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ORIGINAL ARTICLE

Local factors affecting the testate amoeba community (Protozoa: Arcellinida; Euglyphida) in a neotropical floodplain

Rodrigo L. ARRIEIRA,* Geziele M. ALVES, Leilane T.F. SCHWIND, Fábio A. LANSAC-TÔHA

Department of Biology, State University of Maringa, Brazil
*Corresponding author: rodrigoarrieira@yahoo.com.br

ABSTRACT

The objective of this study was to evaluate the possible influential factors on the patterns of temporal distribution of testate amoebae (Protozoa: Arcellinida and Euglyphida) in plankton environments connected to a main river in a Neotropical floodplain. In this context, we hypothesised that the local factors would be the main structural factors for the testate amoebae. Samplings during two hydrological periods were conducted along a longitudinal axis of three environments for aquatic macrophytes, at the edge of the banks. The highest mean values of the richness, diversity and density were recorded for the high water period. Our results suggested that local factors influence the distribution of testate amoebae. These environments were significantly affected by the hydrological regime, where the main structural factors for testate amoebae were the environmental variables, supporting the predicted hypothesis.

Key words: Protozoa, diversity, backwater; flooding, Paraná River.

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INTRODUCTION

In the Neotropics, shallow depth allows for the establishment of large areas colonised by aquatic macrophytes in most floodplains. Studies have defined the main characteristics of different communities associated with aquatic macrophytes, revealing the determinative factors of their structures. The high productivity of these plants depends on the physical, chemical, and biological characteristics of the environment, as well as and the influence of floods on the environment's local factors (Agostinho *et al*., 2007; Lamentowicz *et al*., 2007; Maia-Barbosa *et al*., 2008; Thomaz and Cunha, 2010; Villabona-González *et al*., 2011).

The area colonised by macrophytes hosts a great number of ecological niches and diversity of testate amoebae in the marginal regions of aquatic environments (Hardoim and Heckman, 1996; Souza, 2005). Accordingly, numerous studies reported that these protozoa are strongly influenced and favoured by the location (Dabés and Velho, 2001; Lansac-Tôha *et al*., 2003, 2007, 2009), where the testate amoebae have a high level of species diversity and take advantage of the microhabitats formed by the macrophyte stands. In these habitats, the decomposition process of detritus is intense, while the periphyton flourish and small invertebrates, vertebrates, and other decomposers, such as bacteria, find shelter as well. Comprehending the factors that generate patterns in the testate amoebae community is essential for identifying aspects of the study of the mechanisms that generate and maintain diversity, as well as for predicting how environmental changes affect local and regional diversity (Mac Nally *et al*., 2004). Thus, the present study analysed the structure (species composition and richness, species diversity, and abundance) of testate amoebae. The study also analysed the influence of limnological variables on the community temporal distribution associated with aquatic macrophytes in different environments connected to the Paraná River. In another study, Colares *et al.* (2013) emphasised that the temporal variation of these types of environments is the main influence on the attributes of rotifer and microcrustacean communities.

In this context, we hypothesised that the main structural factors for testate amoebae include the local factors as environment variables. Likewise, the alternative hypothesis was that the community would be structured at random.

METHODS

Study area

This study was conducted in three environments that were connected to the Paraná River (Bilé, Leopoldo and Pau Véio backwater). These environments were included in the Environmental Protection Area of Islands and *Várzeas* of the Upper Paraná River floodplain in Brazil (22°40'-22°50'S and 53°10'-53°40'W) (Fig. 1).

The backwaters are regarded as connected lakes and have a great part of their marginal region occupied by aquatic macrophytes (Thomaz *et al*., 2004). These environments are extremely affected by the water regime of the main river, allowing for a continuous flow between

these two environments (Rodrigues and Bicudo, 2004).

The Bilé backwater is located on Mutum Island. It is 580 m long with variable width and an average depth of nearly 1 m. The marginal region contains large amounts of aquatic macrophytes. The Pau Véio backwater is 1150 m long and roughly 2 m deep, and is also located on the same island with an area of 3 ha. The left bank presents a vegetation gradient from an aquatic to a terrestrial system, composed of aquatic macrophytes (especially *Eichhornia azurea*). The Leopoldo backwater is 965 m long and is located on Porto Rico Island's Channel of the Paraná River, with an average depth of 3 m, a perimeter of 2000 m and an area of roughly 3 ha (Souza-Filho *et al*., 2000).

Sampling

We followed community changes using the three backwaters as replicates. We chose these environments because of their similar characteristics, such as length and limnological variables, as well as their shared influence of the same river in this floodplain system. In each environment, samplings were performed in six stands of aquatic macrophytes, longitudinally arranged and numbered from one to six, with Site 1 located the farthest from the river channel (Fig. 2).

At each sampling point, we measured pH, temperature, dissolved oxygen (% and mg L^{-1}) and conductivity (µS cm^{-1}) using portable digital potentiometers (YSI). Samplings were taken during the low water period (September 2008) and the high water period (March 2009) by means of vertical hauls using a plankton net (68 µm) near the stands. In these same sampling points, three vertical hauls were collected from the lake bottom until reaching the water's surface, subsequently combining the filtered volume obtained in these hauls into a single sample. To calculate the volume of water filtered for each sample where planktonic testate amoebae were obtained, we used the following equation: $Vf=\pi.r^2.d$ (Pinto-Coelho, 2004), where Vf is the volume filtered by the net, r is the radius of the net mouth (0.15 m), and d is the distance run by the net. This material was placed in polyethylene-labelled vials before being fixed with a formaldehyde solution at 4% buffered with calcium carbonate. This study

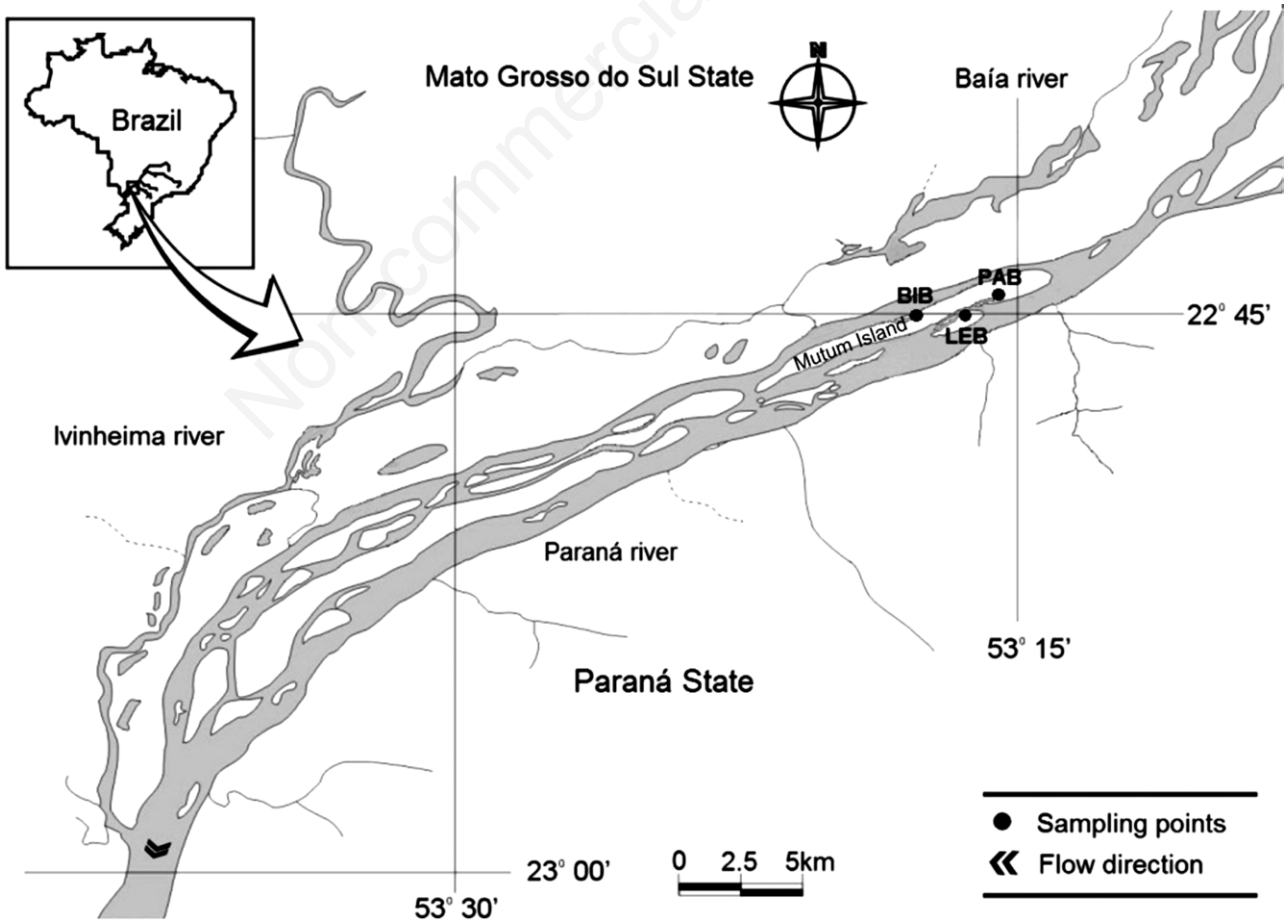

Fig. 1. Area of study and location of the sampling stations (BIB, Bilé Backwater; LEB, Leopoldo Backwater; PAB, Pau Véio Backwater).

is part of a larger project using a collection of other zooplankton communities, such as rotifers, cladocerans and copepods.

Laboratory analysis

The taxonomic classification was based on Adl *et al*.'s (2012) proposed guidelines. Thus, the species were pooled into two categories: Arcellinida Kent, 1880 (Amoebozoa) and Euglyphida Copeland, 1956, emend. Cavalier-Smith 1997 (Rhizaria). In the sample, only the organisms that had an identified stained protoplasm were stained with rose bengal, assuming that the samples were living during collection. For the quantitative analysis of the samples, three sub-samples were obtained using a Hensen-Stempell pipette (2.5 mL), and were analysed in a Sedgewick-Rafter chamber. We sorted the individuals from each sample and prepared glycerine slides for further identification. The identification was performed using the following bibliography: Deflandre (1928, 1929), Gauthier-Lièvre and Thomas (1958, 1960), Vucetich (1973), Ogden and Hedley (1980), Velho *et al*. (1996), Velho and Lansac-Tôha (1996), Alves *et al*. (2007) and Souza (2008). We carried out the analyses using a light microscope (Olympus CX31), assessing at objective lens of 10x to 100x magnification range.

Data analysis

Species diversity was estimated using the Shannon Index (H') (Pielou, 1975). To investigate the differences in the testate amoebae structure in the environment and the hydrological periods, the richness, Shannon Index and density were evaluated during the sampling period using a two-way ANOVA, with $P<0.05$ being deemed as significant. The analyses were taken considering the hydrological period and sampled points, as well as the interaction between them (Sokal and Rohlf, 1991). The assumptions of normality and homoscedasticity (homogeneity of variance) were previously verified through the Shapiro-Wilk and Levene tests, respectively. We conducted this analysis using Statistica 7.1 software (StatSoft Incorporation, 2005).

We applied a Redundancy Analysis (RDA) (Legendre and Legendre, 1998) to assess the relationships between environmental variables and the testate amoebae community. We based the results on the values of total inertia and the significance of the RDA, limnological variables and the percentage of explanation for each axis retained ($P<0.05$). We applied log-transformation for the abundance of species to reduce the effect of the rare species, subsequently processing it according to the Hellinger procedure (Legendre and Gallagher, 2001). In addition, the effect of multicollinearity among environmental variables was analysed through Variance Inflation Factors (VIF). Posteriorly, we carried out a Monte Carlo Permutation Test (999 randomizations) (Borcard *et al.,* 1992) to support the significance of the RDA's association. We used R software, version 2.15.2 (R Development Core Team, 2011) VEGAN package (Oksanen *et al*., 2012) for multivariate analyses. We calculated the beta diversity using the Bray-Curtis index's dissimilarity coefficient to assess the spatial variability of the testate amoebae, considering the environments in the hydrological periods. The Bray-Curtis (dissimilarity) index establishes the relationship between species density and environments - value one (maximum value) indicates the identical environments and value zero indicates samples that have no species in common (Magurran, 2004). We also used R software to carry out these analyses (R Development Core Team, 2011).

RESULTS

In this study, Difflugidae, especially *Cucurbitella dentata* f. *quinquilobata*, *D. muriformis*, *D. pseudogramen*,

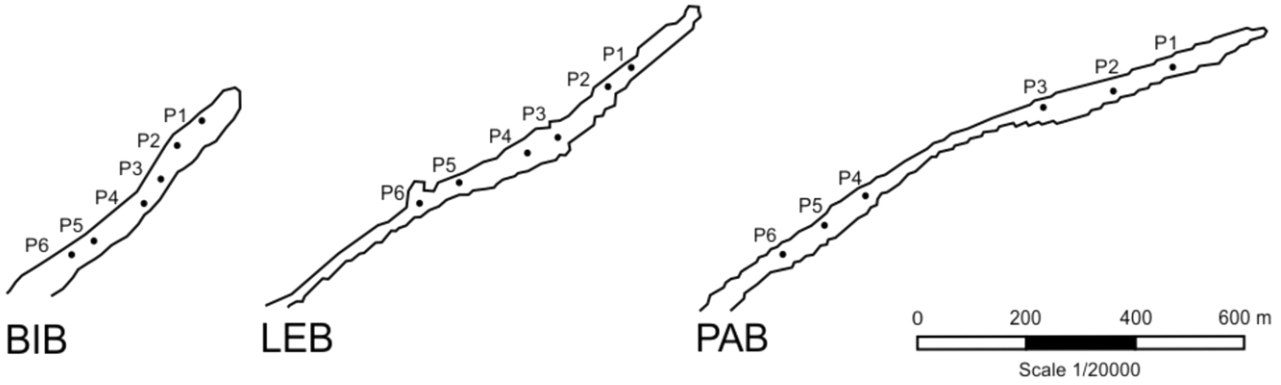

Fig. 2. Sampling points in the backwater of the Upper Paraná river floodplain (BIB, Bilé Backwater; LEB, Leopoldo Backwater; PAB, Pau Véio Backwater).

Difflugia corona and *C. madagascariensis,* were the most common species and had a great density in this study (Fig. 3). The testate amoebae were represented by 53 taxa, distributed among five families, with Difflugiidae as the most representative, with 29 taxa, followed by Arcellidae (9 taxa), Centropyxidae (7 taxa), Lesquereusiidae (7 taxa) and Euglyphidae (1 taxa) (Tab. 1). The depth of the backwaters ranged from 0.6 to 2.3 m, with deeper waters in September 2008 - a period that was previously regarded as having low waters. In contrast, lower waters were indicated for March 2009 - a period that was previously regarded as having high waters. In relation to the limnological variables, a greater concentration of dissolved oxygen was verified during the low water period and higher conductivity values were observed during the high water period (Tab. 2).

The testate amoebae community had the higher values in terms of species richness and species diversity during the high water period (Fig. 4 a,b). The ANOVA results revealed significant differences between the sampling sites and the hydrological periods for species richness (sampling sites*hydrological periods; $F_{(2,30)}$=3.33; P=0.04) (Tab. 3), as well as for species diversity (sampling sites*hydrological periods; $F_{(2,30)}$=7.00; P<0.01) (Tab. 4), showing a significant result for all effects. The studied environments contained testate amoebae with higher mean values of species density during the high water period (Fig. 5). Additionally, the ANOVA results indicated significant differences between the sampling sites and the hydrological periods in terms of density values. Moreover, this same analysis demonstrated that the sampling sites were also significantly correlated with this attribute (sampling sites*hydrological periods; $F_{(2,30)}$=18.94; P<0.01) (Tab. 5).

According to the RDA, the abundance of testate amoebae was correlated with the limnological variables, as well as with the spatial factors in both of the analysed hydrological periods (P<0.05). Furthermore, the analysis results illustrated that the influence of limnological variables influenced 26.5% and 41.2% of the variations in abundance during the low and high water periods, respectively. Some species had an association with environmental variables during the analysed periods. The correlations for the low water period are as follows: *Netzelia oviformis:* correlation with the environments depth; *Difflugia acuminata* and *Difflugia oblonga:* positive correlation with temperature; *Difflugia lobostoma* var. *multilobata:* positive correlation with dissolved oxygen; *Lesquereusia oviformis* negative association with the same variable (Fig. 6a). These association revealed a significant correlation between the abundance of testate amoebae and the limnological variables (Permutest, Pseudo-*F*=1.55; P<0.01). Subsequently, the correlations for the high water period are as follows: *Arcella megastoma*, *Centropyxis aculeata*, *Difflugia acutissima* and *Netzelia oviformis:* negative correlation with conductivity; *Cucurbitella dentata* f. *quinquilobata:*

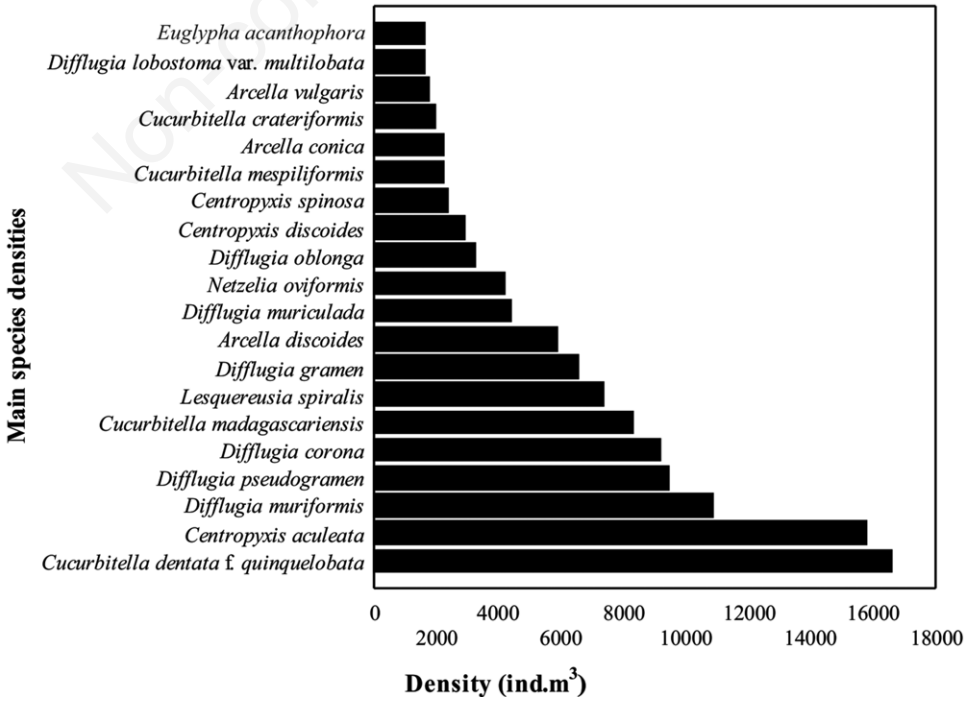

Fig. 3. Main species densities of the testate amoebae during the studied periods.

Tab. 1. List of testate amoebae taxa recorded in the study.

ARCELLINIDA	
Arcellidae	
Arcella arenaria Greeff 1866	*A. mitrata* Leidy 1879
A. conica (Playfair 1917)	*A. vulgaris* Ehrenberg 1830
A. dentata Ehrenberg 1838	*A. vulgaris* f. *elegans* Deflandre 1928
A. discoides Ehrenberg 1843	*A. vulgaris* f. *undulata* Deflandre 1928
A. megastoma Pénard 1902	
Centropyxidae	
Centropyxis aculeata (Ehrenberg 1838)	*C. hirsuta* Deflandre 1929
C. discoides (Pénard 1890)	*C. marsupiformis* (Wallich 1864)
C. ecornis (Ehrenberg 1841)	*C. spinosa* (Cash 1905)
C. gibba Deflandre 1929	
Difflugiidae	
Cucurbitella crateriformis G. L. & T., 1960	*D. fragosa* Hempel 1898
C. dentata f. *crucilobata* G. L. & T., 1960	*D. gramen* Pénard 1902
C. dentata f. *quinquelobata* G. L. & T., 1960	*D. limnetica* (Levander 1900)
C. dentata f. *trilobata* G. L. & T., 1960	*D. lithophila* Pénard 1902
C. madagascariensis G. L. & T., 1960	*D. lobostoma* Leidy 1879
C. mespiliformis Pénard 1902	*D. lobostoma* var. *multilobata* G. L. & T., 1958
Difflugia acuminata Ehrenberg 1838	*D. muriculada* G. L. & T., 1958
D. acuminata var. *inflata* Pénard 1899	*D. muriformis* G. L. & T., 1958
D. acutissima Deflandre 1931	*D. oblonga* Ehrenberg 1838
D. amphoralis var. *globosa* G. L. & T., 1958	*D. pleustonica* Dioni 1970
D. bicruris G. L. & T., 1958	*D. pseudogramen* G. L. & T., 1958
D. capreolata Pénard 1902	*D. stellastoma* Vucetich 1989
D. corona Wallich 1864	*D. urceolata* Carter 1864
D. curvicaulis Pénard 1899	*Protocucurbitella coroniformis* G. L. & T., 1960
D. elegans Pénard 1890	
Lesquereusiidae	
Lesquereusia mimetica Pénard 1902	*L. spiralis* var. *caudata* (Playfair 1917)
L. modesta Rhumbler 1896	*Netzelia oviformis* (Cash 1909)
L. ovalis G. L. & T., 1959	*N. tuberculata* (Wallich 1864)
L. spiralis (Ehrenberg 1840)	
EUGLYPHIDA	
Euglyphidae	
Euglypha acanthophora (Ehrenberg 1841)	

Tab. 2. Mean values and standard deviation (SD) of the limnological variables registered in the environments during the low and high water periods (September 2008 and March 2009, respectively).

Limnological variables	Low water Mean and SD	High water Mean and SD
pH	6.64±0.21	7.06±2.29
Temperature (°C)	28.73±0.58	22.81±1.47
Dissolved oxygen (mg L^{-1})	2.20±1.83	6.60±1.02
Conductivity (µS cm^{-1})	70.55±16.24	55.13±1.85

Tab. 3. ANOVA results on mean richness of testate amoebae in relation to sampling sites and hydrological periods.

Effects	F	P
Sampling sites	8.8	<0.01
Hydrological periods	6.46	0.02
Sampling sites *hydrological periods	3.33	0.04

**Interaction between the effects.*

Tab. 4. ANOVA results on mean diversity of testate amoebae in relation to sampling sites and hydrological periods.

Effects	F	P
Sampling sites	13.02	<0.01
Hydrological periods	10.93	<0.01
Sampling sites *hydrological periods	7.00	0.01

**Interaction between the effects.*

Tab. 5. ANOVA results on mean density of testate amoebae in relation to different sampling sites and hydrological periods.

Effects	F	P
Sampling sites	3.8	0.01
Hydrological periods	1.82	<0.01
Sampling sites *hydrological periods	18.94	<0.01

**Interaction between the effects.*

positive association with the environments depth; *Arcella discoides*, *A. mitrata* and *Euglypha acantophora*: positive correlation with pH; *Cucurbitella mespeliformis:* negative correlation with pH (Fig. 6b). These association shown a significant correlation between the abundance of testate amoebae and the limnological variables (Permutest, Pseudo-*F*=2.62; P=0.01).

In general, considering the beta diversity assessed using the Bray-Curtis index, the major alteration in the community occurred during the low water period, with higher dissimilarity values, for example, a greater similarity for the testate amoebae community occurred at the sampling sites during the high water period (Tab. 6).

DISCUSSION

Difflugiidae was the family with the highest species richness and abundance. Several studies on floodplain environments and marginal regions colonised by aquatic macrophytes indicated its prominence (Lansac-Tôha *et al*., 2001; Velho *et al*., 2004; Snegovaya and Alekperov, 2005; Souza, 2005; Alves *et al*., 2008; Leão *et al*., 2009). While the abundance of *Difflugia* species could be associated with food availability (Dabés and Velho, 2001), a possible association for the *Cucurbitella* species would be the environmental characteristics - lentic and shallow environments with rich organic matter, especially with senescent material macrophytes, would be a good match (Souza, 2008). Previous studies also presented different taxa numbers. This study presented backwaters with 53 taxa, which is a high number compared with other studies on testate amoebae in aquatic macrophytes (Dabés and Velho, 2001; Leipnitz *et al*., 2006; Vieira *et al.*, 2007; Alves *et al*., 2010). The fact that the backwaters presented a higher level of richness and diversity values during periods of high water could be associated with the increased water level leading to an expanded connection to the river. It favours the input of organisms and increases diversity (Velho *et al*., 2004; Alves *et al*., 2005). One example of this was the temperature decrease during this period, which possibly resulted in the decreased metabolic rates of testate amoebae, and consequently, also caused the low feed rates in contrast to the high water period (Torres, 1996).

Generally, in floodplains, the testate amoebae density has no temporal patterns of fluctuation and this attribute is not related to the hydrological cycle (Velho *et al*., 1999; Bini *et al*., 2003). However, the ANOVA results in our study revealed the influence of hydrological periods on density, with higher values found for all of the environments during the high water period. Local factors could explain this temporal pattern of density, since they are predominantly responsible for the testate amoebae community dynamics. In this context, our study demonstrates the association of environmental variables with the most abundant species (*Cucurbitella dentata* var. *quinquilobata* and *Centropyxis aculeata*), supporting the

Tab. 6. Mean Bray-Curtis index values of testate amoebae between the sampling points in the environments and hydrological periods.

Environments	Low water	High water
Bilé backwater	0.51	0.35
Leopoldo backwater	0.37	0.38
Pau Véio backwater	0.44	0.38

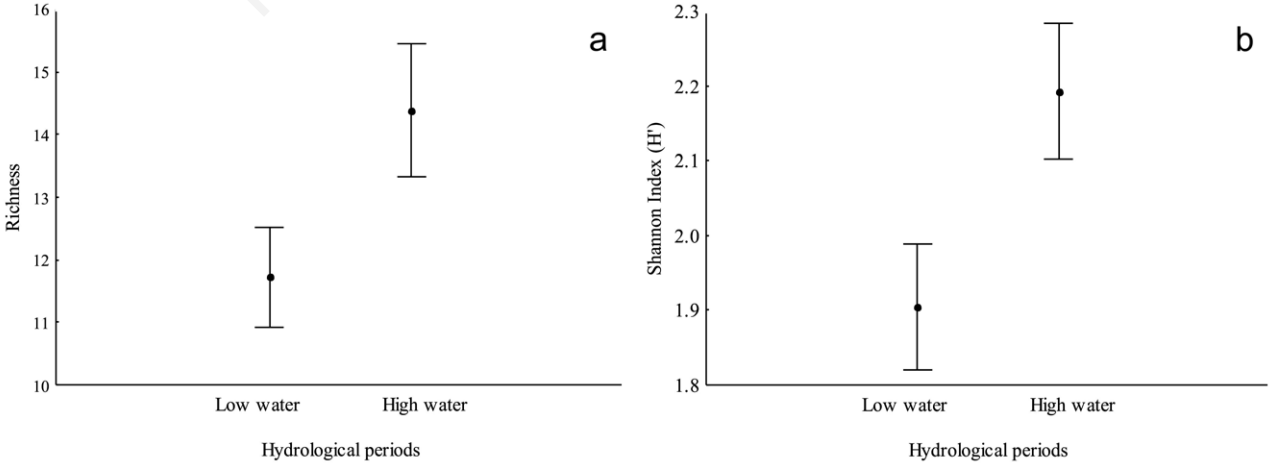

Fig. 4. Richness (a) and Shannon index (b) of the testate amoebae registered during the studied periods. Symbol=mean value of richness and the Shannon index; bar=standard error.

findings for the RDA results during the high water period.

Each hydrological period had environmental variables that influenced their distribution of species, represented as environmental filters that selected those with the most similar characteristics. This promoted the coexistence of those able to adapt to the environmental conditions. Moreover, both the flood pulse and the dry period exerted a direct influence on the filters and established the spatial distribution of the species (Simões *et al*., 2012, 2013). During the low water period, the species were associated with all tested environmental variables, revealing no influence on the testate amoebae. Since only three species represented the association with low abundance, it suggests that other factors could influence the community structure at these sites. The high water period was a large influence on the association between the environmental variables, the most abundant species, and characteristics such as pH. A possible explanation would be that greater decomposition of organic matter in these environments during this hydrological period promoted an increase in the environment's acidification, enhancing the abundance of species that prefer this sort of environment (Lamentowicz and Mitchell, 2005). The beta-diversity similarity results for the high water period revealed the major influence of the connection to the river, as well as the flow variability for the community dynamics in the environments. This especially could be caused by the homogenisation effect, in accordance with other zooplankton studies (Bozelli and Esteves, 1995; Bonecker *et al*., 2005; Lansac-Tôha *et al*., 2009). Still, another study on the Upper Paraná River floodplain's different environments attributed the major alteration in the species composition of testate amoebae to the environment's connectivity to the river during this same period (Costa *et al*., 2011). In contrast, greater dissimilarity among floodplain aquatic communities usually occurs during low water periods (Thomaz *et al*., 2007).

CONCLUSIONS

Our results indicated that local factors were responsible for temporal variation as a preponderant structuring factor in the testate amoebae community. In

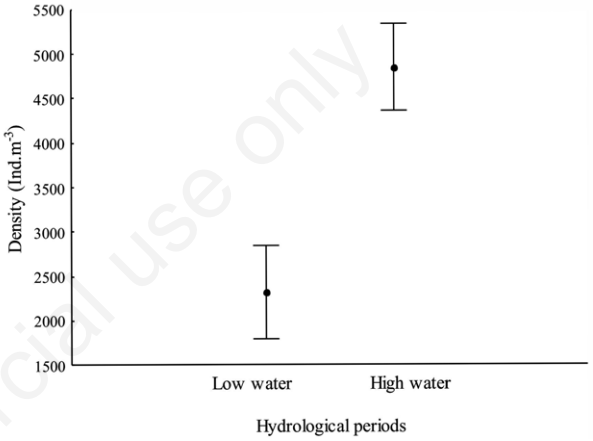

Fig. 5. Density of testate amoebae recorded in the studied environments and periods. Symbol=mean value of density (ind.m^{-3}); bar=standard error.

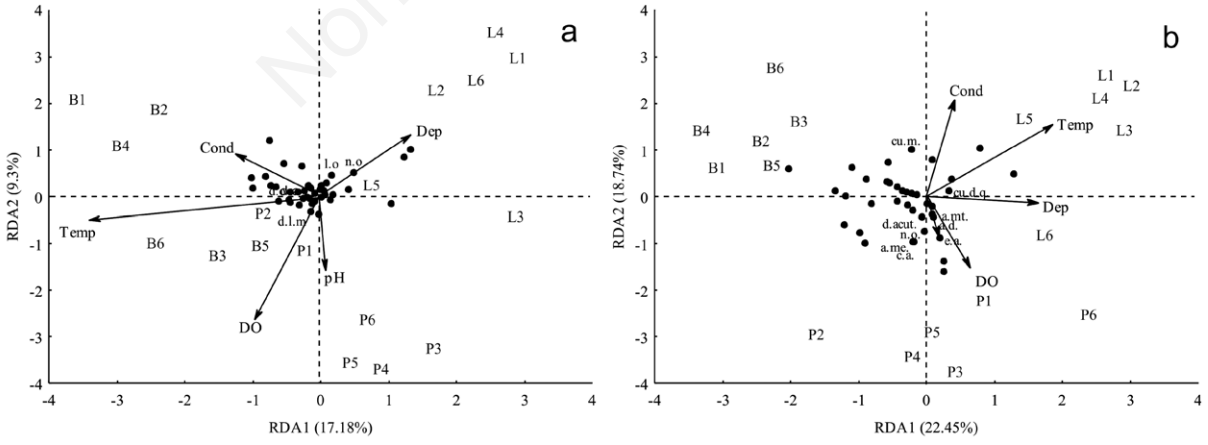

Fig. 6. RDA scores with the dispersion of the limnological variables and species abundance during the low water (a) and high water (b) periods. Cond, conductivity; Dep, depth; DO, dissolved oxygen; Temp, temperature; a.d., *Arcella discoides*; a.me., *Arcella megastoma*; a.mt., *Arcella mitrata*; c.a., *Centropyxis aculeata*; cu.d.q., *Cucurbitella dentata* f. *quinquilobata*; cu.m., *Cucurbitella mespeliformis*; d.a., *Difflugia acuminata*; d.acut., *Difflugia acutissima*; d.l.m., *Difflugia lobostoma multilobata*; d.o., *Difflugia oblonga*; l.o., *Lesquereusia oviformis*; n.o., *Netzelia oviformis*; e.a., *Euglypha acantophora.* We only used subtitles for species most associated with each axis to facilitate the identification of relationships among the species with the limnological variables.

this study, there was an emphasis on the importance of the flood-pulse homogenisation effect during the high water period, corroborating previous hypotheses.

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