Determinants of beta diversity: the relative importance of environmental and spatial processes in structuring phytoplankton communities in an Amazonian floodplain

Determinantes da diversidade beta: a importância relativa de processos ambientais e espaciais na estrutura de comunidades fitoplanctônicas de uma planície de inundação amazônica

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Abstract: Aim: Beta diversity is defined as the change in species composition along environmental gradients, and in the present study, we investigated the influence of local (i.e., environmental) and regional (i.e., dispersal) factors in community structure. The aims of this study were to evaluate the beta diversity of phytoplankton communities in the Curuaí floodplain and to determine the relative importance of environmental and spatial processes in shaping phytoplankton community structure; **Method:** The phytoplankton communities were sampled in 16 lakes of the Curuaí floodplain (Amazon Basin) during high-water periods in 2002 and 2003. We used partial redundancy analysis (pRDA) to evaluate the pure effect of environmental (six variables) and spatial (spatial filter) variability on phytoplankton community composition; **Results:** There were 156 taxa recorded in the two study years, including 122 algae species in 2002 and 66 algae species in 2003. The beta diversity that we measured (β_{SIM} index) was 0.889 in 2002 and 0.789 in 2003. The partitioning variation demonstrated that the majority of variation in phytoplankton community structure was not significantly explained by pure environmental and pure spatial components. However, environmental variables presented a larger coefficient of determination than the spatial variable; **Conclusion:** Other factors than those we measured in this study, such as local variables (i.e., biotic interactions, hydrology, etc.) and stochastic events, affected the absence of significant results in our data. Therefore, we suggest that additional variables, such as biological interactions and other local factors, should be considered in this type of analysis to increase its explanatory power for understanding the variation of diversity in these communities.

Keywords: metacommunity, partitioning variation, rainy season, Amazon.

Resumo: Objetivo: A diversidade beta é definida como as mudanças na composição de espécies ao longo de um gradiente ambiental, e atualmente, ecólogos têm investigado a influência de fatores locais (i.e. ambiente) e regionais (i.e. dispersão) na estrutura de comunidades. Os objetivos desse trabalho foram avaliar a diversidade beta da comunidade fitoplanctônica da planície de inundação do Curuaí e determinar a importância relativa dos processos ambientais e espaciais em sua estrutura; **Método:** A comunidade fitoplanctônica foi amostrada em 16 lagos da planície de inundação do Curuaí (Bacia Amazônica) durante o período de águas altas em 2002 e 2003. Usou-se a análise de redundância parcial (pRDA) para avaliar o efeito do ambiente (seis variáveis) e espacial (filtros espaciais) na variabilidade da composição da comunidade fitoplanctônica; **Resultado:** Foram registradas 156 espécies em dois anos de estudos, 122 espécies em 2002 e 66 espécies em 2003. A beta diversidade (índice β_{SIM}) foi 0.889 em 2002 e 0.789 em 2003. A análise de partição da variância revelou que a maior parte da variação da comunidade fitoplanctônica não foi significativamente explicada pelos únicos efeitos ambientais e espaciais. No entanto, as variáveis ambientais no presente estudo apresentaram maior coeficiente de determinação do que as variáveis espaciais; **Conclusão:** Outros fatores afetaram a ausência de resultados significativos nos presentes dados, como variáveis locais não mensuradas (i.e. interações biológicas, hidrologia e outros) e eventos estocásticos. Dessa forma, sugerimos que variáveis como interações biológicas e outras variáveis locais sejam consideradas nesse tipo de análise para aumentar o poder de explicação e elucidar a variação da diversidade biológica.

Palavras-chaves: metacomunidade, partição da variância, estação chuvosa, Amazônia.

1. Introduction

Species richness is the simpler measurement for quantification and expression of the presence of taxa in a region. However, there are three types of diversity to be considered in biodiversity analyses: alpha, beta and gamma (Magurran, 2004). Beta diversity is an important concept for understanding the functioning of ecosystems and for the conservation of biodiversity. Moreover, ecologists are currently interested not only in analyzing beta diversity, but in interpreting the causes of beta diversity (Legendre et al., 2005). For decades, patterns in the variation of community structure (i.e., beta diversity) were assumed to be mainly controlled by environmental factors and niche differences among species (Tokeshi, 1999). The current neutral theory of biodiversity (Hubbell, 2001) has presented a different point of view, as it assumes that interacting species are equivalent and that population dynamics are driven by random variation in births, deaths, and stochastic, but spatially restricted dispersal.

The Brazilian floodplain lakes provide a good system to test the influence of local (i.e., environmental) and regional factors (i.e., dispersal) in determining metacommunity structure. A metacommunity is a set of local communities within a landscape that are linked by the dispersal of multiple potentially interacting species (Holt, 1991; Wilson, 1992; Cottenie and De Meester,

2004). Currently, four main theoretical paradigms of metacommunity ecology have been proposed (species-sorting, mass-effects, patch-dynamics and neutral), and their difference is based in the importance of local and/or regional factors that affect community structure (Leibold et al., 2004; Thompson and Townsend, 2006).

There have been a number of phycological studies on the Amazon basin (e.g., Ibañez, 1997, 1998; Huszar, 2000; Huszar and Reynolds, 1997; Huszar, 1996a, b; Melo and Huszar, 2000). However, most of these studies only explored phytoplankton composition in a descriptive way (i.e., evaluated the species richness, abundance or dominance of phytoplankton species).

The aims of this study were to evaluate the beta diversity of the phytoplankton community in the Curuaí floodplain and to determine the relative importance of environmental and spatial processes in shaping phytoplankton community structure. Thus, considering the importance of the flood pulse on the homogenization of phytoplankton and limnological attributes (Thomaz et al., 2007), our expectation was that no difference in beta diversity would be found between the years 2002 and 2003 as precipitation levels were similar in both years (see Figure 1 in Materials and Methods), especially when taking into consideration the cumulative effects of this variable. Furthermore, because the

samples were taken during the rainy season in both years, we expected that this environmental component would be observed to be shaping the structure of the phytoplankton community; in other words, in the rainy season, all of the lakes in the floodplains in this region are connected, and it is expected that there is a high dispersal capacity of small aquatic organisms (Finlay, 2002; Figuerola and Green, 2002; Padisák, 2004). Thus, we believe that L. G. M. Baas-Becking´s premise can be used to explain the distribution of phytoplankton in the rainy season: "everything is everywhere, but the environment selects" (Green et al., 2008).

2. Materials and Methods

2.1. Study area

The Lago Grande de Curuaí floodplain (01° 50' S and 02° 15' S and 55° 00' W and 56° 05' W, Pará State) is a complex system with more than 16 interconnected lakes that are linked to the Amazon River by nine channels on the south-eastern side (see map in Maurice-Bourgoin et al., 2005). It drains a total area of 3,610 km², which is covered in the south dense forest.

The Curuaí floodplain is very extensive and shallow, and it is vegetated during the low water season by savannah, shrubs and alluvial forest (RADAMBRASIL, 1976). The inundated area varies from 700 km² during the dry season to 2,300 km² at the time of the flood peak (Martinez et al.,

2003), representing 0.8% of the total flooded area of the Central Amazon basin. The low water phase usually occurs in November, and the water levels rise from December to May–June (Maurice-Bourgoin et al., 2005).

The Lago Grande de Curuaí lake system is approximately 100-m wide and 3-km long during the low water period; its depth varies between 6 m, during the low water period, to 12 m, during the high water period. As the river level rises, several other channels progressively connect different parts of the floodplain to the main river (Bonnet et al., 2008).

The main lakes in the region are classified as "white-water" lakes, including Lago do Poção, Lago do Salé, Lago de Irateua, Lago da Porta, Lago Santa Ana and Lago Grande de Curuaí, because they are mainly fed by waters from Amazon, while Lago Curumucuri, Lago Açaí and, to a lesser extent, Lago Miuá, are considered to be "black water" lakes, in which the main water input comes from the local runoff from an extensive forest drainage area (Sioli, 1984).

Precipitation at Curuaí is influenced by an orographic effect in the south and differs from rainfall received by lakes in the northern part of the system. Precipitation over the floodplain was higher in 2003 than in 2002 (Figure 1), with maximum levels over 500 mm. In the sampling months for both years, rainfall was approximately 200 mm. The highest rainfall in the Amazon Basin is generally
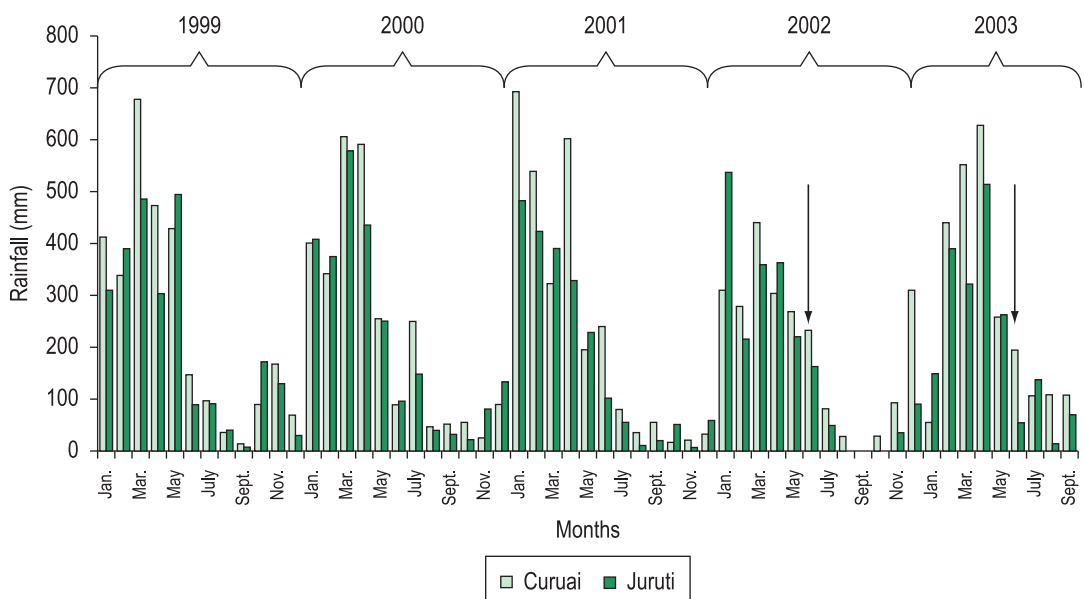

Figure 1. Mean monthly rainfall measured in two floodplain stations. The number above the key indicates years. Arrows indicate the sampling periods.

from January to March. However, in 2003 the highest precipitation was recorded in April.

2.2. Biological, limnological and spatial data

The data in this study were collected in two years (2002 and 2003). In 2002 11 lakes in the Curuaí floodplain were sampled. In 2003, 14 lakes were sampled (Table 1). Phytoplankton richness was estimated from subsurface samples collected during high water periods (23-28 June, 2002 and 20-25 June, 2003) by a selective method using a plankton net of 25-µm mesh size. In this study, we collected only qualitative data, though 50 aliquots were analyzed for each sample.

Samples were preserved with Transeau solution (Bicudo and Menezes, 2005). Taxonomic classes were identified according to the classification system of Van Den Hoeck et al. (1993).

Beta diversity index applied to quantify species composition turnover across all lakes was Simpson Index (β_{SIM}; Lennon et al., 2001). Beta diversity can be caused by nestedness and species turnover, thus, the β_{SIM} is adequate to separate turnover from nestedness processes (Baselga, 2010). The β_{SIM} varies from zero (totally similar lakes) to 1 (dissimilar lakes). We performed the β_{SIM} index using R software (function beta.SIM; developed by Baselga, 2010).

Limnological characterization was conducted according to the HiBAM project (*Hidrologia e Geoquímica da Amazônia*) sampling protocol that followed APHA (1992) methodology. The main aim of this project was to understand the hydrological, sediment and geochemistry processes of the Amazon basin at the continental scale based on a hydrodynamic and geochemistry model of large fluvial systems. The limnological variables analyzed were water temperature (ºC), electrical conductivity (µS/cm), pH, water transparency (m), seston (mg/L) and alkalinity (mg/L).

Spatial variables based on the matrices of Euclidean distance were created using eigenfunction analyses (Borcard and Legendre, 2002; Borcard et al., 2004; Diniz-Filho and Bini, 2005; Dray et al., 2006; Griffith and Peres-Neto, 2006). In these analyses, geographical coordinates were first used to create distance. Then, by following the procedures described in detail by Griffith and Peres-Neto (2006), it was possible to generate distance-based or topology-based eigenvector maps. The eigenvectors (spatial variables, also known as filters) allow the representation of spatial relationships among the sampling units at different spatial scales. In our study, they can be considered to be different and independent propositions of how lakes are geographically related. Positive and negative spatial autocorrelations are represented, respectively, by eigenvectors associated with positive and negative eigenvalues. Small eigenvalues (in absolute terms)

Table 1. Geographic coordinates of the Curuaí floodplain lakes which were studied here.

Stations	Lakes	Latitude S	Longitude W	Year
01	Lago Grande de Curuaí	02°14,063'	55°09,052'	2002 and 2003
02	Lago da Vermelha	02°07,027'	55°28,035'	2002 and 2003
03	Lago Santa Ana	02°05,022'	55°30,036'	2002 and 2003
04	Lago da Porta	02°08,890'	55°46,097'	2002 and 2003
05	Lago São Nicolau	02°10,488'	55°46,008'	2002 and 2003
06	Lago do Salé	02°11,074'	55°48,020'	2002 and 2003
07	Lago de Irateua	02°05,486'	55°45,499'	2002 and 2003
08	Lago do Poção	02°07,017'	55°38,030'	2002 and 2003
09	Igarapé Curumucuri	02°07,442'	55°56,190'	2002 and 2003
10	Lago Miuá	02°02,350'	55°38,388'	2002
11	Lago Açaí	01°56,842'	55°35,196'	2002
12	Lago Cativo	02°10,518'	55°32,532'	2003
13	Lago da Preguiça	02°09,006'	55°32,040'	2003
14	Lago Mari Mari	02°07,002'	55°32,052'	2003
15	Lago Piedade	02°09,006'	55°34,050'	2003
16	Lago Pirapitinga	02°04,010'	55°40,027'	2003

indicate the absence of spatial autocorrelation, and, therefore, they are not suitable for defining spatial structures (Griffith and Peres-Neto, 2006; Dray et al., 2006). Here, all eigenvectors with Moran's I coefficients higher than 0.1 were included in the matrices of spatial predictors. For instance, the results of the eigenvector maps derived from the spatial coordinates of the lakes studied indicate the flexibility of this method in creating spatial variables, where the eigenvector maps indicated different levels of complexity in terms of spatial relationships among the lakes. For both years, two spatial filters were selected. Eigenfunction spatial analyses were performed using the freely available Spatial Analysis in Macroecology v. 4.0, SAM package (Rangel et al., 2010).

2.3. Variation partitioning

To estimate the relative importance of environmental and spatial components in shaping phytoplankton community structure, we used a partial redundancy analysis (pRDA) (Legendre and Legendre, 1998). The percentages of the total variation in the phytoplankton matrix that can be attributed to the different components of variation (pure environmental [described by letter a], pure spatial [c], shared by environment and space [b], and unexplained [d]) were based on the adjusted (unbiased) fractions. The significance of each fraction was tested by permutation tests using 999 randomizations (Peres-Neto et al., 2006). All analyses were conducted using the complete dataset. All environmental variables (except pH) were log-transformed before analysis. We performed the above analyses using R software (function Varpart of Vegan Package).

3. Results

The limnological characteristics in the lakes of the Curuaí floodplain were very similar in both years (2002 and 2003), with neutral pH, high concentration of suspended material and low transparency (Table 2).

There were 156 taxa recorded in the two years of the study. These included 122 algae species in 2002 belonging to the following classes: 46 Chlorophyceae, 28 Cyanophyceae and 17 Bacillariophyceae. In 2003, there were 66 algae species, including 21 Bacillariophyceae, 12 Cyanophyceae and 11 Zygnemaphyceae.

Of the lakes studied in 2002 (Figure 2a), Lago Grande Curuaí and Lago Açaí, which are the only two lakes with black water (fed by local rains and drainage from elevated terrain) in the Curuaí floodplain, had the highest richness with 38 and 31 species, respectively. Lake Vermelho had the lowest richness with only two species. In 2003 (Figure 2b), Lago Grande de Curuaí had the highest richness with 41 species, whereas the richness of Lago da Preguiça was extremely species-poor with only two species.

Lago Grande Curuaí presented the highest species richness in both years. Additionally, there was a high frequency of occurrence of some Cyanophyceae in this lake, including *Dolichospermum spiroides* (Klebahn) Wacklin et al., *Dolichospermum circinalis* (Rabenh.ex Bornet & Flah.) Wacklin *et al.*, *Microcystis aeruginosa* (Kütz.) Kütz, *Microcystis wesenbergii* (Kom.) Kom. in Kondr., *Microcysitis panniformis* Kom. et al., *Radiocystis fernandoi* Kom. et Kom.-Legn. and *Planktothrix agardhii* (Gom.) Kom. et Anagn.

In both 2002 and 2003, none of the species we observed were present in all lakes; however, the most frequent taxa in 2002 were *Aulacoseira italica* (Ehr.) Simonsen¸ *A. herzogii* (Lemm.) Simonsen and *Ulnaria ulna* (Nitz.) Compère, which were found in four lakes. The most frequent species in 2003 was *Aulacoseira granulata* (Ehr.) Simonsen var. *granulata*, which was found in 13 lakes.

Table 2. Coefficient of Variation (CV) and averages of abiotic variables in 2002 (n = 11 lakes) and 2003 (n = 14 lakes).

	2002		2003	
	CV (%)	Mean	CV (%)	Mean
Temperature (°C)	2.54	29.59	1.403	29.75
Conductivity (µS/cm)	6.05	39.17	6.6	47.68
pH	5.75	6.77	13.72	7.12
Transparency (m)	32.54	1.27	9.8	0.62
Suspended Material (mg/L)	51.33	9.57	24.46	15.85
Alkalinity (mg/L)	41.704	9.78	27.71	17.6

The Simpson index (β_{SIM}) for the Curuaí floodplain was 0.889 in 2002 and 0.789 in 2003, showing that the lakes in 2002 were more dissimilar in their phytoplankton communities than in 2003.

In both sampling years, we applied the analysis of variation partitioning (using a partial redundancy analysis) to decompose the pure importance of environmental and spatial components on phytoplankton community variation, thus, we observed, in both years, that phytoplankton community variation in phytoplankton community structure was not significantly explained by pure environmental and pure spatial components (Table 3).

4. Discussion

Floodplains store water during the rising stage of the Amazon River and during the rainy season and release it when the river level is decreasing. It has been estimated that approximately 30% of the water in the Amazon River passes through the connected floodplains (Richey et al., 1989). The limnological variables analyzed in this studied did not present great variation among years, probably because the samples were obtained during high water in both years. Moreover, in the limnological literature, it is very common to analyze and investigate seasonal variation (e.g., Loverde-Oliveira and Huszar, 2007); however, other authors that analyzed interannual variation registered distinct results, such as great interannual variation (Nabout et al., 2007) or no interannual variation (Shoup and Wahl, 2009).

We registered high beta diversity values (β_{SIM} index) in the phytoplankton community of the Curuai floodplain in both years. However, in 2002 beta diversity was higher than in 2003. In 2002, most environmental variables had higher variation coefficients, indicating higher environmental variability. Some authors had observed that more variation in environmental gradients (i.e., a larger coefficient of variation) can promote high beta diversity (Harrison et al., 1992; Bini et al., 2001; Nabout et al., 2007).

In the field of phycology, Huszar et al. (1990) discussed beta diversity in Brazil, focusing on the lower Doce River lakes. They found elevated beta diversity and attributed it to elevated environmental heterogeneity due mainly to anthropic effects. Nogueira et al. (2008) registered elevated beta diversity in artificial lakes (urban lakes), varying from 0.4 to 0.65 using the other index (β-1; Harrinson et al., 1992). For floodplain lakes along the Paraná River (Borges and Train, 2009) and Araguaia River (Nabout et al., 2007), using β-1 index, registered lower beta diversity than we observed in this study.

Table 3. Variation partitioning of the phytoplankton community data with associated *P* values for year 2002 and 2003. The following components are indicated: "a" – variance explained by pure environmental factors, "c" – variance explained by pure spatial variables and "b" – variance explained by the spatially structured environmental variation. Negative values of adjusted coefficients of determination (Adj. R^2) were converted to zero (Legendre, 2008).

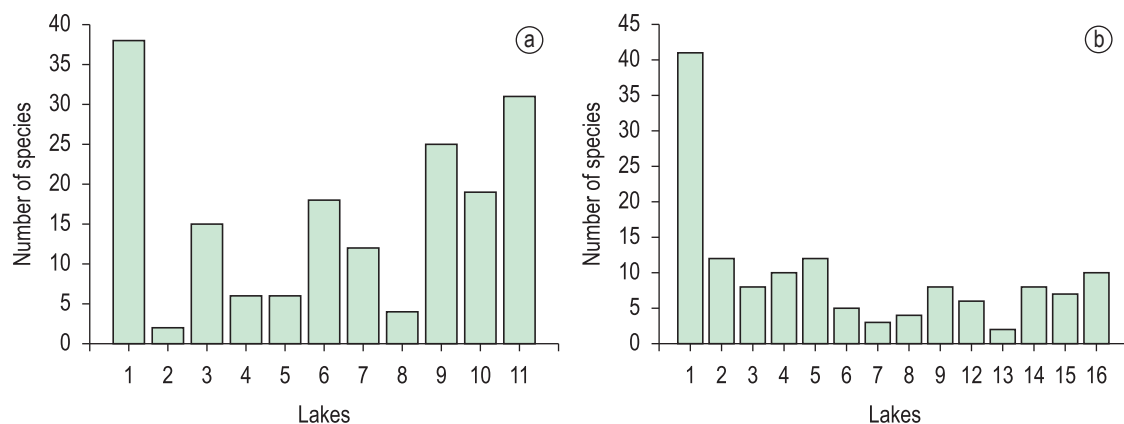| Effects	2002		2003	
	Adj. R^2	P	Adj. R^2	P
a	0.138	0.279	0.132	0.237
c	0	0.807	0	0.483
b	0.178		0.014	
Residual	0.876		0.859	

Figure 2. Species richness by sampling station from each lake of the Curuaí floodplain (α diversity). Species richness in lakes for year 2002 (a) and for year 2003 (b).

Currently, a large number of papers have discussed the determinants of beta diversity utilizing different groups of organisms as models (e.g., Beisner et al., 2006; Soininen et al., 2007; Nabout et al., 2009; Heino et al., 2010). The proposal of the neutral theory (Hubbel, 2001) and statistical advances (i.e., partial RDA, partial Mantel and others) have promoted a new debate about the relative importance of regional (i.e., dispersal) or local (i.e., environmental) components in structuring metacommunities. Despite the great amount of discussion in the scientific literature, the answer to this question is far from final. Clearly, answering questions such as which environmental or local variable (Beisner et al., 2006), temporal and spatial scale (Borcard et al., 2004), and spatial data (Legendre et al., 2005) is important to understand the determinants of beta diversity. The study we present here contributes to this discussion by analyzing the floodplain model and the relative role of environmental and spatial factors in the phytoplankton structure in a floodplain in the Amazon River Basin.

We expected that environmental factors would be the spatial factors that played the largest role in explaining the structure of phytoplankton communities in the Curuaí floodplain in both years. We found that neither environmental nor spatial factors explained a significant proportion of the total variation in phytoplankton community structure, though the results were similar in both years. This result is very similar to the ones found in phytoplankton communities in lakes in Canada (Beisner et al., 2006) and the Araguaia river floodplain (Nabout et al., 2009).

Others authors found significance of spatial or environmental variables utilizing distinct communities. However, in most of these studies, a large portion of the total variation remained unexplained, such as the diatom community in one lake of Scotland (Yang et al., 2009), diatom communities in rivers in Finland (Heino et al., 2010), phytoplankton communities in Canada (Beisner et al., 2006) and Brazil (Nabout et al., 2009), and macroinvertebrates in streams in Brazil (Roque et al., 2008). These papers all discussed the importance of local or regional effect, despite the fact that all of them have one similarity: a large part of the variance was not accounted for. Thus, the high amount of unexplained variation (i.e., residual) observed in our data and in phytoplankton data from other studies causes us to inquire about which local variables are important in order to explain phytoplankton beta diversity.

Other local environmental variables can be relevant to the structure of phytoplankton communities, and these will contribute to reducing the portion of the total variation that is not explained by the environmental variables we utilized. For example, variables such as hydrological aspects, water residence time, lake geomorphology, mixing patterns and soil characteristics can all be drivers of phytoplankton community structure (Padisák, 2004; Gruberts et al., 2007; Cowell and Dawes, 2008). Additionally, investigating biological interactions among phytoplankton, such as zooplankton herbivory or other top-down effects could increase our understanding of the factors structuring phytoplankton communities (Søndergaard et al., 1990; Jeppesen et al., 1997; Padisák, 2004). Besides biological interactions, the phytoplankton community could be regulated by stochastic events, resulting in communities that are randomly assembled (Sloan et al., 2006).

Finally, our analyses agree with other phytoplankton studies (Beisner et al., 2006; Nabout et al., 2009) and provide evidence of the importance of negative results (Young et al., 2008) in discussions of conceptual models of metacommunities. Additionally, we believe that the inclusion of other local variables, such as biological interactions and fine-scale environmental variation, should increase the explanatory power of these models.

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