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ORIGINAL ARTICLE

The structure of planktonic communities of testate amoebae (Arcellinida and Euglyphida) in three environments of the Upper Paraná River basin, Brazil

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ABSTRACT

Ecological communities are constantly restructuring in the short and long term in response to population dynamics and environmental variables. This study evaluated the structure of arcellinid and euglyphid testate amoebae planktonic communities in three environments of the Upper Paraná River basin, Brazil. We hypothesised that the community structure of testate amoebae is differentially influenced by environmental conditions, mainly in isolated lentic ecosystems, due the effect of the low-water period. In addition, we predicted that the response of testate amoeba communities to environmental changes is also affected by the distinct hydrodynamic characteristics of the environment. Plankton were sampled in the low- and high-water periods, and physical and chemical variables were calculated for each site. In order to evaluate the influence of environmental conditions on the variation in testate amoebae community structure over time, a time-lag analytical approach was used and significance was estimated using a Mantel test. A Kendall test coefficient was used to estimate the maintenance of species abundance on each day when sampling was carried out and for each water body. A redundancy analysis was also performed to assess the responses of testate amoeba communities to environmental change in the three studied environments. Bray-Curtis dissimilarity indices were calculated for the testate amoeba communities and the significance of the differences between communities was estimated using a Mantel test. Seventy-five taxa belonging to six families were identified. Environmental conditions influenced the richness, abundance, and dominance pattern of the testate amoebae communities, and distinct hydrodynamic characteristics of the environments affected the establishment of community structure.

Key words: Zooplankton; protozoa; environmental variability; community structure.

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INTRODUCTION

Ecological communities are naturally dynamic and experience constant restructuring in response to population dynamics and environmental variables, in both the short and long term (Brown *et al.*, 2001). Variability is a natural property of ecological communities (Landres *et al.*, 1999). The identification of different time scales is a precondition for understanding the factors and processes that characterise ecosystems and that promote variability in community structure (Levin, 1992; Thrush *et al.*, 1997). Environmental conditions and resources that exceed the tolerance range of organisms that produce an adverse effect on populations and thereby affect ecosystem functioning due to changes in the community structure, biodiversity, and energy flow (Vinebrooke *et al.*, 2004).

Studies carried out on the Paraná (Bonecker *et al.*, 2005; Lansac-Tôha *et al.*, 2009; Dias *et al.*, 2014), Pantanal (Fantin-Cruz *et al.*, 2010), and Amazon (Carvalho, 1983; Bozelli, 1994; Hardy *et al.*, 1994) floodplain have shown that the structure of the zooplankton community changes with variations in physical and chemical attributes of water during the high-water period. Floodplains are characterised by high environmental heterogeneity, including lotic, semi-lotic, and lentic environments. This results in a high biological diversity (Ward and Tockner, 2001; Agostinho *et al.*, 2004). It has been suggested that connectivity to the main river is an important factor for patterns of species richness in these ecosystems (Stanford and Ward, 1993). Thus, habitat diversity is essential for the maintenance of high diversity on the floodplains (Thomaz *et al.*, 2007). In aquatic environments, abiotic variation can prevent well-adapted species from becoming dominant to the exclusion of others (Hays, 1996). Species richness can be affected by the competitive exclusion of species over time that influences community structure in floodplain environments (Tilman, 1982). This process allows species with different competitive strategies to co-exist in a certain environment (Hutchinson, 1961). Testate amoebae are a functional polyphyletic group of free-living protozoa and are distinguished from naked amoebae by their ability to build a shell (Adl *et al.*, 2012). These organisms have a wide distribution and have been recorded in numerous habitats, including planktonic

(Lansac-Tôha *et al.*, 2000; Velho *et al.*, 2000), benthic (Balik and Biyu, 2000; Yangmin *et al.*, 2013), peatland (Bobrov *et al.*, 1999; Mitchell *et al.*, 2008), and soil (Beyens and Meisterfeld, 2001) environments, among others. Testate amoeba species have a short generation time and respond rapidly to changes in environmental conditions.

These responses depend on several factors, such as temperature, nutritional conditions, the availability and quality of food resources, and population density (Pennak, 1953); this highlights the importance of studies that assess the influence of environmental variability on testate amoeba communities (Schonborn, 1992). Environmental change can also occur on small scales; however, studies that analyse these effects on testate amoeba communities are lacking. Thus, this study evaluated the structure of planktonic communities of arcellinid and euglyphid testate amoebae in three different environments of the Upper Paraná River basin, Brazil, in two different periods.

We hypothesised that the community structure of testate amoebae is differentially influenced by environmental conditions, mainly in isolated lentic ecosystems, due to the effect of a low-water period. In addition, we predicted that responses of testate amoeba communities to environmental change are also differentially affected by hydrodynamic characteristics of the environment.

METHODS

Study area

This study was performed at three different sites of the Upper Paraná River basin, Brazil (The Paraná River, Osmar and Pau Véio, Fig. 1). The Paraná River is a lotic ecosystem (22º44'S and 53º13'W, Fig. 1); and is the major river of the La Plata Basin and the second- longest river in South America. This ecosystem has a multichannel lotic pattern, a variable width, contains large islands

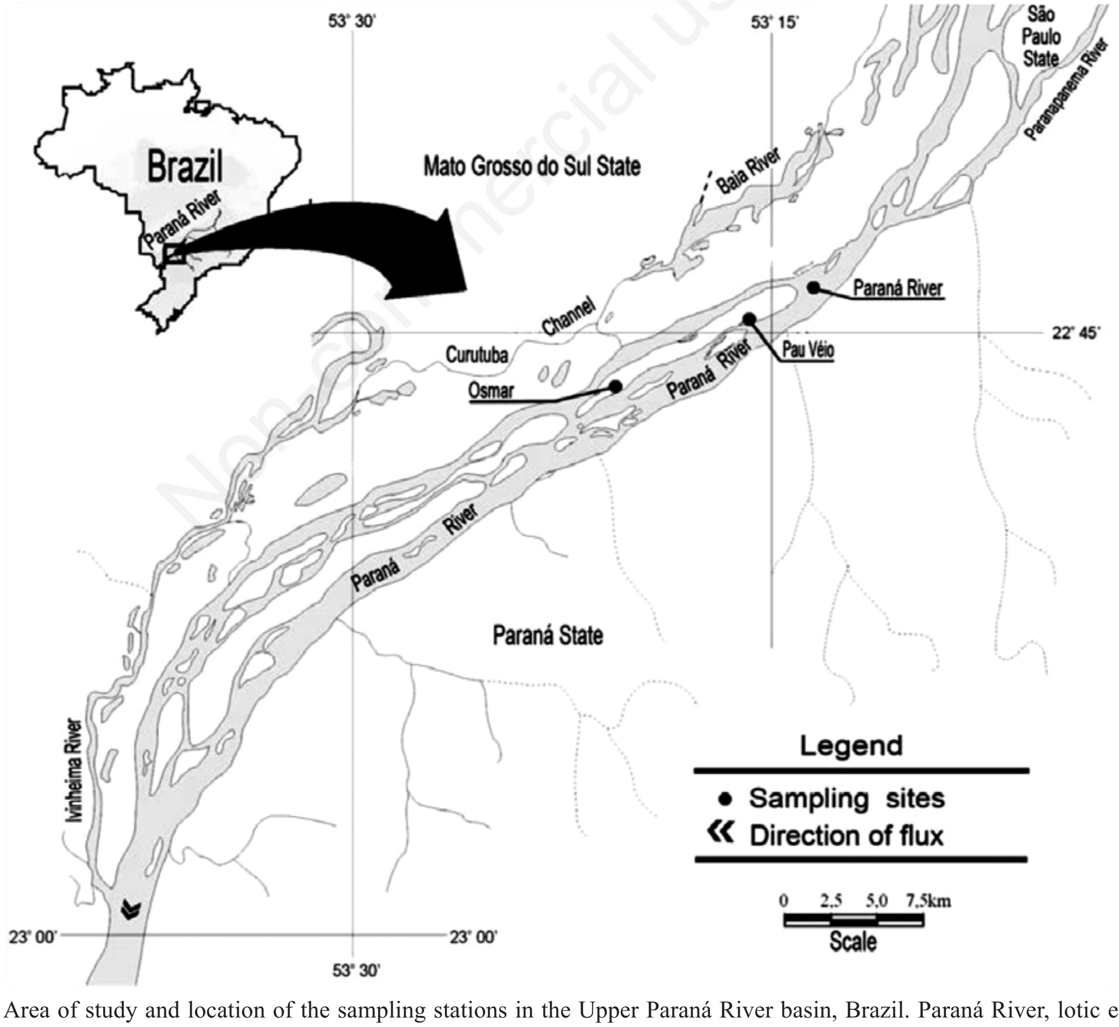

Fig. 1. Area of study and location of the sampling stations in the Upper Paraná River basin, Brazil. Paraná River, lotic ecosystem; Osmar, isolated lentic ecosystem, Pau Véio, connected lentic ecosystem.

and bars, and the water level is strongly influenced by upstream reservoirs (Agostinho *et al.*, 2001).

Osmar is an isolated and shallow lentic ecosystem (22° 46’ S; 53° 19’ W, Fig. 1), with periods of reduced water volume followed by high-water periods. This ecosystem is not directly connected to the river and remains unconnected to the main river channel during low- water periods, with direct contact only during major high-water periods. It has an area of 0.006 ha, a mean depth of 1.5 m and is surrounded by pastures and successional riparian forest remnants (Roberto *et al.*, 2009). Pau Véio is a connected lentic ecosystem (22° 44’ S; 53° 15’ W, Fig. 1) that is directly affected by the river’s water regime. This ecosystem is permanently connected to the river through short canals. It has an area of 3 ha, a mean depth of 1.8 m and contains extensive stands of multispecific aquatic macrophytes (Rodrigues and Bicudo, 2004).

Sampling of testate amoebae

Testate amoebae samples were collected over 15 consecutive days and then on alternate days for a further 15 days at each site. Testate amoebae have a short life cycle, lasting between three and five days (Pennak, 1953). Thus, we sampled the planktonic testate amoebae community at short time intervals. Samples were taken in both the low-water period (winter; September 2009) and high-water period (summer; February 2010). Integrated samples of plankton were collected using a motorised pump (500 L of water per sample filtered through plankton net with 68-μm mesh), placed 0.5 m above the bottom, to avoid capturing benthic organisms. This study is part of the Upper Paraná River Floodplain Long Term Ecological Research (LTER) programme that involves sampling other zooplankton groups, such as rotifers, cladocerans, and copepods. We chose 68-μm mesh in order to sample the widest variety of zooplankton possible, and this method was used for all samples (Chick *et al.*, 2010). Organisms were narcotised by saturating the sample with CO2, fixed with sugar-coated 4% formalin, and buffered with calcium carbonate, to avoid destroying the shell of the testate amoebae. The species richness of testate amoebae was quantified by observing water samples on glass slides under an optical microscope (Olympus CX31) at a magnification of 400×. Species identification was performed based on the following literature: Deflandre (1928, 1929), Gauthier-Lièvre and Thomaz (1958, 1960), Vucetich (1973), Velho and Lansac-Tôha (1996), Velho *et al.* (1996), Alves *et al.* (2007), Souza (2008), and Mazei and Warren (2012, 2014). Where possible, we lumped subspecies together into their respective morphospecies in order to reduce the skew or distortion of the results, because many subspecies have not been verified by description (Mitchell and Meisterfeld, 2005).

The abundance of testate amoebae was quantified using a Sedgewick-Rafter chamber and by counting individual organisms under an optical microscope. For counting, sets of three sequential subsamples totalling 7.5 mL were obtained by Hansen-Stempell and at least 50 individuals were counted per sample (Bottrell *et al.*, 1976). In each sample, only organisms that contained an identifiable protoplasm stained with Rose Bengal were considered alive and were counted (Booth *et al.*, 2010). The total abundance was expressed as individuals per cubic metre (ind m^{-3}).

Physical and chemical variables

We measured the following environmental variables: depth of the sampling site (m), water transparency (m) using Secchi disk depth, water temperature (°C), dissolved oxygen (mg L^{-1}) using portable YSI equipment, and electrical conductivity (μS cm^{-1}) and pH using Digimed potentiometers. Samples of water were collected for the measurement of chlorophyll-*a* (μg L^{-1}), suspended organic and inorganic matter (μg L^{-1}), and total phosphorus and nitrogen (μg L^{-1}). These environmental variables were measured at the surface and bottom of each water body and the mean values were used to run the analyses for all variables except for transparency and depth. The mean values were used because the environments are shallow and show full mixing, and light penetration and physical and chemical differences within the water column are very uncommon (Roberto *et al.*, 2009). The concentration of chlorophyll-*a* was quantified via extraction with 90% acetone and measurement of the absorbance in a spectrophotometer at 663 nm (Golterman *et al.*, 1978). Concentrations of suspended organic and inorganic matter (μg L^{-1}) were determined using gravimetric analysis (Wetzel and Likens, 1991). Total nitrogen was quantified by the persulphate method, which entails the oxidation of all nitrogenous compounds to N-nitrate. This was then reduced to N-nitrite in the presence of cadmium using a flow-injection system (Mackereth *et al.*, 1978), and the concentration of the ion was determined spectrophotometrically. The total phosphorus concentration was determined using an orthophosphate reaction and subsequent spectrophotometric measurement of absorbance at 660 nm (Golterman *et al.*, 1978).

Data analysis

A time-lag analytical approach was performed to evaluate the influence of environmental conditions on temporal variation in the testate amoebae community. This analysis can produce a number of general theoretical patterns with time-series data. If the regression result is significant, positive, and linear, this implies that the assemblage in question is undergoing directional change. If the regression result is not significant or the slope is not significantly different from zero, this implies fluctuation or stochastic variation over time. A negative slope implies that the species composition is converging toward a community-type characteristic of one of the early sampling periods (Collins *et al.*, 2000). The significance was estimated by a Mantel test to compare the relationship between the dissimilarity matrices and the time-lag matrix. A Kendall test was used to estimate the species abundance on each sampled day and for each water body. This analysis encompasses different aspects of the species abundance: a significant positive association suggests that species abundance becomes more similar over time (patterns of species dominance are maintained), whereas a significant negative association indicates a reversal of the dominance pattern among species (Kendall, 1990).

We also performed a Redundancy Analysis (RDA) to assess how testate amoeba communities responded to environmental change in the three environments in both studied periods (Legendre and Legendre, 1998). The relationship between species and water body was evaluated through permutations (999 random permutations). We log-transformed the species abundance data to reduce the influence of rare species. We then processed the data according to the Hellinger procedure (Legendre and Gallagher, 2001), to linearize the data, increase the symmetry of relationships, and reduce the effect of outliers. Environmental data were also log-transformed (except pH). The effect of multicollinearity among environmental variables was analysed using Variance Inflation Factors (VIF). The dissimilarity of the testate amoebae community between different sampling times within each water body was calculated using the Bray-Curtis index (Legendre and Legendre, 1998). The significance of this difference was calculated using a Mantel test (Mantel, 1967; Legendre and Fortin, 1989; Bini *et al.*, 2008). This analysis correlated the relationship between the temporal dynamics of the communities (Bray-Curtis dissimilarity matrix) and the abundance in each environment (abundance matrix), using 999 random permutations. This analysis tested whether the results differed from random relationships (Jackson and Somers, 1989).

Statistical analyses were performed with the statistical environment R version 3.0.2 (R Core Team, 2013) using the Vegan R package version 2.0-6 (Oksanen *et al.*, 2013). Before performing the analyses, all environmental variables were log-transformed (except pH), to minimise the effect of outliers and to avoid statistical problems (Zuur *et al.*, 2010).

RESULTS

Characterisation of environmental conditions

The river and the connected lentic ecosystems showed high variation in most environmental parameters, particularly suspended inorganic matter. The isolated and connected lentic ecosystem showed high variations in total phosphorus (Fig. 2).

Variation in the composition, richness, and abundance of the testate amoebae community

In total, 75 morphospecies were identified, belonging to six families: Difflugiidae (42 taxa), Arcellidae (13 taxa), Centropyxidae (10 taxa), Lesquereusiidae (seven taxa), Plagiopyxidae (two taxa) and Euglyphidae (one taxon) (Supplementary Tab. 1). Higher mean values of species richness were observed during the low-water period (21 species in each lentic ecosystem and 7 species in the river) than during the high-water period (16 species in the isolated lentic ecosystem, 14 in the connected lentic ecosystem and 4 in the river, Fig. 3 a,b). The mean species abundance was greater in the isolated lentic ecosystem (3447 ind m^{-3} in the low-water period; 2242 ind m^{-3} in the high-water period), than in the connected lentic ecosystem (1632 ind m^{-3} low; 734 ind m^{-3} high) or the river (103 ind m^{-3} low; 48 ind m^{-3} high, Fig. 4 a,b).

High oscillations in species abundance were observed in the isolated lentic ecosystem at the beginning of sampling (the first 12 days) and at the end of sampling (day 21) in the low-water period. The connected lentic ecosystem showed the highest abundance at the beginning of sampling and a decrease during the final sampling days. The highest species abundance in the river was observed on days 13 and 17, with a subsequent reduction observed in the final sampling days (Fig. 4a). During the high-water period, all the water bodies showed the greatest species abundance values during the first 11 days, with a decrease in subsequent sampling days (Fig. 4b).

Time-lag analytical approach of testate amoebae dominance

Testate amoeba communities showed distinct changes in dominance patterns over the sampled days in all the water bodies (Tab. 1). The environmental conditions dif-

Tab. 1. Results of Mantel tests between the time-lag matrix and the Kendall similarity coefficient matrix in the environments of the Upper Paraná River basin.

	r-Mantel	P
Winter		
Isolated lentic	-0.24	<0.01*
Connected lentic	-0.20	0.01*
River	-0.02	0.39
Summer		
Isolated lentic	-0.20	0.02*
Connected lentic	0.04	0.32
River	0.03	0.62

**Significant results.*

ferentially influenced these dominance patterns in each water body and studied period. A significant relationship was observed between the matrices of Kendall similarity and time lag in the isolated lentic ecosystem during both studied periods. The dominance of the testate amoeba communities changed, and the distribution of species abundance reversed over time. *Arcella gibbosa* predominated during the first eight sampling days, as well as during the low-water period on day 15. In the interval between days 9 and 12, *Arcella mitrata* showed greater dominance, and on day 14, *Arcella vulgaris undulata* predominated. *Arcella vulgaris* predominated on day 13, and *Arcella discoides* on day 16. From day 17 to day 21, the final sampling day, *Cucurbitella dentata* quinquilobata assumed dominance in the community (Fig. 5a). Higher variation in the concentration of total nitrogen and suspended inorganic matter was correlated with these changes in the dominance pattern. *Arcella gibbosa* predominated for the first three days of sampling, on days 6, 7, and 10, and in the high-water period between days 16 and 21. *Cucurbitella dentata quinquilobata* predominated on days 5 and 9 and between days 11 and 15. A change in the predominant species was also observed on days 4 (*Centropyxis aculeata*), 8 (*Difflugia pseudogramen*), and day 21, which was the final day of sampling (*A. mitrata*) represented the dominant species on the final sampling day (Fig. 5b). Of the environmental parameters considered, total phosphorus was the most highly correlated was with and changes in the dominance pattern in the isolated lentic ecosystem during the high-water period.

In the connected lentic ecosystem during the low-water period; however, the testate amoebae community structure showed a significant difference between these matrices. *Centropyxis aculeata* predominated on almost all the days of sampling, except for day 18, when *A. discoides* predominated (Fig. 6 a,b). High correlations were observed between the matrices of Kendall similarity and depth, electrical conductivity, temperature, chlorophyll-*a*, total nitrogen, and suspended organic matter (low water period). In contrast, the structure of the testate amoebae community in the river showed no significant pattern between the associations of the time lag of samplings and

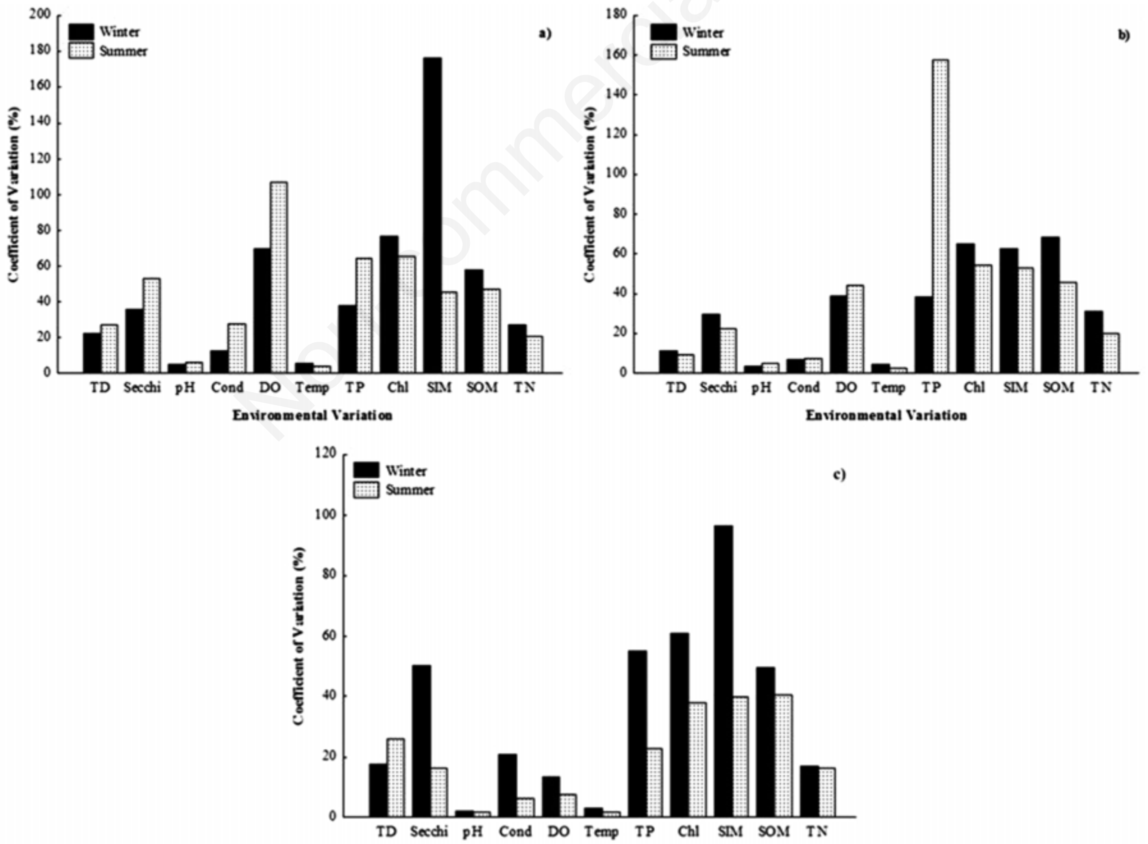

Fig. 2. Coefficient of variation (CV) of environmental conditions in the isolated lentic ecosystem (a), connected lentic ecosystem (b), and river (c) in both studied periods. TD, depth; Secchi, water transparency; Cond, electrical conductivity; DO, dissolved oxygen; Temp, temperature; TP, total phosphorus; Chl, chlorophyll-*a*; SIM, suspended inorganic matter; SOM, suspended organic matter; TN, total nitrogen.

the Kendall correlation matrix. Thus, this lotic ecosystem did not indicate a reversal of the trend in the patterns of community abundance over time (Fig. 7 a,b).

Redundancy analysis between testate amoebae and environmental conditions

Community structure was associated with environmental variables in all the water bodies. The ordination model explained 27% (adjusted R^2) of the data in the low-water period and 22% (adjusted R^2) in the high-water period. Significance values for individual RDA axes were 44.3% (axis 1) and 11.7% (axis 2) in the low-water period and 44.7% (axis 1) and 15.8% (axes 2) in the high-water period. In addition, the results of the permutation tests (999 random permutations) showed a significant difference to RDA ($P<0.05$) in both studied periods.

Most species were distributed on the negative side of the axis in the low-water period; however, a positive association was observed between distributions of these species and electrical conductivity, temperature, depth, and water transparency. The concentrations of dissolved oxygen, pH, and suspended organic and inorganic matter were also positively correlated with the first axis, although with lower importance. The positive correlation was mainly with arcellid species. However, a negative correlation was observed between distributions of these species and chlorophyll-*a* and total phosphorus (Fig. 8a). Only *Arcella brasiliensis*, *A. vulgaris*, and *A. vulgaris undulata* were positively correlated with axis 2. Distributions of these species

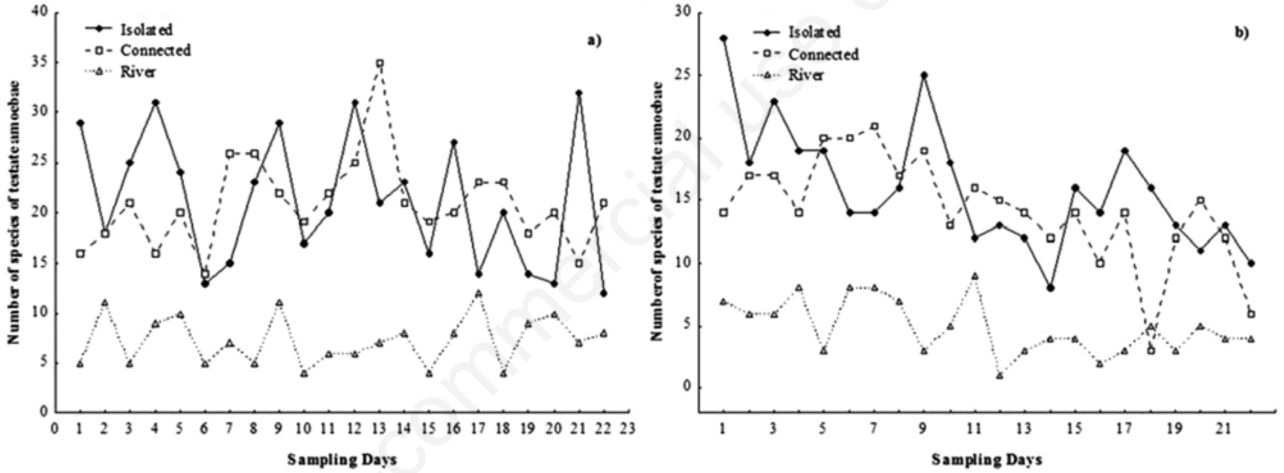

Fig. 3. Mean richness of testate amoebae in the environments: (a) winter and (b) summer.

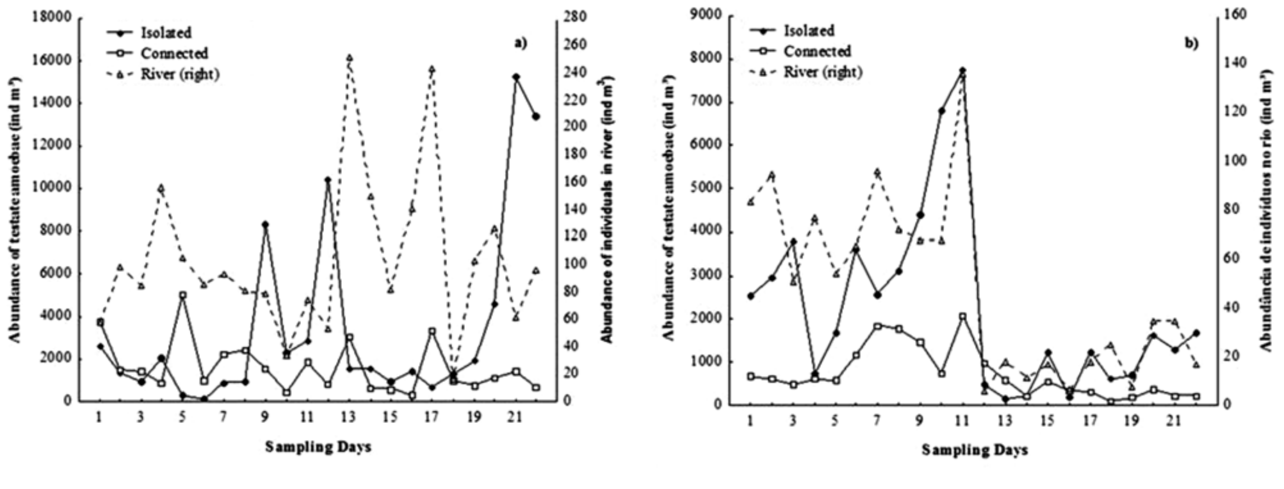

Fig. 4. Mean abundance of all the testate amoebae in the environments: (a) winter and (b) summer.

showed an association with greater values of temperature, depth, and electrical conductivity and lesser values of suspended organic matter. Most species were distributed on the first ordination axis in the high-water period. Species distribution was positively correlated with the concentration of total phosphorus and chlorophyll-*a* and with electrical conductivity on axis 1. This positive correlation was mainly with the distributions of difflugid species. The distribution of some species was negatively correlated with depth, water transparency, and suspended organic and inorganic matter (Fig. 8b). There was no clear explanation for the positive influence of the environmental variables on species distribution on axis 2. A negative association was observed between some testate amoeba species and water transparency and suspended organic matter (Fig. 8b).

Bray-Curtis dissimilarity of the testate amoebae community structure

The mean Bray-Curtis dissimilarity value estimated for each water body indicated different patterns of communities, corroborating the results of RDA. During the low-water period, the river had the greatest mean dissimilarity value (0.58), followed by the connected lentic ecosystem (0.54), then the isolated lentic ecosystem (0.48). During the high-water period, the isolated lentic

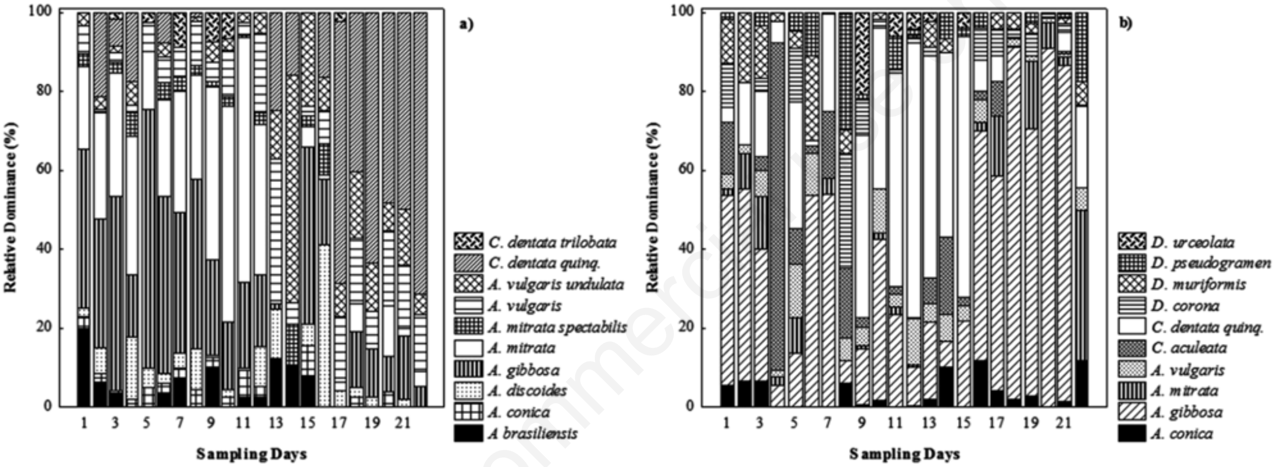

Fig. 5. Dominance pattern of the testate amoebae community in the isolated lentic ecosystem: (a) winter and (b) summer. Only the most dominant species were considered.

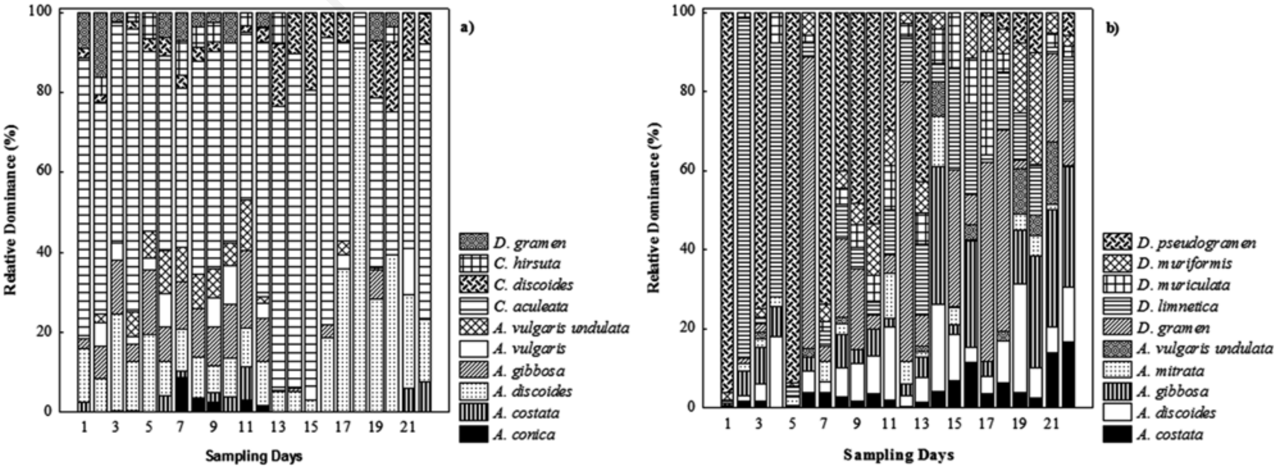

Fig. 6. Dominance pattern of the testate amoebae community in the connected lentic ecosystem: (a) winter and (b) summer. Only the most dominant species were considered.

ecosystem had the greatest dissimilarity value (0.54), followed by the river (0.49), and then the connected lentic ecosystem (0.47). Mantel tests indicated significant results (999 random permutations; P<0.05) for dissimilarity values in all water bodies in the studied periods (Tab. 2).

DISCUSSION

The Difflugiidae, Arcellidae and Centropyxidae had the highest species richness and abundance. Numerous studies have shown that the presence of these families is frequently recorded in freshwater environments (Green, 1975; Dabés, 1995; Landa and Mourguês-Schurter, 2000), particularly in the Upper Paraná River basin (Lansac-Tôha *et al.*, 2004, 2009; Alves *et al.*, 2010, 2012; Arrieira *et al.*, 2015).

During the low-water period, the water bodies in the isolated lentic ecosystem showed the highest mean values of species richness and abundance. These environments had a lower water volume, which may have caused a higher concentration of organisms. Exchange of fauna oc-

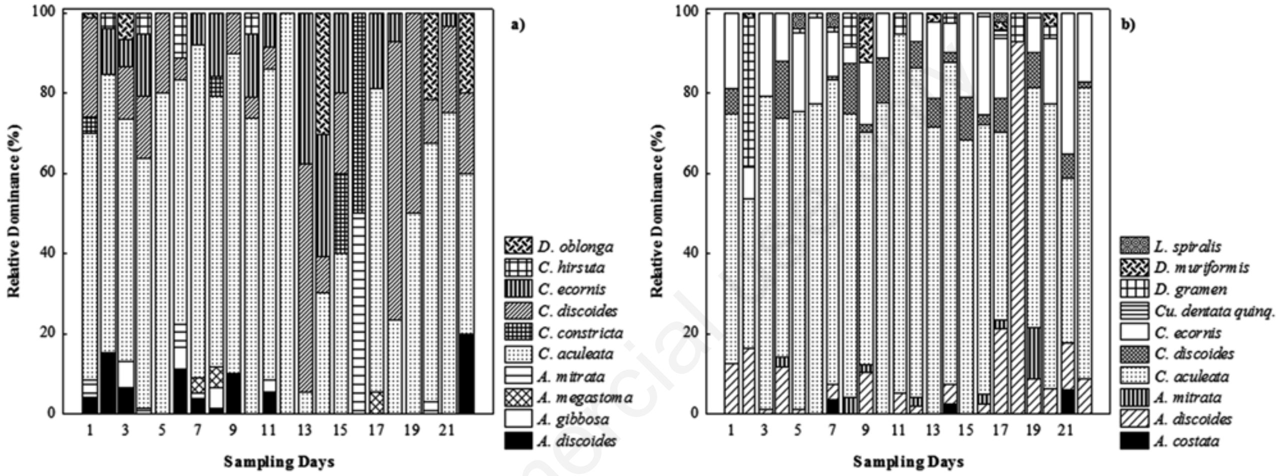

Fig. 7. Dominance pattern of the testate amoebae community in the river: (a) winter and (b) summer. Only the most dominant species were considered.

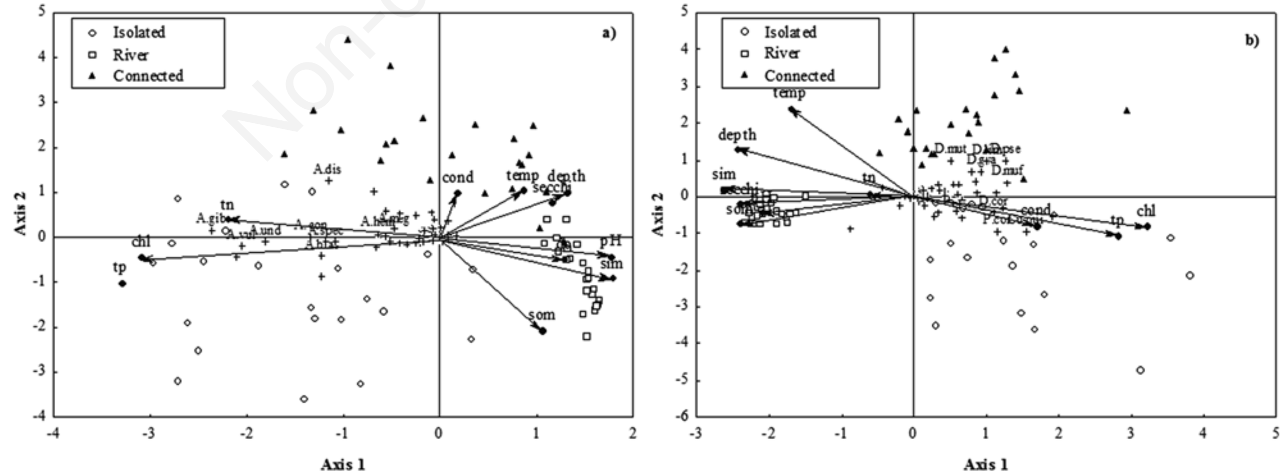

Fig. 8. Ordination diagram of RDA. a) Winter. b) Summer. Variables: temp, water temperature; do, dissolved oxygen; chl, chlorophyll-*a*; tp, total phosphorus; tn, total nitrogen; cond, electrical conductivity; secch, water transparency; sim, suspended inorganic matter; som, suspended organic matter; depth; pH. Species: A.bras, *A. brasiliensis*; A.con, *A. conica*; A.gib, *A. gibbosa*; A.dis, A. *discoides*; A.hem, *A. hemisphaerica*; A.meg, A. *megastoma*; A.spec, *A. megastoma spectabilis*; A.vul, *A. vulgaris*; A.und, *A. vulgaris undulate*; Cu.q, *Cu. dentata quinquilobata*; D.cor, D. *corona*; D.gra, *D. gramen*; D.lim, *D. limnetica*; D.muf, *D. muriformis*; D.mut, *D. muriculata*; D.pseu, *D. pseudogramen*; P.cor, *P. coroniformis*. Only the species most associated with each axis were used, to more easily identify the relationships between species and environmental variables.

curs through the displacement of water masses or the ability of organisms to move between planktonic and littoral zones (Lansac-Tôha *et al.*, 2004). This process might also be aided by water contraction in lentic ecosystems (Simões *et al.*, 2012), reflecting the greater proximity of the littoral vegetation and planktonic zones, as well as reduction of the water column. Thus, the contribution of species associated with vegetation and sediment was greater, increasing the richness and abundance in this studied period. The river showed a lower in the river than in the lentic ecosystems. The lentic ecosystems have greater habitat heterogeneity and stands of aquatic macrophytes in the littoral region. This region shows a greater concentration of nutrients and increased availability of habitats for colonisation (Thomaz and Bini, 1998). Previous studies in this floodplain have shown high zooplankton richness near this vegetation (Bonecker *et al.*, 1998; Lansac-Tôha *et al.*, 2004).

During the low-water period, greater variations in abundance were related to higher variations in environmental conditions. Thus, these water bodies were more unstable, and that variation directly affected the organism density. During the high-water period, the high similarity between the abundance patterns was related to the homogenising effect of flooding (Thomaz *et al.*, 2007). Temporal variation in community structure was observed in all water bodies, with environmental conditions changing the dominance pattern of the community. These results were related to the increased dissimilarity and promoted the reversal of ranks of species distribution as a consequence.

The isolated lentic ecosystem showed high variability in environmental conditions, highlighted by the significant relationships between the matrices of the Kendall similarity and time lag. High variation in phosphorus during the high-water period, and total nitrogen and suspended inorganic matter during the low-water period were correlated with these results. We suggest that this variability in environmental conditions is the main influence on testate amoebae community structure. Floodplains are regularly affected by changes in environmental conditions that can exceed the tolerance limit of some species (Shurin *et al.*, 2007, 2010). Thus, these conditions can inhibit the development of some species, thereby changing the dominance patterns. The high dissimilarity of testate amoeba communities was probably due the effect of low-water period. A high correlation with the variation in electrical conductivity, temperature, chlorophyll-*a*, total nitrogen, and suspended organic matter, likely affected the testate amoebae community. Similarly, Hein *et al.* (2003) demonstrated that autochthonous processes of energy input exceed allochthonous processes, due to the effect of low-water period. The lack of significance in the association between the sampling time lag and the Kendall correlation matrix suggests that an increase in depth, caused by the high- water period, is responsible for maintaining environmental conditions. These conditions favour the lower variability of the community in the high-water period (Simões *et al.* 2012).

Tab. 2. Results of Mantel tests to Bray-Curtis dissimilarity significance in the environments of the Upper Paraná River basin in both studied periods.

	Index	r-Mantel	P
Winter			
Isolated lentic	0.48	0.29	<0.01*
Connected lentic	0.54	0.32	<0.01*
River	0.58	0.12	0.01*
Summer			
Isolated lentic	0.54	0.23	0.01*
Connected lentic	0.47	0.26	<0.01*
River	0.49	0.03	0.05*

**Significant results.*

Other studies have reported high variability in macroinvertebrate and fish communities under relatively constant environmental conditions (Moyle and Vondracek, 1985; Townsend *et al.*, 1987; Weatherley and Ormerod, 1990; Scarsbrook, 2002; Milner *et al.*, 2006). Our results suggest that variability in environmental factors was not detected due to characteristics of the water body. Thus, environmental variations were not sufficiently significant to lead to important changes in the species dominance in the river. The hydrodynamic characteristics of these environments also influenced the establishment of species. This suggests that environmental variation creates a gradient of conditions that promote changes in the structure of the testate amoebae community.

Arcellidae species showed a negative association with the environmental variables that reflect productivity, such as the total concentration of phosphorus, chlorophyll-*a*, and suspended organic matter. Arcellid species construct their shells via an endogenous process. Thus, they do not require suspended matter, and can therefore be frequently found in oligotrophic environments (Reid, 1961; Medioli and Scott, 1983). Difflugiidae species showed a positive association with the concentrations of total phosphorus and chlorophyll-*a*. These species require inorganic particles to construct their shells (exogenous production), and are found in environments with higher productivity (Scott *et al.*, 1991).

The dissimilarity in testate amoebae community composition supports the hypothesis that oscillations in the water level influence the community structure. In addition, the community composition was more dissimilar in the isolated lentic ecosystem, in which high water had a negative effect on community structure. The high water diluted the plankton and caused a lower species composition in this ecosystem compared to the other ecosystems. However, the greater species difference in the river and connected lentic ecosystems was likely due to the absence of exchange of fauna between the lentic and lotic environments, caused by the effect of low water period. Moreover, this result may be related to the sampling of fauna from the littoral and sediment regions, as previously discussed. These results agree with those of Margalef (1983) and Ward *et al.* (2002), who demonstrated that oscillations in the water level typify a continuous physical disturbance.

CONCLUSIONS

Our results suggest that the richness, abundance, and dominance pattern of the testate amoebae community were influenced by environmental conditions. In addition, the results showed that testate amoeba communities responded differentially to environmental conditions and were affected by the distinct hydrodynamic characteristics of the environment.

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