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RESEARCH ARTICLE

Effects of space and environment on phytoplankton distribution in subtropical reservoirs depend on functional features of the species

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Abstract

Environmental factors and dispersal can influence the structure of biological communities. Their effects can depend on the functional features of the species in the community. Since species belonging to the same trophic level, such as phytoplankton, may show functional differences, we investigated whether the effects of environment and dispersal differ among phytoplankton species from different functional groups. We analyzed data from a rainy and a dry period in 30 reservoirs in a subtropical region. In both periods, the environment as well as high and limited dispersal influenced the metacommunity structure. The functional groups had a low correspondence in their response to both dispersal and environment. Our results showed that the influence of the processes underlying the structure of the metacommunities, such as species sorting (environment influence), mass effect (high dispersal), and neutral dynamics (limited dispersal), depended on the functional characteristics of the organisms and could vary even among species of the same trophic level. These findings suggested that species at the same trophic level could not be considered ecological equivalents. This paper includes a Portuguese and Spanish version of the abstract in the online resources.

Keywords Metacommunities · PCNM · Functional diversity · Cyanobacteria · Plankton · Biovolume

Introduction

The structure of biological communities (e.g., species composition and abundance) varies in time and space, being influenced by environmental factors (environmental conditions and biotic interactions) and dispersal (Heino et al. 2015; Datry et al. 2016). Understanding how those processes act on the communities is crucial to conservation and management of ecosystems (Hubbell 2001; Cassemiro and Padial 2008). For instance, by evaluating the influence of local conditions and dispersal on biodiversity, one could determine if conservation efforts should concentrate on restoring the local conditions (e.g., reducing a certain stressor) or enhancing the connectivity among the communities (to guarantee exchange of species).

The effects of environment and dispersal on communities may vary among trophic levels due to particular features of the organisms (e.g., life history) that cause them to react differently to extrinsic factors (e.g., environmental variation and spatial discontinuity). For instance, the distribution of larger organisms would be limited mainly by dispersal (Padial et al. 2014). In the case of microorganisms such as phytoplankton, it has been proposed that mainly environmental conditions drive their distribution, while dispersal could not be an important process (Cermeño et al. 2010; Astorga et al. 2012; Padial et al. 2014) since microorganisms have high dispersal rates (e.g., Finlay 2002; Cermeño et al. 2010).

Alfonso Pineda, Jascieli Carla Bortolini and Luzia Cleide Rodrigues have contributed substantially to this work.

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Recent evidence, however, indicates that microorganisms may exhibit spatial patterns that are not associated exclusively with the spatial variation of environmental conditions, but also with dispersal (Van Der Gucht et al. 2007; Declerck et al. 2013). Spatial proxies have been used as signals of dispersal (see Heino et al. 2015), and with this approach, several studies have provided evidence that space (i.e., dispersal) influences the structure of microorganism assemblages (Beisner et al. 2006; Heino et al. 2010; Padial et al. 2014; Bortolini et al. 2019). However, few studies have explored the question of whether a significant effect of space on community structure was related to high or limited dispersal. This accuracy is important to determine strategies for management and conservation of biological systems (Trakhtenbrot et al. 2005). It is necessary, for instance, to understand if, in a particular case, it would be necessary to increase connectivity among sites (to foster the arrival of species) or to decrease it (to prevent influx of unwanted species, such as toxic algae in aquatic systems).

Species belonging to the same trophic level exploit resources similarly, and according to Hubbell (2001), they should react in the same way to environmental variation and show the same dispersal probability. However, these species can react differently to variations in environmental conditions and space, since they may have morphological, metabolic, and functional differences (Salmaso et al. 2015). For instance, in stratified environments, phytoplankton species will vary in their sedimentation rate, since "heavy" algae (e.g., organisms with a silica carapace) could settle faster than those with some mechanism controlling their position in the water column (e.g., flagella and aerotope) (Padisák et al. 2003). In another example, species with protection from desiccation (e.g., mucilaginous matrix in some colonial algae) may tolerate longer travels and reach more-distant sites (traveling in the feathers of birds, for example) than species without some specialized protection. One can expect that species that share morpho-functional features will have a similar response to external stimuli, and species with low similarity will be influenced by different factors.

We aimed to determine the roles of environmental and spatial processes (high and limited dispersal) in the distribution of phytoplankton species with different morpho-functional characteristics. We hypothesized that, although phytoplankton constitutes a single trophic level, the species are not ecological equivalents and the effects of environment and space vary among different morpho-functional groups of phytoplankton species. We expected that species from different groups could show low concordance in their responses to the environment and space. We were also interested in determining the main environmental and spatial drivers of the variation in each morpho-functional group. To test our hypothesis, we used phytoplankton and environmental data from 30 reservoirs located in six basins in a subtropical region, distributed in an area of ca. 200,000 km^2, with different environmental conditions and degrees of connectivity.

Materials and methods

Study area

The study included 30 reservoirs in an area of ca. 200,000 km^2 in a subtropical region in South America (between 22° and 27° S and 49° and 55° W) (Fig. 1). The reservoirs

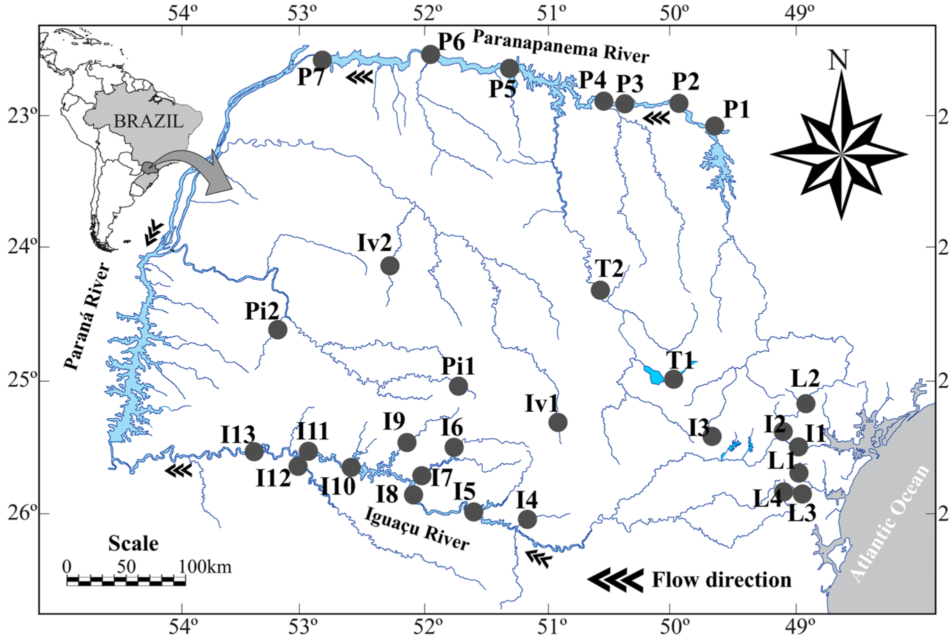

Fig. 1 Distribution of the reservoirs. Table 1 shows details for sites

belong to the Paraná basin, specifically to the sub-basins of the rivers Tibagi, Iguaçú, Paranapanema, Piquirí, Ivaí, and the Litorânea basin. The reservoirs were constructed between 1909 and 2001 and have different degrees of connectivity. While some of them are arranged in cascades (e.g., reservoirs along the Paranapanema and Iguaçú Rivers), others do not show connectivity, either directly or indirectly. The area of the lacustrine zone ranges from 0.1 to 419 km^2, while the water retention time ranges from < 10 to > 300 days (Table 1). Most of the reservoirs are used for electricity production and some of them for recreation, drinking-water supply, and irrigation.

Phytoplankton sampling and analysis

The samples were collected directly with bottles at the subsurface in the pelagic zone of the lacustrine area of the reservoirs. We fixed them with 1% acetic Lugol's solution. We conducted sampling twice in 2001, covering the dry (July) and rainy (December) periods. The counts of individuals (cells, filaments, and colonies) followed Utermöhl (1958) and Lund et al. (1958). Biovolume (mm^3 L^{-1}) was used as a biomass estimate and calculated as the product of the volume of each taxon and its density (individuals mL^{-1}). The volume of each taxon was calculated by approximating its shape to geometric forms (e.g., cylinders and cones) (Sun and Liu 2003).

We categorized the phytoplankton taxa into morphology-based functional groups (MBFG, Kruk et al. 2010). We based the grouping on the shared morpho-functional traits of the species. MBFG includes seven groups of species that differ in size, form, and presence of specialized features (Fig. 2). We chose the MBFG approach since it has shown a better response to environmental variation at broad scales

Table 1 General information about the reservoirs. RT, water residence time (days)

Basin	Reservoir	Code1	Code	Altitude (m)	RT (days)	Area (km^2)	Perimeter (km)	Start of operation
Iguaçú	Piraquara	I1	Pi	742	438	3.3	4	1979
Iguaçú	Iraí	I2	I	918	240	15	20.1	2000
Iguaçú	Passaúna	I3	P	921	420	14	35.3	1991
Iguaçú	Salto do Vau	I4	SV	832	1	2	4	1959
Iguaçú	Foz do Areia	I5	FA	785	150	139	288	1980
Iguaçú	Salto Curucaca	I6	Cu	904	1	2	3.7	Unknown
Iguaçú	Jordão	I7	J	619	183	3.4	21.7	1996
Iguaçú	Segredo	I8	Se	643	47	80.4	175	1992
Iguaçú	Cavernoso	I9	Cv	868	0.5	2.9	3.7	1950
Iguaçú	Salto Santiago	I10	SS	636	110	208	377	1979
Iguaçú	Salto Osório	I11	SO	398	16	51	180	1975
Iguaçú	Foz do Chopim	I12	FC	373	0.5	2.9	5.3	2001
Iguaçú	Salto Caxias	I13	SC	347	33	124	267	1998
Ivai	Rio dos Patos	Iv1	Pa	697	0.2	13	32	1917
Ivai	Mourão	Iv2	Mo	598	70	11.3	60	1964
Litorânea	Guaricana	L1	G	780	13	7	7.2	1957
Litorânea	Capivari	L2	Ca	816	48	12	123.5	1970
Litorânea	Salto do Meio	L3	Sme	850	0.5	0.1	3.9	1949
Litorânea	Vossoroca	L4	V	921	110	5.1	18.5	1949
Paranapanema	Chavantes	P1	X	491	353	400	402	1970
Paranapanema	Salto Grande	P2	SG	407	1.4	12	25	1958
Paranapanema	Canoas II	P3	CII	410	4.4	22.5	66	1992
Paranapanema	Canoas I	P4	CI	384	6	30.8	74	1999
Paranapanema	Capivara	P5	C	360	127	419.3	738	1975
Paranapanema	Taquaruçu	P6	T	313	7.9	80.1	156	1989
Paranapanema	Rosana	P7	R	293	19	220	230	1986
Piquiri	Santa María	Pi1	SM	904	2	0.1	2	Unknown
Piquiri	Melissa	Pi2	M	339	0.5	2.9	3.5	1962
Tibagi	Alagados	T1	A	944	46	7.2	47	1909
Tibagi	Harmonia	T2	H	720	13	3	7.5	1953

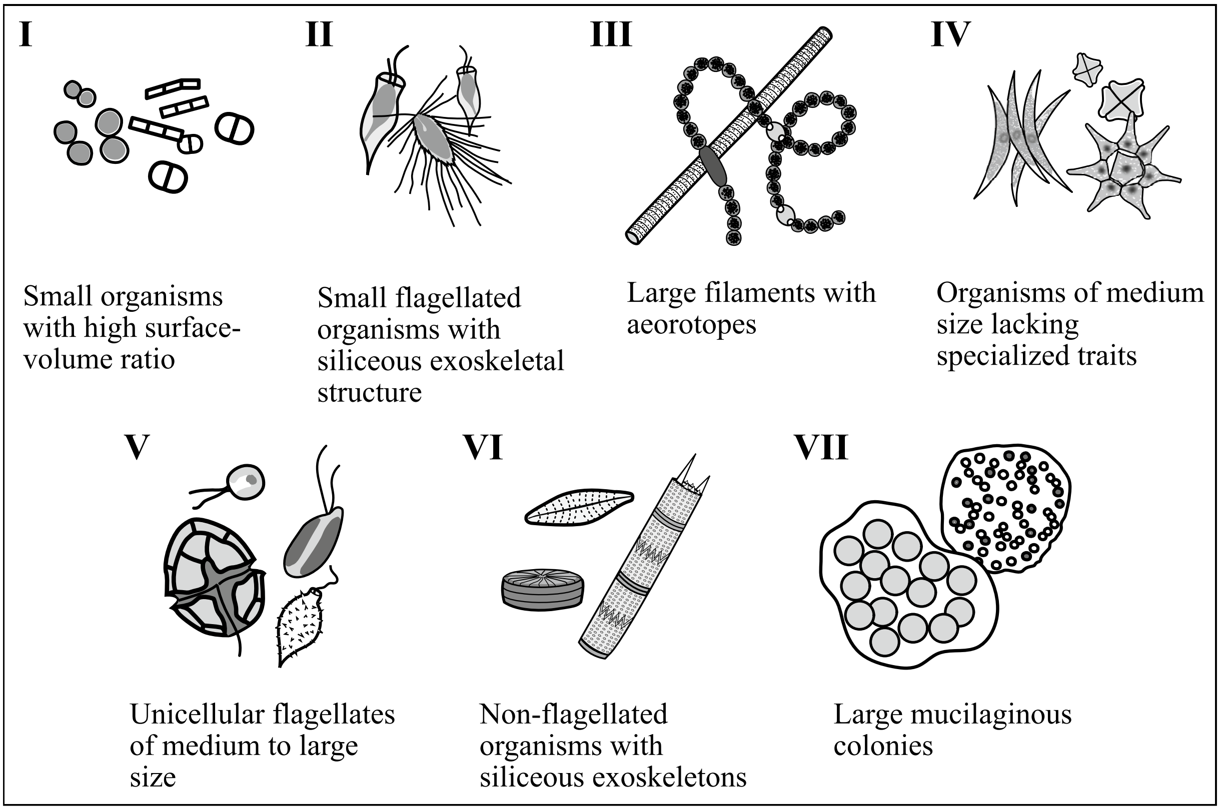

Fig. 2 Seven morphology-based functional groups (Kruk et al. 2010). Algae sizes in the figure do not represent true size–scale relationships among groups

than groups based on other classification methods (Kruk et al. 2011).

The functional-groups approach assumes that species in a specific group react in the same way to external stimuli and that the differences among groups are greater than the differences among species within a group. This approach has allowed identification of the key temporal and spatial processes underlying the community assemblage (e.g., Rodrigues et al. 2018; Pineda et al. 2020), due to the deterministic relationship that can be established between ecological processes and functional traits. For instance, the body size allows identification of the effect of grazing, since smaller phytoplankters (e.g., MBFG I) are more palatable than larger ones (e.g., MBFG VII) (Lehman 1991). In another example, for stagnant water habitats, while silica-shelled organisms (MBFG VI) sink rapidly due to their high weight, organisms with aerotopes (MBFG III) sink slowly due to their buoyancy (Kruk et al. 2010).

Environmental and biotic explanatory variables

Simultaneously with the phytoplankton, we collected samples of zooplankton and environmental variables. We expressed zooplankton density as ind. m^{-3} and separated the zooplankton into nine categories: testate amoebae, rotifers, cladocerans, calanoid nauplii, calanoid copepodites, calanoid adults, cyclopoid nauplii, cyclopoid copepodites, cyclopoid adults, and heterotrophic flagellates. We used different zooplankton groups because each one can graze on different phytoplankton species, based on their size and shape.

We also measured the variables pH, water temperature (°C), conductivity ($\mu S\ cm^{-1}$), turbidity (NTU), depth (Z_{max} in m), wind ($m\ s^{-1}$), P-PO_4 ($mg\ L^{-1}$), N–NO_3^- ($mg\ L^{-1}$), and N–NH_4^+ ($mg\ L^{-1}$). We estimated the euphotic zone (Z_{eu} in m) as 2.7 times the Secchi disk depth (Cole 1994), and we calculated the mixing zone (Z_{mix} in m) from temperature profiles. We used the Z_{mix}:Z_{max} ratio as a measure of the water column stability, with values close to one considered as more unstable. We used the Z_{eu}:Z_{mix} ratio as a measure of light availability in the mixing zone (Jensen et al. 1994). We also recorded the altitude (m), area (km^2), perimeter (km), and water retention time (days) of the reservoirs (provided by the management company of each reservoir). Details about the measured environmental factors and zooplankton sampling can be found in Simões et al. (2015). We classified the environmental factors according to the processes they represented, as chemical (factors affecting metabolism, including light availability) or physical (related to factors with no direct effect on metabolism) (Table 2).

Spatial factors

We used spatial factors as a proxy of the effect of dispersal on the community structure. The spatial variables (eigenvectors) were generated using the analysis of principal coordinates neighbor matrices (PCNM; Borcard and Legendre 2002), which consists of a principal components analysis based on a matrix of geographic distances. The PCNMs obtained for this analysis model different spatial structures (Borcard and Legendre 2002) and can be used together with environmental variables in variation-partitioning analysis (Anderson and Cribble 1998) as a way to understand the processes underlying a community assemblage (Borcard and Legendre 2002).

We obtained 17 PCNMs with positive eigenvalues that were categorized as representing fine or broad spatial scales. PCNMs with smaller eigenvalues (in this study, PCNM 5 to PCNM 17) represented the fine scale (Diniz-Filho and Bini 2005; Griffith and Peres-Neto 2006) and were interpreted as a signal of high dispersal, which indicates the influence of a mass-effect dynamic (Heino et al. 2015). PCNMs with higher eigenvalues (in this study, PCNM 1 to PCNM 4) represented the broad scale (Diniz-Filho and Bini 2005; Griffith and Peres-Neto 2006) and were related to dispersal limitation, which indicates the influence of a neutral dynamic (Heino et al. 2015). To split the PCNMs into these scales, we drew maps with the PCNMs (Online resource 2, S3) and grouped them according to the spatial pattern they represented, as suggested by Borcard et al. (2011).

Table 2 Mean values, standard deviation (SD), and variation coefficient (VC–%) of chemical, physical, and biotic factors measured in the rainy and dry periods for the 30 reservoirs

	Rainy			Dry		
	Mean	SD	VC	Mean	SD	VC
Chemical						
pH	7.5	0.6	8	6.2	1.4	23
$N–NO_3^-$ (mg L^{-1})	251.5	204	81	331.5	183.6	55
$N–NH_4^+$ (mg L^{-1})	14.5	10.9	75	29.4	36.2	123
Z_{eu} (m)	4.3	2.4	56	4.9	2.5	51
Z_{eu}:Z_{mix}	0.9	0.8	89	0.6	1.2	200
Turbidity (NTU)	13.2	25.9	196	9.2	10.8	117
Conductivity (μS cm^{-1})	44.8	20.1	45	38.2	15.2	40
T (°C)	23.8	2.9	12	18	4.8	27
$P–PO_4$ (mg L^{-1})	4.1	5.3	129	2.9	2.1	72
Physical						
Wind (m s^{-1})	2.9	2.1	72	3.5	3	86
Altitude (m)	640.4	227.5	36	640.4	227.5	36
Z_{max} (m)	29.4	32.6	111	30.4	32.8	108
Z_{mix}: Z_{max}	0.5	0.3	60	0.7	0.3	43
Area (km^2)	63.1	111.5	177	63.1	111.5	177
Perimeter (km)	106.9	166.9	156	106.9	166.9	156
Residence time (days)	82	125.7	153	82	125.7	153
Biotic (ind m^{-3})						
Testate amoebae	3885	20,904	538	226	482	213
Rotifera	28,424	42,404	149	22,055	51,429	233
Cladocera	35,479	130,949	369	26,477	101,646	384
Calanoid nauplii	8053	17,561	218	1066	2421	227
Calanoid copepodites	6818	12,387	182	2472	8605	348
Calanoid adults	1056	1908	181	132	256	194
Cyclopoid nauplii	10,714	22,276	208	12,465	32,025	257
Cyclopoid copepodites	5507	15,069	274	4371	13,423	307
Cyclopoid adults	351	862	245	999	4444	445
Heterotrophic flagellates	3185	3734	117	1832	2098	115

Z_{max} depth max, Z_{eu} euphotic zone, Z_{mix} mixing zone, T water temperature

Data analysis

To characterize the temporal variation in environmental conditions and to test for environmental differences between the rainy and dry periods, we used a constrained analysis of principal coordinates (CAP; Anderson and Willis 2003) on the Euclidean distance for scaled variables.

To assess the effects of environmental and spatial factors on the variation of the biomass phytoplankton, we used a partial redundancy analysis (pRDA; Borcard et al. 1992). As response, we used nine matrices of biovolume values: one including all the species, one with all the MBFGs, and one for the species in each MBFG (seven matrices). As explanatory, we used two explanatory matrices: one with environmental factors and one with the PCNMs.

We also used pRDA to evaluate the importance of each kind of environmental factor. For this, we split the environmental factors into three explanatory matrices according to the processes to which they were most related: physical, chemical, and biotic (Table 2). For these pRDAs, we also included as explanatory one matrix with the 17 PCNMs to remove the effect of space from the environment–species (or groups) relationship. Then, we evaluated the effect of the broad and fine spatial scales, again with pRDA, by separating the PCNMs into two explanatory matrices according to the spatial scale they represented. For these pRDAs, we also included one matrix with the total of the environmental factors, since we were interested in determining the pure influence of space on the species (or groups), excluding any interaction of space with environmental factors. For all pRDAs, we used Monte Carlo permutation tests (9999 permutations) to assess the significance of the fractions (Borcard et al. 1992). As a measure of the explained variation of the explanatory matrices, we considered only the pure fractions, as well as the adjusted R^2 values, since this corrects for the effect of differences in the number of independent variables in the explanatory matrices and allows comparison of results (Peres-Neto et al. 2006).

To evaluate the level of concordance of the responses of species in different functional groups to the total of explanatory factors (environmental and spatial factors in a single matrix) in each period, we ran a Procrustean Randomization Test (ProTest; Jackson 1995) on the ordination (sites) generated by the redundancy analysis (RDA), performed separately for each MBFG (seven response matrices). We also tested concordance for the same group between periods. In all cases, we evaluated (9999 permutations) the level of agreement between ordinations as the sum of squares of the residuals, m^2 (Jackson 1995). Lower values of the m^2 statistic indicate a high association between the responses of functional groups, and higher values indicate a low association. For our main objective of understanding whether species react in the same way to the environment and space, the Procrustes analysis complemented the pRDAs, since environment and space can influence two MBFGs with the same force (R^2 adjusted in the pRDA), but how each MBFG relates to those explanatory factors may be different (i.e., differences in the significant explanatory factors and ordination, or RDA).

As a previous step to the pRDA and RDA, we performed a variable selection using a forward procedure ($p < 0.05$, 999 permutations) for each explanatory matrix. The response matrix was Hellinger-transformed and the environmental factors were log-transformed (except the pH and ratios). The Hellinger transformation is a recommended way of handling community data sets with many zeros (as in our case) without overweighting the rare species (Legendre and Gallagher 2001). We investigated the collinearity with the variation inflation factor (VIF). We removed from the analyses all variables with a VIF higher than 10 (Legendre and Legendre 1998). We ran the analyses and plots in the R software (R Development Core Team 2021), using the vegan (Oksanen et al. 2007), ggplot2 (Wickham 2016), and adespatial (Dray et al. 2018) packages.

Results

Environmental variability in reservoirs

In both the rainy and dry periods, environmental conditions showed high spatial variation (Table 2), especially related to light availability (in the dry period, variation coefficient—VC > 100% for turbidity and Z_{eu}:Z_{max}), nutrient concentrations (VC > 70% for P–PO_4 and N–NH_4^+), and zooplankton abundance (VC > 110% in all cases). CAP showed environmental differences between periods ($F = 5.97$, $p = 0.001$). The sites in the rainy period were related mainly to higher temperature, pH, and light availability (Z_{eu}:Z_{max} ratio), while in the dry period, the sites were mainly associated with high nitrate and ammonium concentrations and high water-column mixing (Z_{mix}:Z_{max} ratio) (Fig. 3).

Phytoplankton and MBFG

In total, 140 phytoplankton taxa were recorded, 106 in the rainy and 101 in the dry period (Online resource 1). MBFG IV showed the highest number of taxa (51) and MBFG I the lowest (3). We recorded all the groups in both the rainy and dry periods, although they were not present in all reservoirs (Fig. 4). The biovolume values of all MBFGs showed a high spatial variation (Fig. 4). Filamentous algae (MBFG III, mean values dry = 4.42 $mm^3 L^{-1}$, rainy = 0.82 $mm^3 L^{-1}$), flagellates (MBFG V, mean values dry = 0.35 $mm^3 L^{-1}$, rainy = 0.68 $mm^3 L^{-1}$), and diatoms (MBFG VI, mean values dry = 0.20 $mm^3 L^{-1}$, rainy = 0.40 $mm^3 L^{-1}$) showed the

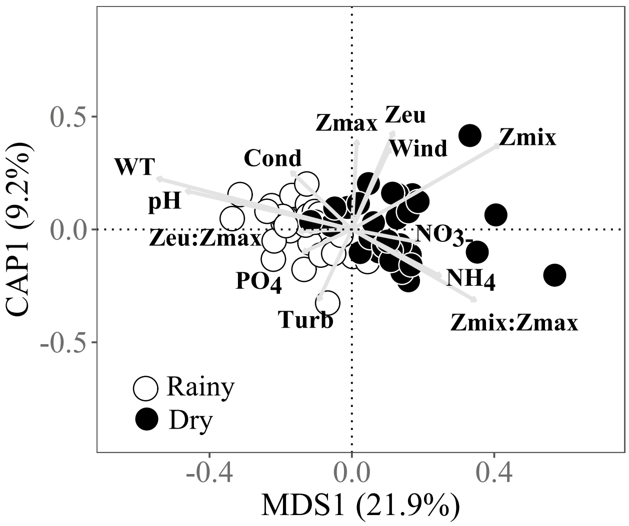

Fig. 3 Environmental temporal variation of the 30 reservoirs represented on the first two axes of a constrained principal coordinates analysis

highest biovolume values (more details in Online resource 1) and dominated in most of the reservoirs (Fig. 4).

Environmental and spatial drivers of the MBFGs

Both environmental and spatial factors were selected as explanatory factors of the phytoplankton community, except for the total MBFG in both the rainy (no spatial factors selected) and dry (none selected) periods and for the species belonging to MBFG I in the rainy period (no spatial factors selected). The selected factors varied among the MBFGs and changed over time (Table 3).

Regarding the total of species, the pRDA showed that the environment was more important for the biovolume variation than space (Table 4). However, the importance of the environment (physical, chemical, and biotic factors) and space (fine-scale—high dispersal and broad-scale—limited dispersal) varied between periods and among MBFGs (Table 4). No relationship between the phytoplankton community and the environment emerged when analyzing the MBFG level in the dry period and MBFG I in the rainy period.

Although initially the effect of the total environment and total space could be significant, the explanation of their split fractions decreased (even turning null) due to the high values of the shared fractions (not shown) that indicate the interaction among factors. In general, ProTest Analysis showed low concordance among the MBFGs (Table 5), and even significant results showed low concordance (m^2 values higher than 73), indicating that species in each MBFG responded in different ways to environmental variation. The MBFGs also showed lower concordance between periods.

Discussion

Are the species from the same trophic level ecological equivalents? By analyzing a polyphyletic community of species that are strongly dependent on light and nutrient availability, such as phytoplankton (including cyanobacteria), and its relationship with environmental and dispersal processes, we found that the answer is no. The influence of the ecological processes, as well as both high and limited dispersal, depended on the features of the phytoplankton species and the period of the year. Our findings contrast with the idea that species at the same trophic level are ecological equivalents and that their distribution would be related exclusively to dispersal and ecological drift, with no relationship to environmental variation (Hubbell 2006).

Effect of environment on phytoplankton variation

One could expect a stronger relationship between the community and the environment at the functional level (e.g., MBFG) than at the species level (Mutshinda et al. 2016), since environmental filtering and biotic interactions shape communities through selection of the functional traits of species (e.g., Noble and Slatyer 1980). In our case, however, this was true only in the rainy period. In the dry period, the environment did not explain the variation of the whole community when the MBFG was analyzed (no factor was selected). Although MBFGs are based on morphological features that reflect some physiological traits of the species (e.g., smaller size is related to higher nutrient uptake) (Kruk et al. 2010), in our case, it appeared that MBFGs did not reflect the species traits that were influenced by the environment. For instance, the selection of environmental factors in the dry period showed that pH and calanoid copepodites were important drivers for the species variation, but the MBFGs were not. Thus, although grouping species based on their morphology can help to understand the processes that shape the communities (such as in the rainy period); in some cases, the species morphological characteristics considered by the MBFG could not allow us to identify the response of some physiological traits (e.g., tolerance to water acidity) to environmental variations (e.g., change in pH) or the influence of significant interspecific dynamics (e.g., grazing). Therefore, identifying the main drivers of the community based on functional groups could be difficult in some cases.

When analyzing the whole community at the species level, we found that mainly environmental factors drove the phytoplankton variation, as found in other studies (Beisner et al. 2006; De Bie et al. 2012; Padial et al. 2014; Huszar et al. 2015; Machado et al. 2016; Santos

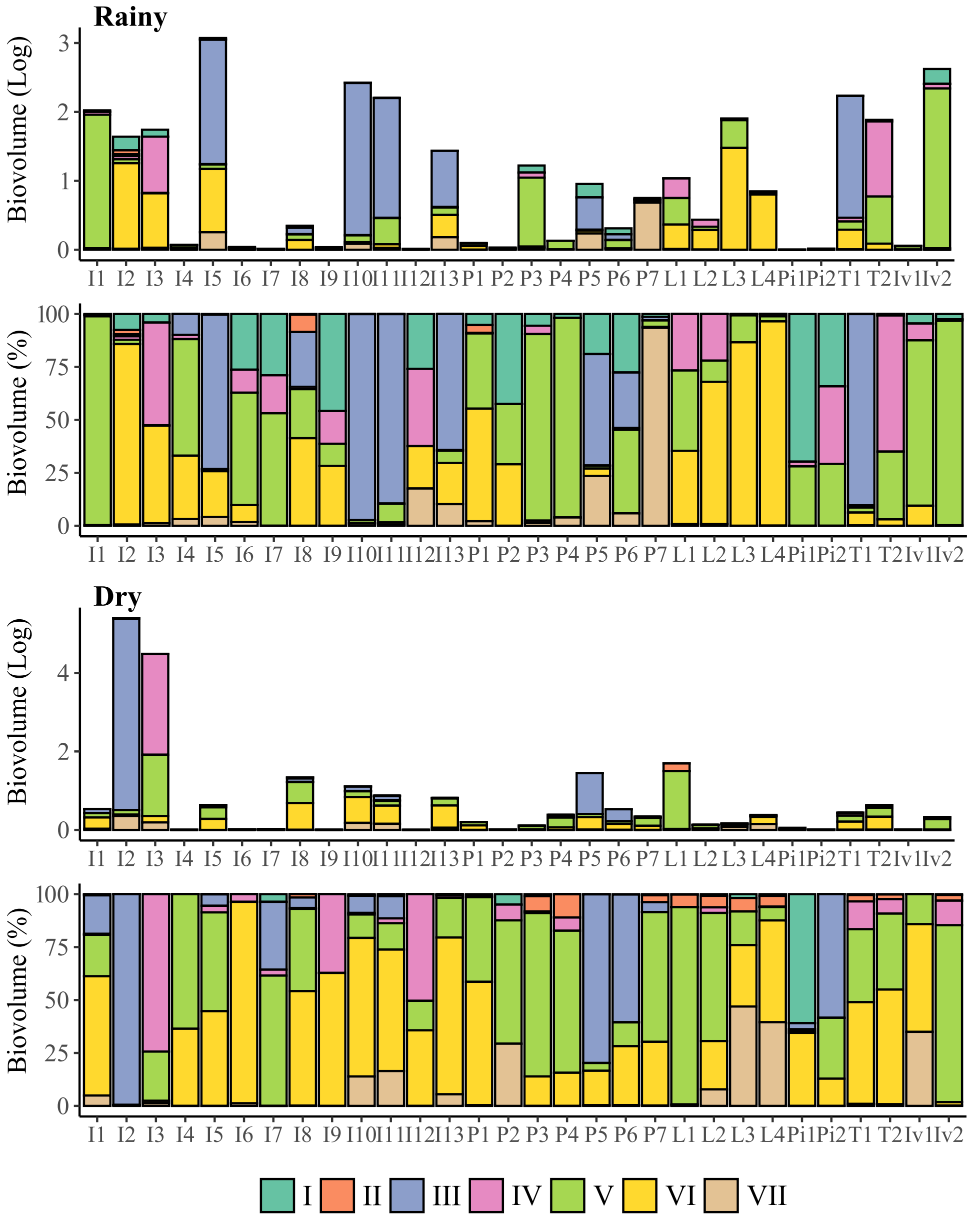

Fig. 4 Spatial variation of the biovolume (mm^3 L^{-1}) total and relative contributions of the morphology-based functional groups (MBFG) in the rainy and dry periods. See code names in Table 1

et al. 2016; Wojciechowski et al. 2017; Santana et al. 2018; Bortolini et al. 2020). However, we also found that the influence of the environment (and space, as we will discuss below) depended on the functional features of the phytoplankton. Moreover, each kind of environmental factor (physical, chemical, and biotic) had a different effect on each MBFG. In fact, in most cases, the species of the different MBFGs did not show concordance in their response to the environment (and space). In other words, phytoplankton species belonging to different MBGFs cannot be considered ecological equivalents. Although all the phytoplankters belong to the same trophic level and exploit the same resources, they show different functional traits (e.g., size, shape, presence of mucilage, flagella, and siliceous exoskeleton) influencing the way that they react to the abiotic and biotic characteristics of the reservoirs. For instance, while filamentous species (MBFG III) seemed to be sensitive to the area of the reservoirs, colonial algae (MBFG VII) showed sensitivity to changes in the abundance of zooplankton and the mixing of the water column.

Effect of space on phytoplankton variation

We showed that other factors aside from the environmental ones influenced the distribution of species. For instance, we observed high residual values in the pRDAs and we found that spatial factors related to broad (dispersal limitation) and fine (high dispersal) scales were important for the distribution of some phytoplankton species.

Table 3 Selected environmental and spatial factors selected by the forward method in the rainy and dry periods

	Environmental			Spatial	
	Physical	Chemical	Biotic	Broad	Fine
Rainy					
All species	Z_{Mix}:Z_{Max}, area	Turbidity	Rotifer	PCNM1	PCNM9
MBFG I	–	–	–	–	–
MBFG II	Z_{max}	–	Cladocera, HF	PCNM1	PCNM9
MBFG III	Area	P–PO_4	Coptocal	PCNM4	PCNM9
MBFG IV	Z_{Max}, area, Z_{Mix}:Z_{Max}	–	Coptocal	PCNM1, PCNM2, PCNM4	PCNM9
MBFG V	–	–	Rotifers, naupcal, HF	PCNM1	–
MBFG VI	Z_{Mix}:Z_{Max}	Turbidity	Adultcycl, adultcal, naupcal	PCNM1	–
MBFG VII	Area	–	Coptocal, HF, cladocera	PCNM1	PCNM13
All MBFGs	Altitude, area	–	Cladocera, coptocal	–	–
Dry					
All species	Area	pH, turbidity, NH_4^+, Z_{eu}:Z_{Mix}	Coptocal, HF	PCNM2, PCNM1	PCNM5, PCNM9
MBFG I	Perimeter	Turbidity, cond	Cladocera	PCNM1, PCNM2	PCNM9
MBFG II	–	–	Adultcycl, cladocera	PCNM1	PCNM9, PCNM15
MBFG III	Area	–	Adultcal	PCNM4, PCNM1	PCNM9,
MBFG IV	–	Z_{eu}:Z_{Mix}	–	–	PCNM8, PCNM5, PCNM9,
MBFG V	Perimeter	–	HF, coptocycl	–	PCNM5, PCNM9
MBFG VI	Area, residence time, Z_{Mix}:Z_{Max}	Z_{eu}:Z_{Mix}, Z_{EU}	Coptocycl, HF	PCNM1, PCNM2	PCNM9,
MBFG VII	–	N–NH_4^+	Coptocycl	PCNM3	PCNM7
All MBFGs	–	–	–	–	–

As spatial factors, 10 PCNMs were selected from the original 17 PCNMs

"–" indicates cases in which no factors were selected

HF heterotrophic flagellates, *Coptocal* calanoid copepodites, *Adultcycl* adult cyclopoids, *Adultcal* adult calanoids, *Naupcal* calanoid nauplii, *Coptocycl* cyclopoid copepodites

The significant effect of dispersal limitation suggests that some species could not reach all the sites that possess the appropriate environmental conditions for their establishment. The influence of dispersal limitation was higher for filamentous (MBFG III), flagellates (MBFG V), and colonial (MBFG VII) phytoplankters. These groups include bloom-forming and toxigenic cyanobacteria (Kruk et al. 2010; Kruk and Segura 2012), such as *Dolichospermum* and *Raphidiopsis* from MBFG III, and *Aphanocapsa* and *Microcystis aeruginosa* (Kützing) Kützing from MBFG VII. In the case of representatives from MBFG VII, they can be efficiently dispersed overland (i.e., with viable inocula) by vectors (e.g., *Aphanocapsa*; Schlichting 1960) and through the air (e.g., *Microcystis*; Chrisostomou et al. 2009). However, the success of this overland dispersal is limited to a few travel hours and short distances (Schlichting 1960; Chrisostomou et al. 2009). On the other hand, *Raphidiopsis raciborskii* (Woloszynska) Aguilera, Berrendero Gómez, Kastovsky, Echenique & Salerno (formerly *Cylindrospermopsis raciborskii*) (MBFG III) disperses successfully due to its ability to tolerate traveling along river courses (Padisák 1997) and it seems that viable inocula can reach sites as much as 400 km distant from the source (Hamar 1977). Although our study area includes several reservoirs with high connectivity (such as those in cascades), in other cases, the reservoirs have no direct connection and are very distant for viable inocula to reach. In general, the effect of dispersal limitation on the distribution of MBFG III suggests that, although some reservoirs have the potential to develop representative populations of toxic filamentous algae (e.g., high phosphorus concentration in Iv2), the increase in biomass did not occur, at least in part because of low levels of incoming inocula.

In other cases, high dispersal among sites influenced the spatial variation of phytoplankton biomass. Since some reservoirs possess characteristics favoring phytoplankter development (Reynolds 1999; Borges et al. 2008), such as high water residence time (Souza et al. 2016), they can develop a high biomass which can be exported through both the air and watercourses. In this study, we found high biomasses in several reservoirs (e.g., Irai with 130.54 mm^3 L^{-1} in the dry

Table 4 Variation partitioning results, showing the relative contributions (%) of the environmental and spatial factors to the variation of the biovolume of the phytoplankton species and MBFGs in the rainy and dry periods

	Total env	Physical	Chemical	Biotic	Total spatial	Fine	Broad	Env and spatial	Residual
Rainy									
All species	**9***	**5***	0	**3***	3	0	3	**17***	83
MBFG I	–	–	–	–	–	–	–	–	100
MBFG II	**17***	2	–	11	**9***	3	**6***	**30***	70
MBFG III	**14***	**6***	3	0	**17***	3	**13***	**38***	62
MBFG IV	**4***	**4***	–	1	**6***	0	**6***	**13***	87
MBFG V	**19***	–	–	**19***	**10***	—	**10***	**27***	73
MBFG VI	**15***	2	2	**9***	**3***	–	**3***	**19***	81
MBFG VII	**13***	**3***	–	**11***	**5***	**3***	1	**19***	81
All MBFGs	**21***	**7***	–	1	–	–	–	**21***	79
Dry									
All species	**13***	**3***	3	3	4	0	0	**23***	77
MBFG I	**34***	0	**15***	0	0	0	0	**50***	50
MBFG II	**12***	–	–	**12***	25	**18***	5	**53***	47
MBFG III	**14***	**6***	–	0	**10***	1	**10***	**35***	65
MBFG IV	3	–	3	–	**15***	**15***	–	**21***	79
MBFG V	**18***	2	–	**14***	**10***	**10***	–	**31***	69
MBFG VI	**29***	**13***	**12***	**5***	**6***	0	**6***	**47***	53
MBFG VII	**8***	–	2	**6***	**13***	**4***	**8***	**28***	72
All MBFGs	–	–	–	–	–	–	–	–	100

In addition, the pure contribution of the environmental (physical, chemical, and biotic) and spatial fractions (fine and broad). Values highlighted in bold and with an asterisk indicate significant fractions. Zero values indicate an explanation lower than 0.05%. – represent cases in which no factors were selected

"–" indicates cases in which no factors were selected

Env environmental

period, and Mourão with 9.50 mm^3 L^{-1} in the rainy period), some of them in cascade (Foz de Areia, 6.97 mm^3 L^{-1} in rainy). The inocula exported from reservoirs may modify the composition and abundance of communities located in the surroundings (Chrisostomou et al. 2009) and in downstream areas (Bovo-Scomparin et al. 2013; Bortolini et al. 2017).

The effect of high dispersal was related to small flagellates with a siliceous exoskeletal structure (MBFG II), phytoplankters with medium body size without special features (MBFG IV), large flagellates (MBFG V), and colonies (MBFG VII, the only group with high dispersal in both periods). We draw attention to the effect on MBFG VII since it includes toxigenic cyanobacteria, such as *Microcystis aeruginosa*, which showed the highest biomass in this group (Online resource 1). This alga has a mucilaginous matrix that protects the cells when they are transported by animals. This means that an aquatic system without conditions favoring the development of *M. aeruginosa* can still contain individuals of this species, due to incoming inocula from sites with larger populations. Management measures to control populations of toxigenic algae in reservoirs should consider the relationship with surrounding habitats with high populations, and then decrease the quantity of incoming alga biomass by controlling the local populations at the source sites.

Although we did not test the pairwise relationships to determine the direction of the high export of biomass, we believe that high dispersal is more likely to occur in reservoirs located in a cascade, since high connectivity and water flow can favor dispersal of phytoplankton (Zorzal-Almeida et al. 2017; Marquardt et al. 2018; Galizia Tundisi 2018). Our biomass plot showed how in both periods, for instance, the biomass of MBFG VII decreased directionally from P5 to P6 reservoirs—the former acting as a possible source of inoculum. Future studies will be necessary to determine if such directional decrease is related to a dilutive effect due to dispersal from a highly populated source. Moreover, further research is necessary to analyze the effect of high dispersal on the homogenization of communities at taxonomic and genetic levels, and to determine, for instance, if populations of cyanobacteria of cascade reservoirs belong to the same clone.

In some cases, we observed that both limitation and high-dispersal processes acted simultaneously, as in the case of large mucilaginous colonies (MBFG VII) in the rainy period. Both the distance and the connectivity among communities

Table 5 ProTest analyses of responses of different MBFGs (or the same between periods) to environmental conditions (based on RDA)

	m^2	p	m^2	p	m^2	p	m^2	p	m^2	p	m^2	p
	II		III		IV		V		VI		VII	
Rainy												
I	1.00	0.82	0.96	0.43	0.99	0.84	0.96	0.45	0.95	0.30	0.99	0.81
II			0.94	0.30	0.96	0.47	0.98	0.19	0.91	0.12	0.97	0.63
III					0.95	0.43	0.91	0.10	**0.74**	**0.001**	**0.80**	**0.01**
IV							**0.87**	**0.04**	0.98	0.75	0.95	0.43
V									0.99	0.89	0.91	0.12
VI											0.95	0.44
Dry												
I	0.91	0.10	0.94	0.26	0.96	0.47	0.99	0.88	**0.87**	**0.04**	0.97	0.64
II			0.98	0.84	0.96	0.44	0.98	0.79	0.96	0.43	0.98	0.73
III					0.94	0.34	0.90	0.10	0.90	0.09	0.94	0.34
IV							0.72	0.00	0.92	0.17	0.97	0.65
V									0.91	0.14	0.92	0.19
VI											**0.87**	**0.04**

Dry–rainy concordance

I		II		III		IV		V		VI		VII	
m^2	p	m^2	p	m^2	p	m^2	p	m^2	p	m^2	p	m^2	p
0.98	0.69	0.99	0.75	0.90	0.10	0.91	0.14	**0.81**	**0.01**	**0.82**	**0.01**	0.99	0.97

The sum of the squared residuals (m^2) is a measure of the concordance between two ordinations (comparison between functional groups). High values of m^2 indicate weak concordance. Significant concordances highlighted in bold

can determine the effects of limited and high dispersal on community structure, since immigration and successful colonization depend on their dispersal efficiency over the surrounding dry land (Naselli-Flores and Padisák 2016). For our study zone, for instance, while some reservoirs were located along the same river, improving connectivity and dispersal, others belong to different basins without direct or indirect connectivity and dispersal could be more difficult.

Finally, we do not discard the possibility that the effect of both broad- and fine-scale spatial factors included in the pRDA could indicate the effect of environmental variables, important for phytoplankton, that we did not measure and that show spatial structuring (Borcard and Legendre 1994; Borcard et al. 2004, 2011).

Conclusion

Together, our results showed that the influence of the processes underlying a metacommunity (communities related by the exchanges of organisms) assemblage, such as species sorting (environmental influence), mass effect (high dispersal), and neutral dynamic (dispersal limitation), depends on the functional characteristics of the species and can still vary for species within the same trophic level. By clarifying the kind of factors with important effects at both the taxonomic and functional levels, as well as for each kind of algae, our study may contribute to the development of management measures for organisms of public-health interest, such as toxigenic cyanobacteria.

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Declarations

Conflict of interest There is no conflict of interest.

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