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ECOSYSTEMS

Environmental heterogeneity drives the distribution of copepods (Crustacea: Copepoda) in the Amazon, Araguaia, Pantanal, and Upper Paraná floodplains

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Abstract: Environmental heterogeneity influences the physiology and behavior of organisms, leading to alterations in populations, communities, and ecosystems. This study was designed to evaluate the effect of the spatial and temporal limnological heterogeneity on the distribution of copepods in the Amazon River floodplain, Araguaia River floodplain, Pantanal floodplain, and Upper Paraná River floodplain. We performed dispersion homogeneity tests (PERMIDISP) to analyze the limnological heterogeneity, a Generalized Linear Mixed Model (GLMM) to test the relationship between limnological heterogeneity and species distribution, and a Canonical Correspondence Analysis (CCA) to analyze which limnological variables explain the variation in the community composition. In our study, we observed higher environmental heterogeneity during dry periods, especially in the Amazon floodplain. The Amazon showed the highest species richness (the total number of species that occurred in each floodplain), with endemic species, also the highest abundance of individuals, especially during dry periods, which was possibly due to the biogeography, the size of the basin, and the heterogeneity of the environments. The Pantanal presented the second highest species richness and showed the highest species richness and abundance of individuals during rainy periods. The distribution of copepods was highly correlated with environmental heterogeneity**.** The species were mainly related to temperature, nutrients, and depth.

Key words: Niche, spatial distribution, temporal distribution, zooplankton.

INTRODUCTION

Environmental heterogeneity plays a key role in the dynamics of freshwater ecosystems (Stein et al. 2014, Gianuca et al. 2017, Peláez & Pavanelli 2019). This means that changes in physical and chemical conditions influence the physiology and behavior of organisms, leading to alterations in the fluctuation of populations, in ecological interactions, in communities' organization and thus, in ecosystem process (Rietzler et al. 2002, Landa et al. 2007, Tundisi & Matsumura-Tundisi 2008). Heterogeneity represents a relevant tool for identifying the biotic variability in freshwater environments (Bozelli et al. 2015). More heterogeneous environments also offer more niches, allowing high species diversity (Heino et al. 2015).

Floodplains are considered highly heterogeneous environments as the environmental variables fluctuate according to the flood pulse (Neiff 1996, Bozelli et al. 2015). During low water periods, rivers, lakes, and blackwaters become isolated, and physical and chemical characteristics diverge among these environments, while during flood periods, these environments are connected, and the limnological variables tend to become more similar (Thomaz et al. 2007). Thus, these fluctuations occur on a spatial (among lakes and rivers) and temporal scale (between periods – dry and rainy). During the dry period, when the lakes became isolated, there is also a more restricted dispersion of microorganisms, increasing the dissimilarity in species composition, but dispersion is still possible by means of wind and animals, such as birds (Pinceel et al. 2016, Hessen et al. 2019). Consequently, in these systems, lakes exhibit large seasonal changes in the water's physical and chemical characteristics that are attributed to morphometry and wind exposure (Bovo-Scomparin & Train 2008). These fluctuations in physical and chemical factors might result in changes in the species composition and in the abundance of individuals in aquatic communities (Thomaz et al. 2007, Lansac-Tôha et al. 2009, Pineda et al. 2019).

Zooplankton communities respond to spatial and temporal variation in environmental characteristics (Landa et al. 2007, Aranguren-Riaño et al. 2011, Lopes et al. 2014, Pineda et al. 2019). Studies in the Upper Paraná River floodplain showed that the zooplankton structure is altered by fluctuations in limnological variables, the flood duration, and the characteristics of the river causing that flood (Lansac-Tôha et al. 2004, 2009, Braghin et al. 2015). Zooplankton displays a role in nutrient cycling, representing the link between the producers and the other components of herbivory and the bacterial food chain (Auer et al. 2004, Segovia et al. 2015), and providing energy for high trophic levels.

For copepods, some studies have demonstrated a strong relationship between these organisms and environmental factors such as the trophic status of the environment (especially for Cyclopoids - Gazonato Neto et al. 2014, Perbiche-Neves et al. 2016, Macedo et al. 2019), biogeography, basin size (Perbiche-Neves et al. 2014b), and the relationships inside aquatic food-webs (Segovia et al. 2015). Despite many studies with copepod distribution, there is still a lack of information related to species distribution in Brazilian floodplains, what are the limnological variables related to these distribution and and whether the differences in copepods' abundance and occurrence are related to environmental heterogeneity, especially during different hydrologic periods.

In this way, this study was designed to evaluate the effect of limnological heterogeneity on the distribution of planktonic copepod species in different Neotropical floodplains (Amazon River, Araguaia River, Pantanal, and Upper Paraná River) during the dry and rainy periods. We hypothesized that the differences in the distribution of species and abundance of individuals will be positively related to the environmental heterogeneity and that copepod species will be related to different limnological variables (such as temperature and depth) that represent each hydrologic period.

MATERIALS AND METHODS

Study area

This study was conducted in four large South American floodplains in Brazil: the Amazon River, Araguaia River, Pantanal, and Upper Paraná River (Figure 1). In the Amazon floodplain, floodable areas of large whitewater rivers, like the Amazon/Solimões and its tributaries, Purus, Juruá and Madeira, cover about 400,000 km^2 and are regionally known as *várzeas*. On the other hand, areas of blackwater rivers, such as the Negro River and its tributaries, cover about 118,000 km^2, have low fertility and are called *igapós* (Junk 1993, Melack & Hess 2010, Junk et al. 2011). The mean annual rainfall ranges from 2,200 mm to 3,500 mm. Samples were collected in whitewater environments and in

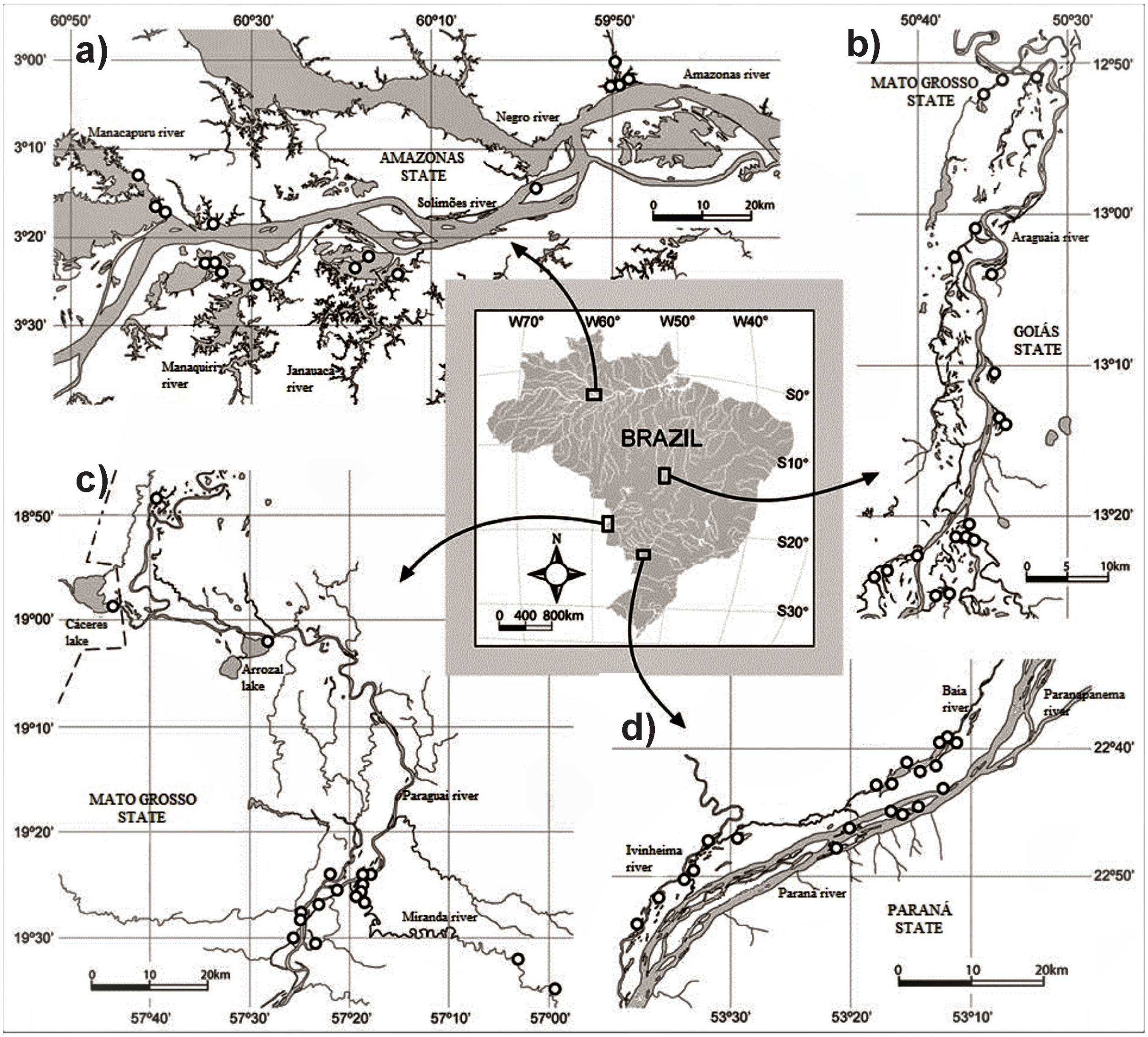

Figure 1. **Study area with the location of the sites sampled in each floodplain: a) Amazon River; b) Araguaia River; c) Pantanal and d) Upper Paraná River, Brazil.**

environments influenced by blackwater rivers. Usually, the flood period begins in November and reaches its maximum in July, with the ebb beginning in August when the water flows from the lake to the river; October is the driest month (Yamamoto et al. 2004).

The Araguaia River basin can be divided into three sub-regions: lower, middle and upper Araguaia, with a total area of approximately 377,000 km^2 and a mean annual rainfall of 2,000 mm. This river is part of the Araguaia-Tocantins watershed, which is one of the most important river systems in South America, since its catchment area includes two phytogeographic regions housing important biodiversity: The Amazon rainforest to the north and the Cerrado to the south. In this floodplain, the flood period occurs between November and April, while the dry period is from May to October (Latrubesse & Stevaux 2002, 2006).

The Pantanal is one of the largest continuous wetlands in the world, occupying, in the Brazilian states of Mato Grosso and Mato Grosso do Sul, an area of 138,183 km^2, with annual rainfall amounts of around 1,000 - 1,500 mm (Silva & Abdon 1998, Leandro & Souza 2012). The study area comprises the sub-regions of the Paraguay and Miranda rivers. In the Upper Paraguay River region, the rainy period is between January and April, and the dry period is between June and September (Assine & Silva 2009).

The Upper Paraná River floodplain shows a large accumulation of sediment in the bed of the main river, forming sandy bars and islands of various sizes (from a few hundred meters to kilometers in length). The floodplain covers an area of about 802,150 km^2 in Brazilian territory, and the mean annual rainfall is 1,500 mm. The flood period is usually between November and March, and the dry period is from May to October (Souza-Filho & Stevaux 2004, Roberto et al. 2009, Souza-Filho 2009).

Sampling design

Samples were taken from 72 lakes connected to the main river or tributary in the four floodplains: Amazon (16 lakes), Araguaia (18 lakes), Pantanal (18 lakes) and Paraná (20 lakes) (Supplementary Material - Table SI). In order to analyze a greater variability in this community, samples were obtained during two hydrological periods (dry and rainy) in the years 2011 and 2012, totalizing 144 samples. Zooplankton was sampled under the water's surface in the limnetic region of each lake. For each sample, a volume of 500 liters of water was filtered through a plankton net (68 μm), with a motorized pump. Samples were stored in polyethylene vials and fixed in 4% formaldehyde buffered with calcium carbonate.

In the laboratory, the identification of copepod species was performed using specialized literature (Brandorff 1978, Sendacz & Kubo 1982, Dussart 1984, Reid 1985, Santos-Silva 2000, Lansac-Tôha et al. 2002, Silva 2003, Perbiche-Neves et al. 2015b). The copepod community abundance was determined by counting organisms in a Sedgewick-Rafter chamber from three subsequent subsamples obtained using a Hensen-Stempell pipette (2.5 mL). In these three subsamples, at least 50 adults were counted. Samples with low numbers of organisms were counted in full. The final density was expressed in individuals m^{-3}.

Environmental variables were measured, and water samples were taken for analysis in the laboratory, concomitant to the zooplankton sampling. Water temperature (°C) and dissolved oxygen (mg L^{-1}) were determined using a portable digital oximeter YSI coupled with a thermometer. The pH and electrical conductivity (μS cm^{-1}) were measured using a portable digital potentiometer (Digimed). Turbidity (NTU) was obtained using a portable turbidimeter. Concentrations of total nitrogen (μg L^{-1}) and phosphate (μg L^{-1}) were determined according to Mackereth et al. (1978), and concentrations of nitrate (μg L^{-1}), ammonia (μg L^{-1}) and total phosphorus (μg L^{-1}) were determined according to Giné et al. (1980), Koroleff (1976) and Golterman et al. (1978), respectively. To determine the concentration of chlorophyll-a (μg L^{-1}), water aliquots were filtered through glass fiber filters (Whatman GF/F), and the pigments were 90% acetone extracted and read on a spectrophotometer at 663 nm, being corrected to other dissolved compounds and turbidity (Golterman et al. 1978).

Data analysis

In order to analyze the environmental heterogeneity in each floodplain (the floodplain being the factor) in the distinct hydrologic periods, two dispersion homogeneity tests (PERMDISP) (Anderson et al. 2006) were performed, one for each period (dry and rainy). A distance matrix was created for each limnological variable (cited above), and the centroid average distance for each floodplain was calculated. The significance of the distances to the centroid among floodplains was tested through a permutation test (999 repetitions) using the function "permutes" and the package "vegan" in R (Oksanen et al. 2019).

We created species accumulation curves for each floodplain and period (dry and rainy) separately to explore spatial and temporal patterns of alpha, beta and gamma diversity, using the package "vegan" (Oksanen et al. 2019) and the function "specaccum" in R. We also performed two PERMIDISP tests (one for each period) to obtain the homogeneity of the dispersions in the abundance of individuals and occurrence of the species; for that, we first transformed the matrix with the abundances/species/sites into distances through the "Bray Curtis" method and then concluded the PERMIDISP tests with the floodplain as centroid (factor). These distances to the centroids are called here species distribution, which are the differences in species composition and the abundance of individuals among the sites sampled inside each floodplain and in each period.

To test the relationship between the distribution of copepods and the heterogeneity in each period (rainy and dry period) two Generalized Linear Mixed Models (GLMM; Schall 1991) (one for each period) with Gaussian family were performed, using the floodplains as the random factor. The response variable was the abundances/species/sites transformed by the PERMIDISP, and the predictor variable was the environmental heterogeneity also generated by the PERMIDISP. The model significance ($p < 0.05$) was tested through an ANOVA. For these analyses, we used the packages "vegan" (Oksanen et al. 2019) "MASS" (Ripley et al. 2019), "car" (Fox et al. 2019) in R.

Finally, to better explore the data and identify the most important limnological variables related to copepod abundances in each hydrologic period (dry and rainy), a Canonical Correspondence Analysis was performed (CCA; Legendre & Legendre 2012). The results were based on the percentage of inertia explained, following the forward selection model, according to the Akaike Information Criterion (AIC). The significance of the association between the matrices and retained axes ($p < 0.05$) was tested using a permutation test with 999 permutations (Legendre et al. 2011). To standardize the abundance of individuals per species, values were transformed into the square root. For these analyses, we used the package "vegan" (Oksanen et al. 2019) in R. The graphics were built using the package "gglopt2" (Wickham et al. 2019). For all analyses and graphics, we used the program R Core Team (2013).

RESULTS

Environmental heterogeneity

The PERMIDISP results revealed that the floodplains displayed different environmental heterogeneity during the dry period ($p = 0.001$). The highest value of environmental heterogeneity was observed for the Amazon, with a mean value of 3.5 and the lowest for the Araguaia (mean value of 2.0) (Figure 2). The Amazon environmental heterogeneity differed from that of the Araguaia and Paraná ($p = 0.001$ and 0.009 respectively), and the Araguaia from the Pantanal ($p = 0.008$). During the rainy period, the environmental heterogeneity was not significantly different between floodplains (Figure 2, for more details please see Table SII).

Copepod community

The copepod community was represented by 31 species in this study, across all samples

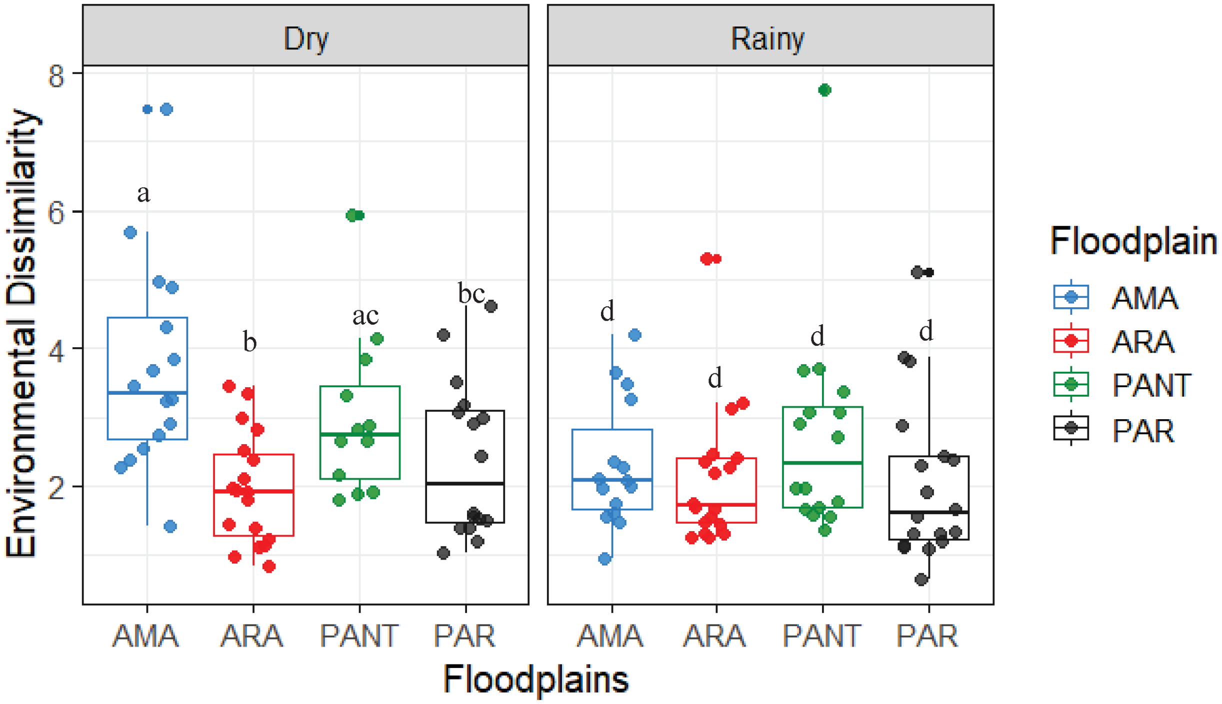

Figure 2. Limnological heterogeneity generated by the PERMIDISP analyses for both hydrologic periods (dry and rainy), in each floodplain. AMA = Amazon, ARA = Araguaia, PANT = Pantanal, PAR = Upper Paraná. The central lines denote the median value, box denotes 25th and 75th percentiles, whiskers represent respectively the smallest and largest value within 1.5 times in interquartile range below and above percentiles, and dots are the observed values. Letters above the columns indicate significant differences in posthoc analyses - floodplains that share a letter do not differ significantly, $p < 0.05$).

(Table SIII); 14 of them occurred in two or more floodplains. The Amazon floodplain presented the highest species richness (gamma diversity) with 17 species (14 in each period). The Amazon floodplain had higher alpha, beta and gamma diversity compared to the other floodplains, in both season (Figure 3). The Pantanal showed the second highest gamma diversity with 14 species (12 during the dry period and 10 during rainy) (Figure 3). In the Paraná floodplain, 13 species were observed (10 during rainy and eight during the dry period), and in the Araguaia floodplain 10 species (eight in each period) (Table SIII). Through the accumulation curve, the Araguaia and Paraná floodplains showed a stabilization trend in the species number (alpha and beta diversity) related to the sampling effort in both hydrologic periods, especially during the dry period (Figure 3).

During the dry period, the highest values for copepod abundance were found in the Amazon River floodplain, which varied between 45 and 133,334 ind.m^{-3}. In the Araguaia River floodplain, copepod abundance during this period ranged from 2 and 27,841 ind.m^{-3}. In the Upper Paraná River floodplain, the values ranged between 5 and 8,777 ind.m^{-3}. In the Pantanal, abundance values varied between 6 and 102 ind.m^{-3}. During the rainy period, the Upper Paraná River floodplain showed the highest abundance values, with values ranging from 10 to 3,300 ind.m^{-3}; followed by the Amazon River floodplain, ranging from 10 to 2,601 ind.m^{-3}. In the Pantanal, the abundance of copepods varied between 2 and 1,281 ind.m^{-3}.

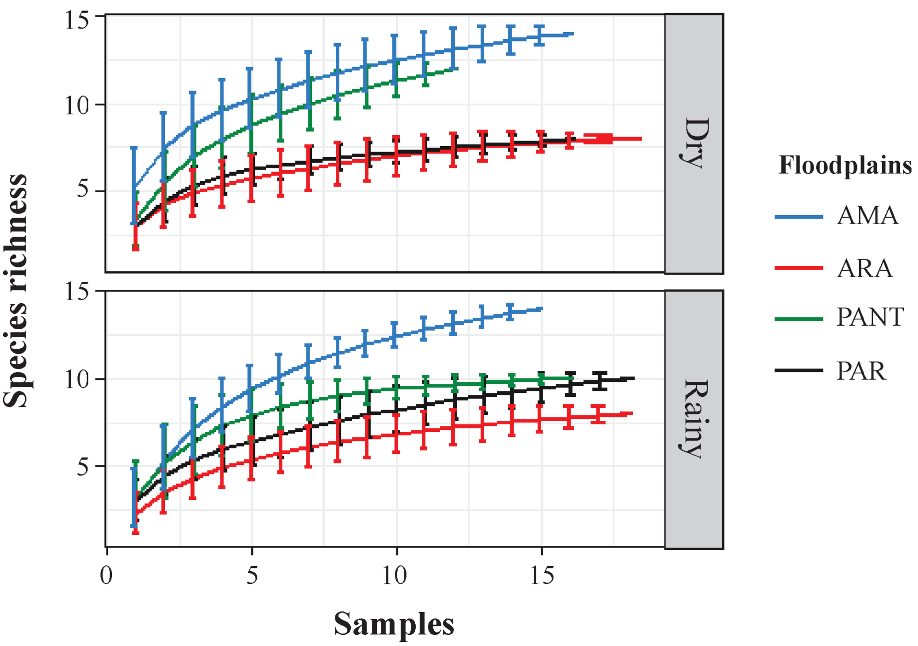

Figure 3. Accumulation curves displaying the species richness (number of species) per sampling effort (samples) in both hydrologic periods (dry and rainy) and in each floodplain (AMA=Amazon, ARA=Araguaia, PANT=Pantanal, and PAR = Upper Paraná). The central lines denote the median value, whiskers represent standard deviation (±SD).

In the Araguaia floodplain, copepod abundance ranged from 4 to 66 ind.m^{-3}.

The contribution of each species to the total abundance of individuals changed depending on the hydrologic period and floodplain. In the Amazon floodplain during the dry period there was a similar distribution in the abundance of individuals of the following species: *Thermocyclops decipiens* (approx. 27%), *Notodiaptomus simmilimus* (approx. 25%) *Oithona amazonica* (approx. 23%), *Notodiaptomus amazonicus* (approx. 20%), contrary to the rainy period, in which only two species contributed most to the total abundance of individuals, *O. amazonica* (approx. 60%) and *Thermocyclops minutus* (approx. 30%).

In the Araguaia, during the dry period two species represented approximately 96% of the total abundance of individuals (*T. minutus* – 70% and *T. decipiens* - 26%) and during the rainy period *T. minutus* represented approx. 53% of the total abundance of individuals, followed by *T. decipiens* (approx. 12%), *Paracyclops finitimus* (approx. 10%), *Micocyclops anceps* (approx. 9%) and *Mesocyclops meridianus* (approx. 5%).

In the Pantanal floodplain, three species represented most of the total abundance of individuals during the dry period, *M. anceps* (approx. 25%), *T. decipiens* (approx. 22) and *Notodiaptomus spinuliferus* (approx. 10%); during the rainy period, two species represented approx. 95% of the total abundance of species (*T. minutus* – 75% - and *M. meridianus* – 20%). In the Paraná floodplain, two species represented the most contribution to the total abundance of individuals during the dry period (*T. minutus* – 70% -and *Notodiaptomus henseni* – 26%) and during the rainy period (*T. minutus* – 73% - and *T. decipiens* – 20%).

GLM and CCA

The GLMM showed that the community dissimilarity (based on the species abundances) was positively related to the environmental heterogeneity (dissimilarity), in all floodplains, in both hydrologic periods (rainy: df = 62, t-value = 3.23, p = 0.001 and dry: df = 57, t-value = 3.97, p = 0.000) (Figure 4). The CCA revealed that 22% and 19% of the variation in the abundance of copepods was explained by environmental

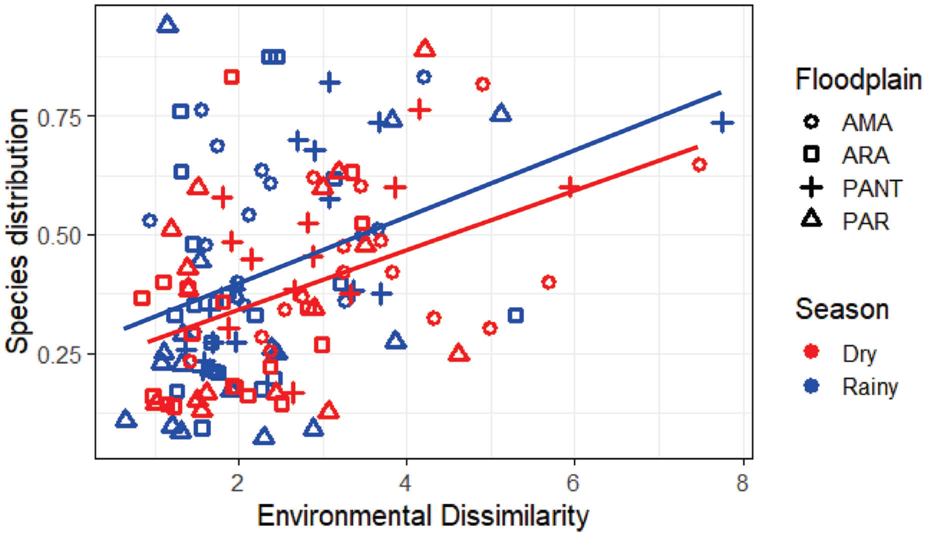

Figure 4. Scatterplot displaying GLMM results between the dissimilarity of copepod communities (PERMIDISP distances, please see methods) and the environmental heterogeneity in both hydrologic periods (dry in red and rainy in blue) in each floodplain, AMA = Amazon, ARA = Araguaia, PANT = Pantanal, PAR = Upper Paraná.

variables during the dry and rainy periods, respectively (Figure 5). The species most related to environmental variables were the ones that presented high abundance values during the corresponding hydrologic period (some species only during dry, other only during rainy, and some during both periods). Similar variables explained the distribution of copepod species in both hydrologic periods (temperature, chlorophyll, depth, and nutrients) (Figure 5).

DISCUSSION

Environmental heterogeneity has an influence on the spatial and temporal distribution of species (Bozelli et al. 2015, Heino et al. 2019), including zooplanktonic species (Gianuca et al. 2017, Pineda et al. 2019). The hydrological regime is considered the main force for limnological variability, creating a temporal fluctuation of environmental heterogeneity (Junk et al. 1989, Simões et al. 2013a). In our study, we observed higher environmental heterogeneity during dry periods, especially in the Amazon floodplain, and higher homogenization during rainy periods. The Amazon showed the highest species richness, with higher alpha, beta, and gamma diversity (independent of the hydrologic period) with endemic species, as well as higher individuals abundance, particularly during dry periods. The distribution of species and individuals was positively related to environmental heterogeneity and also related to the limnological variables, supporting our hypotheses.

In our study we identified 31 copepod species, a significant value considering that there were only two samplings per floodplain (one during dry and one during the rainy period) and only in lakes. Lansac-Tôha et al. (2009) identified 43 copepod species over eight years in different environments in the Paraná floodplain (rivers, lakes, backwaters); Palhiarini et al. (2017) also identified 29 copepods in different environments in this same floodplain over two years of sampling, whereas Perbiche-Neves et al. (2014a) identified 46 copepod species in reservoirs from the entire La Plata river basin.

The Cyclopidae family has a widespread distribution, which includes many cosmopolitan species (Reid 1998, Silva 2008), and more endemic species have been recorded with the advancement of research in places where the local fauna has not been fully exploited yet

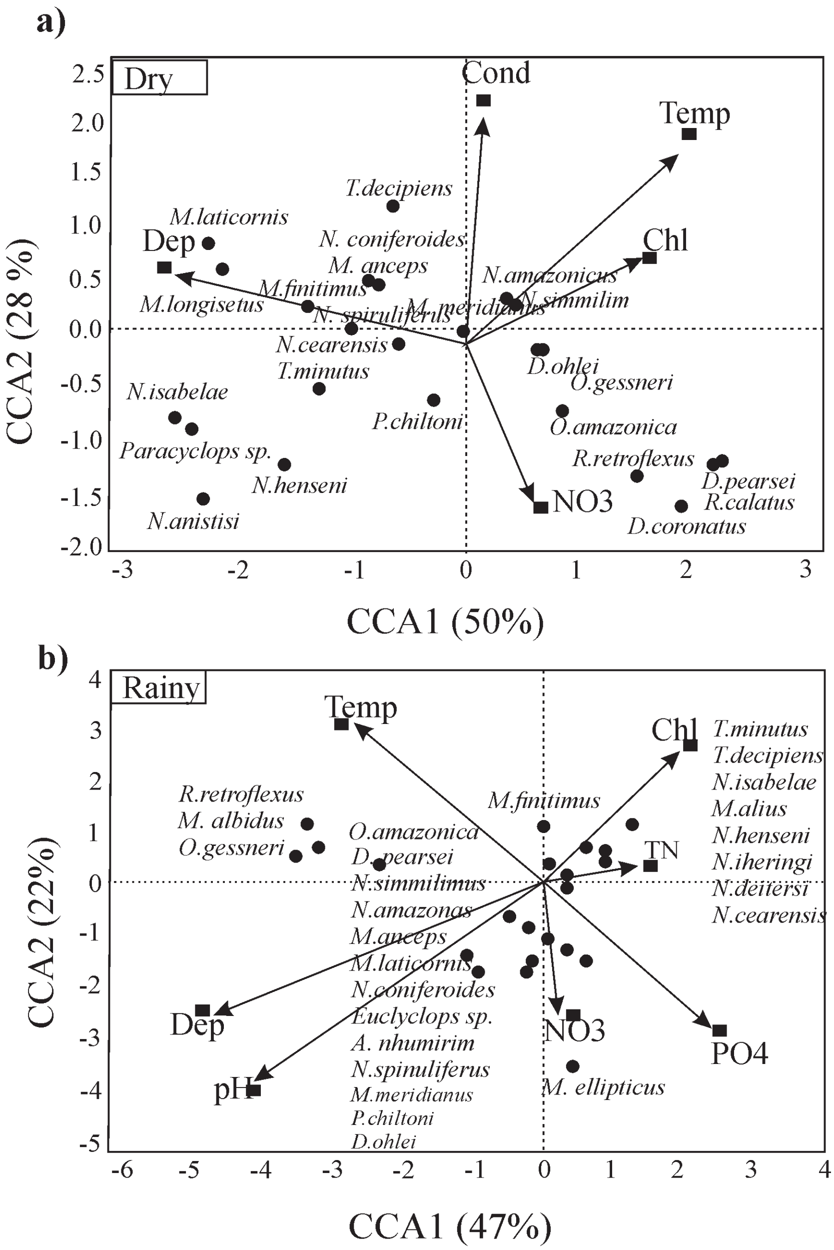

Figure 5. Two-dimensional CCA diagram between the abundance of copepods and environmental variables of the floodplains for each hydrological period (dry, two significant axes; rainy, three significant axes). Cond = electrical conductivity; TN = total nitrogen; Dep = depth; PO4 = Phosphate; NO3 = nitrate; Temp = temperature; Chl = chlorophyll-*a*.

(Suárez-Morales et al. 2004). Many Cyclopidae species recorded in our study are considered from the littoral region of the lakes and are mostly associated with macrophytes, copepods such as *Macrocyclops albidus*, *Microcyclops anceps*, *Microcyclops finitimus*, and *Paracyclops chiltoni* (Lansac-Tôha et al. 2002). Thus, the importance of including fauna samples that are associated with macrophytes is evident, in order to increase the information about rarity and richness of the copepod species, especially the Cyclopidae.

On the other hand, Diaptomidae is represented by 13 genera in South America freshwaters (Suárez-Morales et al. 2005), six of them were recorded in our study, and of these *Notodiaptomus* is the genus with the greatest number of endemic species. In South America, the Diaptomidae copepods are distributed in endemic ecoregions and present great diversity attributed to biogeographic historical events of the Neotropics, and climatic conditions that could limit the species distribution (Previattelli et al. 2013, Perbiche-Neves et al. 2014b).

The Oithonidae family is represented by six species in the continental waters in the Neotropical region, five of them endemic to this region (Boxshall & Defaye 2008). The *Oithona* genus is considered an important component in the plankton of South American seas and coastal lakes (Reid 1985). In Brazil, *Oithona amazonica* presents a high frequency of occurrence and abundance in the Amazon floodplain (Rocha 1985). The extensive interface between marine and freshwater environments and the marine inclusions at the time of the Miocene in the Amazon region are highlighted as important factors in the structuring of communities in this region (Lovejoy et al. 1998, Perbiche-Neves 2014b). Among copepods, freshwater *Oithona* species found only in this region may reflect these historical and biogeographic events and the evolutionary success of copepods in colonizing continental waters (Perbiche-Neves et al. 2014b).

Floodplain lakes have a pattern of seasonal changes in the physical and chemical characteristics of water (Junk et al. 1989, Simões et al. 2013a). During the rainy period, the water level rises (depth values), causing severe changes in the environment, such as, the increase in connectivity throughout the system and the homogenization of species and limnological variables (Thomaz et al. 2007). This was possibly the reason why the limnological heterogeneity was observed to be lower during rainy periods, as the environments became more similar due to the homogenization effect (Bozelli et al. 2015). The opposite occurred with higher environmental heterogeneity during dry periods, when the lakes became isolated and local forces acted in each lake differently (Rodriguez & Lewis-Jr 1997).

Periodic floods or natural periodic disturbances in floodplain systems are responsible for increasing the temporal variability of the zooplankton community (Simões et al. 2013a, b). Thus, the copepods showed replacements (species exchange) in the abundant species in response to temporal environmental variations (dry and rainy period in this case), with different species contributing to the total abundance in the different periods. This species exchange is reinforced by Perbiche-Neves et al. (2015a), in a study that recorded two groups of species occurring in a reservoir influenced by temperature on a large latitudinal scale and water transparency on a local scale, with regional effects on the abundance of individuals.

The disturbances caused by environments are considered one of the mechanisms in the empty niche theory (Hutchinson 1957). For example, drastic changes caused in environments, such as changes in water level, totally or partially eliminating the populations of some species, which are replaced by others that colonize the empty niche, lead to a relatively rapid recovery in response to new environmental conditions. In the floodplain environments studied, there is a pattern of changes in the abundance of individuals, as some species predominate during the rainy period and others during the dry period, as observed by the relative abundance.

According to the niche theory, in the limits of the environmental tolerance or in the extremes of amplitude variation, the effects of environmental variations have a negative relationship with population growth and survival, decreasing the abundance and limiting the spatial distribution of the species (Sexton et al. 2009). This selects the species establishment, leading to differences in the composition over time and space. On the other hand, high heterogeneity produces more niches that could be occupied by more species (Heino et al. 2015). The difference in environmental heterogeneity among environments inside the floodplain and/or among floodplains is responsible for the changes observed in species occurrence and contribution to the total abundance on a spatial scale, while the environmental heterogeneity generated by the hydrologic period reinforces the differences in species distribution over time within the floodplain. Summing up, we observed in this study a replacement (species exchange) among copepod species over time and space, and this was related to environmental heterogeneity. Moreover, this reinforces the findings in accumulation curves; the Amazon floodplain presented the highest environmental heterogeneity and has a special biogeographic history, and it also presented a tendency in species increase, showing potential for biodiversity to increase.

Studies on large spatial scales have demonstrated the restricted occurrence of copepod species in ecoregions, and they have been shown to be highly endemic and very well adapted (Suárez-Morales et al. 2004, 2005, Silva 2008, Previattelli et al. 2013, Perbiche-Neves et al. 2014b, Marrone et al. 2017). The result of the CCA implies a close relationship between environmental variables and species according to the hydrologic period. The high spatial environmental variation indicates a divergence in the spatial distribution of species in floodplains, therefore restricting the copepod species to particular regions or time periods. Moreover, the positive relationships with the variables indicating food resources, such as the concentration of the nutrients (nitrogen and phosphorus), indicate the bottom-up regulation mechanism, favoring the energy flow from primary productivity to the highest levels (Carpenter et al. 1985). High values for these variables in the floodplains in both periods (rainy and dry) were a positive factor, promoting high values for the abundance of most species, as seen from the results.

Several theories are intertwined to determine the limiting factors for the distribution and abundance of species and organisms (Sexton et al. 2009). Studies that focus on tolerance limits of species and their relationships with environmental conditions have reemerged in recent years, because of the anthropogenic changes in climate and natural environments. These have caused significant changes in community structure, facilitating invasion by non-native species (Fey & Cottingham 2011) and the loss of species diversity, with consequent changes in ecosystem functioning (Loreau et al. 2001). In general, Neotropical freshwater ecosystems are very vulnerable to transformation by human activities and lose their natural characteristics by drastic artificial changes, making them even more susceptible to environmental impacts (Agostinho et al. 2004).

CONCLUSION

Local factors (physical and chemical such as depth, temperature, pH, conductivity, chlorophyll, phosphate, and nitrogen) determined the distribution of copepod abundance and showed a close relationship with the spatial and temporal distribution of species. Furthermore, a higher dissimilarity in species distribution was observed at high levels of environmental heterogeneity. This supports the hypothesis that the distribution of copepods could be positively related to environmental heterogeneity and that the copepod species would be related to limnological variables. We also observed the highest species richness in the Amazon floodplain, which presents a large basin area and has an important history in copepod colonization (Perbiche-Neves et al. 2014b). In subtropical freshwater ecosystems, copepods are normally the biggest species among plankton, participating in many ecological interactions; they also respond to environmental gradients (Matsumura-Tundisi & Tundisi 2003, Palhiarini et al. 2017, Perbiche-Neves et al. 2019). In this way, the results of this study contribute to a better understanding of the complexity of the patterns in the distribution of copepod species on a macro-scale in different Brazilian floodplains, and this could be used as a starting point for other studies with copepods.

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SUPPLEMENTARY MATERIAL

Tables SI, SII, SIII.

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