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Spatial distance explains the periphyton metacommunity structure of a neotropical stream network

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Abstract Environmental and dispersal drivers are determinants of periphyton metacommunities. However, the effects of these predictors can vary according to the facet of biodiversity assessed. In this study, we assessed the relative importance of local environment (i.e., limnological variables), regional landscape (i.e., land use), and spatial distance (i.e., overland and watercourse dispersal routes) components for the periphytic community in 30 Cerrado stream sites. For this, we estimated different metrics, such as the total density, beta diversity, local contribution to beta diversity (LCBD), species richness, and composition. This last metric was obtained considering the complete and deconstructed communities according to the type of adhesion to the substrate. We found 128 species with a predominance of the Bacillariophyceae, of which most have loosely adherence to the substrate. The algae community showed a high turnover of species along the hydrographic drainage. Besides, spatial distances were significant for species richness, total density, and species composition metrics using overland or watercourse distances. The spatial distance was also crucial for species composition tightly adhered to the substrate. Nevertheless, any community metric had no local environment and

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regional landscape effects. Therefore, on a large spatial scale, the effect of the spatial component can be attributed to species dispersion limitation, whereas on a finer spatial scale, mass effect was the primary process driving the variation among communities. In this sense, while for some species dispersal is limited by higher distances, for others dispersing to streams with suboptimal conditions can be associated with physiological aptitudes and high reproductive rates, which allow for the maintenance of species in the studied stream sites.

Keywords Brazil · Dispersal limitation · Epilithic algal · Mass effects · Spatial filters

Introduction

The structure of freshwater biological metacommunities can be influenced by local, regional, and spatial components (Leibold et al., 2004; Heino et al., 2015). Limnological variables such as temperature, pH, and turbidity characterize the local environment (Alemany et al., 2006; Huszar et al., 2015; Machado et al., 2016), while land use in the watershed and the spatial distance among sites encompass regional landscape and spatial components, respectively (Blanchet et al., 2014; Heino et al., 2015; Leibold et al., 2017). The relative importance of these components is context dependent in freshwater habitats. For example, in river networks, the dispersal can be influenced by the dendritic landscape of riverine systems and environmental heterogeneity (Brown & Swan, 2010; Altermatt, 2013; Brown et al., 2016; Henriques-Silva et al., 2019; Faquim et al., 2022). Patterns in metacommunity studies are also influenced by interactions among factors associated with the spatial scale of the study, such as the dispersal capacity of organisms, local environmental features, and regional landscape (Heino et al., 2015).

Spatial predictors are expected to explain metacommunity structure (Nakagawa, 2013; Heino et al., 2015; Oliveira et al., 2020). On local scales, such as a stream reach, the high dispersal of organisms among habitat patches homogenize assemblage composition (i.e., mass effect). In contrast, the spatial predictors on large scales tend to be more significant among watersheds, where dispersal limitation may be relevant. Thus, dispersal is one of the

central mechanisms explaining community structure, either by excess at local scales or limitation at regional scales (Soininen, 2012; Heino et al., 2015). Furthermore, the importance of the spatial component for structuring the aquatic metacommunities can be affected by the dispersal dynamic in the river network (Tonkin et al., 2018), as migrants may use both the water corridor and overland routes.

Environmental predictors are considered of great importance on local and intermediate scales as the high frequency of migrants at these scales allows environment conditions to act as filters (Carvalho & Tejerina-Garro, 2015; Heino et al., 2015). Besides, landscape characteristics may influence local environmental factors. For example, the input of allochthonous sediments in streams and the impairment of the chemical and physical integrity of the aquatic habitat may be correlated to the lack of riparian vegetation and intense land use in the watershed (Ward, 1998; Wiens, 2002; Casatti et al., 2006; Cunha et al., 2019). Therefore, changes in the watershed may alter the limnological characteristics of water bodies and, consequently, the dynamics of biological communities (Wiens, 2002; Barbosa et al., 2019; Di Carvalho & Wickham, 2019). Furthermore, the removal of riparian vegetation in lotic water bodies can increase the light incidence in these environments, which can cause changes in algal density and composition (Sabater et al., 2000).

The periphytic algal community represents a suitable model to investigate the influence of local and landscape environmental factors and spatial components on the community structure (Algarte et al., 2014; Padial et al., 2014; Benito et al., 2018; Oliveira et al., 2020). The dispersal mode of these organisms is influenced by the form of adherence to the substrate (Biggs et al., 1998). Species without attachment structures allow the movement to more favorable layers of the biofilm and prevent silting (Biggs et al., 1998; Lange et al., 2016; Dunck et al., 2016a). On the other hand, species with attachment structures are strongly adhered to the substrate and are more likely to remain attached to surfaces under high shear stress conditions (Biggs et al., 1998; Lange et al., 2016; Dunck et al., 2016a). Thus, species with distinct forms of adherence (i.e., loosely or tightly attached algae) may respond differently and their separate analyses should allow a better understanding of the environmental and spatial

contribution on community structure (Algarte et al., 2017).

The periphytic species also respond to environmental conditions and resources (Santos et al., 2018; Dunck et al., 2021). Physical–chemical variables of water such as nutrients, temperature, pH, dissolved oxygen, conductivity, suspended solids, and flow velocity are the main determinants for the diversity patterns of these communities (Biggs, 1995; Algarte et al., 2014; Ren et al., 2021; Zhu et al., 2022). In addition, they are influenced by indirect interference from landscape characteristics. For example, removing riparian vegetation increases the input of nutrients and light in streams, causing changes in the species composition of periphytic communities and increasing the likelihood of blooms and the dominance of some algae taxa (Davies Jr. et al., 2008; Cibils et al., 2015; Guo et al., 2015; Dunck et al., 2022; Pacheco et al., 2022).

Previous studies have investigated the importance of environmental and spatial predictors in explaining periphyton's variation. They pointed out that habitat variables were the main determinants of species composition (Algarte et al., 2014; Benito et al., 2018). However, other diversity metrics of communities also respond to these predictor variables. For example, the beta diversity components may indicate if changes in the community composition among sites occur mainly due to the species turnover or nestedness, the latter indicating whether communities with low species richness are populated by a subset of species occurring in communities with high richness (Baselga, 2010). In addition, it is also possible to estimate the contribution of each community to total beta diversity, which is known as Local Contribution to Beta Diversity (LCBD; Legendre & De Cáceres, 2013). Furthermore, the responses to environmental gradients and species dispersal patterns can be influenced by how they adhere to the substrate (Biggs et al., 1998; Algarte et al., 2014). Thus, the knowledge of spatial patterns helps to understand the dynamics and the structure of aquatic communities (Legendre & De Cáceres, 2013; Legendre, 2014) and to define the main determinants at different levels of organization.

In this context, we evaluated the influence of local environmental, landscape characteristics, and the spatial distances on the variation of periphytic communities, and their biodiversity facets within a riverine dendritic structure. We hypothesize that the local environment, representing the physicochemical aspects of the habitat, is the main determinant for all community metrics, as they provide the habitat template to the biological niches of species. On the other hand, the percentage of remaining riparian native vegetation in streams has a secondary importance, influencing indirectly on the diversity metrics (e.g., high explanation of shared components between variables). However, we expect that this percentage of importance varies according to the type of response metric assessed, since they represent complementary aspects of biodiversity (species richness, total beta diversity, local contribution to beta diversity, total density, and species composition). For the spatial component, we hypothesize that its importance depends on the form of adhesion to the substrate, with less importance for loosely attached species that disperse passively and can reach greater distances when compared to strongly attached species.

Methods

Study area

This study was carried out in the Paranaíba River basin (Fig. 1). It is located in the central region of Brazil (total area of 222,600 km^2), with 63.2% of its extension in the south of the Goiás State (CBH Paranaíba, 2021). We sampled 30 streams in the Piracanjuba River with 120 km length in a straight line (16.43 to 17.02 S and 48.10 to 48.37 W). The Piracanjuba River is inserted in Cerrado biome areas with intense landscape conversion to pasture (Alencar et al., 2020). We selected sampling sites with similar levels of declivity and substrate and located on third-order streams (Dodds & Oakes, 2008). All samplings were carried out during the dry season between August and September, 2019.

Periphyton community

We randomly collected five rocks along a stream reach of 10 m, always in the same direction (upstream to downstream), focusing on the epilithic community. On each rock, we scraped an area of 25 cm^2 corresponding to the side that faces upward with the aid of a brush with soft bristles and distilled water,

Fig. 1 Location of the 30 stream sites sampled along the Piracanjuba River basin in the southern region of the State of Goiás, Brazil. Numbers indicate stream codes
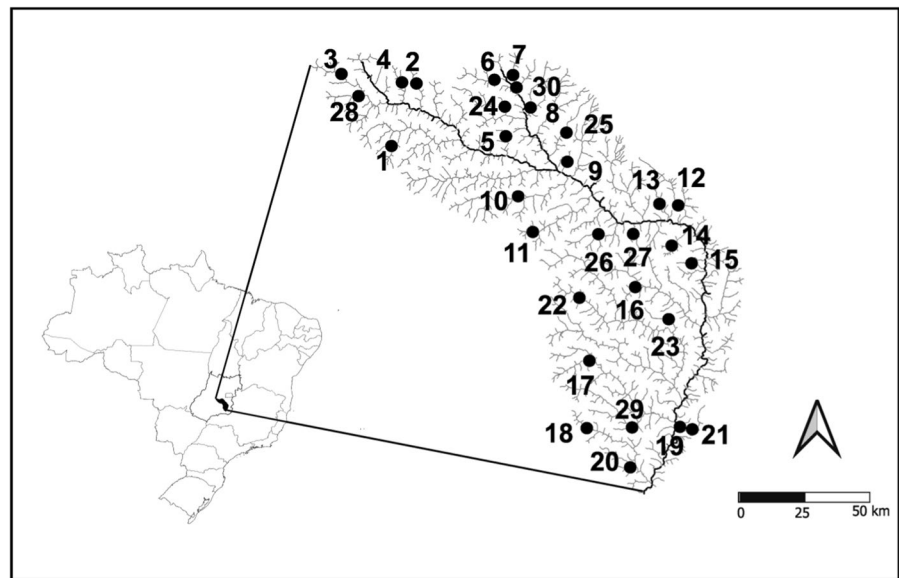
minimizing the fragmentation of filamentous algae (Schneck & Melo, 2012). The periphyton sampled from the five rocks of each stream was fixed with acetic Lugol solution and stored in a 100-mL amber bottle. The periphytic algae community was quantified using the sedimentation technique (Utermöhl, 1958) in an inverted microscope Zeiss Axiovert 25 with a magnification of 400x. Individuals were counted in random fields until we found no new species (species accumulation curve method; Bicudo, 1990).

The algal density was expressed in individuals by cm^{-2} (Ind cm^{-2}). The specimens were classified to the lowest taxonomic level using Round (1965; 1971), Round et al. (1990), Taylor et al. (2007), Laux and Torgan (2011), Sant'Anna et al. (2012), Wehr and Sheath (2013), Taylor & Concquyt (2016), and Aquino et al. (2018). To confirm the diatoms' taxonomic identification, we built permanent slides following the methods described in the European Committee for Standardization (ECS, 2003). For this, samples were washed with distilled water to remove the Lugol solution and digested with hydrogen peroxide (H_2O_2 35%, P.A.) at 90 °C for 24 h. Then, the supernatant was removed and the samples covered with concentrated hydrochloric acid (HCl 37%) for 12 h for cold oxidation. Afterward, the samples were washed again with distilled water and then centrifuged (about 8 min at 1200 rpm). Finally, the samples were placed in a slide and a coverslip and fixed using Naphrax (refractive index 1.5). The taxa were

identified using taxonomic keys and specific scientific literature for this group (Wetzel et al., 2010; Krammer & Lange-Bertalot, 2021; Lange-Bertalot, 2021a, b) under optic microscopic (Zeiss Axiovert 25 model) with 1000× magnification. Periphytic algae were classified according to the form of adhesion to the substrate as tightly adhered or loosely adhered (Sládecková & Sládecek, 1964; 1977). Algae without some type of attachment structure were classified as loosely adhered and with the presence of attachment structure were classified as tightly adhered (Biggs et al., 1998; Algarte et al., 2014; Lange et al., 2016; Dunck et al., 2016a).

Local environmental variables

We measured the local environmental variables using portable sensors (Manta 2 model sub 4.0) for electrical conductivity (µS cm^{-1}), dissolved oxygen (mg l^{-1}), pH, total dissolved solids (mg l^{-1}), water temperature (°C), turbidity (NTU), and depth (m). The water flow (m s^{-1}) was estimated using a flowmeter (General Oceanics R Flowmeter, model 2030) and channel width (m) using a tape measure. We also collected water samples (500 ml) from each site to determine in the laboratory the total phosphorus (µg l^{-1}), ammoniacal nitrogen (mg l^{-1}), nitrate (mg l^{-1}), and orthophosphate (µg l^{-1}) concentrations according to APHA (2005).

The luminosity was determined using five canopy photographs taken around the sampling point. We converted them into black-and-white images to calculate the proportion of black pixels. The images were analyzed with *imageJ* software (Rasband, 2018).

Landscape variable

We considered land use as a regional landscape variable estimated as the percentage of different land uses. In this sense, we considered two spatial landscape scales: (i) a riparian buffer, which is a semi-circular buffer with a 100 m radius encompassing the upstream area of each sampled site and (ii) the drainage, which is the watershed area upstream of the sampling site. For these measures, we used the Mapbiomas database (https://mapbiomas.org/) based on Landsat 30-m images from 2018. We used GIS software to identify and quantify the land use considering the following categories: forest formation, savanna formation, grassland formation, planted forest, pasture, annual and perennial culture, urban infrastructure, and other non-vegetated areas.

Subsequently, we organized the land use categories into four groups considering landscape spatial scale (riparian buffer and drainage) and land use degradation (native and impacted). Thus, we obtained the percentage of remaining native vegetation in the riparian buffer (% RNV buffer) and remaining native vegetation in the drainage (% RNV drainage) by grouping forest formation, savanna formation, and grassland formation from the riparian and drainage buffers, respectively. We also obtained the percentage of buffer impact (% Buffer Impact) and drainage impact (% Drainage Impact) by grouping planted forest, pasture, annual and perennial culture, urban infrastructure, and other non-vegetated areas obtained from the riparian and drainage buffers, respectively.

Spatial variables

We employed two approaches for the spatial data: (i) the Euclidean distance using the geographic coordinates of each stream measured by a GPS and (ii) the distance matrix represented by the distance between each pair of sampling points following the watercourse. We used both datasets separately to generate spatial filters of the Principal Coordinates of Neighbor Matrices type (PCNM; Griffith & Peres-Neto, 2006). Besides, we used spatial filters to represent the dispersal limitation of the periphytic algal community. Thus, the spatial filters generated using the Euclidean distance represent overland dispersal, while those using the watercourse distance represent the dispersal following the watercourse. For each dataset, a total of 19 PCNM filters were generated.

Each PCNM, when plotted against the study area extension, presented a different size and number of patches (Borcard et al., 2004). The size of the patches for each PCNM indicates the spatial scale (extension) that the filter represents. As a result, the first PCNMs represent a large spatial extension, with fewer patches of larger diameter. In contrast, the last PCNMs depict a minor spatial scale indicated by a small number of patches of tinier diameters. We distributed the PCNMs generated into three categories of spatial extension based on a linear transect of 113 km: (i) broad-scale PCNMs, the first six represented by small patches ranging from 20 to 40 km of diameter; (ii) intermediate-scale PCNMs composed by PCNMs 7 to 12 representing patches oscillating between 10 and 20 km of diameter; and (iii) fine-scale PCNMs, represented by PCNMs 13 to 19 exhibiting patches ranging from 1 to 10 km of diameter. The PCNMs and their groups were generated using the overland or the watercourse spatial distance matrices.

Data analysis

We estimated each stream's species richness, total density, and composition of the periphytic algae community. For the composition, we considered the whole community and deconstructed community according to the type of adhesion to the substrate (tightly and loosely adhered). These metrics are complementary and represent different facets of community structure. We assessed the beta diversity using two approaches. First, we estimated the overall multi-sample beta diversity using Jaccard dissimilarity (βJAC), and we partitioned it into turnover (βJTU) and nestedness (βJNE) components (Baselga, 2010). This analysis was performed using presence-absence data of the periphytic community. Second, we used the LCBD (Local Contribution to Beta Diversity), proposed by Legendre & De Cáceres (2013), to estimate the uniqueness of each stream site and its contribution to the overall beta diversity.

The local environmental variables were log-transformed (log $x+1$) except for pH, standardized by scaling the mean to zero and standard deviation to one. We used the variance inflation factor (VIF) to select non-collinear variables. Thus, the selected environmental variables (VIF < 2) were water flow, total phosphorus, ammoniacal nitrogen, nitrate, orthophosphate, dissolved oxygen, pH, water temperature, and luminosity.

We considered only the percentage of impact on the drainage and riparian buffers for regional landscape variables due to their complementarity with the remaining native vegetation in riparian buffer and drainage scales. Initially, we transformed data using the angular method, which is used frequently to analyze proportion data obtained by the arcsine of the square root of the proportion. The impact level in riparian buffer and drainage did not present collinearity (VIF < 2).

For the spatial distance variables, we used a forward selection analysis on the PNCM filters considering the Euclidean distance (overland dispersal) and distance along the water corridor (watercourse dispersal). We retained the PCNM filters correlated to each response variable (p < 0.05 and R^2adj higher than the full model; see Blanchet et al., 2008). For the overland distance, we selected the PCNM filters 9, 11, 16, and 18 for species richness; the PCNM filter 3 for total density; the PCNM filter 11 for LCBD; and the PCNM filters 1, 3, and 7 for total community composition. Considering the community deconstruction according to the forms of adhesion to the substrate, we selected the PCNM filters 1, 7, and 13 for tightly adhered species and filter PCNM 18 for loosely adhered ones. Using the watercourse distance, we selected PCNM filter 15 for species richness; PCNM filter 12 for total density; PCNM filter 15 for LCBD; and PCNM filters 10 and 11 for total community composition. Considering the community deconstruction according to the form of adhesion to the substrate, we selected the PCNM filters 10, 11, and 12 for tightly adhered. No watercourse distance filter was selected for loosely adhered species. To test our hypotheses, we used a partial Redundancy Analysis (pRDA) when the response was a matrix (total species composition and by adherence forms) and a multiple linear regression analysis when the response variables were univariate (species richness, LCBD, total density). We partitioned the total variation into

the pRDA and multiple linear regressions to obtain the shared and the unique contribution of the predictor variables to explain the response variables as follows: explanation purely of local environmental variables [a]; explanation purely of local environmental variables; [b] purely regional landscape; [c] purely space; [d] shared component between environment and landscape; [e] shared component between environment and space; [f] shared component between space and landscape; [g] shared component between environment, landscape and space; and [h] residual variation (Legendre & Legendre, 2012).

All analyses were performed using the R 3.5.1 software (R Core Team, 2021). The overall beta diversity was estimated using the *betapart* package (Baselga & Orme, 2012). The LCBD and the forward selection were obtained using the *adespatial* R package (Dray et al., 2021). We used the "rda" function for RDA and regression analyses and "varpart" function to partition variation, both in the *vegan* package (Oksanen et al., 2016). The VIF was estimated using the *usdm* package (Naimi et al., 2014).

Results

Sampled streams were shallow, with pH close to neutral and low concentrations of nitrate and orthophosphate (Table 1). Most of the physical and chemical characteristics showed slight variation between sites, except for the total phosphorus, orthophosphate, conductivity, and turbidity (Table 1).

The average percentage of remaining native vegetation (RNV) was 40% (ranging from 20 to 73%) and 26% (ranging from 12 to 50%) at the riparian buffer and drainage scales, respectively (Table 1). At the riparian buffer scale, two streams presented RNV > 61% and 12 sites ranged from 40 to 60% of RNV (Fig. S1 in the Online Resource 1). The remaining 16 streams (53.3% of the streams) in the extension of the riparian buffer had RNV < 40% (Fig. S1 in Online Resource 1). Considering the drainage area, 86.6% of the streams have RNV < 40% (Fig. S1 in Online Resource 1).

We found 128 periphytic algae species (See Table S1 in Online Resource 2); the most frequent group was Bacillariophyceae, present in all stream sites. Other frequent classes were Cyanophyceae (83%), Zygnemaphyceae (73%), Chlorophyceae

Table 1 Mean and standard deviation (± SD) values for local environmental and landscape variables measured in 30 stream sites in the Piracanjuba River basin, Goiás State, Brazil

Environmental variables	Mean	± SD	Minimum	Maximum
Conductivity ($\mu s\ cm^{-1}$)	43.16	31.16	5.90	105.40
Water flow ($cm\ s^{-1}$)	11.11	10.95	2.50	53.00
Total phosphorus ($\mu g\ L^{-1}$)	8.31	27.68	0.00	153.74
Width (m)	2.90	0.97	1.00	5.39
Nitrate ($mg\ l^{-1}$)	0.26	0.19	0.20	1.27
Ammoniacal nitrogen ($mg\ l^{-1}$)	0.001	0.004	0.00	0.02
Dissolved oxygen ($mg\ l^{-1}$)	7.19	0.94	3.70	8.10
Orthophosphate ($\mu g\ l^{-1}$)	0.52	1.67	0.00	6.97
pH	6.49	0.48	4.85	7.50
Depth (cm)	23.13	0.39	10.28	40.74
Water temperature (°C)	20.34	1.30	17.80	22.10
Turbidity (NTU)	13.10	16.71	2.03	81.60
RNV riparian buffer (%)	40.80	15.21	20.00	73.84
RNV drainage (%)	26.01	10.66	12.33	50.54
Impacted riparian buffer (%)	59.19	13.66	26.15	80.00
Impacted drainage (%)	73.98	10.66	49.45	87.66

(73%), and Fragillariophyceae (66%). The genus *Pinnularia* was the most frequent in streams (80% of frequency), followed by *Eunotia* (76.6%), *Ulnaria* (66.7%), *Closterium* (56.7%), *Oedogonium* (56.7%), and *Cymbella* (50%). The species with the highest frequency and density in the sampled sites was *Navicula cryptocephala* Kützing, present in 76% of

the streams sampled followed by *Pinnularia microstauron* var *angusta* Krammer (70%), *Eunotia* sp.1 (56%), *Oedogonium* sp.1 (53%), *Navicula radiosa* Kützing (43%), *Phormidium* sp.1 (46.5%), and *Navicula antonii* Lange-Bertalot (40%). Most species were loosely adhered; however, the tight adherence occur with more abundance in most of the streams sampled

Fig. 2 Species density according to the form of adhesion to the substrate sampled in 30 streams in the Piracanjuba River basin, Goiás State, Brazil
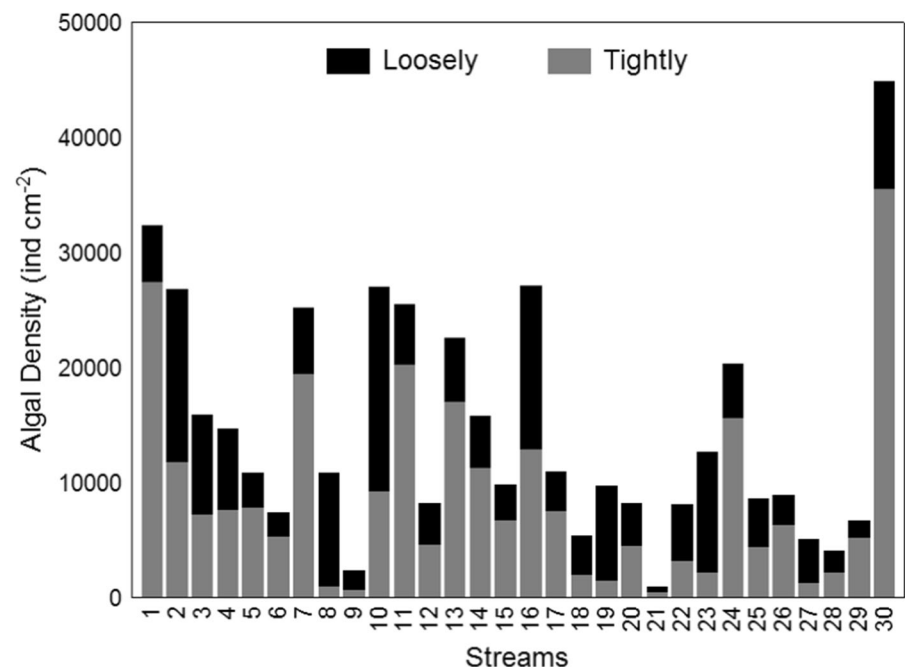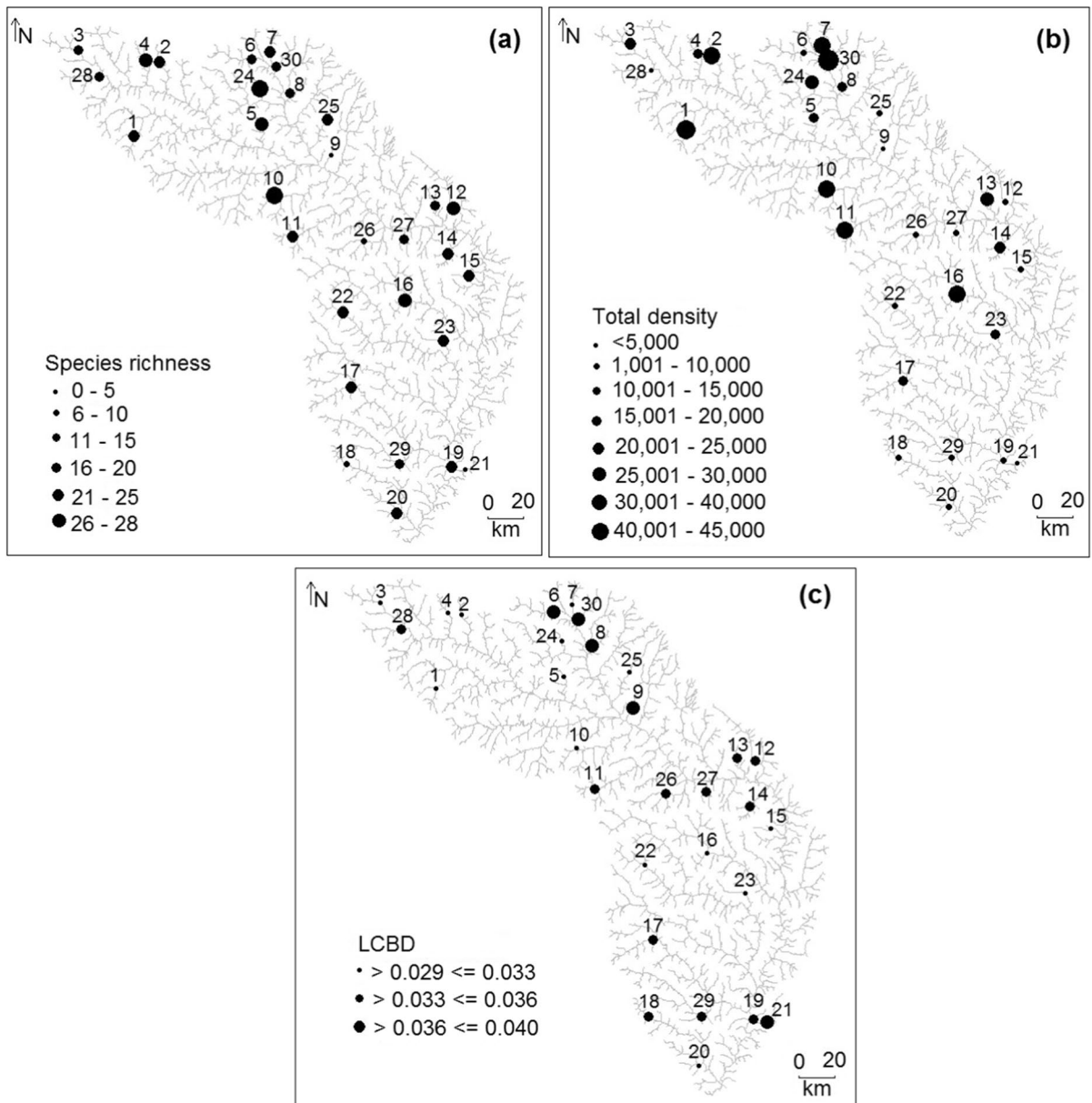
Fig. 3 Variation in periphyton community richness (**a**), total density (individuals by cm^{-2}) (**b**), and LCBD (**c**) measured in 30 streams in the Piracanjuba River basin, Goiás State, Brazil. Circle sizes correspond to the values of each component in the algal community. The numbers indicate the stream code

(Fig. 2). The periphytic algae community showed high variation in species richness, total density, and LCBD values along the drainage basin (Fig. 3). The average species richness value was 16 per sampled site (maximum = 28, minimum = 4; Fig. 2). We found a high total beta diversity value (βJAC = 0.96), mostly due to species turnover (βJTU = 0.95; βJNE = 0.01).

The LCBD had an average value of 0.033 (maximum = 0.040; minimum = 0.029).

The spatial component was the only significant predictor of the community composition, species richness, and total density using both PCNM filters derived from overland (Euclidean distance) and watercourse distances (Tables 2 and 3). The spatial

Table 2 Unique and shared components from the partial Redundancy Analysis (pRDA) and multiple linear regressions for the periphytic algal community

|	a		b		c		d	e	f	g	h
	R^2 adj	P	R^2 adj	P	R^2 adj	P	R^2 adj	R^2 adj	R^2 adj	R^2 adj	R^2 adj
Total density	− 0.027	0.552	0.072	0.169	0.23	**0.019**	0.069	0.000	− 0.080	− 0.058	0.787
Species richness	0.051	0.578	− 0.018	0.197	0.366	**0.014**	− 0.003	0.022	− 0.121	0.162	0.541
LCBD	− 0.170	0.974	− 0.081	0.878	0.159	0.068	0.094	0.009	− 0.076	0.003	1.026
Community composition	− 0.025	0.806	0.001	0.461	0.046	**0.020**	0.006	− 0.002	0.012	− 0.006	0.968
Tightly adhered	− 0.035	0.828	− 0.004	0.547	**0.062**	**0.03**	0.013	− 0.004	0.022	− 0.007	0.953
Loosely adhered	− 0.027	0.744	− 0.003	0.538	0.008	0.297	0.006	0.011	0.013	-0.014	0.99

Bold values indicate statistically significant effects on community composition or diversity ($P < 0.05$). The spatial component was obtained using geographic coordinates of each sampled site (Euclidean distance), representing the overland dispersal mechanism. LCBD is the Local Contribution to Beta Diversity. [a] Explanation purely of local environmental variables; [b] purely regional landscape; [c] purely space; [d] shared component between environment and landscape; [e] shared component between environment and space; [f] shared component between space and landscape; [g] shared component between environment, landscape and space; and [h] residual variation. The PCNM filters 9, 11, 16, and 18 were selected for species richness; the PCNM filter 3 for total density; the PCNM filter 11 for LCBD; and the PCNM filters 1, 7, and 3 for total community composition; and the PCNM filters 1, 7, and 13 for tightly adhered and PCNM filter 18 for loosely adhered

Table 3 Unique and shared components from the partial Redundancy Analysis (pRDA) and multiple linear regressions for the periphytic algal community

	a		b		c		d	e	f	g	h
	R^2 adj	P	R^2 adj	P	R^2 adj	P	R^2 adj	R^2 adj	R^2 adj	R^2 adj	R^2 adj
Total density	− 0.118	0.418	0.033	0.561	0.137	**0.049**	0.010	0.040	0.01	0.000	0.885
Species richness	− 0.059	0.781	− 0.009	0.289	0.103	**0.050**	0.114	0.014	− 0.010	0.044	0.803
LCBD	− 0.236	0.981	− 0.081	0.833	0.156	0.056	0.084	0.010	− 0.010	0.047	1.029
Community composition	0.006	0.412	0.002	0.411	0.056	**0.001**	− 0.002	− 0.003	− 0.018	0.001	0.957
Tightly adhered	− 0.002	0.540	− 0.013	0.696	0.015	0.331	0.011	0.004	− 0.010	− 0.005	0.973
Loosely adhered	0.028	0.208	− 0.009	0.673	–	–	0.003	–	–	–	0.978

Bold values indicate statistically significant effects on community composition or diversity ($P < 0.05$). The spatial component was obtained using the distance among sample sites following the stream watercourse, representing dispersal mechanisms along the drainage basin. LCBD is the Local Contribution to Beta Diversity. [a] Explanation purely of local environmental variables; [b] purely regional landscape; [c] purely space; [d] shared component between environment and landscape; [e] shared component between environment and space; [f] shared component between space and landscape; [g] shared component between environment, landscape and space; and [h] residual variation. The PCNM filter 15 was selected for species richness; PCNM filter 12 for total density; PCNM filter 15 for LCBD; PCNM filters 10 and 11 for community composition; PCNM filters 10, 11, and 12 for tightly adhered; and no PCNM filters was selected for loosely adhered

component derived from overland distance explained species richness (adj $R^2 = 0.366$; $P = 0.014$), total density variation (adj $R^2 = 0.23$; $P = 0.019$), community composition (adj $R^2 = 0.046$; $P = 0.002$), and the composition deconstructed by the form of adhesion to the substrate for tightly adhered (adj $R^2 = 0.062$; $P = 0.030$; Table 2), while the watercourse distance influenced the total density (adj $R^2 = 0.137$; $P = 0.049$), species richness (adj $R^2 = 0.103$; $P = 0.05$),

and total community composition (adj $R^2 = 0.056$; $P = 0.001$; Table 3). The local and regional landscape variables used in the pRDA analyses were not related to the different aspects of the periphytic algal community structure considered ($P > 0.05$; Tables 2 and 3).

Some species were associated with different spatial filters, as shown by the pRDA result performed on the species composition of the periphytic community

Fig. 4 Redundancy analysis (RDA) biplot for selected variables showing the sites (1–30), species (sp1–sp128), and spatial filters (PCNM). **a** RDA using overland spatial and **b** watercourse spatial matrix. The species names and the pRDA scores are available in the Online Resource 1
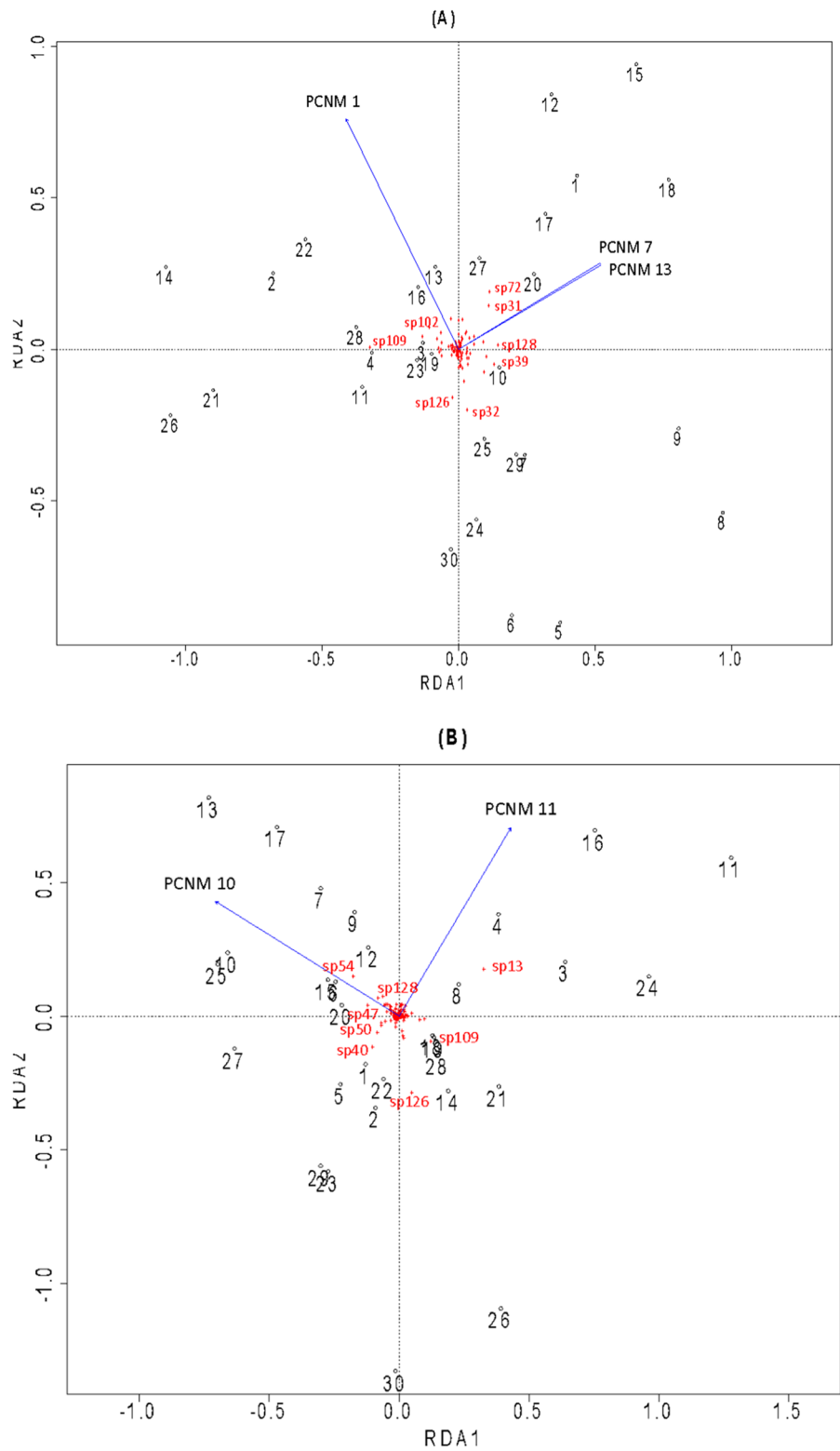
(Fig. 4). According to the pRDA based on the overland spatial matrix (Fig. 4a), the first and second axis of the RDA represented 18 and 15% of the data variation, respectively. The species *Wilmottia stricta* Machado-de-Lima, Martins & Branco (sp128 in Fig. 4a) and *Heteroleibleinia* sp 1. (sp72 in Fig. 4a) were positively associated with the first axis of the ordination, which also is correlated with the PCNM7 and PCNM13. In contrast, *Pseudanabaena limnetica* (Lemmermann) Komárek (sp109 in Fig. 4a), *Ulnaria ulna* (Nitzsch) Compère (sp126 in Fig. 4a), and *Pinnularia microstauron* var *angusta* (Nitzsch) P. Compère (sp102 in Fig. 4a) were negatively associated with the first axis of the RDA, which is also correlated with PCNM1. The pRDA based on the watercourse spatial distance matrix (Fig. 4b) represented 15% of the data variation in the first axis and 13% in the second one. This analysis revealed that *Batrachospermum gelatinosum* (Linnaeus) De Candolle (sp13 in Fig. 4b) and *Pseudanabaena* sp1 (sp109 in Fig. 4b) were positively correlated to the first axis of the pRDA, which is correlated to the PCNM11. Besides, *Eunotia* sp.7 (sp54 in Fig. 4b) was negatively associated with the first axis of the pRDA, which was also associated with PCNM10.

Discussion

We investigated the influence of the local environmental (limnological) variables, regional landscape (land use), and spatial distance (dispersal limitation) components on the periphytic communities in a water basin located in the Brazilian Cerrado. We observed high beta diversity, mainly associated with species turnover across the basin and partially corroborating our hypotheses. In this sense, we found that different metrics of the periphytic algal community were influenced only by the spatial component, considering overland or watercourse distances. However, spatial variables showed different percentages of explanation for the metrics considered. The local and regional environmental predictors were not significant. Thus, we infer that on a large spatial scale, the effect of the spatial component can be attributed to species dispersion limitation, whereas on a finer spatial scale, mass effect was the primary process driving the variation among communities.

Our results indicate that spatial distance (both overland and watercourse) are substantial determinants of stream periphytic communities' metrics. The influence of spatial distance on species dispersal has been acknowledged for many aquatic communities (Soininen et al., 2007; Rocha et al., 2020; Carvalho et al., 2021), showing a greater importance in larger-scale studies (Chase et al., 2005; Heino et al., 2012; Padial et al., 2014; Borges et al., 2020; Ptatscheck et al., 2020). However, its influence has been observed at finer spatial scales (Oliveira et al., 2020; Rocha et al., 2020; Carvalho et al., 2021). High distances among sampled sites can influence the dispersal of propagules throughout the region, possibly causing the differentiation in species composition among communities (Grönroos et al., 2013).

The mass effect and the dispersal limitation are processes associated with space that structure biological communities (Heino et al., 2015). Factors such as the spatial scale considered, beta diversity, and the form of species adherence to substrate can help to understand how processes affect the community structure. In the present study, we found high beta diversity, besides different spatial filters (different spatial extensions) significantly explained species composition. While broad-scale (areas from 20 to 40 km) spatial filters (1 to 6) indicate limited dispersal processes, filters of intermediate (area from 10 to 20 km) or finer (1 to 10 km) spatial scales (filters 11 to 19) are associated with mass effect processes (Heino et al., 2015; Rocha et al., 2020). Furthermore, we found that filters indicating different spatial scales were substantial for explaining species composition (total and tightly adhered in substrate) and other community metrics. The significance of these filters shows that the processes related to dispersal limitation and mass effect are crucial for the structure of the periphytic metacommunity.

The community of periphytic algae has a wide range of adherence to substrates, with loosely attached species capable of exhibiting a wide range of dispersal capacities (Algarte et al., 2014; 2017), linked to mass effect processes (Kristiansen, 1996; Soininen, 2002; Franceschini et al., 2009; Heino, 2010; Dong et al., 2016; Soininen et al., 2016; Jamoneau et al., 2017). On the other hand, species tightly attached to the substrate have a lower dispersal capacity and may be associated with "limited dispersal" processes (Algarte et al., 2014, 2017). We found that

the spatial filters over land are important to explain the composition of species tightly attached to the substrate. These species are associated with filters of intermediate and finer spatial scale. These results confirm the trends expected by our hypothesis and indicate that tightly adhered species have a limited dispersion when compared to loosely adherent ones. Thus, the spatial filters used in the analyses were indicators of how periphytic algal communities are structured in space and, hence, indicators of the processes that regulate the metacommunity.

The spatial predictors used here were surrogates for dispersal of the periphytic community. Many studies have used spatial distances as proxies for the dispersal ability (see Heino et al., 2015). However, it is fundamental to consider that spatial filters may be linked to other non-measured predictors that may show spatial autocorrelation (Nabout et al., 2009; Diniz-Filho et al., 2012; Chang et al., 2013). Despite the fact that our study considered the most common environmental variables used in periphytic community studies, such as temperature, light intensity, and nutrient input (Astorga et al., 2012; Dunck et al., 2013; 2016b), other non-measured local variables may explain the community structure associated with dispersal processes. For instance, features linked with habitat complexity, such as the substrate type (e.g., rock), may be autocorrelated in space and their effects confounded with dispersal limitation (Algarte et al., 2017).

Based on our results, we relate the processes arising from the turnover of species and the possible limitation of the occurrence of organisms to dispersal limitation or mass effect, depending on the scale of spatial filters selected in the analyses. The mass effect is associated with fine-scale filters, implying a large capacity for dispersal. In contrast, the dispersal limitation process is associated with broad-scale spatial filters with large and tightly attached species, suggesting low mobility. Furthermore, the importance of the spatial predictor in explaining other metrics of the periphytic community (e.g., total density and species richness) demonstrates the importance of dispersal and environmental variables associated with the spatial structure in understanding stream periphytic community dynamics.

Author contributions PHFO contributed to conception and design, analysis and interpretation of data, acquisition of data, and drafting of the article. KBM contributed to conception and design, analysis and interpretation of data, acquisition of data, drafting of the article, and revising critically for important intellectual content. FBT contributed to conception and design, acquisition of data, and drafting of the article. RAC contributed to conception and design, analysis and interpretation of data, and drafting of the article. MEF contributed to conception and design, analysis and interpretation of data, and drafting of the article. FLTG contributed to conception and design, analysis and interpretation of data, and drafting of the article. PC contributed to conception and design, analysis and interpretation of data, and drafting of the article. CF contributed to conception and design, analysis and interpretation of data, and drafting of the article. ASM contributed to conception and design, analysis and interpretation of data, and drafting of the article. JCN contributed to conception and design, analysis and interpretation of data, acquisition of data, and drafting of the article.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethical approval Not applicable. The present study did not involve research with humans or animals.

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