

Effect of slackwater areas on the establishment of plankton communities (testate amoebae and rotifers) in a large river in the semi-arid region of northeastern Brazil

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ABSTRACT

Effect of slackwater areas on the establishment of plankton communities (testate amoebae and rotifers) in a large river in the semi-arid region of northeastern Brazil

The increase in discharge of rivers over time and space poses challenges to the establishment of some biotas, because of higher turbulence, turbidity, hydraulic forces and limited food sources, which may directly affect the community structure. In this context, slackwater areas play an important role in the establishment of organisms, acting as refuges, reducing turbulence, turbidity and providing greater availability of food. This study investigated the changes in community structure of testate amoebae and rotifers in relation to the appearance and disappearance of slackwater areas formed by sandbars on a stretch of the Parnaíba River. The appearance of slackwaters promoted suitable environmental conditions for the establishment of rotifers. On the other hand, slackwaters acted as a buffer for testate amoebae, allowing them to colonize the plankton due to a lower suspension of sediment in these areas. We suggest that the intermittent presence of slackwaters in the Parnaíba River channel is an essential driver of abundance and succession patterns of species in the plankton, through the alternation of washing-out effects, taxon-specific potential of reproduction and biological interactions.

Key words: colonization, current velocity, environmental variables, Parnaíba River, zooplankton

RESUMO

Efeito de áreas de baixo fluxo no estabelecimento de comunidades planctônicas (amebas testáceas e rotíferos) em um grande rio na região semi-árida do nordeste do Brasil

O aumento da descarga de rios ao longo do tempo e espaço coloca desafios ao estabelecimento de algumas biotas, devido uma maior turbulência, turbidez, forças hidráulicas e limitadas fontes de alimento, que podem afetar diretamente a estrutura da comunidade. Neste contexto, as áreas de baixo fluxo desempenham um papel importante no estabelecimento de organismos, agindo como refúgio, reduzindo a turbulência, turbidez e proporcionando uma maior disponibilidade de alimento. Este estudo investigou as mudanças na estrutura de comunidades de amebas testáceas e rotíferos em relação ao surgimento e desaparecimento de áreas de baixo fluxo formadas por bancos de areia em um trecho do rio Parnaíba. O surgimento de áreas de baixo fluxo promoveu condições ambientais adequadas para o estabelecimento de rotíferos. Por outro lado, essas áreas atuaram como um tampão para as amebas testáceas colonizarem o plâncton, devido uma menor suspensão do sedimento. Sugerimos que a ausência e a presença de bancos de areia no canal do rio Parnaíba são cruciais para os padrões de abundância e sucessão de espécies no plâncton, através da alternância de

efeitos de “lavagem”, potencial reprodutivo espécie-específico e interações biológicas.

Palavras chaves: *colonização, velocidade de corrente, variáveis ambientais, rio Parnaíba, zooplâncton*

INTRODUCTION

Several studies have demonstrated the role of slackwater areas for the establishment of microfauna in river environments (Thorp & Mantovani, 2005; Humphries *et al.*, 2006; Nielsen & Watson, 2008). Slackwaters are often formed by permanent islands, tree trunks and rocks or even by macrophyte stands, and are important refuge habitat patches for biota (Humphries *et al.*, 2006). The dynamic nature of these habitats is driven mainly by the flow regime (Hill *et al.*, 1991) and has been an important factor related to variability in abundance and biomass of planktonic communities (Nielsen *et al.*, 2010).

The shorter water retention in river channels is often considered the factor responsible for the lower abundance of organisms (Pace *et al.*, 1992). In contrast, associations of slackwater areas with the main channel of rivers have been increasingly recognized as responsible for the secondary productivity of rivers (Nielsen & Watson, 2008). Studies investigating the secondary productivity in slackwaters indicate that these habitats contain a diverse and abundant range of organisms, mainly due to decreased water velocity, with the abundance of organisms frequently higher in slackwater areas compared to the river channel (Ward & Stanford, 1995; King, 2004; Pace *et al.*, 1992). However, these studies have been conducted in rivers with stable hydrological characteristics, unlike the case of rivers in semi-arid regions. Furthermore, the rivers previously studied are usually characterized by the presence of permanent islands and slackwater areas; few studies have demonstrated the effect of ephemeral islands (e.g., formed by sandbars) on the plankton community structure (e.g., Thorp & Mantovani, 2005).

Rivers in the Brazilian semi-arid region are physically rigorous and little favorable for the establishment of planktonic communities due to instability of the sand substrate and high load of suspended sediment. The Brazilian semi-arid region is relatively dynamic, characterized by the predominance of intermittent rivers and streams,

complex weather patterns, low and unevenly distributed rainfall and low thermal amplitude (Maltchik & Medeiros, 2006; Medeiros *et al.*, 2011; Lucena *et al.*, 2015; Picapedra *et al.*, 2017). As a result, many of the tributaries of the Parnaíba River have characteristics ranging from extreme flooding to drought, which contributes to a high degree of spatial variation and habitat heterogeneity (Medeiros *et al.*, 2011). Thus, determining the factors that control the abundance, diversity and distribution of zooplankton can be an important step to understand the ecology of rivers in this region.

Testate amoebae and rotifers have long been recognized as a critical component of freshwater ecosystems, yet information on their ecology and distribution is still limited (Bertani *et al.*, 2011; Schwind *et al.*, 2016a). This is due to issues like inadequate taxonomic and molecular knowledge on the species, difficult identification related to phenotypic plasticity and cryptic speciation as well as insufficiency of reliable biogeographical studies (Segers, 2008; Lahr *et al.*, 2014). These groups consist mostly of organisms with short generation times and rapid reactions to changes in environmental conditions (Bertani *et al.*, 2011; Arrieira *et al.*, 2015). These responses depend on several factors, such as temperature, nutritional conditions, availability and quality of food resources and population abundance (Pennak, 1953). The identification of different time scales is a prerequisite for understanding the factors and processes that characterize ecosystems and promote the variability in community structure (Levin, 1992; Thrush *et al.*, 1997).

Thus, the present study investigated the variation in the community structure of testate amoebae and rotifers between the hydrological periods in the Parnaíba River channel. We assumed that: (i) the structure of communities of testate amoebae and rotifers is driven differently between the hydrological periods, due to the appearance and disappearance of slackwater areas resulting from the formation of sandbars; (ii) the similarity of communities between environments is greater during the high water period, since the displace-

Sampling

Sampling was conducted at 12 sites located in the Parnaíba River in two hydrological periods: low water period (August 2013 - with sandbars) and high water period (January 2014 - without sandbars) (Fig. 1). Samples were taken with the aid of a suction pump to draw 600 liters of water per sample, which were filtered through a conical-cylindrical net (68 µm). The collected material was placed in a polyethylene bottle (500 ml), labeled and fixed in 4 % formaldehyde solution buffered with sodium borate (Na₃BO₃). The following environmental variables were measured: depth of the sampling sites (m); water current velocity (m/s; mechanical flow meter), water transparency (cm; Secchi disk), water temperature (°C; mercury bulb thermometer), dissolved oxygen (mg/L; portable oxymeter), electrical conductivity (µS/cm; portable conductivity meter), pH (portable pH meter), turbidity (NTU; portable turbidimeter), suspended solids (mg/L; Apha, 2005) and chlorophyll-*a* (µg/L; Golterman *et al.*, 1978).

Laboratory analysis

Samples were concentrated to 100 ml and then 20 sub-samples were taken with a Hensen-Stempel pipette (2.5 ml) and counted in a Sedgewick-Rafter chamber, under an Olympus CX 41 microscope, at a 10× to 100× magnification range. For analysis of testate amoebae, only organisms with protoplasm stained with Rose Bengal were identified, assuming that the organisms were alive when the samples were taken. The identification of testate amoebae was based on the following literature: Vucetich (1973), Ogden & Hedley (1980), Velho *et al.* (1996), Velho & Lansac-Tôha (1996), Alves *et al.* (2007), Nicholls (2007) and Souza (2008). Rotifers were identified with the aid of the following literature: Koste (1978), Nogrady & Pourriot (1995), Segers (1995) and Smet (1996).

Data analysis

Species richness (number of species), Shannon Diversity Index (H') and evenness (E) were calculated from the sample data for each site

(Magurran, 1988). To investigate the differences in the zooplankton structure between hydrological periods, the abundance, richness, diversity and evenness of testate amoebae and rotifers communities were evaluated by one-way analysis of variance (one-way ANOVA), with level of significance of $p < 0.05$ (Sokal & Rohlf, 1991). Normality and homoscedasticity (homogeneity of variance) were previously checked by the Shapiro-Wilk and Levene tests, respectively.

The relationship between environmental variables and testate amoebae and rotifers species was explored by means of a Canonical Correspondence Analysis (CCA) (Ter-Braak, 1986). Species abundance data were log transformed [$\log(x + 1)$] to reduce the effect of rare species, since these species were considered the more representative of this environment. The significance of the CCA association was tested with a Monte Carlo permutation test (999 permutations; Borcard *et al.*, 1992).

Beta diversity values were calculated using the Bray-Curtis dissimilarity index to evaluate the spatial variability of the planktonic community, considering the environments in hydrological periods. The Bray-Curtis index establishes the relationship between species abundance and environments, where the value of one (maximum) indicates identical samples and value of zero indicates that the samples have no species in common (Magurran, 2004). Statistical analyses were performed in the statistical environment R version 3.0.2 (R Development Core Team, 2011) using the Vegan R package version 2.0-6 (Oksanen *et al.*, 2012).

RESULTS

Testate amoebae were represented by 46 species of 10 families; Diffugiidae was the most representative, with 13 species, followed by Arcellidae (10 species) and Centropyxidae (8 species). The most common species were *Arcella vulgaris* Ehrenberg, 1830, *Centropyxis aculeata* Ehrenberg, 1838, *C. ecornis* Ehrenberg, 1841 e *Cyclopyxis kahli* Deflandre, 1929. These species were more abundant during the high water period (Fig. 2a). On the other hand, rotifers were represented by 39 species of 13 families; Brachionidae

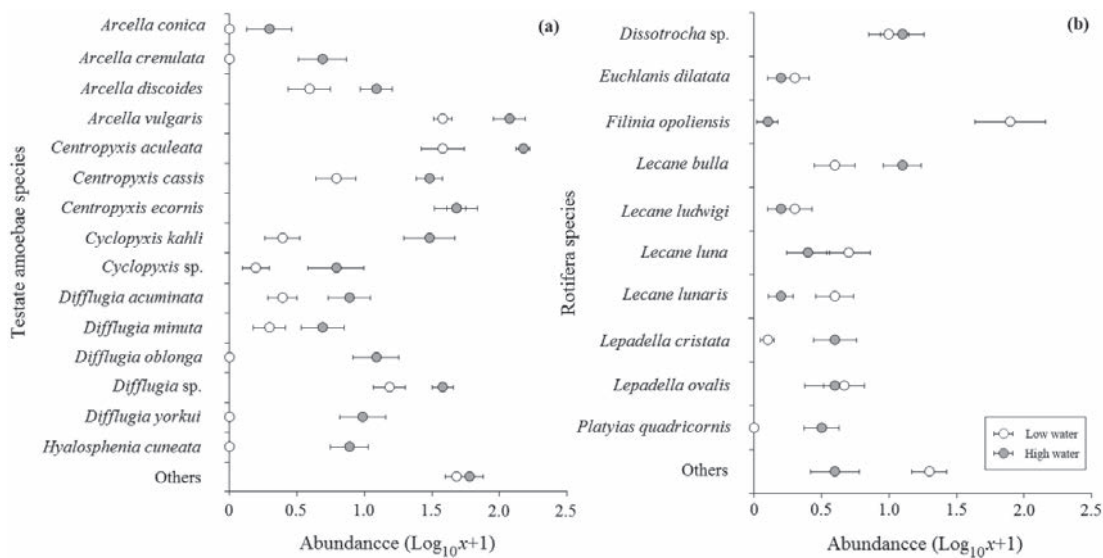


Figure 2. Abundance of the main species of testate amoebae (a) and rotifers (b) recorded during the hydrological periods. Circles = mean values of abundance; bars = standard error. *Abundância das principais espécies de amebas testáceas (a) e rotíferos (b) registradas durante os períodos hidrológicos. Círculos = valores médios de abundância; barras = erro padrão.*

and Lecanidae were the most representative, with 8 each species. The most common species were *Filinia opoliensis* (Zacharias, 1898), *Dissotrocha* sp., *Lecane bulla* (Gosse, 1851) and *Lepadella ovalis* (Müller, 1786). Community abundance was driven mainly by *F. opoliensis* (Fig. 2b) (see Table S1, available at www.limnetica.net/en/limnetica).

The Parnaíba River showed high variability between hydrological periods for most environmental variables. During the high water period, there were higher mean values for almost all environmental variables, except for water transparency, which had the highest mean value during the low water period (Table 1).

Table 1. Environmental data (Mean ± SD) for the different hydrological periods. *Dados ambientais (média ± SD) para os diferentes períodos hidrológicos.*

Environmental variables	Low water	High water
Chlorophyll- <i>a</i> (µg/L)	0.11 ± 0.27	3.56 ± 5.9
Conductivity (µS/cm)	5.25 ± 1.48	9.86 ± 4.94
Depth (m)	1.73 ± 1.01	2.29 ± 1.03
Dissolved oxygen (mg/L)	6.89 ± 0.56	7.27 ± 0.24
pH	5.45 ± 0.17	6.48 ± 0.70
Suspended solids (mg/L)	3.90 ± 2.50	54.46 ± 77.07
Temperature (°C)	24.37 ± 0.91	27.80 ± 1.52
Transparency (m)	1.11 ± 0.30	0.51 ± 0.40
Turbidity (NTU)	6.60 ± 2.65	49.94 ± 51.37
Water velocity (m/s)	0.69 ± 0.26	0.83 ± 0.22

The testate amoebae community had significantly higher values of abundance and species richness (Fig. 3a and Fig. 3b), but lower evenness (Fig. 3d), during the high water period. However, no significant differences in diversity were found between hydrological periods (Fig. 3c). The rotifer community had significantly higher values of abundance and species richness during the low water period (Fig. 3a and Fig. 3b), but a much higher evenness during high water (Fig. 3d). In the case of testate amoebae, no differences were found in terms of diversity. Overall, testate amoebae assemblages were richest and more diversified than rotifers, in both seasons (Fig. 3b and 3c).

According to the CCA, species abundance was correlated with environmental variables, as well as with spatial factors, during the hydrological periods analyzed. The first two CCA axes explained 68.6% of data variability. Some species were associated with environmental variables: *Diffflugia* sp., *Euchlanis dilatata* Ehrenberg, 1832, *Lecane lunaris* (Ehrenberg, 1832), *L. ludwigi* (Eckstein, 1883) and *Lepadella ovalis* were positively correlated with water transparency and negatively correlated with turbidity, water temperature, water velocity and depth; *Arcella conica* (Playfair, 1918), *A. crenulata* Deflandre,

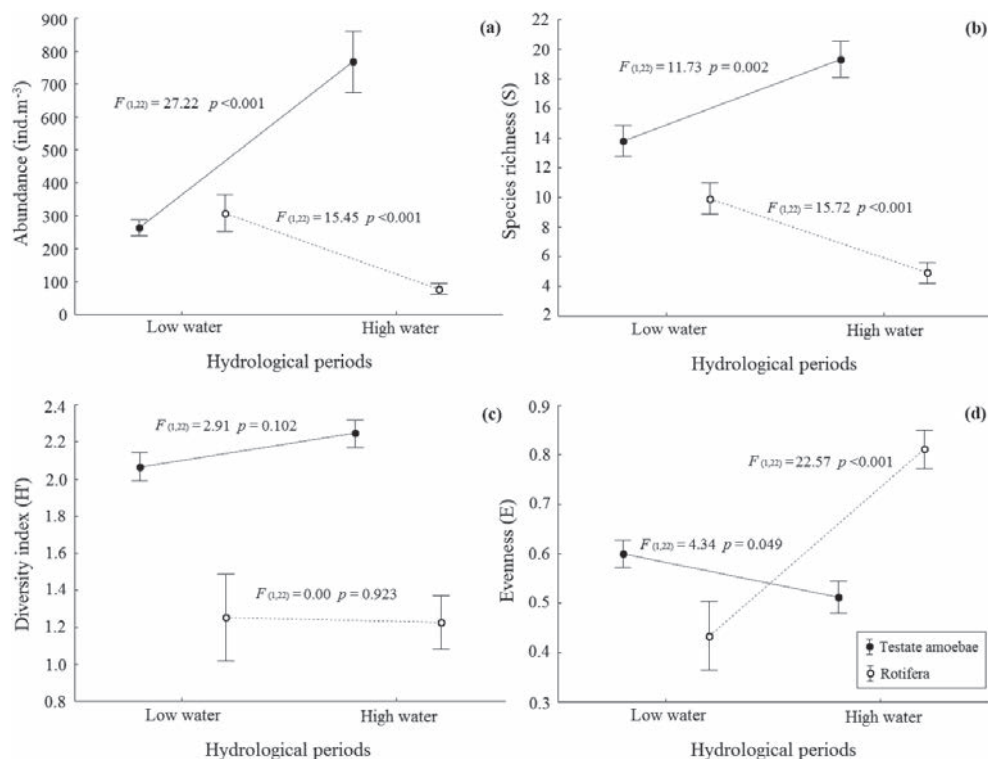


Figure 3. Abundance (a), richness (b), diversity (c) and evenness (d) of the testate amoebae and rotifers recorded during the hydrological periods. Circles = mean values of abundance, richness, diversity and evenness; bars = standard error. *Abundância* (a), *riqueza* (b), *diversidade* (c) e *equitabilidade* (d) de amebas testáceas e rotíferos registrados durante os períodos hidrológicos. Círculos = valores médios de abundância, riqueza, diversidade e equitabilidade; barras = erro padrão.

1928, *A. discoides* Ehrenberg, 1843, *Centropyxis cassis* (Wallich, 1864), *Cyclopyxis* sp. and *Diffflugia yorkui* Nicholls, 2007 were positively correlated with turbidity, water temperature, water velocity and depth, and negatively correlated with water transparency; *Arcella vulgaris*, *Centropyxis aculeata*, *C. eornis*, *Dissotrocha* sp., *Filinia opoliensis* and *Lecane luna* were negatively correlated with chlorophyll-*a*, dissolved oxygen, electrical conductivity, suspended solids and pH; *Cyclopyxis kahli*, *Diffflugia acuminata* Ehrenberg, 1832, *D. minuta* Rampi, 1950, *D. oblonga* Ehrenberg, 1838, *Hyalosphenia cuneata* Stein, 1857, *Lecane bulla*, *Lepadella cristata* (Rousselet, 1893) and *Platylas quadricornis* Ehrenberg, 1832 were positively correlated with chlorophyll-*a*, dissolved oxygen, electrical conductivity, suspended solids and pH (Fig. 4). These associations revealed significant correlations between zooplankton abundance and environmental variables (Permutest, Pseudo- $F=1.94$; $p=0.001$).

In general, according to the beta diversity using the Bray-Curtis index, the main alteration in the plankton community occurred during the low water period, with higher mean values of dissimilarity (0.54). In turn, greater similarity between communities was found during the high water period (0.63).

DISCUSSION

Our results showed that the presence of slackwaters and local environmental conditions are important factors influencing zooplankton community structure. In accordance with other studies (Thorp & Mantovani, 2005; Nielsen & Watson, 2008; Ning *et al.*, 2009; Nielsen *et al.*, 2010), our results confirm our initial hypotheses and suggest that slackwaters formed by the appearance of sandbars during the low water period represent a key habitats for the heterogeneity of the zooplankton structure in the Parnaíba

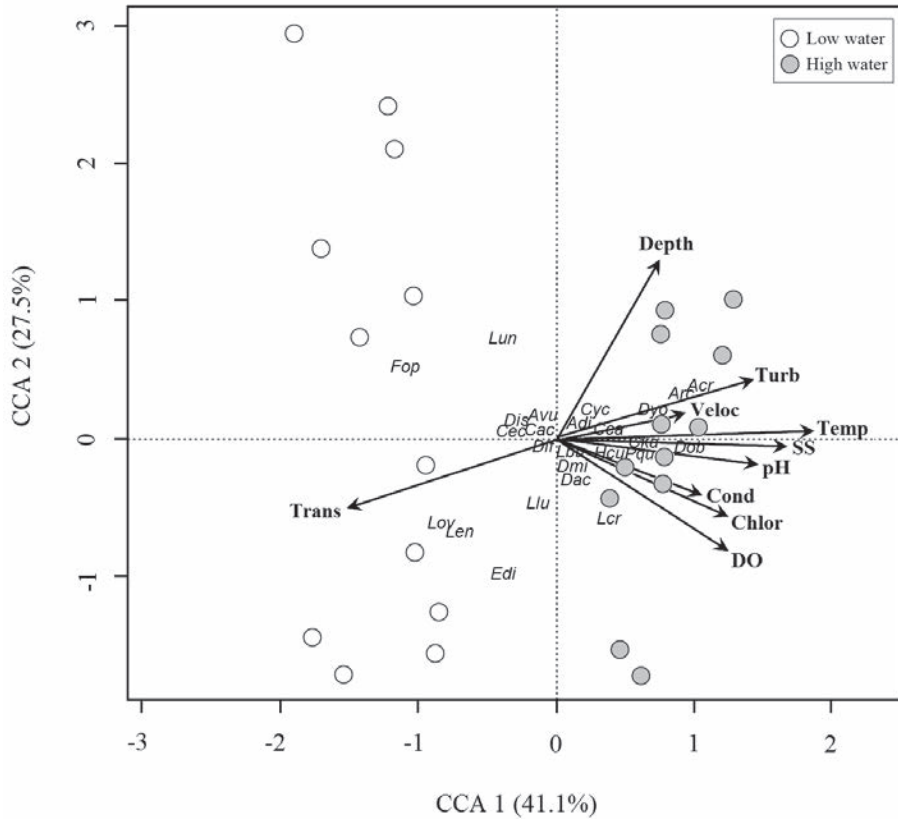


Figure 4. CCA results with the dispersion of the environmental variables and species abundance during the hydrological periods (abbreviations: Trans = water transparency; DO = dissolved oxygen; SS = Suspended solids; Chlor = chlorophyll-*a*; Cond = electrical conductivity; Temp = water temperature; Turb = turbidity; Veloc = water velocity; Testate amoebae: Aco = *Arcella conica*; Acr = *Arcella crenulata*; Adi = *Arcella distenda*; Avu = *Arcella vulgaris*; Cac = *Centropyxis aculeata*; Cca = *Centropyxis cassis*; Cec = *Centropyxis ecornis*; Cka = *Cyclopyxis kahli*; Cyc = *Cyclopyxis* sp.; Dac = *Diffflugia acuminata*; Dmi = *Diffflugia minuta*; Dif = *Diffflugia* sp.; Dob = *Diffflugia oblonga*; Dyo = *Diffflugia yorkui*; Hcu = *Hyalosphenia cuneata*; Rotifera: Dis = *Dissotrocha* sp.; Edi = *Euchlanis dilatata*; Fop = *Filinia opoliensis*; Lbu = *Lecane bulla*; Llu = *Lecane ludwigi*; Lun = *Lecane luna*; Len = *Lecane lunaris*; Lcr = *Lepadella cristata*; Lov = *Lepadella ovalis*; Pqu = *Platylas quadricornis*). Resultados da CCA com a dispersão das variáveis ambientais e abundâncias das espécies durante os períodos hidrológicos (abreviaturas: Trans = transparência da água; DO = oxigênio dissolvido; SS = sólidos suspensos; Chlor = clorofila-*a*; Cond = condutividade elétrica; Temp = temperatura da água; Turb = turbidez; Veloc = velocidade da água).

River. In general, the community structure of testate amoebae and rotifers responded differently to periods of drought and flood. The appearance and disappearance of slackwater areas did not cause evident variability between hydrological periods in terms of species diversity, but this was clearly important for the variability in abundance, richness and evenness of the communities.

The high water period was important for increasing abundance and species richness of testate amoebae. Diffugiidae, Arcellidae and Centropyxidae were the most abundant and species-rich families. These families are consid-

ered common in plankton and are usually associated with sediment and littoral vegetation, and transported to the water column with the suspension of sediment caused by increased water turbulence, especially during periods of floods (Alves *et al.*, 2012; Lansac-Tôha *et al.*, 2014; Arrieira *et al.*, 2015; Schwind *et al.*, 2016a). The decreased abundance and species richness of testate amoebae during the low water period may be related to the emergence of sandbars that promote the formation of slackwaters. As such, these areas may cause a buffer effect for suspension of organisms from benthic and littoral zones.

On the other hand, the abundance and richness of rotifers were positively affected by the emergence of sandbars in the river channel. Brachionidae and Lecanidae were the most species-rich families of rotifers, but, the community abundance during the low water period was mainly driven by *Filinia opoliensis* (family Trochosphaeridae). Brachionidae and Trochosphaeridae species usually have planktonic habits, while Lecanidae species are related to benthic and littoral zones, occasionally occurring in plankton when migrating between these zones (Almeida *et al.*, 2009; Lansac-Tôha *et al.*, 2009; Picapedra *et al.*, 2017). Once the slackwaters are formed, they buffer flow disturbances (Nielsen *et al.*, 2010) and promote suitable conditions for the establishment of organism with planktonic habits. Apart from this, the high adaptability and capacity of rapid colonization of rotifers (Pourriot, 1977; Lansac-Tôha *et al.*, 2009; Medeiros *et al.*, 2011) favors the colonization of these newly formed habitats. By contrast, the disappearance of slackwater areas during the high water promoted a decline in species abundance and richness due to the presence of rigorous physical conditions in the environment (greater suspension of material organic and turbulence, and shorter water retention time) that hinder the establishment of these organisms.

Supporting our findings, the CCA evidenced a strong association of environmental variables with the two hydrological periods. Among testate amoebae, species of the genus *Arcella* and *Diffugia* were the most abundant during the high water period and exhibited strong associations with increased water velocity and turbidity. Studies indicate that greater turbulence and suspension of large sediment loads in the water column act as regulatory factors important to the zooplankton structure (Thorp & Mantovani, 2005; Sluss *et al.*, 2008). Moreover, the presence of gas vacuoles to float (Štěpánek & Jiří 1958) and low density of the shells (Schönborn, 1962) facilitates the displacement of these protozoa to the plankton (Lansac-Tôha *et al.*, 2014; Schwind *et al.*, 2016b).

The results also showed that chlorophyll-*a* was positively linked to several species of testate amoebae during the high water period. The avail-

ability of chlorophyll-*a* is one of the major influences on species distributions (Schwind *et al.*, 2016b). This is because chlorophyll-*a* is directly linked to food resources in aquatic ecosystems (Bastidas-Navarro & Modenutti, 2007). Thus, chlorophyll-*a* can be considered an important factor in the increased abundance of these organisms. Testate amoebae were also associated with higher temperature and pH values. Possibly, a decrease of temperature during the low water period possibly resulted in decreased metabolic rates of testate amoebae and consequent low feed rates in contrast to the high water period (Torres, 1996; Arrieira *et al.*, 2015). In turn, a greater amount of organic matter was loaded into the river bed with floods. This, combined with higher temperatures, led to greater decomposition of organic matter, resulting in increased acidification of the environment during that period, reinforcing the abundance of species that prefer this type of environment (Lamentowicz & Mitchell, 2005).

Rotifers were associated with the low water period, which had the lowest values of turbidity, suspended solids and water velocity. This observation is in line with results of Claps *et al.* (2011), who suggested that high concentrations of particles negatively impact rotifer populations because such insoluble materials interfere with the filtration process. Floods cause major changes in the physical and environmental conditions. Typically deeper areas are more exposed to turbulent conditions in this period because of relatively high water velocity (Frenette *et al.*, 2012; Massicotte *et al.*, 2014), which often promotes high mortality or removal (washing-out) of the zooplankton from the environment. However, the gradual restoration of bed environmental conditions such as reduced sediment resuspension and the appearance of slackwaters enable the re-colonization of this environment (Baranyi *et al.*, 2002). Studies have shown that rapid colonization of slackwaters by organisms happens due to drift (Casper & Thorp, 2007; Nielsen & Watson, 2008; Ning *et al.*, 2009) and hatching of resting eggs (Ning, 2011).

The dissimilarity index of the beta diversity showed a greater dissimilarity in the low water period. The appearance of sandbars may be

contributing to increase the community heterogeneity among environments, possibly promoting natural barriers that hinder the displacement of organisms from littoral and benthic zones to plankton. Greater dissimilarity between aquatic communities during the low water period has been also observed in floodplain environments (Thomaz *et al.*, 2007). Otherwise, higher similarity in the community occurred during the high water period. Increased hydrological discharge results in washing of slackwater areas, resulting in the homogenization of environments and consequent greater similarity between their communities (Saunders & Lewis, 1988; Nielsen & Watson, 2008). During flooding, the homogenization effect of floods is considered to be a general pattern (Schwind *et al.*, 2016b).

The responses of biota to the high natural variability on flow regime, which typifies rivers and streams in the semi-arid region of Brazil, is still poorly known. The major threats to aquatic biota in semi-arid rivers in Brazil are related to historical changes in regional climatic conditions caused by human occupation in this region, which have led to the intensification of arid conditions (Maltchik & Medeiros, 2006; Medeiros *et al.*, 2011). It is worth noting also that failure to recognize the importance of ecological processes and linkages between natural hydrological disturbances and the biodiversity of aquatic systems in semi-arid Brazil will lead inevitably to the extinction of species and the loss or disruption of natural patterns of flow in these environments (Maltchik & Medeiros, 2006).

In this study, we show that slackwaters formed by the appearance of sandbars during the low water period in the Parnaíba River play an important role in structuring communities. We suggest that changes in environmental variables, especially the decrease in water velocity, offered suitable conditions to the establishment of rotifers. On the other hand, slackwater areas act as natural barriers, causing a decline in testate amoebae populations in plankton due to lower sediment suspension in these areas. The opposite effect was found during the high water period; with the disappearance of sandbars, populations of rotifers were not able to establish due to the higher water velocity, while testate amoebae were

more abundant in the plankton in this period, because of the increased sediment suspension.

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