PRIMARY RESEARCH PAPER

# Effects of freshwater eutrophication on species and functional beta diversity of periphytic algae

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**Abstract** Studies about beta diversity and environmental heterogeneity have shown that the strength of the environmental filtering effect may decrease with the increasing scale. These empirical results have related eutrophic aquatic environments to higher values of beta diversity, but never to dissimilarity of species and functional traits of periphytic algae. We tested the hypotheses that periphytic algae have higher dissimilarity of both species and functional traits in eutrophic environments, and that these dissimilarities are related to environmental dissimilarity. To this end, we used richness, density, and four functional traits of periphytic algae and local limnological data from wetlands in the Brazilian savanna (Cerrado). We analyzed the beta diversity and the relationship of species and functional dissimilarities with the environmental dissimilarity and geographic distances. Our hypothesis was confirmed for functional traits dissimilarity and for the importance of the environmental dissimilarity for both species and functional beta diversity. The cultural eutrophication led to a functional homogenization in urban wetlands, which indicates the establishment of species with similar ecological requirements, and consequently, similar 'roles' in the ecosystem, and also that sensitive species may have been replaced by tolerant species, leading to declining biodiversity.

**Keywords** Acidic water · Cerrado · Environmental dissimilarity · Functional homogenization · Savanna · Wetlands

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## Introduction

Algae are important primary producers in the aquatic environment, contributing greatly to the primary productivity in freshwater ecosystems. This group can determine the biomass of invertebrates and overall

food-web structures (Thompson & Townsend, 2005; Harley, 2016) due to its effect on primary production and for being the basis of the trophic web. Brazil has an extensive hydrographic network, and still, the knowledge on microalgae biodiversity is proportionately scarce. The most current list of studies carried out in Brazil on algae and cyanobacteria has reported a total of 4,747 species registered in different environments and regions (Menezes et al., 2015). However, this number may be underestimated, due mainly to the low number of researchers in the area and to the large extent of the country (Menezes et al., 2015).

The Brazilian savanna (Cerrado) encompasses many different phytophysiognomies, ranging from woodlands to open savannas and palm swamps, which occur only in this Biome (Ribeiro & Walter, 2008; Bustamante et al., 2012). The two main characteristics of palm swamps are the presence of "buritizais" (*Mauritia vinifera* L. and *Mauritia flexuosa* Mart.) as predominant phanerogamic flora, and the moist soil, which confer the status of wetlands or marshes in Central Brazil (Ribeiro & Walter, 2008). This subsystem contributes to the continuity and regularity of associated watercourses and the protection of the headwaters (Carvalho, 1991). Some studies have recorded the algae present in these environments (Dunck et al., 2013a, b; Leandrini et al., 2013; Dunck et al., 2016a), but the rapid progress of deforestation and urbanization in this region can extinguish habitats and has affected water quality (Fonseca & Mendonça-Galvão, 2014; Fonseca et al., 2014), a condition which can alter or even extinguish algae communities. In addition, cultural eutrophication is expanding, and may cause harmful alterations to the ecosystem functioning and structure (Dodds et al., 2010).

In response to the growing threat of biodiversity loss, the previous studies have tried at exploring and predicting the consequences of anthropogenic disturbances in ecological communities, and taxonomic diversity and species richness are the most common aspects of diversity considered (Schmera et al., 2016). While most ecological studies aim to estimate means (species richness, alpha-diversity measures) (Rosenzweig, 1995), the use of measures of variability allows to better understand natural ecosystems (Palmer & Poff, 1997). One fundamental concept of variation is beta diversity, defined as the variation in community composition among sites or among time periods (Magurran, 2004; Anderson et al., 2010). Therefore,

the comparison of beta/dissimilarity among assemblages is essential in quantitating the effects of environmental gradients (Villéger et al., 2012), for understanding the driving forces underlying community structure at multiple spatial scales (Buckley & Jetz, 2008), biodiversity change (Hillebrand et al., 2018), as well as for conservation purposes (Devictor et al., 2010).

Recently, studies have indicated that species traits reflect the effect of organisms on ecosystem functioning (Tilman, 2001). A set of functional traits determines where species can live (Lavorel et al., 1997) and how they interact (Cadotte et al., 2011), and can comprise the phenotype, and any morphological, physiological, or phenological characteristics that indirectly affect the species fitness (Weithoff, 2003). Thus, functional traits are crucial to understand a species' niche, for being used as proxies for species requirements (Grinnellian view, Rosado et al., 2016) and effects of a species on the environment (Eltonian view, Rosado et al., 2016) (i.e., niche axes) (McGill et al., 2006). In this way, functional beta diversity (or functional dissimilarity) allows one to analyze if communities can be similar in terms of ecological and evolutionary characteristics (Swenson, 2011; Swenson et al., 2012).

Environmental filtering (or species sorting) act as assembly rules, which are environmental processes underlying the community structure or ecological aspects that regulate the species patterns (Weiher & Keddy, 1995). Therefore, this filter plays an important role for species establishment on a local scale, and its strength may decrease with the increasing scale (Bini et al., 2014; Soininen, 2014; Heino et al., 2015a). The increasing spatial extent also increases the variation in environmental variables, such that ecologists have used spatial extent or geographic distances between sites as surrogates for environmental heterogeneity (Bini et al., 2014).

Patterns associated with species and functional beta diversity for periphytic algae have been poorly explored in general. Therefore, our goals were to evaluate the structure of periphytic algae traits among environments, and to assess species and functional beta diversity in the Brazilian savanna (Cerrado) under different anthropogenic impacts. We expect that species and functional dissimilarity measures will respond to eutrophication. We hypothesized that periphytic algae have higher dissimilarity of both

species and functional traits in eutrophic environments. We expected higher beta diversity in more eutrophic environments, as had been shown in aquatic studies (Langenheder et al., 2012; Bini et al., 2014). Our study was conducted in a medium spatial scale (i.e., among localities or among streams), so we also hypothesized that beta diversity should be associated with environmental dissimilarity. We analyzed beta diversity and tested if these patterns were related to environmental dissimilarity and geographic distance. We used periphytic algal and local limnological data from 23 wetlands in the Brazilian savanna (Cerrado).

## Materials and methods

### Study area

The sampled sites were located in the state of Goiás, west central region of Brazil. We sampled six palm swamps in conserved areas, nine in areas impacted by agriculture and eight in urban areas, totalizing 23 palm swamps (Dunck et al., 2013a). The land use (conserved, agriculture and urban) was used as explanatory variable in our study.

### Sampling

Sampling procedures were conducted on August and September 2008. All details of the study area, sampling time and physical characterizations are presented in Dunck et al. (2013a). The map of study area is presented in electronic supplementary material (ESM1).

### Environmental data

The limnological variables (pH, water temperature, electric conductivity and turbidity) were measured with a multiparameter water analyzer (Horiba model U-22). This procedure was done before biological data sampling. For the estimation of total nitrogen and total phosphorus, we collected 1 l of water at each sampling point, fixed in situ with 0.5 ml of acid sulfuric P.A., and for estimation of silica, we collected 250 ml of water, and then processed all according to APHA (2005).

The trophic status of the palm swamps was evaluated by two indices, one proposed by Lamparelli (2004) and another proposed by Dodds et al. (1997). Lamparelli uses total phosphorus as a parameter, and Dodds et al, use both nitrogen and total phosphorus as parameters.

### Periphytic algae

The periphytic algae were sampling from partially submerged grasses (Poaceae) predominant in the palm swamps. Two petioles of different plants were collected totalizing 46 quantitative samples. The petioles were scraped with a steel blade wrapped in aluminum foil and jets of distilled water, and the scraped areas were measured to be used in the density algae estimation.

The samples (material scraped) were quantified using sedimentation chambers in an inverted microscope (Utermöhl, 1958) and sedimentation time followed Lund et al. (1958). The counting method consisted in random fields until reaching at least 100 individuals (cells, colonies, or filaments) from the most dominant species and until the curve of species accumulation begins to decline (Ferragut & Bicudo, 2012). We counted an average of 3,669 individuals per subsample (minimum = 47, maximum = 14,818, standard deviation = 5,053).

The species density was estimated according to Ros (1979) using the scraped areas for estimation in number of individuals per unit area (ind/cm$^2$). The classification system used was Round (1971). The fifty-seven species of periphytic algae found in the study are presented in electronic supplementary material (ESM2). The algal community was represented by 56 species, distributed into 33 genera and 8 classes. Bacillariophyceae (31%), Cyanophyceae (24%) and Zygnemaphyceae (17%) predominated in density among the Palm swamps, and *Gomphonema* Ehrenberg was the genera with the highest number of taxa (ESM2).

### Functional traits

We used four response functional traits of periphytic algae distributed among 15 categories: (1) size class (pico, nano, micro and meso, based on the phytoplankton classification of Reynolds, 1997), (2) growth form (nonmotile unicellular, filamentous, flagellate, or colonial), (3) intensity of adherence to the substrate (firmly or loosely adhered), and (4) form of adherence

to substrate (motile, entangled, prostrate, stalked, or heterotrichous).

Data analysis

We used a principal component analysis (PCA) to evaluate the variation of limnological variables among palm swamps. We used the broken-stick criteria to interpret the PCA axes. For this analysis, the limnological variables were previously standardized (Legendre & Legendre, 1998). To test if palm swamps differ in relation to the limnological variables, we used Permutational analysis of variance (PERMANOVA; Anderson et al., 2008), using a matrix of standardized Euclidean distance based on the scores generated by PCA as response variables and the land use (conserved, agriculture, and urban) as explanatory variable. We also did subsequent pairwise tests in the case of any significant results, to identify which treatments differ.

For the beta diversity analyses, we used the presence–absence matrix containing 56 species and 23 samples. The Sørensen index was used to calculate species pairwise dissimilarity among all palm swamps (beta diversity, bsor, Legendre & Legendre, 1998).

The matrix of distance among species functional traits was done using the distance coefficient for mixed variables proposed by Pavoine et al. (2009), and then turned into a dendrogram using the average linkage clustering (UPGMA). To calculate the pairwise functional dissimilarity (functional beta diversity) using the Sørensen index (bsor, adapted to functional traits, Melo, 2013), we used the functional dendrogram and the species presence–absence matrix. We tested the differences in species and functional dissimilarity among palm swamps (as response variables) by Permutational analysis of variance (PERMANOVA; Anderson et al., 2008) and the land use (conserved, agriculture and urban) as explanatory variable. We also did subsequent pairwise tests in the case of any significant results, to identify which treatments do differ.

We analyzed the environmental dissimilarity among palm swamps using the limnological variables (water temperature, electrical conductivity, pH, turbidity, total phosphorus, total nitrogen, chlorophyll-a and silica). We transformed the limnological variables centering each one by its mean and scaling by its standard deviation (Legendre & Legendre, 1998).

After this, the dissimilarity matrix was obtained calculating pairwise Euclidean distance from the transformed limnological variables. We also analyzed the spatial dissimilarity among palm swamps through the Euclidean distance based on the geographic coordinates of the sites.

To verify if total dissimilarity (bsor) in species or functional composition was explained by environmental dissimilarity and spatial dissimilarity, we used multiple regressions on distance matrices (MRM; Manly, 1986; Legendre et al., 1994; Lichstein, 2007). MRM involves a multiple regression of a response matrix on any number of explanatory matrices (Lichstein, 2007). Here, the environmental dissimilarity and the spatial dissimilarity were explanatory variables for total dissimilarity (bsor) in species or functional composition (response variables). The significances of regression coefficients and coefficients of determination were evaluated with 10,000 permutations. As these parameters are tested by permutations, no assumption is needed to be tested (Legendre et al., 1994; Legendre & Legendre, 1998).

We used R platform to perform the analyses (R Core Team, 2014). The packages ade4 (Chessel et al., 2004) and picante (Kembel et al., 2010) were used for constructing the functional distance matrix and the dendrogram; betapart for beta diversity (Baselga & Orme, 2012) and CommEcol (Melo, 2013) for functional beta diversity; ecodist (Goslee & Urban, 2007) for multiple regressions on distance matrices; and stats for the t tests.

## Results

### Environmental data

All the palm swamps presented high values of silica and acidic pH (Electronic Supplementary Material-ESM3). Almost all the sites (95.6%) presented low concentrations of total phosphorus and were classified as oligotrophic (Electronic Supplementary Material-ESM3). The total nitrogen concentrations were high, and 30.4% of the palm swamps were classified as hypereutrophic based on this nutrient (Electronic Supplementary Material-ESM3).

PCA results summarized 63.2% of the limnological variability among palm swamps in the first two axes selected by the broken-stick criteria. The first axis was

most related to electric conductivity and turbidity, and the second axis by total phosphorus (Fig. 1). These two axes showed a gradient among the palm swamps, mainly in variables related to trophic status (total nitrogen and phosphorus, electric conductivity and turbidity). The conserved palm swamps (with lower values of total nitrogen) and that in urban areas (with higher values of total phosphorus) were presented at the extremes of the environmental gradient (Fig. 1, Electronic Supplementary Material-ESM3).

The PERMANOVA results demonstrated that the palm swamps differ in relation to the limnological variables (Total df = 22, Residual df = 20, pseudo-$F$ = 2.62, $P$ = 0.07), mainly between the conserved and urban palm swamps (Total df = 13, pseudo-$F$ = 5.66, $P$ = 0.01). Values for the pair conserved–agriculture (Total df = 14, pseudo-$F$ = 0.79, $P$ = 0.42) and for the pair agriculture–urban (Total df = 16, pseudo-$F$ = 2.41, $P$ = 0.12) did not differ.

### Species traits structure

Small individuals (nanoperiphyton) and filamentous forms prevailed in conserved and agriculture areas (Fig. 2). Microperiphyton and unicellular forms prevailed on the urban palm swamps. Firmly adhered algae (mostly stalked species) prevailed in impacted palm swamps, and entangled species in conserved areas (Fig. 2).
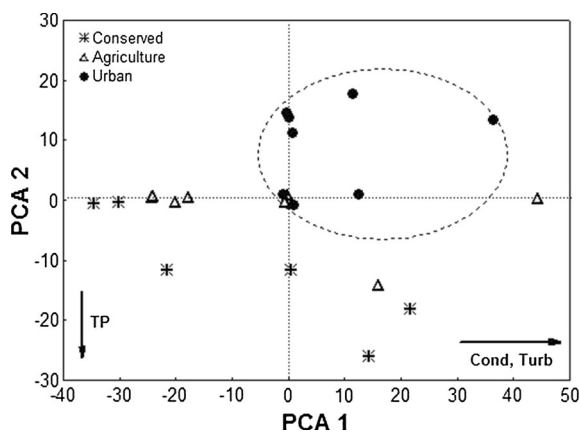
### Species beta diversity

The beta diversity values ranged from 0.81 to 0.91, with an average of 0.81 ($\pm$ 0.15 SD) in urban swaps, 0.87 ($\pm$ 0.17 SD) in agriculture areas, and 0.91 ($\pm$ 0.15) in conserved areas. Beta diversity did not vary among different land uses (Total df = 22, Residual df = 20, pseudo-$F$ = 1.33, $P$ = 0.10).

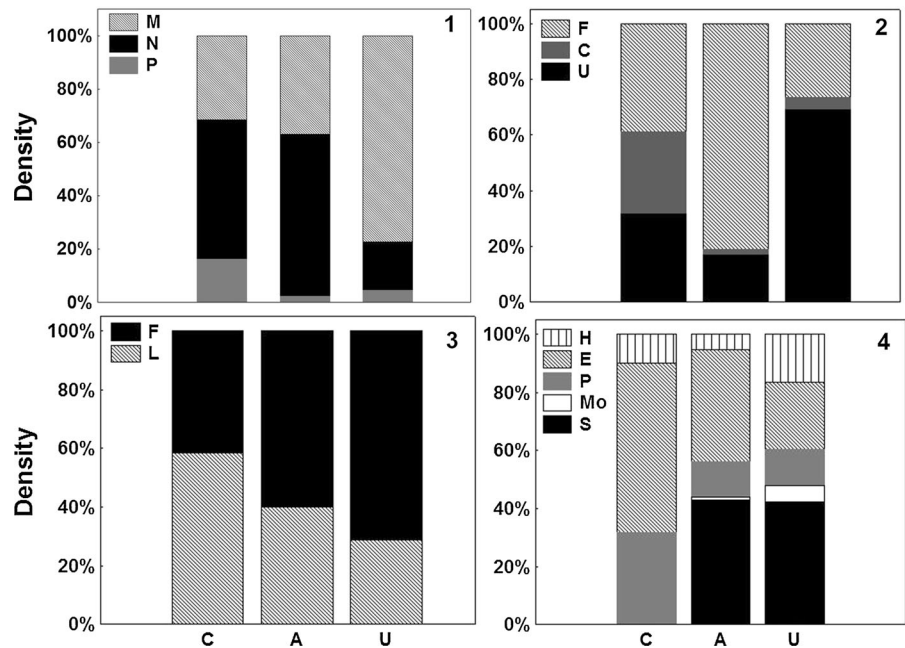### Functional beta diversity

The functional beta diversity values ranged from 0.32 to 0.71, with an average of 0.32 ($\pm$ 0.21 SD) in urban swamps, 0.57 ($\pm$ 0.21 SD) in agriculture areas, and 0.71 ($\pm$ 0.18 SD) in conserved areas. The results of functional beta diversity varied among different land uses (Total df = 22, Residual df = 20, pseudo-$F$ = 2.37, $P$ = 0.012). The differences were observed between the conserved and urban palm swamps (Total df = 13, pseudo-$F$ = 4.04, $P$ = 0.003), where the highest values were recorded in conserved areas. Values for the pair conserved–agriculture (Total df = 14, pseudo-$F$ = 1.84, $P$ = 0.11) and for the pair agriculture–urban (Total df = 16, pseudo-$F$ = 1.55, $P$ = 0.17) did not differ.

### Species beta diversity and Functional beta diversity X environmental dissimilarity and geographic distance

The MRM results showed that environmental dissimilarity was the only determining factor for the taxonomic and functional beta diversity in impacted palm swamps (species beta diversity, Urban $R^2$ = 0.47; environmental dissimilarity $P$ = 0.01*; geographic distance $P$ = 0.19; agriculture area $R^2$ = 0.21; environmental dissimilarity $P$ = 0.03*; geographic distance $P$ = 0.51; conserved areas $R^2$ = 0.07; environmental dissimilarity $P$ = 0.23; geographic distance $P$ = 0.76; functional beta diversity, Urban $R^2$ = 0.43; environmental dissimilarity $P$ = 0.04*; geographic distance $P$ = 0.53; agriculture area $R^2$ = 0.44; environmental dissimilarity $P$ = 0.07; geographic distance $P$ = 0.98; conserved areas $R^2$ = 0.04; environmental dissimilarity $P$ = 0.66; geographic distance $P$ = 0.64).



**Fig. 1** Two first axes of principal component analysis applied to the 23 palm swamps and limnological variables (Cond: conductivity, Turb: turbidity, TP: total phosphorus)

**Fig. 2** Relative density (%) of periphytic algal traits structure among distinct land use in palm swamps (C: conserved, A: agriculture, U: urban, 1- size class, M: micro N: nano; P: pico, 2- growth form, F: filamentous, C: colonial, U: nonmotile unicellular; 3- intensity of adherence to the substrate, F: firmly adhered, L: loosely adhered; 4- form of adherence to substrate, H: heterotrichous, E: entangled, P: prostrate, Mo: motile, S: stalked)



## Discussion

Our results show that cultural eutrophication altered only functional beta diversity, and that species compositional changes were not apparent in this study. Environmental dissimilarity was more important than overland distance (spatial dissimilarity) for both species and functional beta diversity, as reported by several studies on the relationship between beta diversity and environmental heterogeneity (Bini et al., 2014; Heino et al., 2015a, b).

The highest functional beta diversity values were recorded in conserved palm swamps, suggesting a functional homogenization associated to eutrophication. Functional homogenization can be defined as an increased functional similarity due the establishment of species with similar traits (consequently similar 'roles' in the ecosystem), and the loss of species not redundant for determining function (Olden, 2006). Anthropogenic enrichment leads to unfavorable conditions and a loss of environmental heterogeneity, and thus resulted in a significant loss of functional beta diversity in our study. This loss was equivalent to a reduced environmental gradient and the subsequent accommodation of fewer species with similar ecological requirements (Passy & Blanchet, 2007). Consequently, eutrophication led to a functional homogenization in urban swamps.

The palm swamps of the Cerrado biome have unique environmental characteristics such as acidic water and high amounts of silica. However, urban swamps have a higher species richness than the others palm swamps due to a higher light input consequent of the low vegetation cover associated with resource availability (Dunck et al., 2013a). And, despite the higher species richness in these sites, the low beta functional diversity revealed in our results demonstrated that cultural eutrophication, the process usually involved with global patterns of biotic homogenization (Dornelas et al., 2014), can also cause functional homogenization of periphytic algal communities. Dunck et al. (2013a) also showed that these sites have the predominance in biomass and density of some diatom species (*Encyonema silesiacum* (Bleisch) Mann, *Eunotia bilunaris* (Ehrenberg) Mills, *Gomphonema lagenula* Kützing, *Gomphonema gracile* Ehrenberg), etc. that have similar forms of resource acquisition and resistance to disturbances. And these results also corroborate our pattern of functional homogenization.

Patterns associated to eutrophication and functional beta diversity of periphytic algae are still unknown. This relationship has been evaluated for species beta diversity, and some insights have been reported. A negative relationship between beta diversity of benthic diatoms and productivity (biotic homogenization) has

been reported in a study of benthic diatoms from sediments in 23 reservoirs under artificial eutrophication, located in southeastern Brazil (Zorzal-Almeida et al., 2017). Environmental heterogeneity and dispersal limitation (spatial factor) were also reported—the likely main factors to determine the beta diversity of diatoms in tropical reservoirs (Zorzal-Almeida et al., 2017). In addition, Passy & Blanchet (2007) evaluated periphytic algae under a human-impacted context, in stable and unstable reaches within Batavia Kill, before and after streambed restoration. They indicated that the loss of environmental heterogeneity in partially to completely deforested reaches caused a prominent reduction in beta diversity. They concluded that human-impacted stream ecosystems suffer a reduction in the beta diversity of periphytic algae.

In our study, the environmental dissimilarity was more relevant than the spatial factor for species and functional beta diversity, on the scale evaluated. This result corroborates with patterns reported for several communities when environmental variables are more important in the structuring than spatial variables (Heino et al., 2015b). The relevance of environmental heterogeneity structuring microorganisms is evident in several aquatic ecosystems (see Dunck et al., 2015 for examples). Abiotic environmental filters may define if a species has the determinant traits that allow colonization, establishment, and persistence in a given habitat, and the coexisting species may have common requisite adaptations to abiotic conditions. As more abiotic heterogeneous, more niches are available in the environments, providing greater variation in species composition among sites (Chase & Leibold, 2003, Leibold et al., 2004).

Functional dissimilarity (functional beta diversity) could be explained by environmental gradients and abiotic environmental filters that drive the species turnover with particular traits (Swenson et al., 2011). The results of more functionally dissimilar, indicates that deterministic processes, as abiotic environmental filters, related to environmental gradients are driving periphytic algal functional organization.

Eutrophication also shifts the prevalence of different traits within the community. Studies pointed out that eutrophication leads to an increase in density of larger species over nanoperiphytic species (Cattaneo et al., 1997; Ferragut & Bicudo, 2010; Lange et al., 2015). This can explain the prevalence of nanoperiphyton in less eutrophic environments (conserved and agriculture areas) and microperiphyton in urban palm swamps. A factor able to cause a prevalence of smaller species in less eutrophic palm swamps is light input, which was lower in these environments (Dunck et al., 2013a). Small body cell size has the advantage over larger cells in light harvesting, because the amounts of pigments contained in the chloroplasts become less effective as unit size increases (Niklas, 2000). Thus, the light input and the body cell size may have contributed to the predominance of smaller species in less eutrophic palm swamps.

Filamentous life forms prevailed in conserved and agriculture areas, and unicellular forms prevailed in urban palm swamps. The prevalence of filamentous species in conserved and agriculture environments may have been favored by the species position (i.e., height) within the periphyton matrix, enabling higher access or increasing the individual probability of accessing light or obtaining other resources in the water column or within the periphyton matrix (Margalef, 1983; Stevenson, 1996). Filamentous life forms ensure many benefits in acquisition of light and space, favoring the competition with other species for these resources (Niklas, 2000). This type of life form also dominated sites under high farming intensities in streams of Manuherikia River catchment (Central Otago; New Zealand) (Lange et al., 2015) due to low waterflow and nitrogen (Snelder et al., 2014; Lange et al., 2015). Our results support these findings, once most sites in agricultural areas are lentic, and both urban and preserved sites had meso to eutrophic characteristics for nitrogen concentrations (Dunck et al., 2013a).

The unicellular forms prevailing in urban palm swamps may have been fostered by the higher nutrient and light availability in these environments. Unicellular organisms are generally associated with disturbed environments and rapid environmental changes, and this can be explained by the metabolism and growth rates related to small bodies. Regardless of shape or geometry, unicellular individuals have large surface area/body volume ratio, which favors obtain nutrients and metabolize them more rapidly than other life forms, and they can also reproduce faster (Niklas, 2000).

Firmly adhered algae (mostly stalked species) prevailed in impacted palm swamps. Studies have related stalked species with higher total solids in the water (Dunck et al., 2016b), which can be favored by

generally positioning at higher layers of the periphyton matrix (Passy, 2007), and their access to the nutrients of the water column. Most of these impacted sites had higher turbidity values (Dunck et al., 2013a), and the stalked species may have adaptive advantages over other species under these conditions. For Tuji (2000), the prevalence of stalked species refers to a second successional phase, in which stalked species prevail.

Periphytic algal communities were good indicators of eutrophication in palm swamps of the Brazilian savanna (Cerrado). Community attributes such as species richness or density of individuals, which are normally addressed in ecosystem health evaluation, may not be effective, as pointed by Passy & Blanchet (2007). Higher species richness and biomass related to the urban palm swamps considered in this study (Dunck et al., 2013a) have possibly masked a pattern, i.e., that eutrophication caused a functional homogenization in urban palm swamps. Thus, spatially explicit diversity measures frequently ignored in applied ecology (e.g., beta diversity), should be considered for conservation actions, also including the functional aspect. Anthropogenic reshuffling of the earth's biota has been reported to cause a taxonomic homogenization, regardless of taxonomic group and spatial scale (Baiser et al., 2017). That was not observed for the scale we considered in our study using periphytic algae, but we found indications of strong functional homogenization in eutrophic environments. The increasing species traits similarity, with the establishment of species with similar ecological requirements and, consequently, similar 'roles' in the ecosystem, have serious ecological implications. Sensitive species may be being altered by tolerant species following limnological change, which may be an indicative of declining biodiversity.

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