

Temporal stability in beta diversity does not guarantee surrogacy or compositional stability in a micro-phytoplankton metacommunity

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ABSTRACT

Temporal stability in beta diversity does not guarantee surrogacy or compositional stability in a micro-phytoplankton metacommunity

Temporal stability in beta diversity does not guarantee surrogacy or compositional stability in a micro-phytoplankton metacommunity. In this study, we evaluated phytoplankton community organization (i.e., microalgae filtered in 20 µm mesh-sized plankton net) in a highly dynamic subtropical tidal river over three years. Specifically, we assessed temporal stability in the spatial organization of phytoplankton, the diatoms' efficiency as an indicator (surrogate group) of ecological patterns of other phytoplankton groups, the temporal variation in species composition, and the beta diversity of a metacommunity. We performed six sampling occasions at the end of the summers and winters from 2017 to 2019 at 16 sampling points comprising a strong environmental gradient in the Guaraguaçu River, South Brazil. We tested for correlations of community structures from different periods and for correlations between diatoms species and those from other phytoplankton groups using Mantel tests. Species compositions were compared among periods using a permutational multivariate analysis of variance, and temporal variation in metacommunity beta diversity was evaluated using null models. There was temporal stability in the spatial dissimilarities of communities. Diatoms were poorly correlated with the other phytoplankton groups. The temporal stability in spatial structure, a facet of beta diversity, was in line with the temporal stability in compositional variation – a measurement of metacommunity beta diversity. Our results also showed that such stability was not static, since community compositions varied over time, mainly between seasons. We conclude that even in a highly dynamic tidal river, the temporal stability of spatial organization may indicate that the spatial gradient is so strong that it maintains spatial structuring over time. Such patterns were maintained even with the dynamic species changes over seasons. The fact that different phytoplankton groups do not respond similarly to the spatial gradient reinforces that microalgae should be analyzed separately in ecological studies, and long-term monitoring should consider different algal groups for a complete assessment of ecological patterns.

Key words: biotic homogenization, compositional variation, diatoms, environmental filtering, freshwater algae

RESUMO

A estabilidade temporal na diversidade beta não garante indicadores ou estabilidade composicional na metacomunidade do fitoplâncton

A estabilidade temporal na diversidade beta não garante indicadores ou estabilidade composicional na metacomunidade

do fitoplâncton. Neste estudo, avaliamos a organização da comunidade de fitoplâncton (i.e., microalgas filtradas em rede de plâncton de malha de 20 μm) em um rio subtropical de maré altamente dinâmico ao longo de três anos. Especificamente, avaliamos a estabilidade temporal na organização espacial do fitoplâncton; a eficiência das diatomáceas como indicador de padrões ecológicos de outros grupos fitoplancônicos; a variação temporal na composição das espécies, e a diversidade beta da metacomunidade. Realizamos seis esforços amostrais no final de verões e invernos de 2017 a 2019 em 16 pontos de amostragem compreendendo um forte gradiente ambiental no Rio Guaraguaçu, Sul do Brasil. Testamos correlações de estruturas de comunidades de diferentes períodos e correlações entre espécies de diatomáceas e aquelas de outros grupos de fitoplâncton usando testes de Mantel. As composições das espécies foram comparadas entre os períodos usando uma análise de variância multivariada permutacional, e a variação temporal na diversidade beta da metacomunidade foi avaliada usando modelos nulos. Houve estabilidade temporal nas dissimilaridades espaciais das comunidades. As diatomáceas foram mal correlacionadas com os outros grupos de fitoplâncton. A estabilidade temporal na estrutura espacial, uma faceta da diversidade beta, estava em linha com a estabilidade temporal na variação composicional - uma medida da diversidade beta da metacomunidade. Nossos resultados também mostraram que essa estabilidade não era estática, pois as composições das comunidades variaram ao longo do tempo, principalmente entre as estações. Concluímos que mesmo em um rio de maré altamente dinâmico, a estabilidade temporal da organização espacial pode indicar que o gradiente espacial é tão forte que manteve a estruturação espacial ao longo do tempo. Esses padrões foram mantidos mesmo com as mudanças dinâmicas das espécies ao longo das estações. O fato de diferentes grupos fitoplancônicos não responderem de forma semelhante ao gradiente espacial, reforça que as microalgas devem ser analisadas separadamente em estudos ecológicos; e o monitoramento de longo prazo deve considerar diferentes grupos biológicos para uma avaliação completa dos padrões ecológicos.

Palavras chave: *homogeneização biótica, variação composicional, diatomáceas, filtragem ambiental, algas de água doce*

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INTRODUCTION

Understanding spatial and temporal variation of communities is one of the main goals of community ecology (Vellend, 2010). Particularly, microalgae in aquatic systems vary depending on several natural environmental conditions that are being increasingly changed due to anthropogenic impacts (Boyer *et al.*, 2009). Since phytoplankton respond quickly to environmental gradients (Leung *et al.*, 2003), their structure is usually understood within a metacommunity framework (Howeth & Leibold, 2008). Relatedly, long-term studies aim to understand phytoplankton response to disturbance gradients such as pollution and eutrophication (Schelske & Stoermer, 1971), or transition gradients from freshwater to saltwater (Chakraborty *et al.*, 2011) in tidal estuarine rivers.

Over the last years, there have been studies focusing on phytoplankton variation. There are studies involving spatial variation that often focus on how microalgae vary over a spatial gradient (Sá *et al.*, 2013), those that involve temporal variation that present differences in phytoplankton composition through the seasons (Temponeras, 2000), and there is also recurring variation, referring to the

increasing similarity amongst communities or decrease in beta diversity over time – a phenomenon called biotic homogenization (Olden *et al.*, 2018).

Considering the above, it is possible to assume that ecological assessment and community monitoring are common approaches in ecological studies. However, monitoring species composition can be costly considering both the time used to identify species and the financial resources for field campaigns and specialist expertise (Souza *et al.*, 2019). The use of surrogate groups has recently been revealed to be quite attractive to circumvent such shortcomings (Leal *et al.*, 2010). The taxon surrogacy hypothesis is based on the assumption of a concordance among the species richness or compositional patterns across different taxonomic groups (i.e. cross-taxon congruence, Howard *et al.*, 1998; Lamoreux *et al.*, 2006; Lund & Rahbek, 2002; Prendergast *et al.*, 1993; Olsgard *et al.*, 2003; Su *et al.*, 2004), and is one of the basic tools for quick and economic measurements (Favre & O’Doherty, 1999; Favreau *et al.*, 2006; Lindenmayer *et al.*, 2000). Research such as that done by Lowe (1974) and Weber (1971) indicate that, unlike most other algal groups, diatoms can be identified at the species level, since

taxonomy of diatoms is based on the ornamentation of the inert silica cell wall – although identification was not easy for diatoms and many other algal groups. Also, diatoms are typical and powerful indicators of environmental changes (Dixit et al., 1992). Therefore, diatoms can simplify phytoplankton biomonitoring if diatom patterns represent those of other phytoplankton groups that are more difficult to identify (Stenger-Kovács et al., 2007; Machado et al., 2014).

Understanding the mechanisms shaping local communities can be difficult due to environmental filters acting on a small scale encompassing local environmental conditions, including biotic and abiotic variables (Logue et al., 2011; Bortolini et al., 2019) and the structure of local communities varying over time (Padial et al., 2014). An alternative is a study involving the concept of metacommunity, which means a set of local communities that are linked by dispersal of multiple combined local and regional processes (Leibold et al., 2004). The concept has helped to better understand mobile communities (Tonkin et al., 2018). For instance, analyzing the spatial variation of local communities in a metacommunity perspective may inform better the causes for local organization than using local environmental features to explain species organization (see Leibold et al., 2004).

The Guaraguaçu River is a tidal river with a strong and clear environmental gradient of anthropogenic impact and transition from freshwater to saltwater (Tremarin et al., 2010), thus a model ecosystem to study the spatial and temporal variation of phytoplankton communities (Saifullah et al., 2019). The present work has three main objectives: i) to evaluate the temporal stability in the spatial organization of the phytoplankton communities of the Guaraguaçu River; ii) test the effectiveness of the use of diatoms - sampled in the sub-surface - as an indicator of the spatial pattern of the other phytoplankton groups; and iii) describe the temporal changes in species composition and in the total variation of metacommunity.

MATERIALS AND METHODS

Study site

The Guaraguaçu River (25° 37' 36.4" S, 48° 30'

29.2" W, Fig. 1) is a subtropical river with strong tidal influence and strong ecological variation from upstream to downstream (see also Vitule et al., 2006; Araújo et al., 2021; Galvanese et al., 2022). The Guaraguaçu River is the largest river of the Paraná State coastal basin in South Brazil. Its headwaters are located in the Serra da Prata/Serra do Mar high hills at 766 m above sea level, inside the Saint-Hilaire/Hugo Lange National Park, and the river discharges at Paranaguá Bay in an extensive mangrove area (Bigarella, 1999). The region has a tropical, super-humid climate, without real dry seasons (IAPAR, 1978). The accumulated rain average is 2300 mm per year, being distributed throughout the year. The rainy season is summer (around 800 mm per year) and the dry season is winter (around 280 mm per year); the mean temperature is between 17 and 21 °C (Maack, 1981). Seasonality occurs not only in precipitation but also in temperature (milder in winter, as a subtropical ecosystem). Moreover, anthropogenic nutrient enrichment occurs due to the higher effluent discharges from tourism in summer - Guaraguaçu River receives the most untreated domestic effluents of the population from the main beach cities of Paraná (Elste et al., 2019).

The environmental gradient is strong considering changes from areas near headwater streams and mangroves. Sampling occurred in 16 sampling sites located along all navigable stretch of the river (Galvanese et al., 2022, see Fig. 1 for location and coordinates). The upstream sampling sites (Fig. 1) are located in a near-pristine region popularly known as “caixetal” (i.e. ecosystem characterized by the abundance of the endangered amphibious tree *Tabebuia cassinoides* Lam. (DC.) (Bignoniaceae)) with a high concentration of humic and fulvic acid compounds (Silva, 2008; unpublished data). The water quality of the intermediate zone of the river has strong degradation associated with anthropic disturbances (e.g., Singo et al., 2020), and the brackish water at the downstream mangroves has low degradation. Unfortunately, due to logistic and financial constraints, we were not able to measure abiotic variable to better define the environmental gradient of Guaraguaçu River (see description of sampling below). Even so, evidence for the strong gradient abovementioned was already described by the

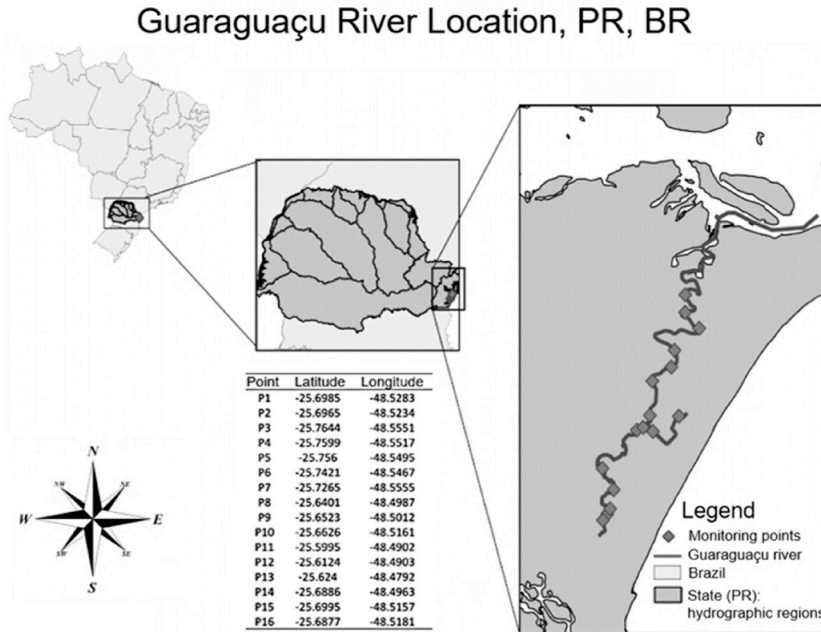


Figure 1. Guaraguaçu River (Paraná, Brazil) and location, with geographical coordinates in decimal degrees, of sampling sites. *Rio Guaraguaçu (Paraná, Brasil) e localização, com coordenadas geográficas em graus decimais, dos pontos de amostragem.*

high spatial turnover of aquatic macrophyte community (Galvanese *et al.*, 2022).

Samplings and data analyses

We sampled phytoplankton in the aforementioned 16 sampling sites by filtering c. 200 L of water in a phytoplankton net of 20 μm , using a 10 L bucket. The filtered water was preserved in 100 mL plastic pots with 10 % Lugol solution. Samplings occurred in six periods: March/April (end of summer in Southern hemisphere) of 2017, 2018 and 2019; and September/October (end of winter in Southern hemisphere) of 2017, 2018 and 2019. As part of a long-term monitoring project, samplings are planned to occur periodically, but in 2020 sampling campaigns were not done due to the Sars-COV-2 pandemic. All data is available for use by the academic community; see details of the long-term monitoring project and metadata in <<https://lasbufprbio.wixsite.com>>. As said, aforementioned, environmental data was not sampled in this long-term monitoring given logistic and financial restrictions, particularly the lack

of equipment and support in Brazilian research centers. Even so, data on aquatic macrophytes are available and demonstrate great turnover along the 16 sampling sites (Galvanese *et al.*, 2022). Indeed, the locations sampling sites were chosen following an adaptation of the RAPELD protocol for long-term monitoring (Magnusson *et al.*, 2005), and were selected to represent meaningful ecological gradients (Galvanese *et al.*, 2022).

Also, it is important to note that small taxa can go through the 20 μm mesh-size net, so our samplings represent only the largest organisms of the phytoplankton community and eventual small-sized organisms trapped in the net (for simplicity, we refer to our such ‘micro-phytoplankton’ community only as ‘phytoplankton community’ along the text). Due to our goals of comparison, and to the fact that sampling was standardized across sites and periods, patterns and conclusions are valid for such taxa. Indeed, if samplings were not standardized across sites, community structuring comparisons would be biased. But we do assume the limitations of our sampling effort for representing all phytoplankton community. Relatedly,

in March/April of 2018, we had made a one-liter sampling of unfiltered water in each sampling site using a dark plastic bottle. Most taxa encountered in this sampling were also recorded in the samplings using nets, but with extremely low abundances given the difference of volume investigated (see data in Supplementary Material). Therefore, we believe the 200 L samplings composed mainly by to organisms larger than 20 μm is a suitable representation of the Guaraçu River phytoplankton community, at least for comparisons purposes. We also highlight that given the hydrodynamics of this tidal river, and also to the intense macrophyte colonization in the margins, our samplings usually sampled species typical from periphyton. (see results below). We kept such taxa in our represented community given this is a natural feature of the river and given the standardization of samplings described above.

The quantitative analysis followed the method of Utermöhl (1958), but using the filtered samplings as mentioned. Cells were enumerated in settling chambers, using an inverted light microscope Olympus IX70 at 600 \times magnification, until the rarefaction curve of species (Bicudo, 1990). The taxa were identified at the lowest possible taxonomic level. Phytoplankton densities (cel/ml) were estimated according to Ross (1979). In total, we generated six tables (one for each sampling period) with species abundance (or the lowest identified taxon) per sampling site. The taxa were organized in tables according to their taxonomic class (Bacillariophyceae, Cyanobacteria, Chlorophyceae, Euglenophyceae, and Zygnemaphyceae).

We standardized data using Hellinger transformation prior to analyses (Legendre & Gallagher, 2001). We first applied the Bray-Curtis dissimilarity index to generate dissimilarity matrices for each period considering the phytoplankton community composition recorded according to the sampling method described above. Dissimilarities represent compositional spatial organization over the sampling sites or over time (*sensu* Tuomisto et al., 2006). We evaluated the temporal stability of compositional spatial organization by testing if pairwise Mantel correlations among dissimilarity matrices were different than expected by a null model that randomizes sampling sites of one dis-

similarity matrix. We applied several Mantel tests considering the possible combination of pairs of matrices from the different periods. The Mantel tests correlate the pairwise dissimilarities of sites of one period with the pairwise dissimilarities of the correspondent sites of a different period. We made such analyses also considering presence-absence data only, thus using correspondent Sørensen dissimilarity. However, the Mantel test does not evaluate how correspondent sites differ over time. For that, we used the temporal beta diversity index (TBI; Legendre, 2019) to describe and investigate temporal variation in community organization considering how the sampling sites vary over time. In summary, in this index, a dissimilarity index is calculated for the same sites between two sampling occasions, and then, through permutations, the sites which had an unusual (and significant compared to a null model) level of dissimilarity in relation to the others are identified. The analysis quantified the role of losses (B) and gains (C) of species to the dissimilarity index; and such components can be differentiated through a permuted paired *t*-test. TBI analysis informed us if there were more losses or gains in abundance-per-species for each sampling site between the distinct times or dates, thus clarifying the reasons (loss of gain of species) for temporal changes in community. We investigated TBI considering the possible combinations of pairs of matrices from the different periods.

For each period, we also tested correlations (as aforementioned) of the Bacillariophyceae dissimilarity matrix with the dissimilarity matrices of the other phytoplankton classes (both for abundances and presences-absences). If correlations are always significant, then spatial organization of diatoms may represent the spatial organization of other phytoplankton groups, and diatoms can be considered a surrogate group for monitoring (see Ribas et al., 2015). For that, we correlated the diatom dissimilarity matrix to i) cyanobacteria dissimilarity matrix and ii) dissimilarity matrix of the other groups (see above). We did so given the low number of individuals in some groups apart from cyanobacteria, preventing us from making comparisons considering community spatial organization in all 16 sampling sites in all sampling periods.

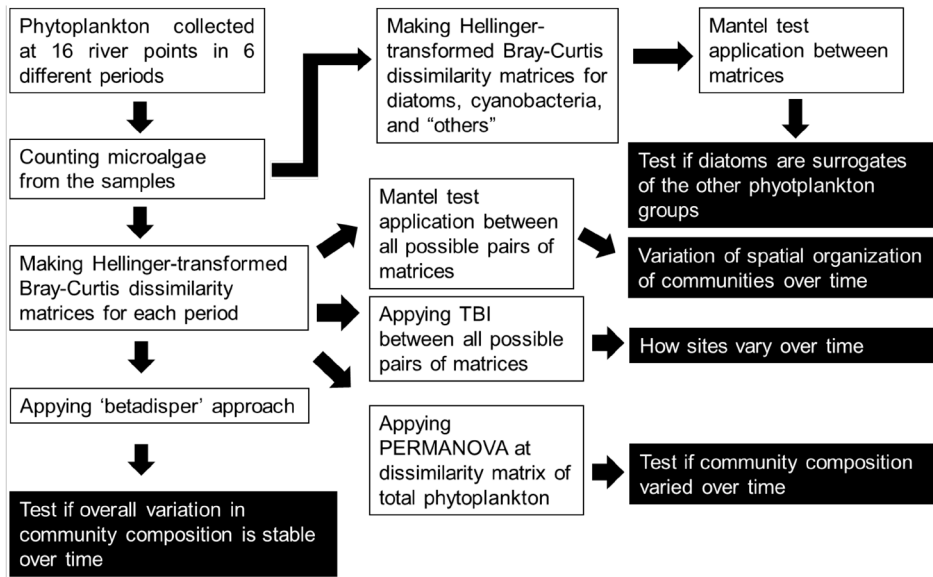


Figure 2. Summary diagram showing the approach and rationale of analyses applied in this study (example for abundances, the Sørensen index was used for presence-absences). *Diagrama sumariizado mostrando a abordagem e o raciocínio das análises aplicadas nesse estudo (exemplo para abundância, o índice de Sørensen foi usado para presença-ausência).*

We then tested if community composition (described by abundances or presences-absences) varied over time by applying a Permutational multivariate variance analysis (PERMANOVA, Anderson, 2001) at the dissimilarity matrix of total phytoplankton, using the sampling period as the predictor factor. Finally, we tested if the overall variation in community composition was stable over time. For that, we estimated phytoplankton compositional variation by applying the ‘betadisper’ approach as described in Anderson *et al.* (2006), and tested if compositional variation differed among periods also using permutations. Differences in species composition and metacommunity compositional variation among periods were visualized in Principal Coordinate Analysis (PCoA, Gower, 1966).

Significant values for all analyses were considered if type I error was lower than 5 %. However, given that we made five comparisons with the same dataset in mantel and TBI pairwise correlations for temporal stability (one period was compared with the other five periods), we applied Bonferroni correction and thus considered significant correlations when type I error was lower

than 1 %. Given we made two comparisons with the same dataset for diatom surrogate analysis (the same diatom matrix was correlated to ‘cyanobacteria’ and ‘other groups pooled’ in two mantel correlations), we applied Bonferroni correction and thus considered significant correlations when type I error was lower than 2.5 %. We performed analyses using the software R, version 3.4.3 (R Core Team 2017) with the packages “vegan” (Oksanen *et al.*, 2019), “betapart” (Baselga *et al.*, 2018), “labdsv” (Roberts, 2015), “adespatial” (Dray *et al.*, 2021) and “ape” (Paradis & Schliep, 2019). Our analytical approach (exemplified for abundances) is summarized in Figure 2.

RESULTS

After summer of 2017, spatial organizations of communities were similar in almost all comparisons according to Mantel tests (see full results in Table 1, presence-absence comparisons were lower than abundance comparisons and non-significant in two comparisons after summer of 2017). Changes in phytoplankton composition along sites considering loss and gains of species

Table 1. Pearson's correlation coefficient (r) and probability of type I error (P) derived from Mantel tests between compositional dissimilarities matrices (Bray-Curtis for abundances and Sørensen for presences-absences) among periods. Significant correlations after Bonferroni correction (see methods) are highlighted in bold. *Coefficiente de correlação de Pearson (r) e probabilidade de erro do tipo I (P) dos testes de Mantel entre as matrizes de dissimilaridade composicional (Bray-Curtis para abundâncias e Sørensen para presenças-absências) entre períodos. Correlações significativas após a correção de Bonferroni (veja métodos) estão destacadas em negrito.*

Pairwise comparison of periods	Abundances		Presence-absence	
	r	P	r	P
Summer 2017 – Winter 2017	0.099	0.205	0.048	0.334
Summer 2017 – Summer 2018	0.092	0.218	0.231	0.043
Summer 2017 – Winter 2018	0.207	0.044	0.170	0.075
Summer 2017 – Summer 2019	0.154	0.046	0.279	0.014
Summer 2017 – Winter 2019	0.171	0.063	0.129	0.179
Winter 2017– Summer 2018	0.722	0.001	0.546	0.001
Winter 2017– Winter 2018	0.500	0.001	0.265	0.008
Winter 2017 – Summer 2019	0.409	0.002	0.216	0.009
Winter 2017 – Winter 2019	0.397	0.003	0.077	0.212
Summer 2018 – Winter 2018	0.598	0.001	0.298	0.006
Summer 2018 – Summer 2019	0.464	0.001	0.254	0.007
Summer 2018 – Winter 2019	0.344	0.003	0.053	0.301
Winter 2018 – Summer 2019	0.654	0.001	0.487	0.001
Winter 2018 – Winter 2019	0.427	0.001	0.326	0.004
Summer 2019 – Winter 2019	0.326	0.001	0.341	0.003

for all possible comparisons are available as Supplementary Material (Available at <http://www.limnetica.net/en/limnetica>). Significant loss-gain change was observed in only one site and in only one comparison; site 7 had higher loss than gains of species between winter of 2017 and summer of 2018 (see table S6 in Supplementary Material).

The correlation of diatom dissimilarity matrices with the matrices from other phytoplankton groups are shown in Table 2. Diatoms spatial organization is related to the spatial organization of other groups in only three out of the 12 possible scenarios for abundances, and in only two out of 12 possible scenarios for presence-absences (Table 2).

Species composition significantly differed among periods (PERMANOVA: $F = 5.99$, $R^2 = 5.9\%$, $P < 0.001$ for abundances; $F = 5.87$, $R^2 = 5.8\%$, $P < 0.001$ for presences-absences). Visually in the PCoA plot, it was possible to see that variation in community composition is sea-

sonal, given the higher overlap of periods in the same season (i.e., see that filled circles representing summers overlap little with open circles representing winters, mainly in the second PCoA axis, Fig. 3). Although there were differences in community composition, the compositional variation (shown by the size of the cloud of sampling distribution points of the same color and shape in Fig. 3) did not vary among periods for abundances ($F = 2.144$; $P = 0.065$). For presence-absences, there was evidence for compositional variation ($F = 3.049$; $P = 0.017$), with winter of 2017 as the most variable, and the summer of 2019 as the least variable (see below). Comparing the values of average distance to the centroid, it can be observed that, for a same year, the summer is always less variable than the winter (Averages distances for 2017: summer = 0.448 and winter = 0.549; Averages distances for 2018: summer = 0.508 and winter = 0.536; Averages distances for 2019: summer = 0.417 and winter = 0.483).

Table 2. Pearson's correlation coefficient (r) and probability of type I error (P) from Mantel tests between compositional dissimilarities matrices (Bray-Curtis for abundances and Sørensen for presences-absences) between diatoms and Cyanobacteria; and between diatoms and the other phytoplankton groups pooled. Significant correlations after Bonferroni correction (see methods) are highlighted in bold. *Coefficiente de correlação de Pearson (r) e probabilidade de erro do tipo I (P) dos testes de Mantel entre as matrizes de dissimilaridade composicional (Bray-Curtis para abundâncias e Sørensen para presenças-ausências) entre diatomáceas e cianobactérias, e entre diatomáceas e os outros grupos fitoplantônicos juntos. Correlações significativas após a correção de Bonferroni (veja métodos) estão destacadas em negrito.*

Period	Correlation between diatoms and:	Abundances		Presence-absence	
		r	P	r	P
Summer 2017	Cyanobacteria	-0.078	0.613	-0.168	0.914
Summer 2017	Other groups pooled	-0.193	0.915	-0.209	0.927
Winter 2017	Cyanobacteria	0.461	0.020	0.294	0.054
Winter 2017	Other groups pooled	-0.057	0.660	0.015	0.412
Summer 2018	Cyanobacteria	0.231	0.054	-0.034	0.592
Summer 2018	Other groups pooled	0.013	0.447	0.058	0.326
Winter 2018	Cyanobacteria	0.026	0.404	0.197	0.404
Winter 2018	Other groups pooled	0.016	0.384	0.041	0.379
Summer 2019	Cyanobacteria	0.061	0.240	0.212	0.094
Summer 2019	Other groups pooled	0.277	0.033	0.161	0.156
Winter 2019	Cyanobacteria	0.332	0.003	0.238	0.027
Winter 2019	Other groups pooled	0.537	0.001	0.513	0.001

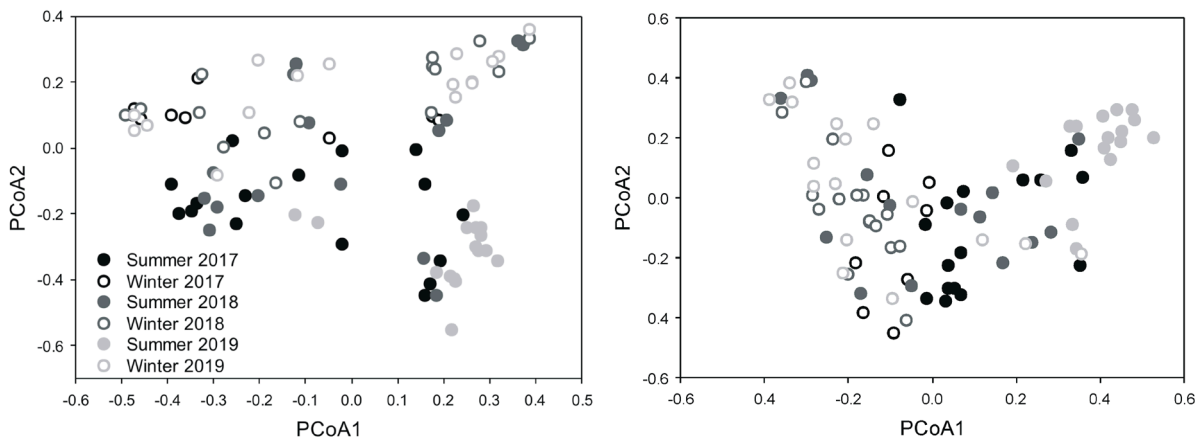


Figure 3. Community organization (abundances – left; presence-absences – right) of phytoplankton in the six periods analyzed according to a principal coordinate ordination analysis (PCoA). Dots indicate position of sampling sites; filled dots indicate samplings of summer and open dots indicate samplings of winter; from 2017 (black dots), 2018 (dark-gray dots) and 2019 (light-gray dots). *Organização da comunidade (abundâncias – esquerda; presenças-ausências – direita) de fitoplâncton nos seis períodos analisados de acordo com uma análise de ordenação de coordenadas principais (PCoA). Pontos indicam a posição das unidades amostrais: pontos preenchidos indicam amostragens de verão e pontos não preenchidos amostragens de inverno; de 2017 (pontos pretos), 2018 (pontos cinza-escuro) e 2019 (pontos cinza-claro).*

DISCUSSION

Here, we scrutinized community organization and temporal variation in microalgae in a highly dynamic ecosystem – a subtropical tidal river. Firstly, and in line with many previous studies (e.g. Heino, 2010), we discard the use of surrogate groups in aquatic systems to simplify biological assessments considering the representation of community structuring patterns of multiple biological groups. Therefore, the first recommendation is for a complete assessment of phytoplankton community structuring along ecological gradients; one should analyze all recorded species from different taxonomic classes. Given that we did not have environmental data to infer which group better respond to major environmental gradients, future studies with the goal of investigating microalgae responses to abiotic drivers are still necessary. Surely, rapid assessments of biological groups should be searched, given the increasing budget cuts in basic science, particularly in Brazil (Andrade, 2019). Apart from the disregard by governments of basic biological assessments that inform conservation efforts (Azevedo-Santos et al., 2019), actions can be quickly and effectively implemented if rapid and straightforward assessments are done. If a surrogate group is found – considering the representation of community structuring patterns – then efforts can be made to focus on this target group to effectively inform and improve conservation of other groups (Souza et al., 2019). Also, if community composition is relatively stable over time, then monitoring can be done with lower frequency.

Still, we found that community spatial organization was quite stable over three years (and six sampling efforts). Our results indicate that only the first sampling effort resulted in a different spatial organization; comparing species loss and gains changes in each site, only one out of the 16 sites and in one out of 14 comparisons significantly changed, which reinforces that the spatial organizations of communities are stable over time. Surely, continuous monitoring may better reveal long-term changes over a longer time span. At first, the relative stability found here may be conflicting with most literature on phytoplankton responses to environmental varia-

tion. Indeed, phytoplankton is one of the aquatic biological groups that mostly respond to environmental variation in aquatic ecosystems (Cardoso et al., 2017). Among the main ecological factors driving species composition are those related to temperature, nutrient availability and constraining variables such as salinity (Costa et al., 2015; Vallina et al., 2017). Therefore, high species variation is expected in a subtropical tidal river with strong spatial heterogeneity in nutrient and salinity concentrations, as well as daily changes due to tides, and seasonal changes in both anthropogenic nutrient enrichment and temperature, such as the Guaraguaçu River (Vitule et al., 2006). It indeed seems that the variation in community composition is seasonal, given the ordination we made. Even so, we reinforce that spatial organization (i.e., the dissimilarities of sampling sites) – a facet of beta diversity – of phytoplankton is relatively stable. The most likely explanation is that the spatial-environmental gradient in the Guaraguaçu River is so strong that dissimilarities among sampling sites are mostly maintained over time. Such interpretation is highlighted by the stability of each site over time according to TBI analyses (see rationale in Legendre, 2019; and results in Supplementary Material). This does not mean that environmental filtering is not occurring, actually it is the opposite: the known spatial variation described before in this river (see for instance Vitule et al., 2006) selected species for each sector of the river (e.g. Araújo et al., 2021; Galvanese et al., 2022), and such differences are relatively stable over time even though species composition varies over seasons. Here, we did not compare sectors of the river for microalgae (see such comparison for macrophytes in Galvanese et al., 2022), but it was already shown the responses of taxa to tides in Guaraguaçu River (Tremarin et al., 2008a, 2008b). Thus, we reinforce the hypothesis that seasonal or other temporal variation in environmental features can change species composition, but not disrupt the strong spatial structuring role of the set of environmental factors that likely define community organization in the Guaraguaçu River. Relatedly, it was already shown that the role of spatial gradients in communities (if strong enough) may be retained even in highly dynamic ecosystems (e.g., floodplains with seasonality in

precipitation, Padial *et al.*, 2009; Dittrich *et al.*, 2016). It was unfortunate that quantitative environmental variables were not available for a direct relationship between community changes and the environmental shifts along the river, which could demonstrate the eco-regional differences caused by the gradient described in Methods. Indeed, many papers using quantitative data on abiotic conditions have demonstrated that microalgae communities respond effectively indicate major shifts in key environmental drivers both in temperate (e.g. Abonyi *et al.*, 2014) and tropical rivers (e.g. Santana *et al.*, 2016).

Even so, such ‘temporal equilibrium’ in community organization as explained above may not be static, and the species composition sampled in one period may vary from those sampled in another season. Indeed, we did observe there were temporal changes in community composition, and those changes are apparently seasonal, i.e., species compositions of summers were similar as well as species compositions of winters, and differences were mainly among different seasons (see Fig. 3). Relatedly, seasonality has been commonly reported for microalgae in subtropical ecosystems (Bortolini & Bueno, 2013). Surely, a definitive conclusion on seasonality effects in community composition may be reached after long-term samplings, but we have at least shown that species composition is changing over time, even with some stability in community organization.

Finally, we also evaluated another facet of phytoplankton beta diversity – the overall compositional variation. We did so to analyze if there was a period in which total compositional variation – the measurement of metacommunity beta diversity (see Anderson *et al.*, 2001) – is lower or higher. For instance, in a scenario of increasing anthropogenic pressures, it is expected a decrease in the overall compositional variation, as a consequence of the biotic homogenization phenomenon (Olden *et al.*, 2018) so pervasive over aquatic environments (Padial *et al.*, 2020). Here, even with the high anthropogenic pressures in some stretches of the river, there is no evidence that the biotic homogenization phenomenon is occurring during the study periods at the scale of river metacommunity (see also Daga *et al.*, 2015). The only pattern we observed were also related to season-

ality: presences-absences compositions were less variable in summers than in winters of a same year. Given that our standardized monitoring is relatively recent, it is uncertain if biotic homogenization does not occur in this dynamic tidal river (as we intended to analyze) or if it occurred in the past just after the main human pressures in the river. For some years, the drainage of the river for sand extraction, installations for water supply, the destination of most organic loads from domestic effluents, biological invasion of fish and macrophyte species have been causing changes in the ecosystem (Vitule *et al.*, 2006; Elste *et al.*, 2019). Indeed, it has been reported in the Guaraguaçu River an overwhelming impact of an invasive ecological-engineer aquatic tanner grass – the *Urochloa arrecta* (Hack. ex T. Durand & Schinz) Morrone & Zuloaga in decreasing biological diversity (Araújo *et al.*, 2021; Sato *et al.*, 2021; Galvanese *et al.*, 2022). Therefore, the temporal stability in phytoplankton metacommunity beta diversity only reinforces that spatial ecological filtering of species due to several factors prevail over temporal changes in the Guaraguaçu River. Unfortunately, due to resources and logistic limitations, we were still unable to make a complete spatial description of the river, which would be essential to understand the role of the different anthropogenic pressures in community composition. We thus encourage future studies with this particular purpose, hoping that basic research can be supported by Brazilian agencies. Even so, we hypothesize that particularly species sorting may prevail over the other likely metacommunity dynamic mechanisms (see a detailed description in Leibold *et al.*, 2004), given the strong gradient of the river and the expected responses of microalgae to abiotic features.

In summary, we demonstrated the complex phytoplankton variability patterns in a subtropical tidal river. Taken together, our results reinforce that surrogate groups are ineffective (at least in aquatic ecosystems and to represent cross-taxa community structuring), and emphasize the role of spatial ecological filtering in determining species composition. We demonstrated that even with low temporal changes in local community organization or metacommunity compositional variation (two facets of beta diversity), species

identity changes, which show the dynamic equilibrium of dynamic aquatic ecosystems. Even with a temporal stability in community organization, we suggest continuous monitoring of phytoplankton for the understanding of this community in a crucial area for conservation such as the Guaraguaçu River, and also for a better understanding of spatial and temporal dynamics in aquatic communities.

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