Zygnematales		
Family Zygnemataceae		
Netrium sp.	x	
Octacanthium mucronulatum (Nordstedt) Compère 1996	x	
Spirogyra sp.	x	
Species richness	272	209

Table S3 List of zooplankton species recorded between the periods of prolonged drought (2000-2001) and extreme floods (2010-2011) of the 10 lakes studied in Paraná sub-basin of the Upper Paraná River floodplain, Brazil.

Taxa	**Period**	
	Prolonged drought	**Extreme floods**
Rotifera		
Family Lecanidae		
Lecane amazonica (Murray, 1913)		x
Lecane bulla (Gosse, 1851)	x	x
Lecane cornuta (Müller. 1786)	x	x
Lecane curvicornis (Murray, 1913)	x	x
Lecane doryssa Harring, 1914	x	
Lecane elsa Hauer, 1931	x	
Lecane furcata (Murray, 1913)	x	
Lecane haliclysta Harring & Myers, 1926	x	
Lecane hastata (Murray, 1913)	x	
Lecane hornemanni (Ehrenberg, 1834)		x
Lecane inopinata Harring & Myers, 1926	x	
Lecane leontina (Turner. 1892)	x	x
Lecane ludwigii (Eckstein. 1883)	x	x
Lecane luna (Müller. 1776)	x	x
Lecane lunaris (Ehrenberg. 1832)	x	x
Lecane mira (Murray, 1913)		x
Lecane monostyla (Daday. 1897)	x	x
Lecane ohioensis (Herrick. 1885)	x	
Lecane papuana (Murray. 1913)	x	x
Lecane proiecta Hauer, 1956	x	x
Lecane quadridentata (Ehrenberg, 1830)	x	x
Lecane signifera (Jennings, 1896)	x	x
Lecane scutata (Harring & Myers, 1926)	x	
Lecane stenroosi (Meissner, 1908)	x	
Lecane stichaea Harring,1913	x	x
Lecane thienemmani (Hauer, 1938)		x
Lecane ungulata (Gosse, 1887)	x	
Lecane sp.	x	
Family Brachionidae		
Anuraeopsis fissa (Gosse.,1851)	x	
Anuraeopsis navicula Rousselet, 1911	x	x
Brachionus angularis Gosse, 1851	x	
Brachionus bidentatus Anderson. 1889	x	x
Brachionus budapestinensis Daday, 1885	x	
Brachionus calyciflorus Pallas, 1766	x	x
Brachionus caudatus Barrois & Daday, 1894	x	x
Brachionus austrogenitus Ahlstrom, 1940		x

Taxa	Period Prolonged drought	 Extreme floods
Brachionus dolabratus Harring, 1914	x	x
Brachionus falcatus Zacharias, 1898	x	x
Brachionus forficula Wierzejski, 1891	x	
Brachionus mirus Daday, 1905	x	x
Brachionus mirus f. *angustus* Koste, 1972	x	
Brachionus quadridentatus Kertész, 1894	x	x
Brachionus urceolaris Müller, 1773	x	
Kellicottia bostoniensis (Rousselet, 1908)	x	x
Keratella americana Carlin, 1943	x	x
Keratella cochlearis (Gosse, 1851)	x	x
Keratella lenzi Hauer, 1953	x	x
Keratella tropica (Apstein, 1907)	x	x
Plationus patulus macracanthus (Daday, 1905)	x	x
Plationus patulus (Müller, 1786)	x	x
Platyias leloupi Gillard, 1957	x	x
Platyias quadricornis (Ehrenberg, 1832)	x	x
Family Trichocercidae		
Trichocerca bicristata (Gosse, 1887)	x	x
Trichocerca bidens (Lucks, 1912)	x	x
Trichocerca capucina (Wierzejski & Zacharias, 1893)	x	
Trichocerca cylindrica (Imhof, 1891)	x	x
Trichocerca chattoni (Beauchamp, 1907)	x	x
Trichocerca dixonnuttalli (Jennings, 1903)	x	
Testudinella elongata De Smet, 2009	x	
Trichocerca braziliensis (Murray, 1913)	x	x
Trichocerca heterodactyla (Tschugunoff, 1921)	x	x
Trichocerca iernis (Gosse, 1887)	x	x
Trichocerca inermis (Linder, 1904)	x	x
Trichocerca insignis (Herrick, 1885)	x	x
Trichocerca insulana (Hauer, 1937)	x	
Trichocerca intermedia (Stenroos, 1898)	x	
Trichocerca mus Hauer, 1938	x	
Trichocerca myersi (Hauer, 1931)		x
Trichocerca pusilla Harring, 1914	x	
Trichocerca rattus (Müller, 1776)	x	
Trichocerca rousseleti (Voigt, 1902)	x	
Trichocerca ruttneri Donner, 1953		x
Trichocerca scipio (Gosse, 1886)	x	
Trichocerca similis (Wierzejski, 1893)	x	x
Trichocerca similis grandis Hauer, 1965	x	x
Trichocerca stylata (Gosse, 1851)	x	
Trichocerca tigris (Müller, 1786)	x	
Family Euchlanidae		

Taxa	Period	
	Prolonged drought	Extreme floods
Beauchampiella eudactylota (Gosse, 1886)	x	
Dipleuchlanis propatula (Gosse, 1886)	x	x
Dipleuchlanis propatula f. *macrodactyla* Hauer. 1965	x	
Euchlanis dilatata Ehrenberg, 1830	x	x
Euchlanis dilatata lucksiana Hauer, 1930		x
Euchlanis incisa Carlin, 1939	x	x
Family Mytilinidae		
Lophocharis salpina (Ehrenberg, 1834)		x
Lophocharis oxysternon (Gosse, 1851)		x
Mytilina acanthophora Hauer, 1938		x
Mytilina bisulcata (Lucks, 1912)	x	
Mytilina macrocera (Jennings, 1894)		x
Mytilina mucronata (Müller, 1773)		x
Mytilina ventralis (Ehrenberg, 1830)	x	x
Family Testudinellidae		
Testudinella ahlstromi Hauer, 1956	x	
Testudinella discoidea Ahlstrom, 1938	x	
Testudinella mucronata (Gosse, 1886)	x	x
Testudinella ohlei Koste, 1972	x	x
Testudinella patina (Hermann, 1783)	x	x
Testudinella patina dendradena Beauchamp, 1955		x
Testudinella truncata (Gosse, 1886)	x	
Pompholyx complanata Gosse, 1851	x	x
Pompholyx triloba Pejler, 1957	x	x
Family Trochosphaeridae		
Filinia longiseta (Ehrenberg, 1834)	x	x
Filinia opoliensis (Zacharias, 1898)	x	x
Filinia pejleri Hutchinson, 1964	x	
Filinia saltator (Gosse, 1886)	x	
Filinia terminalis (Plate, 1886)	x	x
Family Synchaetidae		
Ploesoma truncatum (Levander, 1894)	x	x
Polyarthra dolichoptera Idelson, 1925	x	x
Polyarthra vulgaris Carlin, 1943	x	x
Polyarthra remata Skorikov, 1896		x
Synchaeta pectinata Ehrenberg, 1832	x	x
Synchaeta oblonga Ehrenberg, 1832		x
Synchaeta stylata Wierzejski, 1893	x	x
Family Flosculariidae		
Floscularia sp.	x	
Ptygura libera Myers, 1934	x	
Ptygura sp.	x	x
Sinantherina spinosa (Thorpe, 1893)		x

Taxa	Period	
	Prolonged drought	Extreme floods
Family Notommatidae		
Cephalodella forficula (Ehrenberg, 1838)	x	x
Cephalodella gibba (Ehrenberg, 1830)	x	x
Cephalodella anebodica Bērziņš, 1976	x	
Cephalodella gracilis (Ehrenberg, 1830)	x	
Cephalodella hiulca Myers, 1924		x
Cephalodella mucronata Myers, 1924	x	
Cephalodella tenuiseta (Burn, 1890)		x
Monommata dentata Wulfert, 1940	x	x
Monommata maculata Harring & Myers, 1930		x
Monommata actices Myers, 1930	x	x
Monommata grandis Tessin, 1890		X
Notommata cerberus (Gosse, 1886)	x	
Notommata copeus Ehrenberg, 1834	x	x
Notommata pachyura (Gosse, 1886)	x	x
Notommata pseudocerberus Beauchamp, 1908	x	
Notommata saccigera Ehrenberg, 1830	x	
Notommata tripus Ehrenberg, 1838	x	
Notommata stitista Myers, 1937	x	
Pleurotrocha robusta (Glascott, 1893)	x	
Taphrocampa selenura Gosse, 1887	x	
Family Tetrasiphonidae		
Tetrasiphon hydrocora Ehrenberg, 1840	x	
Family Lepadellidae		
Colurella sp.	x	
Lepadella benjamini Harring, 1916	x	
Lepadella dactyliseta (Stenroos, 1898)	x	
Lepadella donneri Koste, 1972	x	
Lepadella imbricata Harring, 1914		x
Lepadella ovalis (Müller, 1786)	x	x
Lepadella patella (Müller, 1773)	x	x
Lepadella patella oblonga (Ehrenberg, 1834)		x
Lepadella rhomboides (Gosse, 1886)	x	
Family Conochilidae		
Conochilus coenobasis (Skorikov, 1914)	x	x
Conochilus dossuarius Hudson, 1885	x	x
Conochilus natans (Seligo, 1900)	x	x
Conochilus unicornis Rousselet, 1892	x	x
Family Gastropodidae		
Ascomorpha ecaudis Perty, 1850	x	x
Ascomorpha ovalis (Bergendal, 1892)	x	x
Ascomorpha saltans Bartsch, 1870	x	x
Gastropus hyptopus (Ehrenberg, 1838)	x	x

Taxa	Period	
	Prolonged drought	Extreme floods
Family Proalidae		
Proales minima (Montet, 1915)	x	
Proales sigmoidea (Skorikov, 1896)	x	
Proales sp.	x	
Family Dicranophoridae		
Dicranophoroides caudatus (Ehrenberg, 1834)		x
Dicranophoroides claviger (Hauer, 1965)	x	
Dicranophorus forcipatus (Müller, 1786)	x	
Dicranophorus prionacis Harring & Myers, 1928	x	
Family Trichotriidae		
Macrochaetus collinsii (Gosse, 1867)	x	x
Macrochaetus longipes Myers, 1934		x
Macrochaetus sericus (Thorpe, 1893)	x	x
Macrochaetus subquadratus Perty, 1850	x	
Trichotria tetractis (Ehrenberg, 1830)	x	x
Family Collothecidae		
Collotheca ornata (Ehrenberg, 1830)		x
Collotheca sp.	x	x
Family Hexarthridae		
Hexarthra intermedia (Wiszniewski, 1929)	x	x
Hexarthra mira (Hudson, 1871)	x	x
Family Trochosphaeridae		
Horaella thomassoni Koste, 1973	x	
Family Asplanchnidae		
Asplanchna sieboldii (Leydig, 1854)	x	x
Family Epiphanidae		
Epiphanes clavulata (Ehrenberg, 1831)	x	x
Epiphanes macroura (Barrois & Daday, 1894)	x	x
Epiphanes senta (Müller, 1773)		x
Family Philodinidae		
Dissotrocha sp.	x	
Rotaria sp.	x	
Family Scaridiidae		
Scaridium grande Segers, 1995	x	
Family Ituridae		
Itura aurita (Ehrenberg, 1830)	x	
Itura deridderae Segers, 1993	x	
Itura myersi Wulfert, 1935	x	
Bdelloidea	x	x
Cladocera		
Family Moinidae		
Moina minuta Hansen, 1899	x	x
Moina micrura Kurz, 1874		x

Taxa	**Period** **Prolonged drought**	 **Extreme floods**
Moina sp.		x
Moina reticulata Daday, 1905	x	x
Moinodaphnia macleayi King, 1853		x
Family Bosminidae		
Bosmina hagmanni Stingelin, 1904	x	x
Bosmina sp.		x
Bosmina frey De Mello & Hebbert, 1994	x	x
Bosmina tubicen Brehm, 1939	x	x
Bosminopsis deitersi Richard, 1895	x	x
Family Daphnidae		
Ceriodaphnia cornuta Sars, 1886	x	x
Ceriodaphnia reticulata Jurine, 1820	x	
Ceriodaphnia silvestrii Daday, 1903		x
Ceriodaphnia pulchela Sars, 1862		x
Ceriodaphnia richardi Sars, 1901		x
Daphnia gessneri Herbst, 1967	x	x
Daphnia laevis Birge, 1878	x	
Daphnia lumholtzi Sars, 1885		x
Scapholeberis cf. *armata freyi* Herrick, 1882		x
Simocephalus serrulatus Koch, 1841	x	x
Simocephalus latirostris Stingelin, 1906	x	
Family Sididae		
Diaphanosoma birgei Korineck, 1981	x	x
Diaphanosoma brevireme Sars, 1901		x
Diaphanosoma fluviatile Hansen, 1899	x	x
Diaphanosoma spinulosum Herbst, 1975	x	x
Family Chydoridae		
Acroperus tupinamba Sinev & Elmoor-Loureiro, 2010		x
Magnospina dentifera (Sars, 1901)	x	x
Alona ossiani Sinev, 1998	x	x
Karualona muelleri (Richard. 1897)	x	x
Coronatella monocantha (Sars, 1901)	x	x
Nicsmirnovius paggii Sousa & Elmoor-Loureiro. 2017	x	
Alona cf. *guttata*	x	x
Alona intermedia Sars, 1862		x
Coronatella rectangula (Sars, 1861)	x	
Anthalona verrucosa (Sars, 1901)	x	x
Coronatella poppei (Richard, 1897)	x	x
Alona sp.1	x	
Alona sp.2	x	
Alonella dadayi Birge, 1910	x	x
Alonella sp.	x	x

Taxa	Period	
	Prolonged drought	Extreme floods
Camptocercus australis Sars, 1896	x	
Chydorus eurynotus Sars, 1901	x	x
Chydorus parvireticulatus Frey, 1987		x
Chydorus sp.		x
Chydorus nitidulus Sars, 1901		x
Chydorus pubescens Sars, 1901		x
Chydorus cf. *sphaericus*	x	
Disparalona hamata Birge, 1879		x
Dunhevedia odontoplax Sars, 1901	x	x
Ephemeroporus tridentatus Bergamin, 1932	x	x
Ephemeroporus barroisi Richardi, 1894	x	x
Ephemeroporus hybridus (Daday, 1905)	x	x
Euryalona brasiliensis Brehm & Thomsen, 1936		x
Euryalona orientalis Daday, 1908	x	x
Graptoleberis ocidentalis Sars, 1901		x
Kurzia polyspina Kurz, 1974	x	x
Kurzia longirostris Daday, 1898		x
Leydigiopsis brevirostris Brehm, 1938	x	
Leydigiopsis megalops Sars, 1901		x
Notoalona globulosa Daday, 1898	x	
Notoalona sculpta (Sars, 1901)		x
Oxyurella longicaudis Birge, 1910	x	x
Family Ilyocryptidae		
Ilyocryptus spinifer Herrich, 1884	x	x
Family Macrothricidae		
Grimaldina brazzai Richard, 1892		x
Macrothrix elegans Sars, 1901	x	x
Macrothrix laticornis Jurine, 1820		x
Macrothrix superaculeata Smirnov, 1992	x	
Macrothrix squamosa Sars, 1901	x	x
Macrothrix sp.	x	x
Copepoda		
Family Cyclopidae		
Eucyclops solitarius Herbst, 1959	x	
Macrocyclops albidus Jurine, 1820		x
Mesocyclops longisetus var. *longisetus* Thiébaud, 1914	x	x
Mesocyclops longisetus var. *curvatus* Dussart, 1987	x	
Mesocyclops aspericornis Daday, 1906		x
Mesocyclops meridianus Kiefer, 1926	x	x
Mesocyclops ogunnus Onabamiro, 1957	x	
Mesocyclops ellipticus Kiefer, 1936		x
Microcyclops anceps Richard, 1897	x	x

Taxa	**Period**	
	Prolonged drought	**Extreme floods**
Microcyclops ceibaensis Marsh, 1919	x	
Microcyclops sp.		x
Metacyclops mendocinus Wierzejski, 1892	x	
Paracyclops chiltoni Thomson, 1882		x
Paracyclops sp.		x
Thermocyclops decipiens Kiefer, 1929	x	x
Thermocyclops minutus Lowndes, 1934	x	x
Thermocyclops inversus Kiefer, 1936		x
Family Diaptomidae		
Argyrodiaptomus azevedoi Wright, 1935	x	x
Argyrodiaptomus furcatus Sars, 1901	x	
Argyrodiaptomus sp.		x
Notodiaptomus cearensis Wright, 1936	x	x
Notodiaptomus conifer Sars, 1901	x	
Notodiaptomus deitersi Poppe, 1891		x
Notodiaptomus henseni Dahl, 1894	x	x
Notodiaptomus iheringi Wright, 1935	x	x
Notodiaptomus jatobensis Kiefer, 1956		x
Notodiaptomus incompositus Pesta, 1927		x
Notodiaptomus isabelae Wright, 1936	x	
Notodiaptomus kieferi Brandorff, 1973	x	
Notodiaptomus spiniger Brian 1925		x
Notodiaptomus spinuliferus Dussart & Matsumura-Tundisi, 1986	x	
Total richness	**217**	**190**

Table S4 List of fish species recorded between the periods of prolonged drought (2000-2001) and extreme floods (2010-2011) of the 8 lakes studied in Paraná sub-basin of the Upper Paraná River floodplain, Brazil. In addition, we classify fish when migrating: Yes = long-distance migratory species, No = sedentary species.

Taxa	**Period**		**Migration***
	Prolonged drought	**Extreme floods**	
Order Perciformes			
Family Sciaenidae			
Plagioscion squamosissimus (Heckel, 1840)	x	x	No
Order Characiformes			
Family Acestrorhynchidae			
Acestrorhynchus lacustris (Lütken, 1875)	x	x	No
Family Anostomidae			
Leporinus friderici (Bloch, 1794)	x	x	No
L. lacustris Campos, 1945	x	x	No
Megaleporinus macrocephalus (Garavello, Britski, 1988)		x	Yes
M. obtusidens (Valenciennes, 1836)		x	Yes
M. piavussu (Britski, Birindelli, Garavello, 2012)	x	x	Yes
Schizodon altoparanae Garavello, Britski, 1990	x	x	No
S. borellii (Boulenger, 1900)	x	x	No
Schizodon nasutus Kner, 1858	x	x	No
Family Bryconidae			
Brycon orbignyanus (Valenciennes, 1850)		x	Yes
Salminus brasiliensis (Cuvier, 1816)		x	Yes
Family Characidae			
Aphyocharax anisitsi Eigenmann & Kennedy, 1903	x	x	No
Aphyocharax sp.	x		No
A. dentatus Eigenmann & Kennedy, 1903		x	No
Astyanax affinis	x	x	No
A. aff. *fasciatus* (Cuvier, 1819)	x		No
A. lacustris (Lütken, 1875)	x	x	No
A. schubarti Britski, 1964	x		No
Hyphessobrycon eques (Steindachner, 1882)	x	x	No
Piabucus analis (Eigenmann, 1914)		x	No
Moenkhausia bonita Benine, Castro, Sabino, 2004		x	No
M. forestii Benine, Mariguela, Oliveira, 2009		x	No
M. aff. *intermedia* Eigenmann, 1908	x	x	No
M. cf. *gracilima* Eigenmann, 1908		x	No
M. sanctaeflomenae (Steindachner, 1907)	x	x	No
Psellogrammus kennedyi (Eigenmann, 1903)		x	No
Family Characinae			
Roeboides descalvadensis Fowler, 1932	x	x	No
Family Cheirodontinae			
Serrapinnus calliurus (Boulenger, 1900)		x	No
Crenuchidae			
Characidium aff. zebra Eigenmann, 1909	x		No
Family Stevardiinae			
Piabarchus stramineus (Eigenmann, 1908)	x	x	No
Odontostilbe sp.	x	x	No
Serrapinnus notomelas (Eigenmann, 1915)	x	x	No
Family Curimatidae			

Taxa	**Period**		**Migration***
	Prolonged drought	**Extreme floods**	
Cyphocharax modestus (Fernández-Yépez, 1948)	x	x	No
Cyphocharax nagelii (Steindachner, 1881)	x	x	No
Steindachnerina brevipinna (Eigenmann, Eigenmann, 1889)	x	x	No
S. insculpta (Fernández-Yépez, 1948)	x	x	No
Stevardiinae			
Diapoma guarani (Mahnert, Géry, 1987)	x	x	No
Family Cynodontidae			
Rhaphiodon vulpinus Spix & Agassiz, 1829	x	x	Yes
Family Erythrinidae			
Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)	x	x	No
Hoplias mbigua Azpelicueta, Benítez, Aichino, Mendez, 2015		x	No
H. argentinensis Rosso, Mabragaña, González-Castro, Bogan, Cardoso, Mabragaña, Delpiani & Díaz de Astarloa, 2018		x	No
Hoplias sp.	x	x	No
Hoplias sp.1	x	x	No
Family Hemiodontidae			
Hemiodus orthonops Eigenmann & Kennedy, 1903		x	No
Family Lebiasinidae			
Pyrrhulina australis Eigenmann & Kennedy, 1903	x		No
Family Prochilodontidae			
Prochilodus lineatus (Valenciennes, 1836)	x	x	Yes
Family Serrasalmidae			
Metynnis lippincottianus (Cope, 1870)	x	x	No
Myloplus tiete (Eigenmann, Norris, 1900)	x	x	No
Piaractus mesopotamicus (Holmberg, 1887)		x	Yes
Serrasalmus maculatus Kner, 1858	x	x	No
S. marginatus Valenciennes, 1837	x	x	No
S. sp.1	x	x	No
S. sp.2	x	x	No
Order Gymnotiformes			
Gymnotus sp.	x		No
Family Rhamphichthyidae			
Rhamphichthys hahni (Meinken, 1937)	x	x	No
Family Sternopygidae			
Eigenmannia trilineata López & Castello, 1966	x	x	No
E. virescens (Valenciennes, 1836)	x	x	No
Order Myliobatiformes			
Family Potamotrygonidae			
Potamotrygon amandae Loboda & Carvalho, 2013	x	x	No
Order Cichliformes			
Family Cichlidae			
Apistogramma commbrae (Regan, 1906)		x	No
Astronotus crassipinnis (Heckel, 1840)	x	x	No
Cichla kelberi Kullander & Ferreira, 2006	x	x	No
C. piquiti Kullander & Ferreira, 2006	x	x	No
Cichla sp.		x	No
Cichlasoma paranaense Kullander, 1983	x	x	No
Crenicichla britskii Kullander, 1982	x	x	No
Geophagus sveni Lucinda, Lucena & Assis, 2010		x	No
Laetacara araguaiae Ottoni & Costa, 2009	x		No

Taxa	**Period**		
	Prolonged drought	**Extreme floods**	**Migration***
Satanoperca sp.	x	x	No
Family Poeciliidae			
Pamphorichthys hollandi (Henn, 1916)		x	No
Order Pleuronectiformes			
Family Achiridae			
Catathyridium jenynsii (Günther, 1862)	x	x	No
Order Siluriformes			
Family Auchenipteridae			
Ageneiosus militaris Valenciennes, 1835		x	No
Auchenipterus osteomystax (Miranda Ribeiro, 1918)	x	x	No
Parauchenipterus galeatus (Linnaeus, 1766)	x	x	No
Family Callichthyidae			
Hoplosternum littorale (Hancock, 1828)	x	x	No
Family Clariidae			
Clarias gariepinus (Burchell, 1822)		x	No
Lepthoplosternum pectorale (Boulenger, 1895)		x	No
Family Doradidae			
Ossancora eigenmanni (Boulenger, 1895)		x	No
Platydoras armatulus (Valenciennes, 1840)		x	No
Trachydoras paraguayensis (Eigenmann & Ward, 1907)	x	x	No
Family Heptapteridae			
Pimelodella gracilis (Valenciennes, 1835)	x		No
Rhamdia quelen (Quoy & Gaimard, 1824)		x	No
Family Hypostominae			
Hypostomus ancistroides (Ihering, 1911)	x		No
Pterygoplichthys ambrosettii (Holmberg, 1893)	x	x	No
Family Loricariinae			
Loricaria sp.	x		No
Loricariichthys platymetopon Isbrücker, Nijssen, 1979	x	x	No
Loricariichthys rostratus Reis, Pereira, 2000		x	No
Family Pimelodidae			
Hemisorubim platyrhynchos (Valenciennes, 1840)		x	Yes
Hypophthalmus oremaculatus Nani, Fuster, 1947	x	x	No
Iheringichthys labrosus (Lütken, 1874)	x	x	No
Pimelodus maculatus Lacépède, 1803	x	x	No
P. mysteriosus Azpelicueta, 1998		x	No
Pseudoplatystoma corruscans (Spix & Agassiz, 1829**)**		x	Yes
Sorubim lima (Bloch & Schneider, 1801)	x	x	Yes
Family Rhinelepinae			
Rhinelepis aspera Spix & Agassiz, 1829		x	Yes
Order Synbranchiformes			
Family Synbranchidae			
Synbranchus marmoratus Bloch, 1795		x	No
Total richness	**65**	**86**	

*To Classify fish species as long-distance migratory or sedentary, we use the following references: Oliveira et al. 2018; Suzuki et al. 2002

Oliveira AG, Baumgartner MT, Gomes LC, Dias RM, Agostinho AA (2018) Long-term effects of flow regulation by dams simplify fish functional diversity. Freshw. Biol. 63: 293–305. https://doi.org/10.1111/fwb.13064

Suzuki HI, Pelicice FM, Luiz EA, Latini JD, Agostinho AA (2002) Estratégias reprodutivas da assembléia de peixes da planície de inundação do alto rio Paraná. Pesquisas Ecológicas Longa Duração – PELD. A planície alagável do rio Paraná: estrutura e processos ambientais. Maringá: PELD, 113:116

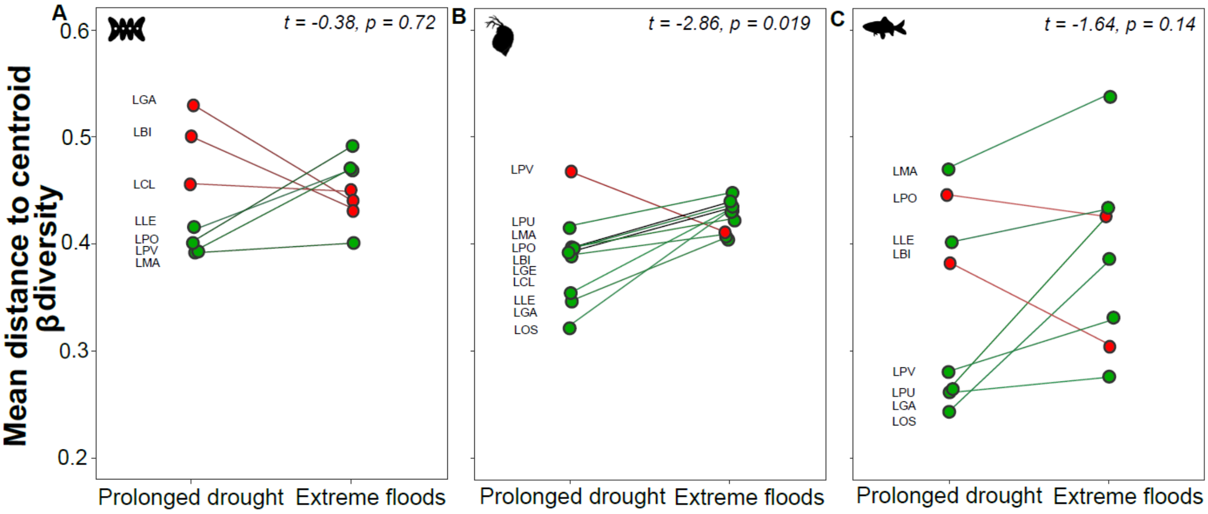

Figure S1. β diversity (mean distance to the centroid), with the number of standardized collections, considering the period of prolonged drought (2000-2001) and the period with extreme flood events (2010-2011) in the Upper Paraná River floodplain, Brazil. A - phytoplankton; B - zooplankton; C - fish. In green, the lakes that showed lower β diversity in the prolonged drought period (as expected), and in red, those that showed the opposite pattern. LGA – Garças; LMA – Manezinho; LPO – Pombas; LPV – Pau Véio; LBI – Bilé; LLE – Leopoldo; LOS – Osmar; LCL – Clara; LGE – Genipapo; LPU – Pousada.

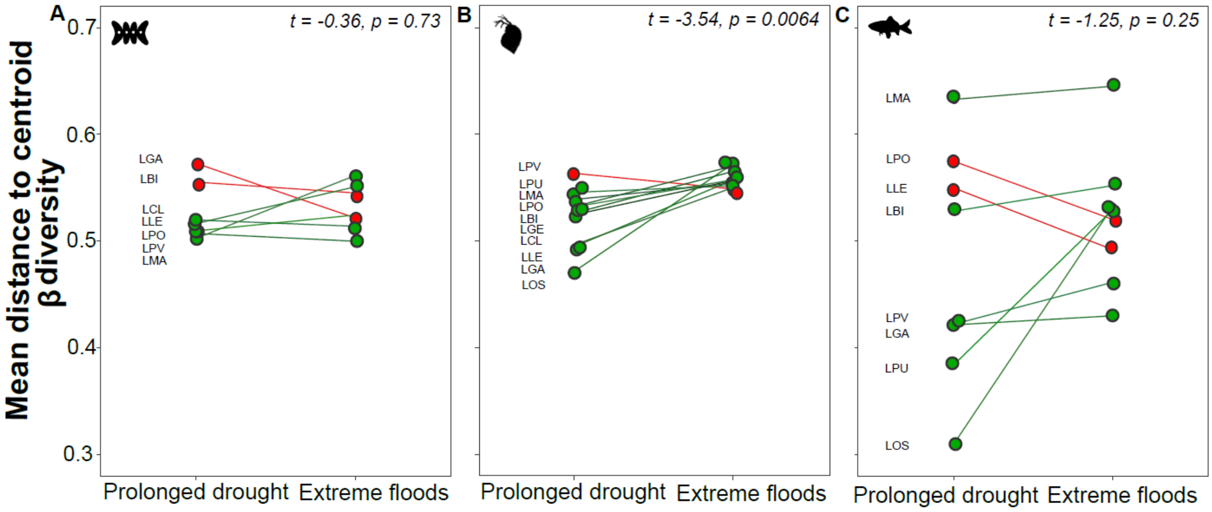

Figure S2. β diversity (mean distance to the centroid), considering the species abundance matrix, in a period of prolonged drought (2000-2001) and a period with extreme flood events (2010-2011) in the Upper Paraná River floodplain, Brazil. A - phytoplankton; B - zooplankton; C - fish. In gree, the lakes that showed lower β diversity in the prolonged drought period (as expected), and in red, those that showed the opposite pattern. LGA – Garças; LMA – Manezinho; LPO – Pombas; LPV – Pau Véio; LBI – Bilé; LLE – Leopoldo; LOS – Osmar; LCL – Clara; LGE – Genipapo; LPU – Pousada.

5 FINAL CONSIDERATIONS

We evaluated the patterns of β diversity and metacommunity at different spatial and temporal scales. In the first manuscript, it was found that regardless of the hydrological period and the spatial scale, the structure of the zooplankton metacommunity remained practically constant throughout the four years, with a predominance of species range turnover (Clementsian pattern). In the smallest spatial scale (sub-basins), we found quasi-structural patterns (quasi-Clementsian and quasi-Gleasonian patterns). The predominance of the Clementsian pattern suggests that the associations of zooplankton species in the floodplain responded similarly to the environmental gradient and the responses differed among species groups. Furthermore, it was found that when considering only the river, at discrete moments (single sample), the flood events showed biotic homogenization in the floodplain. However, over two years of prolonged drought (time scale), the process of biotic homogenization (at least for one sub-basin) was also recorded. This shows that biodiversity changes over time, on large and small scales, and those studies based on single instants can mask critical ecological processes.

In the second manuscript, it was observed, in general, that higher taxonomic (LCBD-t) and functional uniqueness (LCBD-f) were related to lower species and trait richness, respectively. Although we expected this to occur only in the dammed sub-basin, we observed that the sites with the lowest zooplankton richness are the ones that most contribute to β diversity. This negative relationship between richness and LCBD is commonly found in the literature, but this study stands out for showing this relationship for functional data as well. Although taxonomic uniqueness was seen to be cyclical over time in the dammed sub-basin, the role that species play is not changing. Thus, we suggested that the species in this sub-basin perform similar functions. In contrast, in the free-flowing sub-basin, there was a cyclical renewal of the species and their respective traits, following the natural dynamics of an environment with more conserved features. Furthermore, the ecological uniqueness of zooplankton (LCBD-t and LCBD-f) over the 19 years in the floodplain is being driven mainly by temporal processes. This reinforces the importance of long-term ecological studies to better monitor the dynamics of aquatic biota and establish more robust ecological standards.

In the third manuscript, we verified that only zooplankton underwent biotic homogenization in the period of prolonged drought (2000-2001). The β diversity of phytoplankton and fish did not change between the different hydrological periods, indicating that the dispersion type (active or passive) does not interfere with drought homogenization. As the response between the biological groups was different, it is reinforced that the groups are not surrogates of each other, not even within the “planktonic” category, since phytoplankton and zooplankton did not present the same response. In the face of limited resources in conservation planning, there is a debate over how many biological groups need to be considered to represent the dynamics of the ecosystem. It was observed that the response between the groups is not congruent and that the pattern found for one group cannot be extrapolated to the others, especially in the establishment of environmental conservation measures. Furthermore, the reduction of environmental heterogeneity and β diversity of zooplankton, in the period of prolonged drought, emphasizes the importance of natural flood events for maintaining ecosystem functioning and aquatic heterogeneity.

Our results also showed the importance of considering different spatial and temporal scales in ecological studies, and this is highlighted in the interests of obtaining more representative patterns. Although the floodplain of the upper Paraná River has been studied for a considerable time (more than 20 years), the ecological patterns registered in it are still not completely clear. Depending on the selected scale, the β diversity or the structuring of the metacommunity may fluctuate. This reinforces the high spatial and temporal heterogeneity of the floodplain and the need for caution in extrapolating results that may be specific to certain periods of time or biological groups. In addition, a recommendation in one of the manuscripts is to consider functional traits of the species (such as body length, type of reproduction, feeding type, and predation avoidance behavior), since they can maximize understanding of ecosystem dynamics and thus better assist in conservation strategies.

The flood pulses and the temporal heterogeneity induced by extreme rains can increase the β diversity of zooplankton over time and, thus, reduce the negative effects of anthropic action on the floodplain. Thus, the importance of maintaining the natural dynamics in floodplains is reinforced, especially of the free-flowing stretches. Given this, the climate change scenario and its changes in precipitation rates, in addition to the prediction of increased construction of dams, are of major concern.

Finally, the insights promoted by the studies of β diversity and metacommunity help to understand the events that change diversity, such as dam construction and extreme climate events, allowing conservation and environmental management measures to be better designed. The results were found to provide important baselines for the conservation of aquatic biodiversity and the maintenance of the natural dynamics of metacommunities. In addition, the importance of long-term ecological studies is emphasized, since they allow the detection of ecological patterns that are masked in snapshots moments.

APPENDIX D – Scientific divulgation

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*Texto a ser submetido para revista de divulgação científica *Ciência Hoje*, na categoria Seções “Resultados imediatos”.

A incrível biodiversidade, presente em uma única gota de água, ameaçada!

Você já deve ter ouvido falar que estamos vivendo um período de perda da nossa incrível biodiversidade. Os impactos dos seres humanos na natureza são cada vez maiores, trazendo prejuízos para todos os seres vivos. E você sabia que até animais microscópicos podem ser prejudicados por esses impactos? Pois é! Hoje vamos falar sobre um grupo de pequenos animais que possuem uma diversidade extremamente elevada nos mananciais aquáticos e que são bastante sensíveis as alterações ambientais.

O planeta Terra possui uma elevada diversidade de ambientes, desde os terrestres até os aquáticos. E habitando esses diferentes ambientes aquáticos destacamos um grupo composto por animais muito pequenos, o zooplâncton. Apesar de serem menores que um grão de arroz, desempenham um papel ecológico nada pequeno. Esses animais microscópicos representam uma ligação importante na produção e consumo de alimento nas cadeias alimentares. Eles se alimentam das algas (que são os organismos microscópicos produtores de alimentos, através da fotossíntese, nos ambientes aquáticos) e são consumidos por outros animais invertebrados (como algumas larvas de insetos que também habitam os ambientes aquáticos) ou mesmo para peixes.

Desde uma gota de água até nos diferentes ambientes aquáticos, como pequenas poças de água, até lagos, reservatórios e grandes planícies de inundações, o zooplâncton está presente. Ops, você sabe o que é uma planície de inundação? É o nome dado a uma região plana, mais baixa, que fica inundada durante a época de cheia das águas, estando localizada na margem de algum curso de água. Planícies de inundações, também chamadas de várzea, são conhecidas por serem ecossistemas aquáticos altamente dinâmicos. Isso mesmo! Em um único ano eles podem passar por diferentes fases entre seca e cheia (veja a Figura 1). Apesar desses eventos de seca e cheia fazerem parte da dinâmica natural desses ecossistemas, os eventos climáticos extremos podem acabar intensificando as mudanças ambientais nestes ecossistemas.

Você sabe que eventos são esses? Estamos falando do *El Niño* e *La Niña*. O *El Niño* é um fenômeno de aquecimento das águas do oceano e na região sul e sudeste do Brasil causam inundações extremas. Enquanto *La Niña*, é o resfriamento das águas no oceano, mas que no sul e sudeste é responsável por causar secas extremas. Mas, os efeitos desses eventos climáticos, que já não são poucos, podem ser intensificados diante da construção de reservatórios. Você sabia? Quando um reservatório é construído ele causa a inundação de uma área bastante extensa. Isso prejudica tanto a biota aquática quanto a terrestre, que acabam morrendo ou migrando para outros lugares. Além disso, após a construção de reservatórios a dinâmica natural do rio é prejudicada e os eventos de cheia se tornam escassos.

Diante de todas essas mudanças das condições ambientais, você sabia que a diversidade do zooplâncton está ameaçada? Pois é! Você já ouviu falar em um acontecimento chamado “homogeneização biótica”? É quando a diversidade entre os ambientes é muito parecida, e isso pode acontecer com o zooplâncton, reduzindo sua biodiversidade, quando as condições ambientais mudam. Essas mudanças podem ser causadas por diferentes impactos ambientais, entre eles o barramento do curso natural dos rios ou mesmo eventos climáticos extremos, que abordamos anteriormente. Mas, será que há prejuízo ambiental ao se perder espécies tão pequenas? A resposta é sim e sim! Como o zooplâncton possui uma forte relação com outros grupos aquáticos, perder uma espécie pode trazer problemas para o funcionamento do ambiente. O zooplâncton é a prova viva daquele velho ditado: “tamanho não é documento”.

Através de um projeto de Pesquisas Ecológicas de Longa Duração (PELD), estudamos um trecho da planície de Inundação do Alto Rio Paraná, entre os estados do Paraná, Mato Grosso do Sul e São Paulo, e que tem suas condições ambientais afetadas pelos reservatórios construídos no canal do rio Paraná em São Paulo. Analisamos o zooplâncton durante quatro anos: dois anos com seca prolongada (2000-2001) e dois anos com cheias extremas (2010-2011). E sabe o que observamos? No período de seca prolongada, resultante do período de *La Niña* e intenso controle de água pelos reservatórios, a biodiversidade do zooplâncton foi homogênea entre os ambientes. Portanto, um longo período sem água na planície de inundação leva a redução da diversidade do zooplâncton (veja Figura 2). Achou grave? Mas, essa situação pode se tornar ainda mais preocupante se lembrarmos que esses animais, ao longo do tempo, podem interferir diretamente outros grupos biológicos que dependem dele, como as larvas de inseto e peixes. Na natureza tudo está interligado. Perder espécies, seja qual for, pode trazer prejuízos para dinâmica natural do ambiente.

Aqui fica um recado: precisamos estar atentos a perda na biodiversidade, pois muito mais que perder espécies da natureza perdemos também os serviços que o ecossistema proporciona para os seres humanos, como a pescaria.

Figura 1. Planície de inundação do Alto Rio Paraná. Foto: Horácio Ferreira Júlio Júnior.

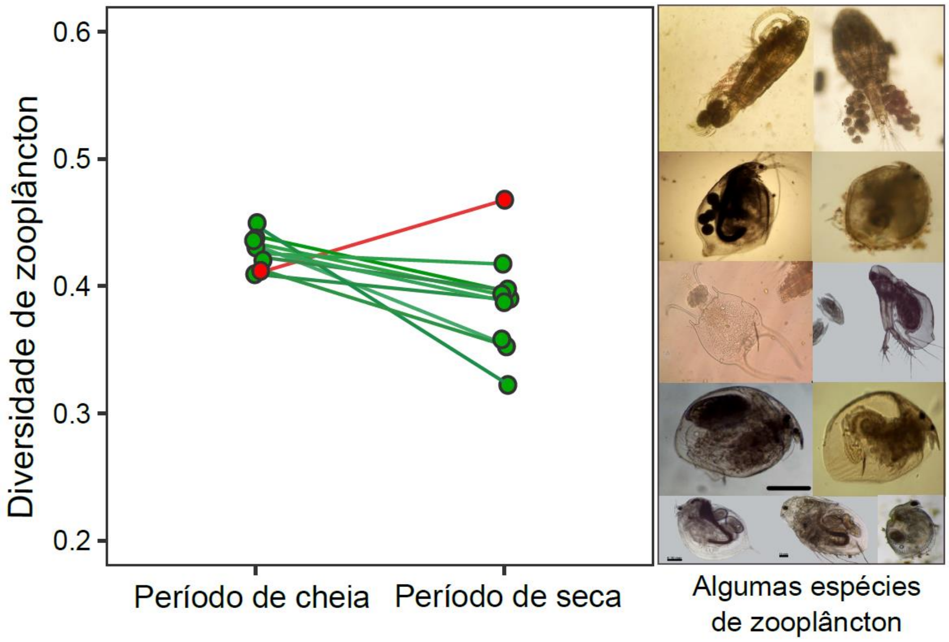

Figura 2. Diversidade do zooplâncton nos 10 lagos estudados. Note, pela linha vermelha, que apenas um único lago que não sofreu a redução na diversidade no período de seca.

ANNEX A - Teaching and Research Development during the doctorate degree which contributed to the execution of this thesis.

ENSINO

1. MESSAGE, H. J.; **DINIZ, L. P.**; MANTOVANO, T. Participação em banca de trabalho de conclusão de curso de Gabriela Naomi Tanaka dos Santos. Importância da raridade de espécies zooplanctônicas em uma planície de inundação neotropical. Curso de Ciências Biológicas, Universidade Estadual de Maringá, PR. 2021.

2. **DINIZ, L. P.** Trajetória acadêmica e a importância da pesquisa científica: zooplâncton enfoque. 2020. (Palestra proferida no Centro de Ensino Superior do Vale do São Francisco – CESVASF, Belém do São Francisco, PE).

3. **DINIZ, L. P.** A incrível diversidade de zooplâncton no bioma Caatinga. 2020. (Palestra proferida na Faculdade de Ciências Humanas do Sertão Central – FACHUSC, Salgueiro, PE).

4. VELHO, L. F. M.; **DINIZ, L. P.**; BIALETZKI, A. Participação em banca de Patrícia Frazão Ferreira. Tecnologias na Piscicultura visando à redução dos impactos na qualidade da água. 2019. Monografia (Aperfeiçoamento/Especialização em Curso de Especialização a Distância em Piscicultura) - Universidade Estadual de Maringá, PR.

5. **DINIZ, L. P.** Participação nos Ciclos de debates de ecologia de água doce – Universidade Estadual de Maringá, PR (2017, 2018 2019).

6. **DINIZ, L. P.** Organismos Aquáticos como Ferramenta de Avaliação de Impactos Ambientais. 2017. (Curso de curta duração ministrado, na Universidade Estadual do Paraná – UNESPAR/Campus Paranavaí, PR).

PESQUISA

(i) Papers published during the doctorate degree

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(ii) Book chapter published during the doctorate degree

1. PADIAL, A. A.; COSTA, A. P. L.; BONECKER, C. C.; NOGUEIRA, D. G.; DE OLIVEIRA ROQUE, F.; **DINIZ, L. P**.; CAVALCANTE, L. L.; VALLEJOS, M. A. V.; OTA, R. R.; LUDWIG, T. A. V. Freshwater Studies in the Atlantic Forest: General Overview and Prospects. The Atlantic Forest. 1ed: Springer International Publishing, 2021, p. 205-230.

(iii) Award

1. Prêmio Harald Sioli e prêmio de Primeiro Lugar nas Sessões Orais no XVII Congresso Brasileiro de Limnologia & 2º Congresso Ibero-americano de Limnologia. O trabalho premiado foi o artigo apresentado na **qualificação do doutorado** da pós-graduanda: "*Environmental filter drives the taxonomic and functional β-diversity of zooplankton in tropical shallow lakes*".

EXTENSÃO

1. Confecção de vídeo de divulgação científica para revista de popularização da ciência LimnoEcos, da Associação Brasileira de Limnologia (ABLimno), sobre o artigo da qualificação do doutorado: "*Environmental filter drives the taxonomic and functional β-diversity of zooplankton in tropical shallow lakes*". Disponível em: <https://www.youtube.com/watch?v=_f3yfHaq_d8&t=54s>

2. VII Mostra Científica – Querência do Norte. 2019. (Exposição projeto PELD-PIAP).

3. Participação no projeto de extensão: Se todos camPEArem (Capacitação e Ação Motivada à Preservação, Educação Ambiental e Recuperação de Ecossistemas aquáticos), a conservação acontece - SOS Riachos de Maringá. 2018-2019.

4. UEM na Expoingá – mostra científica de diferentes grupos biológicos durante a Expoingá, Pró-Reitoria de Extensão e Cultura da UEM, Maringá, PR. 2019.

5. Ciência na Praça - Mostra de Atividades da Pós-Graduação da Universidade Estadual de Maringá. A planície de inundação do Alto Rio Paraná. 2017.