Drivers of zooplankton functional and taxonomic β-diversity in two neotropical floodplains: implications for conservation

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Abstract

Floodplains are among the most biodiverse systems on the planet and offer several eco-system services; however, they are threatened by anthropic actions such as dam construction. We investigated zooplankton taxonomic and functional β-diversity, environmental heterogeneity, and the drivers of β-diversity in response to the hydrological period in the Amazon (without dams) and Paraná (with several dams) floodplains. We also discuss the implications of biodiversity-environment relationships for ecological conservation. We sampled 36 lakes during the drought and rainy periods (72 samples). The 180 zooplankton taxa found were classified into six functional traits. We calculated taxonomic and functional β-diversity (total, replacement, and richness) and the importance of different drivers (physical-chemical variables, food availability, predation, and spatial component). We also determined the environmental heterogeneity in each floodplain and hydrological period. The functional and taxonomic β diversity of the zooplankton community exhibited different patterns in response to the hydrological period. The Amazon floodplain presented greater environmental heterogeneity but not greater beta diversity. The Paraná floodplain presented the lowest functional β diversity during the drought period, where predation and the spatial component were the variables that most explained this variation. A greater contribution of replacement, regardless of the hydrological period, should lead to efforts to preserve as many lakes as possible in both floodplains, as they present unique compositions of species and traits. We emphasize the need to plan conservation strategies in these floodplains, especially considering that dams can lead to homogeneous environmental and biological conditions.

Keywords Environmental heterogeneity · Hydrologic regime · Dams · Ecosystem functioning

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Communicated by David Hawksworth

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Introduction

Floodplains are among the most biodiverse systems on the planet and offer several ecosystem services (Junk et al. 1989; Petsch et al. 2023). This great biodiversity is associated with the spatial and temporal variability caused by flood pulses (Junk et al. 1989; Opperman et al. 2010; Bomfim et al. 2021). The flood pulse, in turn, is linked to the hydrological regime and leads to severe changes in the physical-chemical conditions of waterbodies (Junk et al. 1989; Neiff 1990; Bozelli et al. 2015). In these systems, during the rainy season and flooding periods, the environments (main rivers, lakes, ponds, and tributaries) become connected, which leads to more similar environmental and biological conditions (Thomaz et al. 2007) and stronger effects of regional factors on community dynamics (Rodriguez and Lewis-Jr 1997; Bozelli et al. 2015). During the drought season, the environments become isolated from each other, leading to greater environmental heterogeneity and distinct biological compositions among sites (Simões et al. 2013; Bozelli et al. 2015). Thus, local environmental factors such as species interactions can strongly affect community structure during the drought season (Thomaz et al. 2007; Bozelli et al. 2015). Additionally, greater environmental heterogeneity during drought periods is expected to increase species diversity by increasing niche availability (Heino et al. 2015a).

Despite their importance, floodplains, like other freshwater environments, suffer from several anthropic activities, such as land use and dam construction, that alter their physical-chemical and biological structure (Winemiller et al. 2016; Moi et al. 2022; Zhang et al. 2023). Regarding dam construction, in Brazil, the Paraná River basin has several dams along the main river and its tributaries, which has caused a cascade effect with consequent abiotic and biotic changes from upstream to downstream (Agostinho et al. 2004, 2009; Winemiller et al. 2016). The main impacts are the alteration of the natural flood pulse by dams and the sedimentation of nutrients, which led to an oligotrophication process in this system (Roberto et al. 2009). Whereas in the Amazon, many areas that are still preserved are threatened by dam construction projects, which can consequently alter ecosystem functioning and cause a reduction in fish, including endemic and commercial species, disrupting energy flow in the entire system (Almeida et al. 2009; Winemiller et al. 2016).

In this context, beta diversity can be used to measure biodiversity, better understand ecological patterns, and establish conservation strategies (Heino et al. 2015a; Socolar et al. 2016; Gomes et al. 2020), especially in impacted and threatened systems such as the abovementioned floodplains. Beta diversity is defined as the variation in species/trait composition among sites (Anderson et al. 2006) and can be analyzed through taxonomic and/or functional perspectives; these two approaches can reflect different processes acting on community structure (Braghin et al. 2018; Diniz et al. 2021). Besides ecological and biogeographic processes, historical gradients can also be accessed by partitioning total beta diversity into components such as replacement (replacement of species/traits between sites) and richness difference (difference in richness due to loss/gain of species/traits) (Podani and Schmera 2011; Carvalho et al. 2012; Heino et al. 2019). High values of beta replacement can be attributed to species tolerance to environmental filters or historical events, whereas high values of beta richness reflect the diversity of available niches or physical barriers that limit dispersal (Gaston and Blackburn 2000; Qian et al. 2005; Lansac-Tôha et al. 2019). For conservation purposes, when the greatest proportion of beta diversity is the replacement

component, it should be preserved as many sites as possible; when it is richness-difference, the richest sites must be preserved (Socolar et al. 2016).

Several biological groups, including zooplanktonic organisms, have been used to investigate beta diversity patterns. Zooplankton are highly diverse in aquatic environments (Lansac-Tôha et al. 2009) and are the most abundant primary consumers in these systems; thus, changes in these communities can impact other levels inside food chains and alter the cycling of matter and energy (Litchman et al. 2013). Through zooplankton functional traits, it is possible to evaluate ecosystem conditions and identify any disruptions in ecosystem functioning (Barnett et al. 2007; Kiørboe 2011; Litchman et al. 2013; Hébert et al. 2017). Thus, evaluating variations in the taxonomic and functional beta diversity of zooplankton is a way to protect regional diversity, contribute to conservation plans, and ensure the maintenance of ecosystem services. Zooplankton are very sensitive and can be influenced by many spatial and local factors that filter the final set of species and traits (Bomfim et al. 2021; Deosti et al. 2021; Diniz et al. 2021). However, the factors determining the structure of zooplankton taxonomic and functional beta diversity can change depending on the intrinsic characteristics of floodplains, such as the presence of dams (Braghin et al. 2018; Souza et al. 2021), the set of species, the physical-chemical structure of the environment (Lansac-Tôha et al. 2019), and the influence of hydrological periods (Bomfim et al. 2021). Little is known about the abovementioned drivers of zooplankton taxonomic and functional composition in different floodplains; thus, further investigations can help to identify disruptions in ecosystem functioning and create strategies for conservation.

Here, we investigated zooplankton taxonomic and functional beta diversity in response to the hydrological period (drought and rainy) in two different floodplains, the Amazon River and Upper Paraná River. We also investigated the drivers of zooplankton beta diversity (functional and taxonomic) in these two floodplains during hydrological periods of drought and rain and discussed the implications of biodiversity-environment relationships for ecological conservation. We hypothesize that (1) the Amazon floodplain would present greater environmental heterogeneity and beta diversity due to the greater spatial extent sampled and the absence of dams. The Upper Paraná River floodplain would present lower environmental heterogeneity and beta diversity because this system suffers from the effects of several dams, which could lead to species and trait homogenization (Braghin et al. 2018). Additionally, (2) during the rainy season, we expected to observe lower values of taxonomic and functional beta due to the homogenization effect; the opposite was also true, higher beta values would be observed during periods of drought due to greater environmental heterogeneity. Finally, (3) during the rainy season limnological variables would be important in structuring functional and taxonomic beta diversity. During the dry period, factors related to ecological interactions (food availability and predation) and spatial components would be more important in structuring zooplankton taxonomic and functional beta diversity due to the strength of local factors and the limitation of dispersal.

Methods

Study area

This study was conducted on two large Brazilian floodplains, the Amazon River and the Upper Paraná River (Fig. 1). The geographic coordinates of each sampling site are shown in Supplementary material Table S1. The Amazonian floodplain includes areas flooded
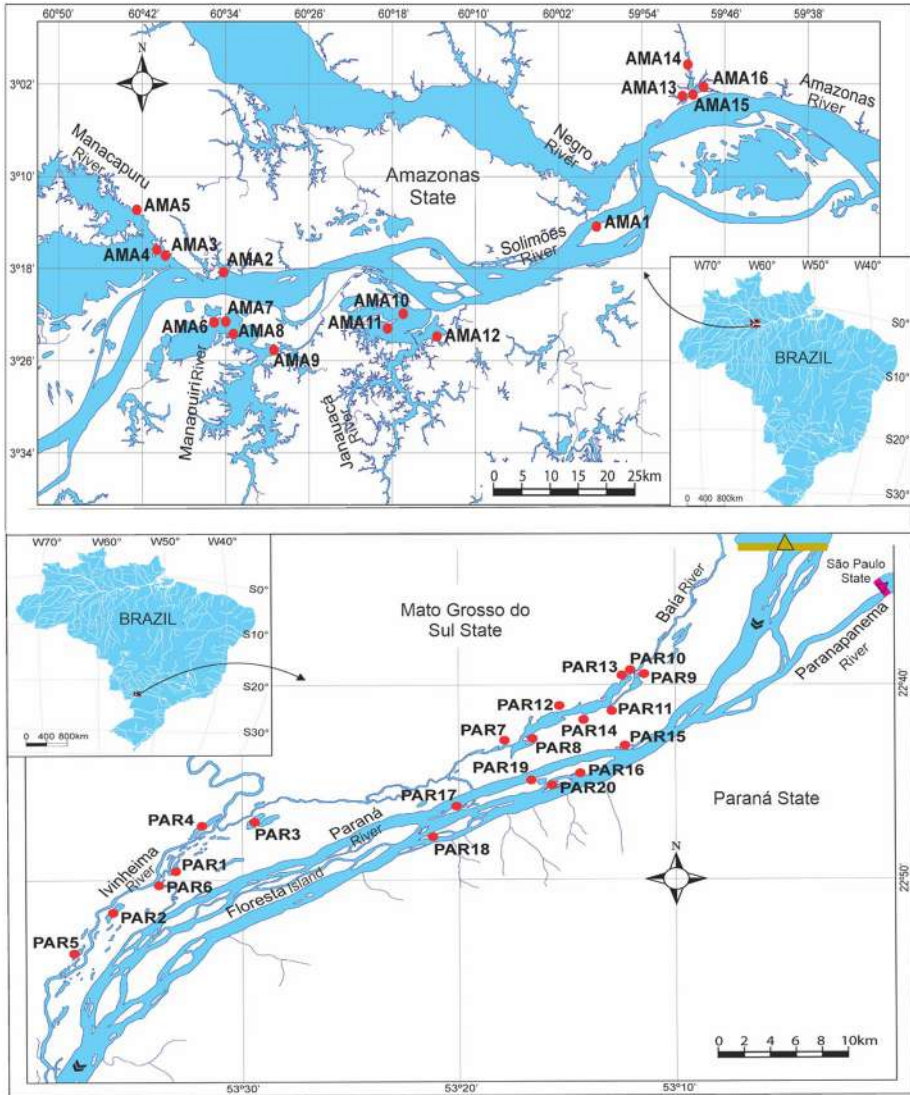

Fig. 1 Sampling sites (red points) in the **(a)** Amazon floodplain (AMA) and **(b)** Upper Paraná River floodplain (PAR), Brazil. The dams in the Paraná system are also shown in the upper right corner of the Paraná sites, the yellow bar and triangle show the 'Engenheiro Sérgio Motta' dam and the pink bar and triangle show the 'Rosana' dam

by large rivers of "white waters" (brownish), such as the Amazonas/Solimões River and its tributaries, the Purus, Juruá, and Madeira River, which together cover approximately 400,000 km^2. The Amazonian floodplain also includes areas flooded by rivers with black waters that have low nutrient availability, such as the Negro River and its tributaries, which together cover approximately 118,000 km^2 (Junk 1993; Melack and Hess 2010; Junk et al. 2011). The annual average rainfall varies between 2,200 mm and 3,500 mm. The flood period starts in November and reaches its peak in July; in August, the water starts to flow from the lake back to the river, and October is the driest month (Yamamoto 2004). We have samples from white and black water.

The Upper Paraná River floodplain contains a large accumulation of sediments on the main riverbed, creating islands of many sizes (from a few hundred meters to kilometers in extension). The Paraná River floodplain covers a drainage area of 802,150 km^2 in the Brazilian territory. The average annual precipitation is 1,500 mm, the flood period occurs between November and March, and the dry period occurs from May to October (Roberto et al. 2009; Souza Filho 2009). This floodplain is highly impacted by the numerous dams upstream that are leading to great sedimentation of nutrients and changing the water characteristics of the Paraná River to oligotrophic conditions (Roberto et al. 2009), with possible consequences for the development of aquatic communities and ecosystem functioning.

Sampling of biological and environmental variables

Zooplankton were sampled in 36 shallow lakes, 16 connected to the Amazon/Solimões River in the Amazon floodplain and 20 in the Upper Paraná River floodplain, which included connected and isolated lakes (Fig. 1). More information about each sampling site can be found in Supplementary material Table S1. Samples were taken during two hydrological periods (drought and rain) in the years 2011 and 2012, a total of 72 samples. Zooplankton were sampled on the surface of the pelagic region at each site. For each sample, 500 L of water were filtered through a plankton net (68 μm) using a motorized pump. The samples were stored in polyethylene bottles and fixed in 4% formaldehyde buffered with calcium carbonate. We followed the methodology described in Lansac-Tôha et al. (2009) for zooplankton identification (species from rotifers, cladocerans, and copepods) and the determination of individual densities.

The limnological variables (physical-chemical), fish (potential predators), and phytoplankton (food availability) were sampled simultaneously with the zooplankton sampling. The physical and chemical variables included depth (m), water temperature (°C), dissolved oxygen (mg/L), pH, electrical conductivity (μS/cm), turbidity (NTU), total nitrogen (μg/L), nitrate (μg/L), ammonia (μg/L), total phosphorus (μg/L), and phosphate (μg/L). The physical-chemical parameters were sampled following the methodology described by Roberto et al. (2009), and the minimum and maximum values of each physical-chemical parameter are shown in Supplementary material Table S2. The sampling method, abundance determination, and phytoplankton characterization can be found at Moresco et al. (2017). Fish were sampled with 20-meter fishing nets with a standardized effort in each lake. After capture, the fish were anesthetized with diluted benzocaine following the guidelines of the American Veterinary Medical Association (Avma 2007). The abundance of individuals was defined by the catch-per-unit effort (CPUE). All individuals captured were deposited in the Ichthyological Collection of the Research Group in Ichthyology, Limnology, and Aquaculture (Nupé-

lia) at the State University of Maringá. All the biological communities were sampled with authorization from the Brazilian Ministry of the Environment and Chico Mendes Institute for Biodiversity Conservation (ICMBio), a protocol registered under the number 29,652 in the System of Biodiversity and Information (SISBIO).

Zooplankton functional traits

We recorded 180 zooplankton taxa, 98 rotifers, 57 cladocerans, and 25 copepods. These taxa were categorized into six functional traits following previous methods described at Barnett et al. (2007) and Braghin et al. (2018). The traits were body size (mm), habitat (littoral or pelagic), type of feeding (filter-Rotifer, suctor-Rotifer, predator-Rotifer, filter-Cladocera, scraper-Cladocera, filter-Copepod, or raptorial-Copepod), escape response to the predator (low, medium, high, or maximum), reproduction (sexual or asexual), and life span (short or long) (the species list with the classification of each functional trait is shown in Supplementary material Table S3). The type, category, and ecosystem importance of each trait are described in Braghin et al. (2018). Habitat, type of feeding, escape response to the predator, reproduction, and life span were determined via literature research, while body size was obtained by measuring the body length of 20 individuals of each species. The average of these values was used in the analysis. For rotifers and cladocerans, measurements were taken according to the shape of the body, and the individuals were measured between the upper part of the head and the end of the carapace without helmets or spines when present (Ruttner-Kolisko 1974; Hardy 1989). For copepods, body length measurements were taken between the head and the last abdominal segment, except for the spines of the caudal branch (Bonecker et al. 2011).

Data analysis

All analyses in our study were performed using the R program (R Core Team, 2020), and all steps are shown in two flowcharts in Supplementary material Fig. S1. First, we calculated the total beta diversity (taxonomic and functional dissimilarity between sites) and its components for each floodplain in each hydrologic period using Sorensen's dissimilarity and incidence data (presence/absence) (R function 'beta', packages "FD" (Laliberté et al. 2014), "BAT" (Cardoso et al. 2020) and "stats" (Bolar 2019). We applied the approach proposed by Podani and Schmera (2011) and Carvalho et al. (2012), which divides the total beta component (β-total) into the components of replacement (β-repl) and richness difference (β-rich). β-repl refers only to the substitution in the identities of species/functional traits, and β-rich refers only to differences in loss or gains in the richness of species/functional traits. Thus, twenty-four dissimilarity matrices were created: three betas (total, replacement, and richness) × two approaches (taxonomic and functional) × two periods (rainy and drought) × two floodplains (Amazon and Paraná).

Second, we prepared and selected the drivers of zooplankton β-diversity. The limnological matrix was composed of the standardized physical-chemical variables using the 'decostand' function from the package "vegan" (Oksanen et al. 2019). We tested for multicollinearity between limnological variables through variance inflation factor (VIF) analysis, and variables with a VIF > 5 were excluded before statistical analysis (Oksanen et al. 2019). Food availability (matrix with phytoplankton abundance-composition) and potential fish

predation (matrix with fish abundance-composition) were summarized through Principal Coordinate Analyses (PCoA), these analyses were performed for each floodplain in each hydrologic period. The first two axes from PCoA for phytoplankton and fish were used in the analyses. For that purpose, we applied the 'pcoa' function from the "ape" package (Paradis and K. Schliep 2018).

The spatial component was obtained with the following steps: (1) the distances in kilometers between all points of each floodplain were determined with the 'path' function from "Google Earth"; (2) the distances (km) were transformed into a triangular matrix using the 'as.dist' function; (3) the triangular matrix was transformed using the Principal Coordinate Analysis of Truncated Distance Matrix (PCNM), creating a rectangular matrix through the function 'pcnm'; and (4) the axes from PCNM were selected using the Moran criterion with the function 'moran.randtest'. All functions mentioned are from the "vegan" (Oksanen et al. 2019), "adespatial" (Dray et al. 2020), and "stats" (Bolar 2019) packages. The Moran criterion ($p < 0.05$) selected the axes PCNM1, PCNM2, PCNM11, and PCNM13 for the Paraná floodplain. For the Amazon floodplain, the Moran criterion selected the axes PCNM1, PCNM2, PCNM10, PCNM11, and PCNM12.

Thus, our predictors of zooplankton taxonomic and functional β diversity were composed of four matrices for each floodplain and each hydrological period. (1) The limnological variables (Lim), (2) the phytoplankton community as food availability (Food) (PCoA axes 1 and 2, total abundance of individuals per site, and species richness per site), (3) the fish community as a variable for potential predation (Pre) (PCoA axes 1 and 2, total abundance of individuals per site, and species richness per site) and (4) the spatial component variable (Spa) (PCNM axis). For graphic representation, please see Supplementary material.

Final analysis

The environmental heterogeneity in the floodplains and hydrological periods was calculated through a permutational analysis of variance (PERMANOVA; R function 'adonis2', "vegan" package). To analyze environmental heterogeneity, we included all physical-chemical variables mentioned above, phytoplankton density and richness, and fish density and richness. The data were first standardized through the 'decostand' function. PERMANOVA was performed using "Euclidian" distance and two predictors—the floodplain and hydrological periods. $p < 0.05$ was considered to indicate statistical significance, and the results were tested using 999 permutations. We displayed the environmental heterogeneity through NMDS (nonmetric multidimensional scaling; R function 'isoMDS', package "MASS") (Ripley et al. 2019).

The distance matrices generated from functional and taxonomic beta diversity were used as response variables in the distance-based redundancy analysis (db-RDA partial, Legendre and Anderson 1999) (R function 'varpart', packages "adespatial", "ade4" (Bougeard and Dray 2018). For the final set of variables (preditors) used in the db-RDA partial, we applied forward selection with two-stop rules. The final sets of limnological variables (Lim), food availability (Food), potential predators (Pred), and spatial components (Spa) that influence the taxonomic and functional beta diversity (β-total, β-repl, and β-rich) in each hydrological period and each floodplain are shown in Supplementary material Table S4. To analyze the relative contributions of the pure and shared effects of the variables Lim, Food, Pred, and Spa to explaining the taxonomic and functional beta diversity, we performed variance par-

titioning (Peres-Neto et al. 2006) (R function 'capscale' and 'varpart' of package "vegan")
and tested the results using ANOVA (R function 'anova').

Results

Environmental heterogeneity

The Amazonian floodplain showed greater environmental heterogeneity than the Paraná
floodplain (PERMANOVA: pseudoF = 8.08; $p < 0.001$). Similarly, the drought period
exhibited greater environmental heterogeneity than did the rainy period (pseudoF = 14.69;
$p = 0.001$; Fig. 2).

Zooplankton functional and taxonomic β-diversity

In general, zooplankton taxonomic β-diversity presented higher values than functional
β-diversity and both had similar patterns related to the hydrologic periods and floodplains,
except for the Upper Paraná during drought (Fig. 3). Additionally, in general, β-replacement
contributed more than β-richness to the β-total.

When we compared taxonomic β-diversity between floodplains, during the rainy period,
β-total and β-replacement were slightly greater in the Paraná floodplain (β-Tot: 0.60, β-repl:
0.42) than in the Amazon floodplain (β-Tot: 0.53, β-repl: 0.39); i.e., during the rainy period,
greater species dissimilarity/replacement was observed between sites in the Paraná flood-
plain than in the Amazon floodplain. During drought, the β-richness (taxonomic) contrib-
uted more to the β-total in the Paraná than in the Amazon floodplain; i.e., large differences
in species richness between sites were observed. Additionally, in the Amazon floodplain,
the values of β-total taxonomic was slightly greater during drought (0.60) than during the

Fig. 2 Environmental hetero-
geneity for each floodplain and
hydrological period. AMA = Am-
azon floodplain, PAR = Upper
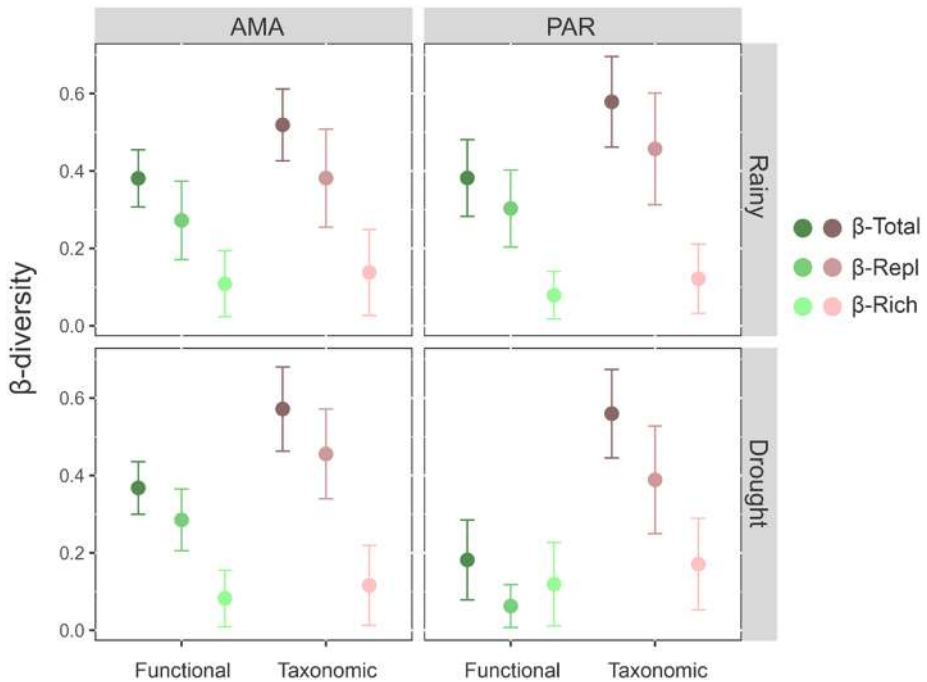Paraná River floodplain
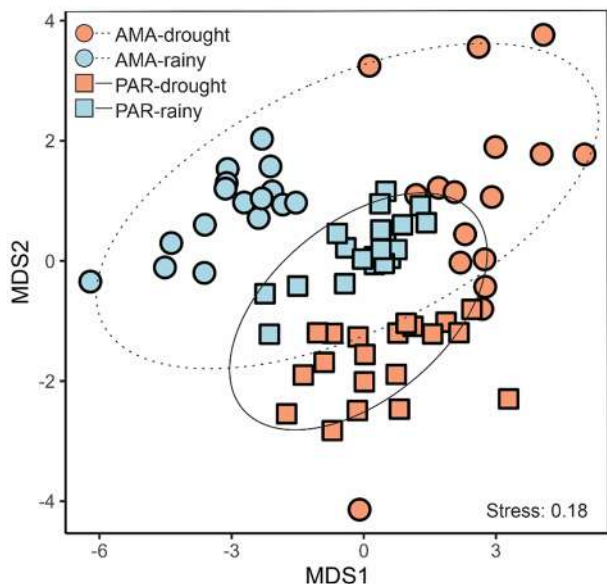
Fig. 3 Zooplankton functional and taxonomic beta diversity in the Amazon River floodplain (AMA) and Upper Paraná River floodplain (PAR) in the two hydrological periods. Total beta diversity=β-total, replacement=β-repl, and richness difference=β-rich. The central lines denote the median values, boxes denote the 25th and 75th percentiles, and whiskers represent the smallest and largest values, respectively, within 1.5 times the interquartile range below and above the percentiles

rainy period (0.53), i.e., greater differences in species composition occurred between sites during the drought period. In the Paraná floodplain, no differences were observed in the total β-taxonomic between the hydrological periods (Fig. 3).

For functional β-diversity, more expressive changes were observed in the Paraná floodplain during the drought period, which presented a very low β-total (0.18) with a greater contribution of β-richness (0.11) than β-replacement (0.06); i.e., differences in trait richness contributed more to total dissimilarity than trait replacement. The values of functional β-total were the same in the rainy period for both the Amazonian floodplain and the Upper Paraná River (0.38). Amazon also had similar functional β-total values between the rainy and drought periods (Fig. 3).

Drives of zooplankton taxonomic and functional beta diversity

The variables chosen by the forward selection method were different for each predictor (limnological, food, predation, and spatial component), hydrological period (drought and rainy), beta component (β-total, β-repl, and β-rich), and taxonomic and functional beta diversity. In general, limnological variables were more related to nutrient availability, depth, temperature, and dissolved oxygen. The variables selected for food availability were the density and richness of phytoplankton and the axes from PCoA (see methodology). Vari-

ables selected for predation were related to the PCoA axes. The variables selected for the spatial component were the PCNM axes 1, 2, and 11 (for more details, see Supplementary material Table S4).

The models with greatest explanation for β-taxonomic were observed for the β-richness component in the Paraná floodplain during the rainy period (70%) and the drought period (41%), as well as in the Amazon floodplain during the drought (63%) and rainy periods (53%) (Fig. 4). In general, the limnological variables were the most important component for structuring the variation in zooplanktonic taxonomic β-diversity in both floodplains and during both periods, especially for β-richness in the Paraná floodplain (drought=18%, rainy=21%; Fig. 4k, l). The second most important driver of β-taxonomic was food availability, especially for β-richness in the Amazon floodplain during the drought period (24%) and in the Paraná floodplain during the rainy period (31%) (Fig. 4e, l). Predation was important for explaining the variation in β-richness in the Amazonian floodplain in both periods (drought=13% and rainy=12%; Fig. 4e, f). The spatial component explained 9% of the variation in β-replacement in the Amazon floodplain during the rainy period and 7% of the variation in β-richness in the Paraná floodplain during the drought (Fig. 4d, k).

The models with greatest explanation for β-functional was observed in the Upper Paraná River floodplain for β-richness (rainy=62% and drought=56%; Fig. 5k, l). The shared
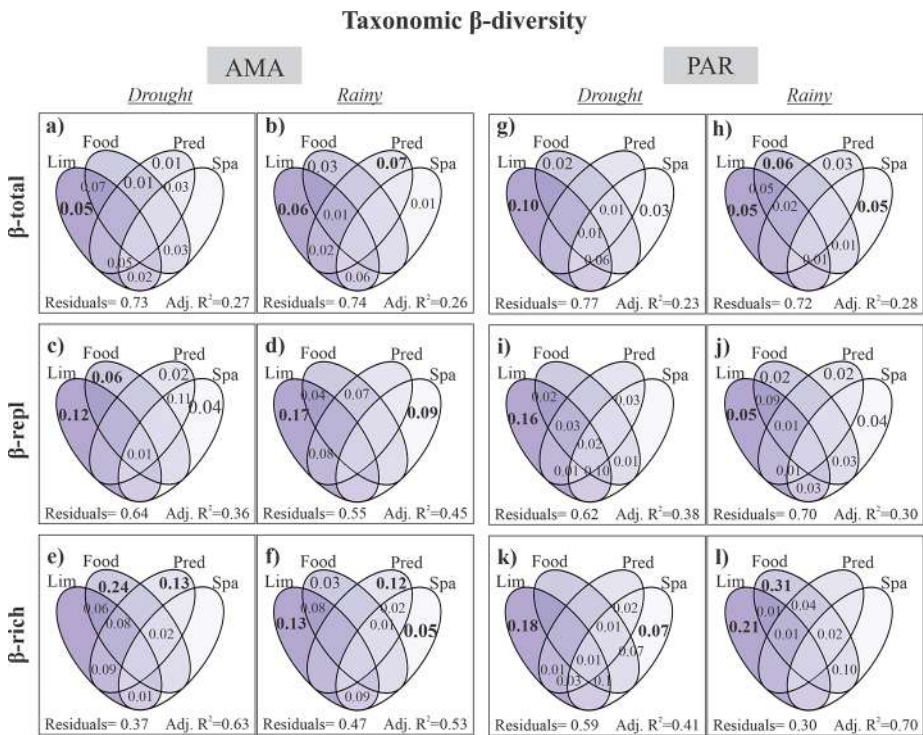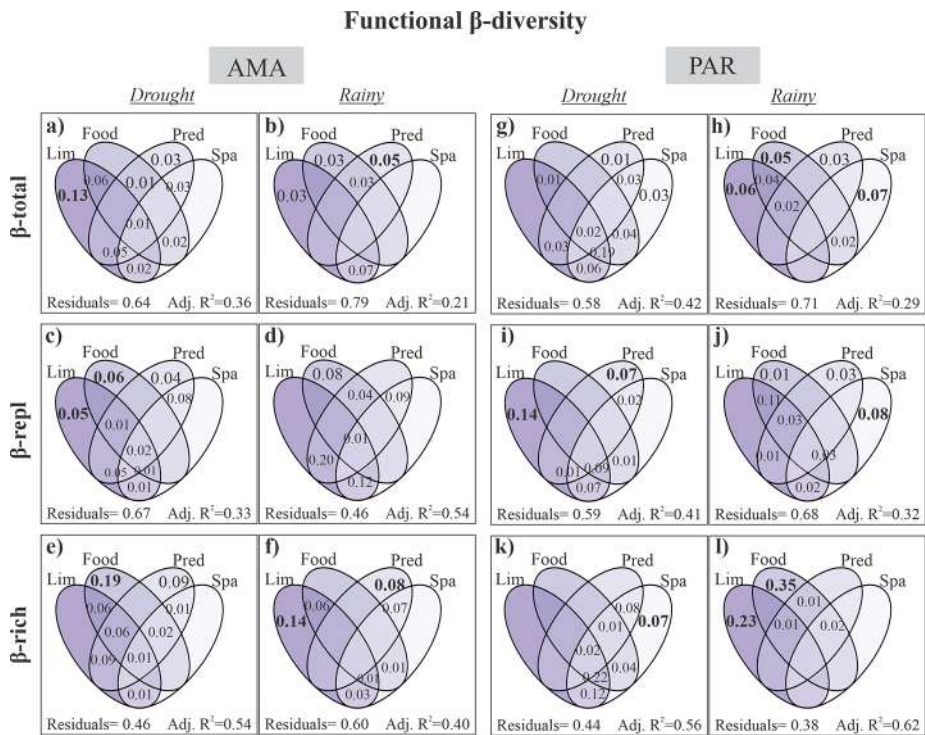

Fig. 4 Relative contributions of limnological variables (Lim), food availability (Food), predation (Pred), and spatial component (Spa) to zooplankton taxonomic beta diversity (β- Total, β-repl, and β-rich) in each hydrological period. a, b, c, d, e, and f are the results of the Amazon River floodplain (AMA), and g, h, I, j, k, and l are the results of the Upper Paraná River floodplain (PAR). The values represent the adjusted R^2 values. Negative fraction values are not shown. Values in bold represent significant results ($p < 0.05$)

Fig. 5 Relative contributions of limnological variables (Lim), food availability (Food), predation (Pred), and spatial component (Spa) to zooplankton functional beta diversity (β-Total, β-repl, and β-rich) in each hydrological period. a, b, c, d, e, and f are the results of the Amazon River floodplain (AMA), and g, h, I, j, k, and l are the results of the Upper Paraná River floodplain (PAR). The values represent the adjusted R^2 values. Negative fraction values are not shown. Values in bold represent significant results ($p < 0.05$)

proportions between predictors had great importance in explaining the variation in zooplankton functional β-diversity (Fig. 5). The limnological variables in the Paraná floodplain explained 23% of the variation in β-richness during the rainy period and 14% of the variation in β-replacement during the drought period (Fig. 5l, i). In the Amazon floodplain, limnological variables explained 14% of the variance in β-richness during the rainy season (Fig. 5f). Food availability explained the variation in β-richness in the Amazonian floodplain during the drought period (19%) and in the Upper Paraná River floodplain during the rainy period (35%) (Fig. 5e, l). Predation explained 9% and 8% of the functional β-richness in the Amazon floodplain during the drought and rainy periods, respectively (Fig. 5e, f). The spatial component explained 7% of the variation in the β-total and 8% of the variation in the β-repl in the Paraná floodplain during the rainy period (Fig. 5h, j); moreover, it explained 7% of the β-richness in this floodplain during the drought period (Fig. 5k).

Discussion

In general, we observed that the two functional and taxonomic approaches produced different patterns for the zooplankton community in response to hydrological periods, and the functional approach was more sensitive to catch environmental changes, especially the differences between beta richness and replacement. As expected, the Amazon floodplain presented greater environmental heterogeneity; however, this heterogeneity was not reflected in greater beta diversity, which partially corroborates our first hypothesis. We did not observe significant differences of environmental heterogeneity and beta diversity between the seasons (rejecting our second hypothesis), except for functional beta diversity in the Paraná floodplain during the drought period that presented the lowest values. This low functional beta was explained by predation and the spatial component. Moreover, different than expected, all factors influenced the taxonomic beta diversity (total and its components) in both floodplains in both hydrological periods, without a clear pattern. However, physical-chemical variables were important drivers of functional beta diversity during the rainy period, while food resources, predation, and spatial components explained functional beta diversity during the drought period, partially corroborating our third hypothesis.

The Amazon and Paraná floodplains have different historical characteristics, geomorphologic formations, species colonization, sizes, rainfall volumes, and basin use (Perbiche-Neves et al. 2014). All these factors create distinct environmental conditions that can reflect different spatial and temporal environmental and biological heterogeneity (Thomaz et al. 2007; Bozelli et al. 2015; Heino et al. 2015a), as observed. The Amazon floodplain presented great environmental heterogeneity and slightly greater taxonomic beta diversity during the drought period than during the rainy period, with a greater contribution from the replacement component. Taken together, these findings show that, in general, the environments of the Amazon floodplain strongly replace species and traits throughout the hydrological period; however, during drought periods, replacement can increase. The factors that drove species replacement in the Amazon during drought were related to limnological variables (most related to nutrients; see Supplementary material) and predation. The flood period creates severe changes in physical-chemical variables, increasing depth, turbidity, and nutrient availability, which affect zooplankton (Lansac-Tôha et al. 2009; Simões et al. 2013). Nutrients such as phosphate and nitrate are proxies for productivity and are linked to increased food availability, favoring the development of zooplanktonic organisms (Jeppesen et al. 2000; Auer et al. 2004). Predation by fish has already been reported to drive zooplankton functional traits (Bomfim et al. 2021; Deosti et al. 2021). During flood periods, there is great dispersion of these predators and the arrival of their offspring (Fernandes et al. 2009), which can increase predation on zooplankton.

In general, the Paraná floodplain also presented a greater contribution of the replacement component than richness-difference, except during the drought period, when beta richness was greater than beta replacement and the total functional beta was very low. This pattern was not observed for taxonomic beta diversity, which showed a high substitution of species between the environments in the Paraná floodplain, but they were functionally similar. This low functional dissimilarity can be a reflection of the dam effects that control flood pulses and lead to prolonged periods of drought (Bertoncin et al. 2019), strengthening environmental filters (Chase 2007) and selecting functional traits. Braghin et al. (2018) reported that dams can decrease zooplankton functional beta diversity. Additionally, Bomfim et al.

(2021) and Diniz et al. (2023) showed that extreme drought periods also reduce zooplankton functional and taxonomic beta diversity, in agreement with our data.

Dams in the Paraná River have caused several environmental changes in recent years, especially related to oligotrophication and the consequent loss of biodiversity (Roberto et al. 2009; Braghin et al. 2018; Bertoncin et al. 2019). A natural flood pulse is essential for maintaining environmental heterogeneity, the exchange of functional traits among environments, and ecosystem functions in the Paraná floodplain (Pineda et al. 2019; Bomfim et al. 2021; Diniz et al. 2023). Another point to be considered is that extreme droughts are expected to increase with climate change (Cai et al. 2015; Cavalcantti et al. 2015), which can aggravate this scenario. Predation and spatial components were important for explaining this low functional beta diversity. The nonexistent connection between environments limits zooplankton and fish dispersion; therefore, no species arrives at these sites, and the conditions are harsh, which leads to stronger filtering (Chase 2007; Gianuca et al. 2017) and the selection of a few traits, reflecting low zooplankton beta diversity. This effect is stronger during drought and milder in other seasons, which can explain the replacement of species and traits between sites during the rainy season in this system.

Regarding the drivers of beta diversity in the hydrological periods, although the taxonomic beta diversity did not show a clear pattern, the functional beta diversity had different drivers depending on the hydrological period. The highest explanatory power during the rainy period, regardless of the floodplain, were related to food availability and physical-chemical variables (Fig. 5l and f), while during the drought period, food availability, spatial component, and predation were important for explaining zooplankton functional beta diversity (Fig. 5e and i). Our findings reinforce the sensitivity of the functional approach to environmental changes and the strength of niche processes during drought periods (Heino et al. 2015b; Gianuca et al. 2017).

The flood period leads to drastic changes in physical-chemical variables and can strongly influence the structure of the zooplankton community (Lansac-Tôha et al. 2009; Simões et al. 2013), as mentioned above. Phytoplankton, which represents food availability, are the preferred type of food for zooplankton, especially nanoplanktonic and picoplanktonic unicellular algae (Colina et al. 2016; Bomfim et al. 2018), and have already been reported to drive zooplankton functional beta diversity (Bomfim et al. 2021). Predation is another main driver of zooplankton structure shaping β-diversity (Antiqueira et al. 2018; He et al. 2018) in both hydrological periods, as reported by Bomfim et al. (2021). Predation can influence the distribution of functional traits (Sodré and Bozelli 2019) because selects large-bodied organisms (Iglesias et al. 2011), species with slow growth, large clutches, and a slow-scape response (Santangelo et al. 2018). The spatial component was important in the Paraná floodplain in both periods and across approaches (taxonomic and functional); this component is more related to dispersion processes and can work on both sides, favoring or restricting dispersion (Hill et al. 2019). During drought, the sites become more isolated, and dispersion is restricted, leading to a more dissimilar community composition, while the flood pulse during the rainy season leads to greater dispersion and lower dissimilarity (Padial et al. 2014). However, at some level, the influence of dispersion on community structure can be weakened during flood periods. This occurs because floods also intensify environmental filters such as depth and turbidity (Simões et al. 2013). Thus, when organisms reach sites through dispersion, environmental filters select the species able to survive those conditions (Bonecker et al. 2009; Cadotte and Tucker 2017), and the communities can be dissimilar.

Despite the environmental differences in the two systems and seasons, we observed that the genera *Lecane* and *Brachionus* were the most common when considering all samples (Table S3). Similar for the traits small-bodied, filter feeders, asexual reproduction, and short life-cycle. These species and traits reflect opportunistic strategy, organisms with low predation risk and that take advantage of sudden environmental changes such as increased food availability, they respond to these fluctuations with fast growth and reproduction becoming dominant in the communities (Ciros-Perez et al., 2015). This can explain their prevalence throughout our samples.

Conclusions and implications for ecosystem conservation

The biodiversity and ecosystem services of both floodplains analyzed are threatened; the Amazon, by future hydroelectric projects; and the Paraná, by several dams transforming this system. In general, zooplankton beta diversity had a greater contribution from replacement than richness differences, regardless of the hydrological period, except for functional richness in the Paraná floodplain during drought. Therefore, for conservation purposes, efforts should consider preserving as many lakes as possible in both floodplains, as they present unique compositions of species and traits, and priority should be given to sites with complementary communities (Socolar et al. 2016; Ambrožová et al. 2022). Additionally, high values of beta replacement can be attributed to the species' tolerance to environmental filters or historical events (Gaston and Blackburn 2000; Qian et al. 2005). In our case, we believe that the high values of beta replacement are due to the hydrological dynamics of the flood pulse that maintain the exchange of species and traits between environments, creating a heterogeneous composition over time (Pineda et al. 2019; Bomfim et al. 2021; Diniz et al. 2023). Zooplankton is essential for ecosystem functioning, and alterations in this community can disrupt energy flow, affecting other levels inside the food chain (Declerck and de Senerpont Domis 2023). Thus, we emphasize the need to plan conservation strategies in these floodplains, especially considering that the functional homogenization observed in the Paraná floodplain is an effect of dams and that the Amazon floodplain is threatened by the same problem.

Author contributions Conceptualization: DCA, FFB, FALT; Data curation: DCA; Formal analysis: FFB; Funding acquisition: FALT; Investigation: DCA, FFB; Methodology: DCA, FFB; Project administration: FALT; Resources: FALT; Supervision: FALT; Visualization: FFB; Roles/Writing - original draft: DCA, FFB, FALT, and Writing - review & editing: DCA, FFB, FALT.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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