Journal of Freshwater Ecology

ISSN: 0270-5060 (Print) 2156-6941 (Online) Journal homepage: https://www.tandfonline.com/loi/tjfe20

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**To cite this article:** Rodrigo Leite Arrieira, Leilane Talita Fatoreto Schwind, Claudia Costa Bonecker & Fábio Amodêo Lansac-Tôha (2017) Temporal dynamics and environmental predictors on the structure of planktonic testate amoebae community in four Neotropical floodplains, Journal of Freshwater Ecology, 32:1, 35-47, DOI: 10.1080/02705060.2016.1236758

**To link to this article:** https://doi.org/10.1080/02705060.2016.1236758

JOURNAL OF FRESHWATER ECOLOGY, 2017
VOL. 32, NO. 1, 35–47
http://dx.doi.org/10.1080/02705060.2016.1236758

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# Temporal dynamics and environmental predictors on the structure of planktonic testate amoebae community in four Neotropical floodplains

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**ABSTRACT**

Understanding the environmental factors that control community structure has become a major focus of ecological research in recent decades. Here, we aimed to analyze the structure of planktonic testate amoebae community and the impact of environmental variables on the diversity of planktonic species in four floodplains of Brazil (Amazonian, Araguaia, Paraná, and Pantanal) over two hydrological periods (2011 and 2012). We hypothesized that biological diversity (richness, abundance, and diversity) of the testate amoebae community is higher during drought periods. Samples were collected from the subsurface of the limnetic region of 72 lakes in the four floodplains during both drought and flood periods in both years. We identified 109 species, belonging to 11 families. Difflugiidae and Arcellidae exhibited higher species composition and abundance. ANOVA results showed noticeable temporal variation in testate amoebae community structure. We confirmed that the highest richness, abundance, and diversity were primarily recorded during drought periods, with significant differences being documented among floodplains and across the two hydrological periods. Multiple regression analysis also indicated that testate amoebae diversity is related to the productivity of the environments in the Amazonian, Araguaia, and Paraná floodplains. Depth of lakes and phosphorus appeared to be limiting factors in the Paraná and Araguaia floodplains, while dissolved oxygen limited species diversity in the Pantanal floodplain. Our results highlight that testate amoebae community exhibit the greatest biological diversity during drought periods, while species diversity is influenced by the environmental conditions (primarily productivity) of each floodplain.

**ARTICLE HISTORY**
Received 4 May 2016
Accepted 13 August 2016

**KEYWORDS**
Protist; Arcellinida; zooplankton; diversity; testate amoebae

## Introduction

Identification of the processes that drive the assembly of communities is becoming one of the main objectives of ecological studies in recent decades (Rohde 2011). Increased understanding of broad-scale diversity is essential to determine the mechanisms that control diversity at different scales (Gaston & Blackburn 2000). Floodplains exhibit high species diversity (Tundisi & Matsumura-Tundisi 2008). These aquatic environments are characterized by heterogeneous river habitat microsystems that have great functional and structural complexity (Tockner et al. 2000; Ward et al. 2002). These ecosystems have seasonal effects, marked by the flood pulse, which is considered to be the

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Supplemental data for this article can be accessed at http://dx.doi.org/10.1080/02705060.2016.1236758.

main force that influences the functioning of these ecosystems (Ward & Tockner 2001). Therefore, floodplains are excellent model systems for investigating potential factors that regulate the organization of aquatic communities.

Changes to the water level lead to alterations of several environmental variables, such as productivity variables (Arrieira et al. 2016), which, in turn, affect the aquatic communities (Junk et al. 1989; Neiff 1990). Consequently, fluctuations to the water level facilitate the development of high species diversity in floodplains (Rocha & Thomaz 2004; Lansac-Tôha et al. 2009). However, species diversity may be influenced by the environmental characteristics of each region, due to differences in environmental factors and the strength of biotic interactions, both of which influence the physiology and behavior of organisms (Gering et al. 2003). These factors determine species richness and promote the replacement of species composition (Simões et al. 2013). Thus, the environmental characteristics of floodplains may serve as a good predictor on the structure of aquatic communities including those of testate amoebae (Neiff 1996). These organisms occupy a variety of trophic roles in the food chain, ranging from decomposers to consumers (Gimenes et al. 2004; Jassey et al. 2013). Furthermore, testate amoebae quickly respond to changing environmental conditions, showing that environmental variability influences community structure (Schonborn 1992).

Although several studies have been conducted in the Brazilian floodplains, knowledge about the diversity and ecology of testate amoebae remains limited. Most studies on testate amoebae have been conducted in the Paraná River floodplain (e.g. Velho et al. 2000, 2003; Lansac-Tôha et al. 2004, 2014; Alves et al. 2010, 2012; Schwind et al. 2016). Other studies on testate amoebae diversity are still at the early stages in other Brazilian floodplains, including the Amazon, Araguaia, and Pantanal (Machado et al. 2015; Patterson et al. 2015; Vieira et al. 2015). Thus, studies investigating the community structure of testate amoebae in floodplains could enhance taxonomic knowledge and characterize the main predictors of these communities.

Here, we aimed to analyze temporal variability in the structure of planktonic testate amoebae community and identify how environmental variables influence species diversity in four floodplains of Brazil. We hypothesized that biological diversity (richness, abundance, and diversity) of the testate amoebae community is higher during periods of drought, when isolation of the lakes and greater impact of environmental conditions (e.g. primary productivity) would increase effects on the community. We also predicted that the species diversity would be influenced by the distinct environmental conditions of each floodplain.

## Methods

### *Study sites*

The study sites (Figure 1) used in this investigation are located in four major floodplains in Brazil: Amazonian (3°02′–3°34′S; 59°38′–60°50W), Araguaia (12°49′–13°25′S; 50°28′–50°43′W), Pantanal (18°46′–19°34′S; 56°58′–57°46′W), and Paraná (22°35′–22°50′S; 53°05′–53°40′W).

The Amazonian floodplain is composed of a complex network of lakes, and covers an area of 350,000 $km^2$. It has the largest river basin ($6.1 \times 10^6$ $km^2$) and greatest discharge volume in the world ($6.3 \times 10^{12}$ $m^3$/yr; Melack & Hess 2010). The Araguaia floodplain is elongated in shape, divided into three segments (Upper, Middle, and Lower), the last of which is located next to the confluence of the Tocantins River. The Middle Araguaia floodplain has a mean discharge of 6,420 $m^3$/s. Precipitation ranges between 1,300 mm/yr in the Upper Araguaia to 2,000 mm/yr in the Lower Araguaia (Latrubesse & Stevaux 2002; Aquino et al. 2008). The Pantanal floodplain is one of the largest continuous wetlands in the world, and covers an area of 140,000 $km^2$. This ecosystem is separated into 10 different sub-regions due to edaphic, hydrological, and biogeographical variations (Hamilton et al. 1995). The meandering and anastomosing rivers, lakes, and small temporary channels connect lake waters with nearby rivers during floods (Carvalho 1986). The Paraná River is the main river of the Plata basin, which was formed by the joining of the Grande and Paranaiba rivers. It has the tenth

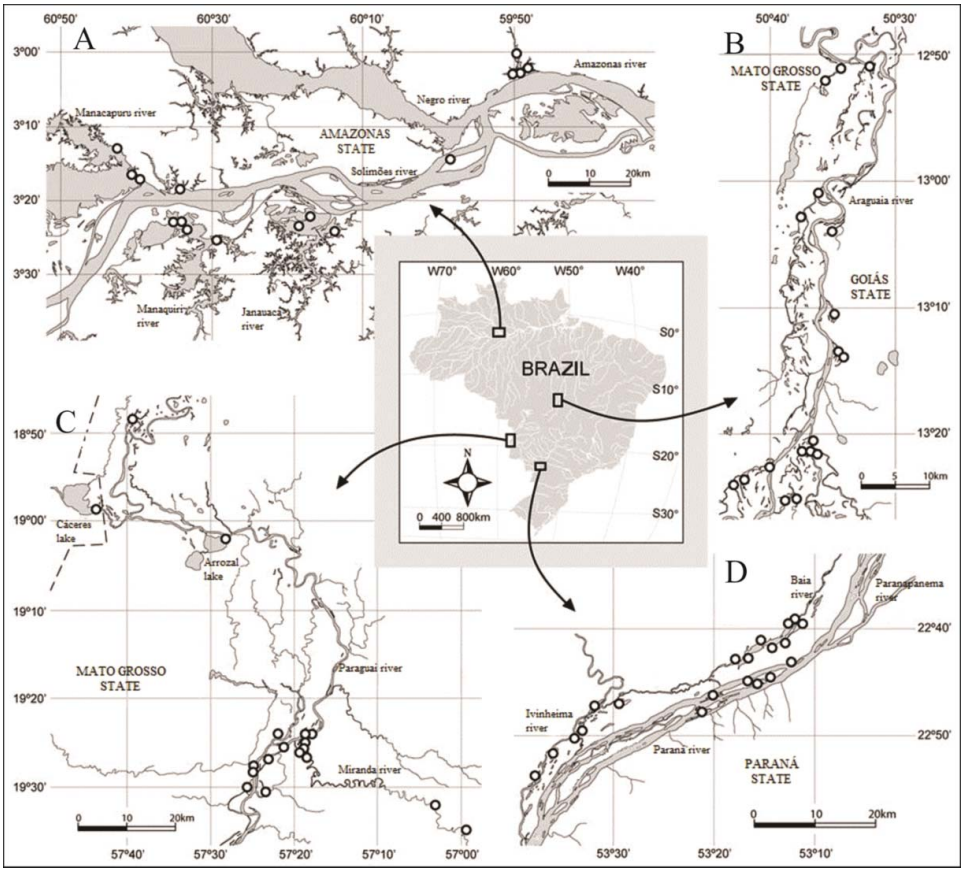


**Figure 1.** Location of the sampling sites in four floodplains of Brazil: (A) Amazonian; (B) Araguaia; (C) Pantanal; (D) Paraná.

largest discharge volume in the world ($5 \times 10^8$ $m^3$/yr) and has a $2.8 \times 10^6$ $km^2$ drainage area. This river has a wide anastomosing main channel, numerous secondary channels, lakes, and tributary rivers, and includes the Ivinhema and Baía rivers (Agostinho et al. 2001).

## *Sampling design*

Water samples were obtained from the subsurface of the limnetic region: (1) in 16 lakes located between the Solimões and Amazon Rivers, during October 2011 (drought period) and May 2012 (flooding period); (2) in 18 lakes located in the Araguaia River floodplain, during November 2011 (drought period) and May 2012 (flooding period); (3) in 18 lakes located in the Paraguay and Miranda River floodplains, during August 2011 (drought period) and March 2012 (flooding period); and (4) in 20 lakes located in the Paraná, Baía, and Ivinhema Rivers of the Upper Paraná River floodplain, during September 2011 (drought period) and February 2012 (flooding period). We collected a total of 144 samples (72 samples * 2 periods). More detailed characterization of study sites is available in Supplemental Table S1.

For each sample, 500 L water were filtered through a plankton net with 68 µm mesh, using a motorized pump. We chose the 68 µm mesh to sample the widest range of planktonic community possible and this bias was standardized for all samples. This study is part of a larger project, which involves sampling of other planktonic communities such as rotifers, cladocerans, and copepods. A sample fraction was collected from the net, transferred into polyethylene-labelled vials, and fixed

with 4% formaldehyde solution buffered with calcium carbonate. The samples were stained with Rose Bengal. Only living testate amoebae with a cytoplasm stained by the dye were counted and identified to the species level.

Testate amoebae abundance was determined using a Sedgewick–Rafter counting chamber placed under an optical microscope at a magnification of 400× (Olympus CX31). Counting was performed using sets of three sequential sub-samples obtained by a Hensen–Stempel pipette. Samples of 7.5 ml were used to count the testate amoebae; at least 50 individuals were counted per sample. Samples were fully quantified when the minimum number of individuals per sample was not achieved (Bottrell et al. 1976). Total abundance was expressed as individuals per cubic meter (ind/$m^3$).

We measured the environmental variables at the same sampling point from which water samples were obtained: water temperature (°C), dissolved oxygen concentration (mg/L) (portable oxygen meter, YSI 550A, YSI, Inc., http://www.ysi.com), depth of lake at the sampling site (m), water transparency (Secchi disk), turbidity (NTU), conductivity (mEq/L), total nitrogen (µg/L), ammonia (µg/L), total phosphorus (µg/L), phosphate (µg/L), pH (portable pH meter, DM-2, DigiMed, http://www.digimed.ind.br), and chlorophyll-*a* (µg/L). Total nitrogen was quantified by the persulfate method, which involves the oxidation of all nitrogenous compounds to nitrate-N. Samples were reduced to nitrite-N in the presence of cadmium using a flow-injection system (Mackereth et al. 1978), and the concentration of the ion was determined spectrophotometrically. Total phosphorus concentration was determined using an orthophosphate reaction and subsequent spectrophotometric measurement of absorbance at 660 nm (Golterman et al. 1978). The concentration of chlorophyll-*a* was quantified by extraction with 90% acetone, and absorbance was measured in a spectrophotometer at 663 nm (Golterman et al. 1978).

## Data analysis

We performed a principal components analysis (PCA) to establish the differential environmental characteristics of the studied floodplains. The data used for this analysis were previously log-transformed (x + 1), with the exception of pH. The Broken-Stick model was used as the selection of the significant axes (Jackson 1993), and the significance of the axes was verified by Analysis of Variance (ANOVA, Sokal & Rohlf 1991). These statistical analyses were performed using the 'vegan' package version 3.2.1 (Oksanen et al. 2015) in R version 3.0.2 software (R Core Team 2015).

Species diversity was estimated using the Shannon Index (H'; Pielou 1975). Two-way ANOVA (Sokal & Rohlf 1991) was used to investigate differences in richness, diversity, and abundance of testate amoebae among floodplain lakes and across the two hydrological periods, with $\alpha = 0.05$ being set as the significance threshold. The analyses considered the hydrological periods and sampled lakes, as well as the interaction between them. The Fisher's test was used to compare significant differences *a posteriori*. Assumptions of normality and homoscedasticity (homogeneity of variance) were previously tested through Shapiro-Wilk and Levene's tests, respectively.

The relationship between species diversity and the environmental variables in each floodplain was assessed by multiple regression (Sokal & Rohlf 1991). For this analysis, a stepwise backward selection procedure was performed to produce a parsimonious model. This procedure included all available factors (independent variables), and progressively excluded non-significant factors ($p < 0.05$), to derive the simplest model with the most representative variables. After setting the complete model, the variables without a significant relationship were removed from the model, to obtain a model that only contained statistically significant parameters. The data employed were log-transformed. Assumptions of linearity, normality, homoscedasticity, and independence were tested. These analyses were carried out using Statistica Software 7.0 (Statsoft Inc. 2005).

## Results

### Characterization of the environmental variables

The mean measured values of environmental variables of the floodplains during drought and flooding are shown in Table 1. The PCA results (Figure 2) indicated distinct characteristics between the environmental variables in each floodplain during both hydrological periods. The PCA 1 axis explained 36% of environmental variability, while the PCA 2 axis explained 14.8% of environmental variability, totaling 50.8% when both axes were combined during the drought period. The following associations were observed for PCA axis 1: Amazonian and Araguaia floodplains showed positive correlations with water transparency and depth; Pantanal and Paraná floodplains showed negative correlations with turbidity, chlorophyll-*a*, total phosphorus, and phosphate. For PCA axis 2 Paraná and Araguaia floodplains showed positive correlations with water transparency, dissolved oxygen, and chlorophyll-*a*, whereas Pantanal and Amazonian floodplains showed negative correlations with conductivity, water temperature, and pH (Figure 2a).

PCA 1 axis explained 46.25% of environmental variability, while PCA 2 axis explained 17.75% of environmental variability, totaling 64% when combining both axes during the flooding period. PCA axis 1 indicated that the Pantanal floodplain was positively correlated with depth and transparency, whereas the Amazonian floodplain was negatively correlated with turbidity, chlorophyll-*a*, temperature, and total nitrogen (Figure 2b).

### Composition and structure of testate amoebae community

We identified 109 testate amoebae species belonging to 11 families (Supplemental Table S2). Difflugiidae had the highest number of species (50), followed by Arcellidae (24), Lesquereusiidae (14), Centropyxidae (13), Hyalospheniidae (two species), Heleoperidae (one species), Phryganellidae (one species), Plagiopyxidae (one species), Trigonopyxidae (one species), Euglyphidae (one species), and Trinematidae (one species).

The testate amoebae community exhibited higher richness during drought in most of floodplains, with the highest richness being detected in the Pantanal floodplain. During flooding, the lowest testate amoeba richness was detected in the Amazonian floodplain. The ANOVA results (Figure 3) indicated significant differences for species richness interactions among the four floodplains and across the two hydrological periods ($F = 4.72$; $p < 0.01$).

Most floodplains had a higher abundance of organisms during the drought period, with the exception of the Paraná floodplain, where abundance was higher during the flooding period. The Amazonian floodplain had the highest abundance of all four floodplains during the drought period. During the flooding period, the lowest abundance was observed in the Amazonian floodplain. The ANOVA results (Figure 4) indicated significant results to species abundance interaction between floodplains and hydrological periods ($F = 7.70$; $p < 0.01$).

The most abundant species in each floodplain are shown in Figure 5, with *Cucurbitella dentata* f. *quinquilobata* being the most abundant in Amazonian floodplain (102,838 ind/m$^3$), *Cucurbitella madagascariensis* in the Araguaia floodplain (1,260 ind/m$^3$), *Centropyxis aculeata* in the Pantanal floodplain (9,409 ind/m$^3$), and *Difflugia pseudogramen* in the Paraná floodplain (31,408 ind/m$^3$; Figures 5 and 6).

The testate amoebae community also showed higher species diversity in most of floodplains during the drought period, with the exception of the Pantanal floodplain. The highest species diversity was detected in the Pantanal floodplain, whereas the lowest species diversity was detected in the Araguaia floodplain. During the flooding period, the lowest species diversity was detected in the Araguaia floodplain. The ANOVA results (Figure 7) indicated significant differences in the interaction of species diversity with the four floodplains and two hydrological periods ($F = 5.11$; $p < 0.01$).

**Table 1.** Mean measured values and standard deviation (SD) of environmental variables in the floodplains during drought (2011) and flooding (2012) periods.

| | Amazonian | | Araguaia | | Pantanal | | Paraná | |
|---|---|---|---|---|---|---|---|---|
| Environmental variables | Drought | Flooding | Drought | Flooding | Drought | Flooding | Drought | Flooding |
| Water temperature (°C) | 32.37 ± 1.78 | 31.94 ± 0.43 | 29.64 ± 0.49 | 28.98 ± 0.79 | 28.96 ± 1.65 | 20.98 ± 0.96 | 28.13 ± 0.51 | 23.43 ± 0.48 |
| Dissolved oxygen (mg/L) | 89.54 ± 3.05 | 23.28 ± 8.86 | 75.67 ± 1.66 | 30.67 ± 1.39 | 53.71 ± 2.32 | 38.53 ± 1.54 | 69.55 ± 1.21 | 85.99 ± 8.03 |
| Water transparency (m) | 0.38 ± 0.19 | 1.14 ± 0.23 | 0.53 ± 0.14 | 1.27 ± 0.53 | 0.50 ± 0.09 | 1.74 ± 0.48 | 0.86 ± 0.04 | 0.79 ± 0.02 |
| Depth (m) | 1.22 ± 0.76 | 12.61 ± 1.13 | 2.06 ± 0.68 | 4.77 ± 0.82 | 2.06 ± 0.11 | 3.02 ± 0.88 | 2.71 ± 0.64 | 2.35 ± 0.83 |
| Turbidity (NTU) | 72.08 ± 4.89 | 7.09 ± 0.38 | 29.18 ± 1.63 | 9.40 ± 0.50 | 19.92 ± 0.95 | 4.96 ± 0.28 | 21.17 ± 1.10 | 22.56 ± 1.63 |
| Conductivity (mEq/L) | 59.79 ± 39.73 | 53.28 ± 8.32 | 39.13 ± 6.98 | 40.34 ± 4.40 | 81.23 ± 3.42 | 86.04 ± 2.98 | 36.78 ± 1.04 | 35.65 ± 1.53 |
| pH | 6.31 ± 0.89 | 7.23 ± 1.01 | 6.91 ± 0.20 | 6.39 ± 0.23 | 6.71 ± 0.40 | 7.60 ± 0.28 | 6.15 ± 0.30 | 6.94 ± 0.34 |
| Total nitrogen (μg/L) | 2579 ± 147.0 | 698.1 ± 28.0 | 1272 ± 22.7 | 776.9 ± 40.2 | 1081 ± 58.3 | 1078 ± 32.4 | 895 ± 22.8 | 1181 ± 29.5 |
| Ammonia (μg/L) | 36.82 ± 3.59 | 15.96 ± 6.91 | 30.20 ± 2.55 | 8.23 ± 0.48 | 33.49 ± 2.65 | 21.40 ± 5.61 | 11.92 ± 0.50 | 19.11 ± 1.60 |
| Total phosphorus (μg/L) | 113.8 ± 5.42 | 22.5 ± 7.22 | 81.0 ± 18.7 | 23.5 ±6.26 | 54.91 ± 1.60 | 60.28 ± 3.33 | 69.41 ± 2.28 | 46.28 ± 1.72 |
| Phosphate (μg/L) | 14.80 ± 4.75 | 8.14 ± 0.33 | 12.49 ± 3.55 | 7.79 ± 2.80 | 17.35 ± 0.75 | 26.08 ± 1.36 | 14.05 ± 4.56 | 12.01 ± 6.53 |
| Chlorophyll-*a* (μg/L) | 48.52 ± 2.95 | 2.78 ± 0.19 | 18.31 ± 7.29 | 5.91 ± 3.55 | 10.27 ± 3.52 | 4.90 ± 0.35 | 16.97 ± 0.91 | 10.70 ± 0.55 |

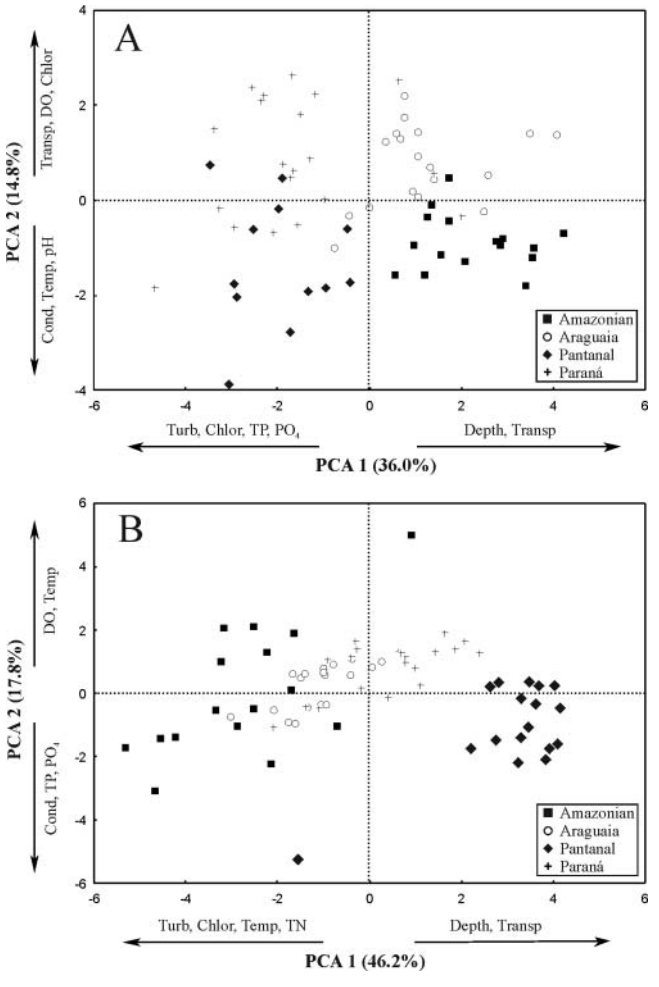


**Figure 2.** Principal components analysis ordination showing the environmental differences in each floodplain during drought (a) and flooding (b) periods. Environmental variables: Chl = chlorophyll-*a*; Cond = conductivity; DO = dissolved oxygen; $PO_4$, phosphate; TP, total phosphorus; Temp = water temperature; Transp, water transparency; Turb = turbidity.

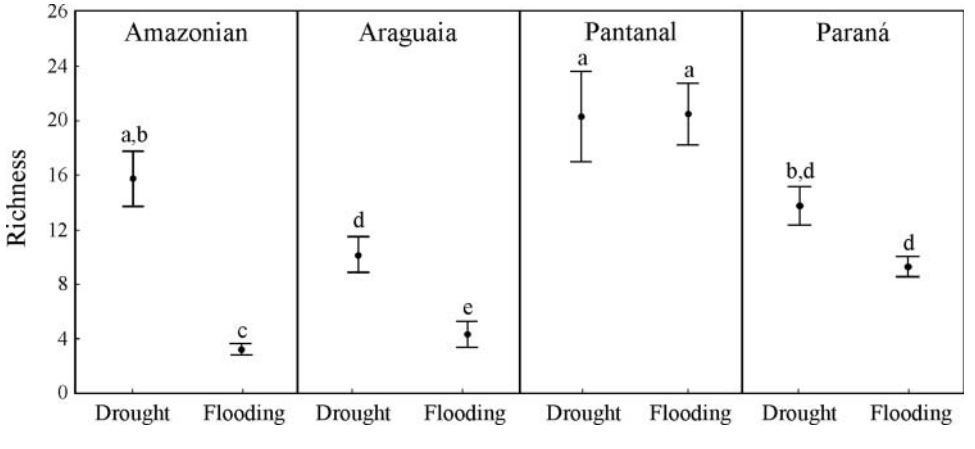


**Figure 3.** Species richness recorded during the drought and flooding periods in the four floodplains. Symbol = richness average; bar = standard error; letters = represents statistically significant differences at $p < 0.05$.

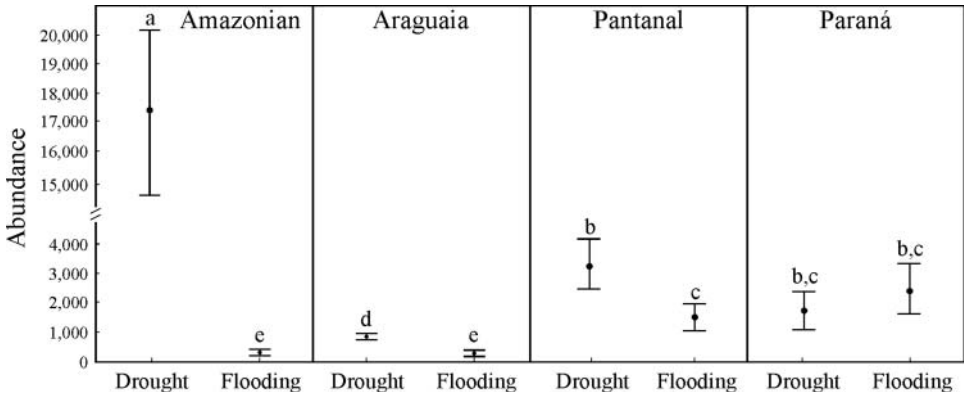


**Figure 4.** Abundance of organisms recorded during the drought and flooding periods in the four floodplains. Symbol = abundance average; bar = standard error; letters = represents statistically significant differences at $p < 0.05$.

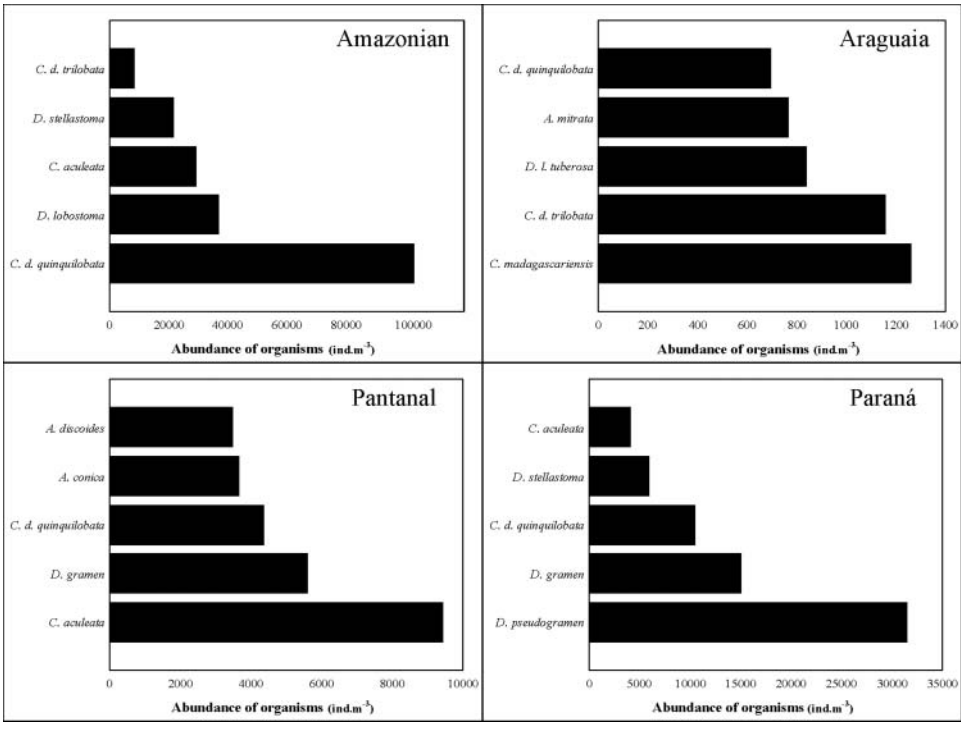


**Figure 5.** Most abundant testate amoeba species in each floodplain.

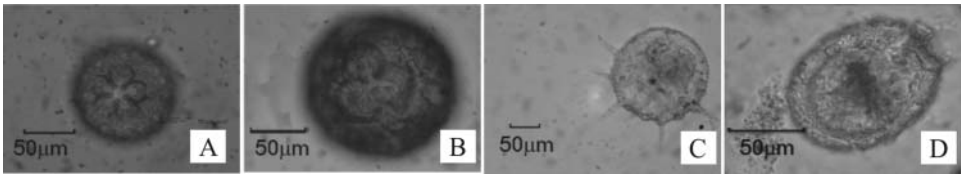


**Figure 6.** Light microscopy images of the most abundant species in each floodplain: (A) *Cucurbitella dentata* f. *quinquilobata* (Amazonian floodplain), (B) *Cucurbitella madagascariensis* (Araguaia floodplain), (C) *Centropyxis aculeata* (Pantanal floodplain), and (D) *Difflugia pseudogramen* (Paraná floodplain).

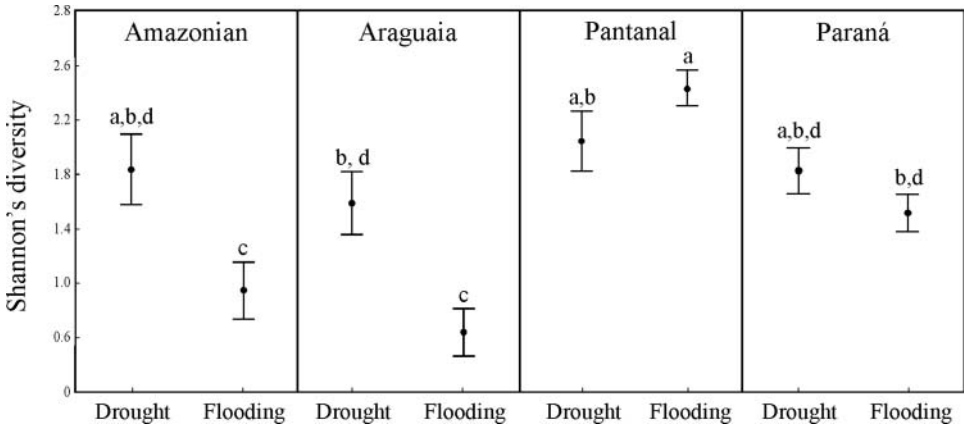


**Figure 7.** Species diversity recorded during the drought and flooding periods in the four floodplains. Symbol = diversity average; bar = standard error; letters = represents statistically significant differences at $p < 0.05$.

### *Relationship between species diversity and environmental variables*

The variables related to the productivity of environments (total nitrogen, ammonia, total phosphorus, phosphate, chlorophyll-*a*, and turbidity) were selected by multiple regression analysis (Table 2) as the main predictors of testate amoebae diversity in the Amazonian, Araguaia, and Paraná floodplains. In the Amazonian and Araguaia floodplains, species diversity was negatively affected by depth and total phosphorus. In the Pantanal floodplain, species diversity was negatively affected by dissolved oxygen. The equations of the multiple regression models, as well as the percentage of explanation for data variability, are presented in Table 2.

## Discussion

Our results indicate that changes to environmental variables were associated with how the hydrological periods influenced the environmental characteristics of each floodplain, as evidenced by the PCA results. The hydrologic regime causes major changes to the environmental variables of the aquatic environments (Thomaz et al. 2007). Hydrological dynamics directly and indirectly influence the structuring of aquatic communities, including biotic interactions and species distribution (Dunson & Travis 1991; Schwind et al. 2016). Thus, the considerable changes in environmental variables related to floodplains and the hydrological periods should have a strong influence on the testate amoebae community.

Difflugiidae and Arcellidae had the highest species richness and abundance. These testate amoeba families are considered to be major planktonic species in floodplains (Dabés 1995; Landa & Mourguês-Schurter 2000; Velho et al. 2004; Arrieira et al. 2015a). The high abundance of *Cucurbitella dentata* f. *quinquilobata* (Amazonian floodplain), *Cucurbitella madagascariensis* (Araguaia

**Table 2.** Contents of the multiple regression model between testate amoebae diversity (response variable) and environmental variables (explanatory variables) in each floodplain; $r^2$ indicates the explanatory ability of the model; *t* corresponds to the value of the *t*-test parameter; *p* indicates the significance of parameters ($\alpha = 0.05$). Div = testate amoebae diversity; D = depth; TN = total nitrogen; PO4 = phosphate; Chl-a = chlorophyll-*a*; NH4 = ammonia; TP = total phosphorus; DO = dissolved oxygen; Turb = turbidity.

| Floodplain | Model equation | $R^2$ | *t* | *p* |
|---|---|---|---|---|
| Amazonian | $\log_{10}(Div) = 1.14 - 0.04 * \log_{10}(D) + 0.01 * \log_{10}(TN) - 0.01 * \log_{10}(TP) + 0.05 * \log_{10}(PO4)$ | 0.37 | 5.04 | < 0.01 |
| Araguaia | $\log_{10}(Div) = 2.27 - 0.21 * \log_{10}(D) + 0.06 * \log_{10}(Chl\text{-}a) + 0.01 * \log_{10}(NH4) - 0.01 * \log_{10}(TP)$ | 0.42 | 6.30 | < 0.01 |
| Pantanal | $\log_{10}(Div) = 3.03 - 0.02 * \log_{10}(DO)$ | 0.43 | 3.30 | < 0.01 |
| Paraná | $\log_{10}(Div) = 2.55 + 0.02 * \log_{10}(Turb) + 0.01 * \log_{10}(DO) + 0.01 * \log_{10}(TN) + 0.06 * \log_{10}(PO4)$ | 0.58 | 3.95 | < 0.01 |

floodplain), and *Difflugia pseudogramen* (Paraná floodplain) might be linked to their spherical shell morphology (Lansac-Tôha et al. 2014). Similar results were obtained by Velho et al. (2003), who found that the predominance of spherical and hemispherical testate amoebae was related to their greater capacity to adapt to the limnetic region of floodplains lakes. The highest abundance of *Centropyxis aculeata*, (Pantanal floodplain) could be attributed to shell compression, which is regarded as an adaptation of these organisms. This characteristic could minimize its resistance to water as well as facilitating longer floatation in the water column (Lampert & Somer 1997).

The highest average richness, abundance, and diversity were observed in most floodplains during the drought period. During this period, floodplain lakes are shallow, and are subject to inputs of seston and nutrients to the water column (Carvalho et al. 2001; Roberto et al. 2009). This nutrient input into the aquatic environment leads to an increase in primary productivity of plankton (Bonecker et al. 2013). Consequently, these factors could promote an increase in the biological diversity of the testate amoebae community during drought.

In contrast, the lowest average biological diversity during flooding might be related to the homogenizing effect of the flood pulse, which promotes dilution of water bodies (Thomaz et al. 2007). As a result, biological diversity of the testate amoebae community declines (Costa et al. 2011). Multiple regression analyses showed that lower species diversity was negatively related to the water level of the Amazon and Araguaia floodplains, and might be due to the homogenizing effect. Consequently, an increase in the water level promoted lower testate amoebae diversity.

The multiple regression results also indicated a predominant relationship between the variables related to productivity (chlorophyll-*a*, total nitrogen, and total phosphorus) as the main predictors of testate amoebae diversity in the Amazonian, Araguaia, and Paraná floodplains. Previous studies on aquatic environments have suggested that ecosystem productivity is directly linked to the availability of food resources, from which protozoan communities benefit (Auer et al. 2004; Bastidas-Navarro & Modenutti 2007). Food resource availability is considered to be the predominant environmental filter in the organization of the testate amoebae community in floodplains (Arrieira et al. 2015b). Moreover, the current study verified that total phosphorus is a limiting environmental factor, based on the negative effects between species diversity and total phosphorus in the Amazonian and Araguaia floodplains. These results support those obtained by Mieczan (2012), in which phosphorus was one of the environmental factors that restricted the occurrence of these protozoa in aquatic environments.

An indirect contribution was observed for species diversity with phosphate (Amazonian and Paraná floodplains) and ammonia (Araguaia floodplain). Higher concentrations of phosphate and ammonia may favor the occurrence of bacteria in aquatic environments, because these organisms are able to absorb these soluble ions, which are excreted by zooplankton (Pinto-Coelho et al. 1997; Torres et al. 2007). As a result, the higher bacterial biomass leads to an increase in the supply of food resources, as they represent important food items in the diet of many testate amoebae (Gilbert et al. 2000; Mieczan 2009).

Another indirect relationship was observed between species diversity and dissolved oxygen in the Pantanal floodplain. Oxygen depletion in water might be related to the increased decomposition of organic matter, which is favored by the presence of large macrophyte biomass and the climatic conditions found in the lakes of the Pantanal floodplain, a process locally known as the *Dequada* process (Hamilton et al. 1995). The areas colonized by macrophytes promote a higher diversity of testate amoebae (Dabés & Velho 2001; Lansac-Tôha et al. 2009; Arrieira et al. 2015a) because macrophyte stands provide a large number of ecological niches (Souza 2005) and, therefore, offer a greater availability food resources to testate amoeba species.

Our results confirmed the hypothesis that the highest richness, abundance, and diversity of planktonic testate amoebae community predominantly occurred during drought periods. The greater abundance of organisms might also be related to the morphological adaptations of the species found in these aquatic environments.

The environmental variables related to primary productivity appeared to be important for testate amoebae diversity, with more productive environments being associated with higher species diversity due to the greater availability of food resources. Other environmental variables, such as phosphate, ammonia, and dissolved oxygen, were indirectly related, operating as environmental filters on testate amoebae diversity in floodplain lakes.

## Acknowledgements

We appreciate comments by Dra. Geziele M. Alves, Dra. Juliana D. Dias, Dr Luiz F. M. Velho, Dra. Paulina M. M. Barbosa, Dr Daniel J. G. Lahr, and two anonymous reviewers who helped us to improve this paper. The authors are also grateful to National Program for Research in Biodiversity (Sisbiota Brazil), Nucleus of Research in Limnology, Ichthyology and Aquaculture (Nupélia), and State University of Maringa for the logistic and financial support. We also thank the National Council of Scientific and Technological Development (CNPq), Coordination for the Improvement of Higher Education Personnel (CAPES), and Araucaria Foundation for their research fellowships.

## Disclosure statement

No potential conflict of interest was reported by the authors.

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