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Trait structure and functional diversity of periphytic algae in a floodplain conservation area

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Abstract

We aimed to evaluate the structure of periphytic algae communities, the trait distribution and the patterns of functional diversity in the last non-dammed stretch of the Upper Parana´ River floodplain. We hypothesize that there is an increase in the functional diversity and a change of the traits and environmental variables structure along this floodplain. We expected an increase in the functional diversity due to the increase in tributaries propagule input leading to a functional divergence, provided by deterministic processes. The sampling was in channels, lakes and rivers in a floodplain area covering 230 km of extension of the main river. The periphyton was obtained from scraping petioles of the floating macrophyte Eichhornia azurea (Sw.) Kunth. The traits evaluated were life form and strength and form of adherence to the substrate. The functional diversity was calculated from a functional dendrogram and assembly rules. The hypotheses proposed in this study were partially accepted, since there was no increase in functional diversity along the sampled area, but we observed a change in the structure of the functional traits along the different stretches of the floodplain. The results showed diatoms as the dominant algae, and functional convergence as the assembly rule prevalent for this community. There was a large difference between local environmental factors along the floodplain. The protected areas housed the greatest functional diversity values, which was apparently influenced by the increase in functional diversity, which can be explained by the limnological factors and the input of propagules from the tributaries to the Paraná River. We noted the importance of the protected areas and local factors for assembly of this community.

Keywords Assembly rules · Bioindication · Diatoms · Functional diversity

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1 Introduction

Biotic communities are organized by the combination of abiotic factors, biotic interactions and dispersal processes (Soininen [2012;](#page-9-0) Padial et al. [2014](#page-8-0)). To explain those mechanisms in species composition, several models and alternative theories have been proposed (Chase et al. [2005](#page-7-0)). One of the theory proposed for microorganisms is based on niche models, in which mechanisms are deterministic, with two main processes affecting community composition: limiting similarity—assuming that biotic interactions tend to disfavour the coexistence of species with similar niches, leading to a functional divergence; and environmental filters—which imply that communities are primarily structured by local environmental control (Hillebrand and Blenckner [2002](#page-8-0); Pavoine et al. [2011](#page-8-0); Soininen [2012\)](#page-9-0). One of the patterns resulting from environmental filtering is convergence, in which coexisting species display ecological strategies more similar than expected by chance

(Weiher and Keddy [1995\)](#page-9-0). This point of view recovers the theory of Baas-Becking ([1934\)](#page-7-0), which states that for microorganisms ''everything is everywhere, but the environments selects''.

Understanding which factors are more relevant in structuring communities (biotic or abiotic), e.g. community assembly rules, can help predict community structure (Weiher and Keddy 1995) and ecosystem functioning (Díaz et al. [2007\)](#page-8-0). However, the roles of geographic distance (restricting through dispersal), and the environment affecting the community structure of microorganisms remain controversial. One of the tools facilitating the quantification of patterns and processes along environmental and spatial gradients is the use of species functional traits and functional diversity (Díaz and Cabido [2001](#page-7-0)).

Functional diversity plays an important role, since it measures the values and range of species traits capable of influencing ecosystem functioning (Tilman et al. [2001](#page-9-0)). That is, it measures the magnitude of functional trait dissimilarity among species (Petchey and Gaston [2002\)](#page-8-0). It is directly related to community ecological processes and the maintenance of ecosystem functioning (Balvanera et al. [2006;](#page-7-0) Petchey and Gaston [2006](#page-8-0); Díaz et al. [2007;](#page-8-0) Sobral and Cianciaruso [2012;](#page-9-0) Lavorel et al. [2013](#page-8-0)).

The knowledge of the temporal and spatial dynamics of functional strategies of periphytic algae contributes to predicting, generalizing and understanding processes structuring these communities (Dunck et al. [2013](#page-8-0); Cibils et al. [2015](#page-7-0); Cibils-Martina et al. [2017\)](#page-7-0). Because they have a sessile life style (for the most part) and short life cycle, periphytic algae respond rapidly to environmental changes and are directly influenced by environmental alterations in temperature, water velocity, light and nutrient availability (Biggs [1996;](#page-7-0) Stevenson [1996;](#page-9-0) Bourassa and Cattaneo [2000;](#page-7-0) Moresco et al. [2009](#page-8-0); Ferragut and Bicudo [2010](#page-8-0); Lange et al. [2011;](#page-8-0) Larson and Passy [2012;](#page-8-0) Algarte et al. [2013;](#page-7-0) Dunck et al. [2013](#page-8-0); Moresco and Rodrigues [2013](#page-8-0); Rodrigues et al. [2013;](#page-9-0) Zanon et al. [2013\)](#page-9-0). They exhibit different biological traits, varying in size, life form (unicellular, filamentous and colonial) and forms of adherence to the substrate (loosely attached and firmly attached). Moreover, these algae are responsible for high rates of aquatic primary productivity (Moschini-Carlos [1999](#page-8-0); Rodrigues et al. [2003](#page-8-0)) and are considered good indicators for the analysis of environmental conditions in highly dynamic aquatic ecosystems, such as river-floodplain systems.

River-floodplain systems are important ecosystems, since they harbour high diversity in aquatic and adjacent terrestrial areas (Agostinho et al. [2005\)](#page-7-0). However, an interruption in this natural gradient can often occur by anthropogenic influences, such as the disposal of chemical waste or reservoir construction (Straškraba et al. [1993](#page-9-0); Malmqvist and Rundle [2002](#page-8-0)), whose effects potentially alter the patterns and processes of abiotic and biotic factors in ecosystems (Ward and Stanford [1983](#page-9-0)). However, due to lateral, vertical and latitudinal gradients (wetland and tributaries from conservation units) in a floodplain, the river can recover from the effects caused by the damming (e.g. increasing in the water column transparency and nutrients levels, see Roberto et al. [2009](#page-8-0)), which would tend to decrease with increasing distance from the reservoir (Stanford and Ward 2001). Although the Paraná River is a system with a fluvial dynamic altered by reservoir construction, it exhibits a large non-dammed area, such as the region of the Upper Paraná River floodplain. In environments located in the fluvial plains, the integrity of the system is dependent on the connectivity between the channels and the wetland and this connectivity is represented by the flood pulse (Junk et al. [1989](#page-8-0); Tundisi and Matsumura-Tundisi [2008\)](#page-9-0). This area encompasses three large conservation units (the Área de Proteção Ambiental das Ilhas e Várzeas do Rio Paraná, the Parque Nacional de Ilha Grande and the Parque Estadual do Ivinhema) covering around 230 km extension, with numerous secondary channels, lakes and rivers (Baı´a, Ivinhema, Amambaı´ and Iguatemi rivers in the right margin, and Paranapanema, Ivaı´ and Piquiri rivers in the left margin) (Souza-Filho and Stevaux [1997\)](#page-9-0).

In this paper, we aimed to evaluate the structure of periphytic algae communities and trait distribution downstream from a dam in the last non-dammed stretch of the Upper Paraná River floodplain. In addition, considering that the functional diversity is a tool to quantification the changes in environment gradients, we assessed the patterns of the functional diversity of these communities (functional convergence or divergence). Specifically, we hypothesize that there is an increase in functional diversity of periphytic algae along this stretch, as well as a change in the structure of the functional traits and their relations with environmental variables. We expect the occurrence of functional divergence, provided by deterministic processes, a positive relationship between the increase in the functional diversity with distance from the dam, due to the input of propagules from the tributaries.

2 Materials and methods

Study area $-$ The Upper Parana^{α} River encompasses the stretch between downstream from Porto Primavera reservoir, situated between Mato Grosso do Sul and São Paulo states, and upstream from Itaipu reservoir, between Mato Grosso do Sul and Paraná states (Fig. [1](#page-2-0)), and constitutes the last non-dammed stretch of the river in Brazilian

Fig. 1 Location of the spatial gradient along the corresponding study area to the upper Paraná River floodplain. Sampling points: (1) Garças Lake; (2) Baía River; (3) Xirica Lake; (4) Ivinhema River; (5) Ivinhema River (medium); (6) Ivinhema Lake; (7) Ivinhema River (bass); (8) Amambaí River; (9) Paraná River 1; (10) Paraná River 2; (11) Iguatemi River and (12) Paraná River 3

territory (Souza-Filho and Stevaux [1997](#page-9-0)), between the coordinates 22°38'-22°57'S and 53°05'-53°36'O.

Its floodplain is 20 km wide, with numerous secondary channels, lakes and rivers. Among them, Baía, Ivinhema, Amambaí and Iguatemi rivers are on the right margin, and Paranapanema, Ivaí and Piquiri rivers on the left margin (Souza-Filho and Stevaux [1997\)](#page-9-0).

Samplings – Samplings were performed in November 2014, period considered high waters, and the sampling sites

were distributed on the right side of the plain, as follows: three are located in the Paraná River main channel (P9, P10) and P12), six located at the mouth of the main tributaries [Baía (P2), Ivinhema Complex (P4, P5 and P7), Amambaí (P8) and Iguatemi rivers (P11)], and three are lentic environments [Garças (P1), Xirica (P3) and Ivinhema lakes (P6)] (Fig. 1). In all sampling sites, the aquatic macrophyte Eichhornia azurea (Sw.) Kunth is the dominant species, which was a substrate to obtain periphytic algal community. We also measured the geographic coordinates of each sampling site.

Limnological variables $-$ At each sampling site, the following variables were measured in the field: depth (m) (digital sonar—HawkEye); water temperature (°C) (digital oximeter—YSI55A); dissolved oxygen (% saturation and mg L^{-1}) (digital oximeter—YSI55A); pH (digital portable pH meter—Digimed); conductivity $(\mu S/cm)$ (digital portable conductivity meter—Digimed); transparency (m) (Secchi disc); turbidity (NTU) (digital turbidimeter— LaMotte2020e); alkalinity (μ Eq L⁻¹) (Carmouze [1994](#page-7-0)); nitrate (Giné et al. [1980](#page-8-0)), orthophosphate (Mackereth et al. [1978\)](#page-8-0), total nitrogen and total phosphorus (μ g L⁻¹) (Bergamin et al. [1978;](#page-7-0) Mackereth et al. [1978\)](#page-8-0). To analyse dissolved nutrients and determine suspended materials (Teixeira et al. [1965](#page-9-0)), samples were filtered under low pressure $(< 0.5$ atm) using Whatman GF/F filters and kept cool for further laboratory analyses (Supplementary Material, Table S1).

Biological variables – Samples for the periphytic algal community were obtained of the aquatic macrophyte E. azurea, always in a mature stage. For each sampling site, two petioles were collected in different macrophyte mats and represented a regular sample. The petioles were placed in Wheaton bottles (150 mL) and transported to the laboratory in Styrofoam box containing ice. The periphytic material was removed scraping the surface of the petioles with stainless-steel blade wrapped in aluminium foil and jets of distilled water. A total of 24 samples were analysed.

The removed material designated to the quantitative analyses was preserved in 5% acetic Lugol solution and in 1:1 Transeau solution for qualitative analyses, according to Bicudo and Menezes [\(2006](#page-7-0)). The length and diameter of the petioles were measured to calculate the area of periphytic colonization.

The quantification of periphytic algae was performed according to the Utermöhl (1958) (1958) method, using an inverted microscope (Olympus $^{\circledR}$ M021) in sedimentation chambers at $400 \times$ magnification. To analyse the samples, horizontal and vertical transects were defined, until reaching at least 100 individuals of the predominant taxon and the stabilization of the species accumulation curve (Bicudo [1990\)](#page-7-0).

Qualitative analyses were performed by mounting temporary slides and analysing them in a binocular optical microscope with ocular micrometres at $400 \times$ and $1000 \times$ magnification (Bicudo and Menezes [2006](#page-7-0)). For diatom species identification, the material was oxidized according to the technique proposed by Simonsen [\(1974](#page-9-0)), modified by Moreira-Filho and Valente-Moreira [\(1981](#page-8-0)), and further mounted on permanent slides. Identification

was performed to the lowest taxonomic level possible (species), according to classical literature and regional studies, following classification proposed by Round [\(1965](#page-9-0)).

Community attributes – The equation for density calculation followed that proposed by Ros ([1979\)](#page-9-0), adapted to the substrate area. Results were expressed per area unit (individuals per square centimetre—ind/cm²). Species richness was obtained through the quantitative analysis.

Selection of periphytic algae functional traits comprised three different aspects of species niche: life form, strength of adherence and form of adherence to the substrate (Biggs et al. [1998](#page-7-0); Burliga and Schwarzbold [2013](#page-7-0)). The functional matrix of species was composed of three algal functional traits distributed in 14 categories: life form (unicellular, filamentous and colonial), strength of adherence (firmly, loosely and mobile), form of adherence (mobile, prostrate, entangled, stalked, mucilaginous pad, mucilage tubes, heterotrichous and differentiated basal cell). These functional traits were analysed directly in each species during sample counting and identification.

The choice of traits was based on studies on periphytic algae approaching functional traits (Ferragut and Bicudo [2010](#page-8-0); Passy and Larson [2011](#page-8-0); Schneck and Melo [2012](#page-9-0); Dunck et al. [2013,](#page-8-0) [2015a,](#page-8-0) [2016;](#page-8-0) Algarte et al. [2014;](#page-7-0) Lange et al. [2016\)](#page-8-0).

Data analyses – Values of functional diversity were calculated for the environments through a measure proposed by Faith ([1992\)](#page-8-0) (PD), which is similar to the measure of mean pairwise distance (MPD) proposed by Webb [\(2000](#page-9-0)). PD values are calculated through the sum of the branch length of a functional dendrogram generated from a matrix of functional traits (Webb [2000\)](#page-9-0). The relationship between functional diversity and geographic distance among environments was tested through a simple linear regression.

We tested the community assembly (functional convergence and divergence) through the analysis described by Pillar et al. [\(2009\)](#page-8-0). This analysis also evaluates the correlation between communities based on functional traits and ecological gradients and distinguishes the fractions representing the trait-convergence assembly patterns (TCAP), trait-divergence assembly patterns (TDAP) and the interaction of assembly patterns (TCAP * TDAP) through a partial correlation. This method was performed using three matrices: W matrix, containing species abundance; B matrix containing species functional traits; and E matrix containing environmental variables at each site (for more robust data, we used the scores of axis 1 of a principal coordinate analysis (PCoA), representing the environmental gradient). Correlations between matrices were tested through permutations (1000) for measures of trait-convergence and trait-divergence. Null model used to

measure TDAP preserves trait-convergence in fuzzy types (fuzzy weighting), community abundance and autocorrelation. It is noteworthy that abundance was log transformed prior to this analysis and environmental matrices were standardized by centering each variable by its mean and scaling each variable by its standard deviation.

To verify the relationship between the functional traits, selected by the prior analysis, and environmental variables, we performed a RLQ analysis (Dolédec et al. [1996](#page-8-0)). This multivariate technique is based on the ordination of three independent matrices: R matrix, containing environmental variables of each site; L matrix, containing species abundances; and Q matrix, containing species functional traits. The result of this analysis is a linear combination of R and O matrices, which maximizes covariance between groups of variables, mediated by the L matrix. This analysis was performed in two steps: (a) a PCA was performed for matrix R; and (b) a correspondence analysis (CA) was performed for matrix L. R and L matrices were standardized prior to the analysis, whereas Q matrix was not subject to any transformations. We further evaluated the degree of significance of correlation between matrices through a Monte Carlo test (9999 permutations). Permutations were performed using model 6 (Dray et al. [2014\)](#page-8-0), which is a combined model (models 2 and 4), which allow lower rates of type I error, if compared to the use of only one of the models or using them separately (Braak et al. [2012](#page-7-0)).

All analyses were performed using software R (R Development Core Team [2015](#page-7-0)). Packages ade4 (Chessel et al. [2004](#page-7-0)) and picante (Kembel et al. [2010](#page-8-0)) were used to construct the functional distance matrix and dendrogram; ade4 was also used to perform RLQ analysis and picante used to calculate functional diversity. Package SYNCSA (Debastiani and Pillar [2012](#page-7-0)) was used to test for metacommunity assembly patterns. Graphs were constructed using software Statistica, version 7.1 (StatSoft [2005\)](#page-8-0).

3 Results

Periphytic community – A total of 358 species were registered during the study. The periphytic community present in the tributaries corresponded to 179 species divided in eight classes (Bacillariophyceae, Chlamydophyceae, Chlorophyceae, Chrysophyceae, Cyanophyceae, Oedogoniophyceae, Xanthophyceae and Zygnemaphyceae). Lakes were represented by 159 species divided in nine classes (Bacillariophyceae, Chlorophyceae, Chrysophyceae, Cyanophyceae, Dinophyceae, Euglenophyceae, Oedogoniophyceae, Xanthophyceae and Zygnemaphyceae). Sampling sites of the main channel of the Paraná River showed 139 species divided in nine classes (Bacillariophyceae, Chlorophyceae, Chrysophyceae, Craspedomonadophyceae, Cyanophyceae, Oedogoniophyceae, Rhodophyceae, Xanthophyceae and Zygnemaphyceae). Bacillariophyceae showed the highest richness in all the studied environments, with 174 species. Considering species density, Bacillariophyceae was the most abundant class too and dominant in all environments (Supplementary material, Figs. S1 and S2), except at P12, where it represented around 40% of total density. Among the species found in the sampling sites, only two, belonging to class Bacillariophyceae, were common to all environments: Achnanthidium minutissimum (Kützing) Czarnecki complex and Eunotia incisa W. Smith ex W. Gregory complex.

Functional diversity – Results of the simple regression did not show an increase in PD values along the area $(F_{1,10} = 3.14, P = 0.107, r^2 = 0.163)$. The evaluation of convergence and divergence traits demonstrated higher ρ values of optimal subset of traits for the trait-convergence patterns, and for the interaction between trait-convergence and trait-divergence, and selected life form (LF) and form of adherence (FA) as the best traits explaining metacommunity assembly of periphytic algae in this study (Table [1\)](#page-5-0).

Relationship between functional traits and environmental variables – RLQ analysis showed significant correlations between species functional traits and environmental variables determining community composition and species distribution. Patterns of PCoA demonstrated the same tendency of distribution of environments, which were ordinated according to their locality inside the stretch (Fig. [2a](#page-6-0)). Results of both RLQ models were significant (model 2, $P = 0.0027$; model 4, $P = 0.0001$ Monte Carlo test).

RLQ analysis also demonstrated significant correlations between life form and form of adherence (differentiated basal cell, mobile and prostrate) in relation to environmental variables. Turbidity showed negative correlations for colonial species, species with differentiated basal cells and mobile species, and positive correlations for unicellular species. Temperature showed positive correlations for species with differentiated basal cells. Conductivity showed positive correlations for colonial and filamentous species, with differentiated basal cells or that are mobile. On the other hand, conductivity showed negative correlations for unicellular prostrate species. Nitrate showed negative correlations for colonial species and for forms of adherence mobile and differentiated basal cells, whereas unicellular species were positively correlated with this variable (Fig. [2](#page-6-0)b).

P1 and P3 exhibited the higher percentages of species with colonial life form and differentiated basal cells and mobile forms of adherence (Fig. [3](#page-6-0)). Sampling sites P2 and

TCAP Set of optimal traits	ρ PCoA	TDAP Set of optimal traits	ρ PCoA	TCAP * TDAP Set of optimal traits	ρ PCoA		Gradient	
LF	0.38	LF	0.28	LF	0.44	$\rho(TE)$	0.18	0.16
LF FA	0.26	SA	0.28	LF FA	0.29	$\rho(XE)$	0.16	0.20
SA	0.24	LF FA	0.27	FA	0.23	$\rho(XE.T)$	-0.14	0.86

Table 1 Correlation (ρ) and the significance tests ($P \le 0.05$) for the patterns of convergence (TCAP), divergence (TDAP) and interaction (TCAP * TDAP) of the periphytic algae functional traits

FA form of adherence, LF life form, SA strength of adherence, TE trait-convergence, ρ (XE) interaction of traces, ρ (XE.T) trait-divergence, ρ PCoA (sets of traits and their correlations with the gradient represented by axis 1 of PCoA)

P11 showed higher abundances of unicellular prostrate species (Fig. [3](#page-6-0)). Sites P8 and P12 showed higher abundances of filamentous and entangled species (Fig. [3](#page-6-0)). There was also an increase in entangled and stalked species with an increase in the distance from the reservoir, while there was a reduction in prostrate species (Fig. [3\)](#page-6-0).

4 Discussion

The results supported partially the hypothesis, and there was a relationship between functional traits and environmental variables, such as life forms and adherence traits with turbidity, temperature, conductivity and nitrate. Functional diversity was related to trait-convergence pattern generated by deterministic processes (abiotic filters provided by the large variation among local environmental factors). This indicates that the periphytic algal community respond to changes in environmental variables, emphasizing the importance of local factors for assembly of the periphyton community.

The presence of upstream damming provides a series of changes as the increasing in the water column transparency and nutrients levels, in the fluvial system (Ward and Stanford [1983](#page-9-0); Roberto et al. [2009\)](#page-8-0). Both PCoA and RLQ results showed a tendency of regional segregation relative to the distance from the reservoir. These patterns may be attributed for two possible explanations, first to the proximity of the sample sites in each group, which share similar environmental characteristics. Second, by the influence of the tributaries and their flow regimes which, contrary to the Paraná River, do not have their hydrological regime controlled by cascading reservoirs (Agostinho et al. [2008](#page-7-0)).

Results show a difference in the functional assembly occupied by periphytic algal communities among sampling sites; however, an increase in the functional diversity along the sampled area was not observed. According to Vanormelingen et al. [\(2008](#page-9-0)), local environmental factors are fundamental to determine patterns of community distribution with high turnover rates, such as periphytic algae.

Additionally, under the effect of environmental filters, species more adapted to a certain habitat are more prone to share similar functional traits, resulting in functional convergence (Petchey et al. [2007\)](#page-8-0).

Functional convergence is usually related to environmental filters, which are assembly rules that represent the set of environmental conditions that restrict the establishment of species with unsuited trait values (Cornwell and Ackerly [2009](#page-7-0)), and this could reflect the importance of abiotic local forces in the structuring of these communities. The results of assembly rules showed functional convergence of these communities (also known as functional clustering), with co-occurring species with functional traits more similar than expected by chance.

We observed a change among the functional traits in the sampled area. Two functional traits were most important in explaining species distribution along the study area: life form and form of adherence to the substrate. The RLQ analysis showed a correlation between higher percentage of colonial species, species with differentiated basal cells and mobile species and low turbidity, low nitrate concentrations and high values of conductivity in Lakes located in the beginning of the stretch (P1 and P3). Colonial species usually have a mucilage, which controls mobility and colony suspension (Reynolds [2006;](#page-8-0) Dunck et al. [2013](#page-8-0)), favouring a competitive advantage for light capture and in environments with low nutrient concentrations (Kruk et al. [2010](#page-8-0)). Species with differentiated basal cells (Oedogoniophyceae) are excellent competitors for light and space, and are associated with high values of conductivity, intermediate levels of nutrients and low water flow (Biggs [1996](#page-7-0); Biggs et al. [1998](#page-7-0); Cavati and Fernandes [2008](#page-7-0); Bichoff et al. [2016\)](#page-7-0). Mobile forms have greater adaptive advantage in oligotrophic environments, since their movement within the periphytic matrix allows access to different sources of resource (Ferragut and Bicudo [2010\)](#page-8-0).

Sites P8 and P12, where conductivity values were intermediate, showed higher abundances of heterotrichous, filamentous and entangled species. This could be associated with an increase of turbidity and reduction of light

Fig. 2 RLQ analysis. a Analysis of principal coordinates (PCoA); b correlation between functional traits and environmental variables. Black frames: significant positive correlation; Gray frames: significant negative correlation. CON conductivity, DO: dissolved oxygen, NO3 nitrate, PO4 orthophosphate, TEM temperature, TUR turbidity, Col colonial, Fil filamentous, Uni unicellular, Dcb differentiated basal cell, Ent entangled, Het heterotrichous, Mob mobile, Sta stalked, Mup mucilaginous pad, *Pro* prostrate, *Mut* mucilage tubes, (1) Garças Lake, (2) Baía River, (3) Xirica Lake, (4) Ivinhema River, (5) Ivinhema River (medium), (6) Ivinhema Lake, (7) Ivinhema River (bass), (8) Amambaí River, (9) Paraná River 1, (10) Paraná River 2, (11) Iguatemi River, (12) Paraná River 3

penetration in the water column. Entangled species are more subject to disturbances, since they do not possess any structures to adhere to the substrate, remaining more superficially in the periphytic matrix, usually stuck to

Fig. 3 Relative density of the functional traits in the sampling points. Life form (a) and form of adherence (b). Col colonial, Fil filamentous, Uni unicellular, Dcb differentiated basal cell, Ent entangled, Het heterotrichous, Mob mobile, Sta stalked, Mup mucilaginous pad, *Pro* prostrate, *Mut* mucilage tubes, (1) Garcas Lake, (2) Baía River, (3) Xirica Lake, (4) Ivinhema River, (5) Ivinhema River (medium), (6) Ivinhema Lake, (7) Ivinhema River (bass), (8) Amambaí River, (9) Paraná River 1, (10) Paraná River 2, (11) Iguatemi River, (12) Paraná River 3

stalked species (Tuji [2000;](#page-9-0) Dunck et al. [2013\)](#page-8-0). Filamentous species are favoured by their vertical growth, which contributes to the access to light and nutrients, rapid growth in size and biovolume maintenance (Margalef [1983](#page-8-0)).

Bacillariophyceae, whose species dominated in all sites, usually have a higher capacity of resisting physical perturbations than other groups and are almost always the first algae colonizing the substrate (Schneck and Melo [2012](#page-9-0)). They are excellent strategists and have adaptive advantages which allow better adhesion to the substrate. Specialized structures, such as mucilaginous peduncles (short or long), allow species to reach the interface of the periphytic matrix, where there is higher light and nutrient availability (Hoagland et al. [1982](#page-8-0); Hudon and Legendre [1987\)](#page-8-0).

Species complex A. minutissimum and E. incisa are the only organisms present in all sampling sites. A. minutissimum is among the most registered diatoms in the world and may occur in acid or alkaline environments, and in oligotrophic to eutrophic environments (Round [2004;](#page-9-0) Dunck et al. [2015b](#page-8-0); Bichoff et al. 2016). Eunotia incisa is common in acid habitats, with great variation in conductivity values (Ortiz-Lerín and Cambra 2007); however, in this study, it was found in oligotrophic to mesotrophic environments.

It was evident the importance of local factors in the fragmentation of the functional traits of periphytic algae. Considering that research has indicated that low values of functional diversity cause a reduction in ecosystem services and function (Díaz and Cabido 2001; Moretti et al. [2013\)](#page-8-0), monitoring biological diversity is a viable manner to assure a long-term maintenance of several ecosystem services (Duffy [2009\)](#page-8-0). Thus, knowing the components of periphytic algae biodiversity is a fundamental step for studies of ecosystem management and conservancy.

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Author's contributions Bichoff, A. was responsible for the analysis of biological material and formulation of goals and hypothesis. Bichoff, A. Osório, N.C., and Ruwer, D.T. contributed with the article conceptualization, including ideas, and all the writing structure of the manuscript. Bichoff, A., and Dunck, B. applied the statistics, and Dunck, B reviewed the article. Rodrigues, L. supervised, and was responsible for the research activity planning and execution.

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