

# Phytoplankton structure is more influenced by nutrient enrichment than by temperature increase: an experimental approach upon the global changes in a shallow subtropical lake

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## ABSTRACT

### Phytoplankton structure is more influenced by nutrient enrichment than by temperature increase: An experimental approach upon the global changes in a shallow subtropical lake

Climate change is considered one of the greatest threats to aquatic ecosystems around the globe. Among the expected changes, including the dynamics of phytoplankton, the growth of cyanobacteria is often cited. This study evaluated the individual and combined effects of increased temperature and nutrients on phytoplankton community structure in a large, oligo-mesotrophic subtropical shallow lake (Mangueira Lake, southern Brazil). The study was conducted in microcosms to simulate possible scenarios of climate change, alone and in combination with nutrient enrichment (N and P); water samples were collected in winter and summer. Phytoplankton total biomass, species richness and diversity did not vary significantly with manipulation of temperature alone, either in winter or in summer. Only cyanobacteria biomass increased significantly with an increase in temperature, in the winter experiments. In summer, phytoplankton total biomass, species richness, Bacillariophyceae and Cyanobacteria increased significantly with enrichment of N and P. The interaction between temperature increase and nutrient addition did not significantly affect phytoplankton attributes. Temperature increase alone was not sufficient to cause structural changes in the phytoplankton community. Instead, nutrient addition (N and P) proved to be the most significant influence on most phytoplankton attributes, even though turnover of bloom-forming cyanobacteria was not observed. Further studies on the resilience of aquatic ecosystems to climate changes may contribute to the conservation and management of these environments.

**Key words:** climate change, cyanobacteria, diversity, microcosms, resilience, lentic ecosystem

## RESUMO

### A estrutura do fitoplâncton é mais influenciada pelo enriquecimento de nutrientes do que pelo aumento de temperatura: uma abordagem experimental sobre as mudanças globais em um lago raso subtropical

A mudança climática é considerada uma das maiores ameaças aos ecossistemas aquáticos em todo o mundo. Entre as mudanças esperadas, incluindo a dinâmica do fitoplâncton, o crescimento de cianobactérias está entre os mais citados. O objetivo deste estudo foi avaliar os efeitos isolados e combinados do aumento de temperatura e nutrientes na estrutura da comunidade fitoplanctônica em um grande lago raso subtropical oligo-mesotrófico (Lagoa Mangueira, sul do Brasil). O estudo foi realizado em microcosmos para simular possíveis cenários de mudança climáticas, sozinhos e em combinação com enriquecimento de nutrientes (N e P), a partir de amostras de inverno e verão. Em ambas estações, a biomassa total do fitoplâncton, a riqueza e diversidade de espécies não variaram significativamente sob a manipulação isolada da temperatura. O aumento da temperatura elevou significativamente a biomassa de cianobactérias em experimentos de inverno. No verão, a biomassa total do

*fitoplâncton, a riqueza de espécies, Bacillariophyceae e Cyanobacteria aumentaram significativamente sob o enriquecimento de N e P. A interação entre aumento de temperatura e adição de nutrientes não promoveu efeito significativo sobre os atributos fitoplanctônicos estudados. O aumento isolado da temperatura não foi forte o suficiente para promover mudanças estruturais na comunidade fitoplanctônica. Entretanto, a adição de nutrientes (N e P) demonstrou influenciar mais significativamente na maioria dos atributos do fitoplâncton, embora não tenha sido observado o recrutamento de cianobactérias formadoras de florações. Nesse sentido, mais estudos enfatizando a resiliência dos ecossistemas aquáticos quanto às mudanças climáticas podem contribuir para a conservação e manejo desses ambientes.*

**Palavras chave:** mudança climática, cianobactérias, diversidade, microcosmos, resiliência, ecossistemas lênticos

## INTRODUCTION

One of the most serious threats to natural ecosystems is climate change, due to its implications for the structure, function, and ecosystem services provided by lakes (ACIA, 2004; Rosenzweig *et al.*, 2007; Havens & Jeppesen, 2018). Monitoring and understanding the effects of climate change are ongoing challenges, as is predicting the many consequences that climate change may cause in different ecosystems (Adrian *et al.*, 2009; Havens & Jeppesen, 2018). Indeed, the Intergovernmental Panel on Climate Change (IPCC, 2007) estimated that the mean temperature of the atmosphere increased by 0.6 °C during the twentieth century.

Freshwater ecosystems are particularly vulnerable to climate changes because they are relatively isolated and fragmented physically within large terrestrial landscapes (Woodward *et al.*, 2010). Eutrophication processes and increased temperature might affect the structure and function of lakes and ponds (Carvalho & Kirika, 2003; Gomes *et al.*, 2017). Some studies have examined the different aspects of intensifying global eutrophication (Pasternak *et al.*, 2009), but little is known about the actual effects that this interaction (temperature and eutrophication) may cause in aquatic ecosystems (Carvalho & Kirika, 2003).

Attempts to predict the possible effects of global climate change in temperate aquatic environments have involved experimentation (Davis *et al.*, 2009; Feuchtmayr *et al.*, 2010) and the use of modeling (Domis *et al.*, 2007; Elliott & Defew, 2011). However, the drivers of climate change will have varied effects on lakes, depending on the geographical location, altitude, morphometry, climate, vegetation and land use (Adrian *et al.*,

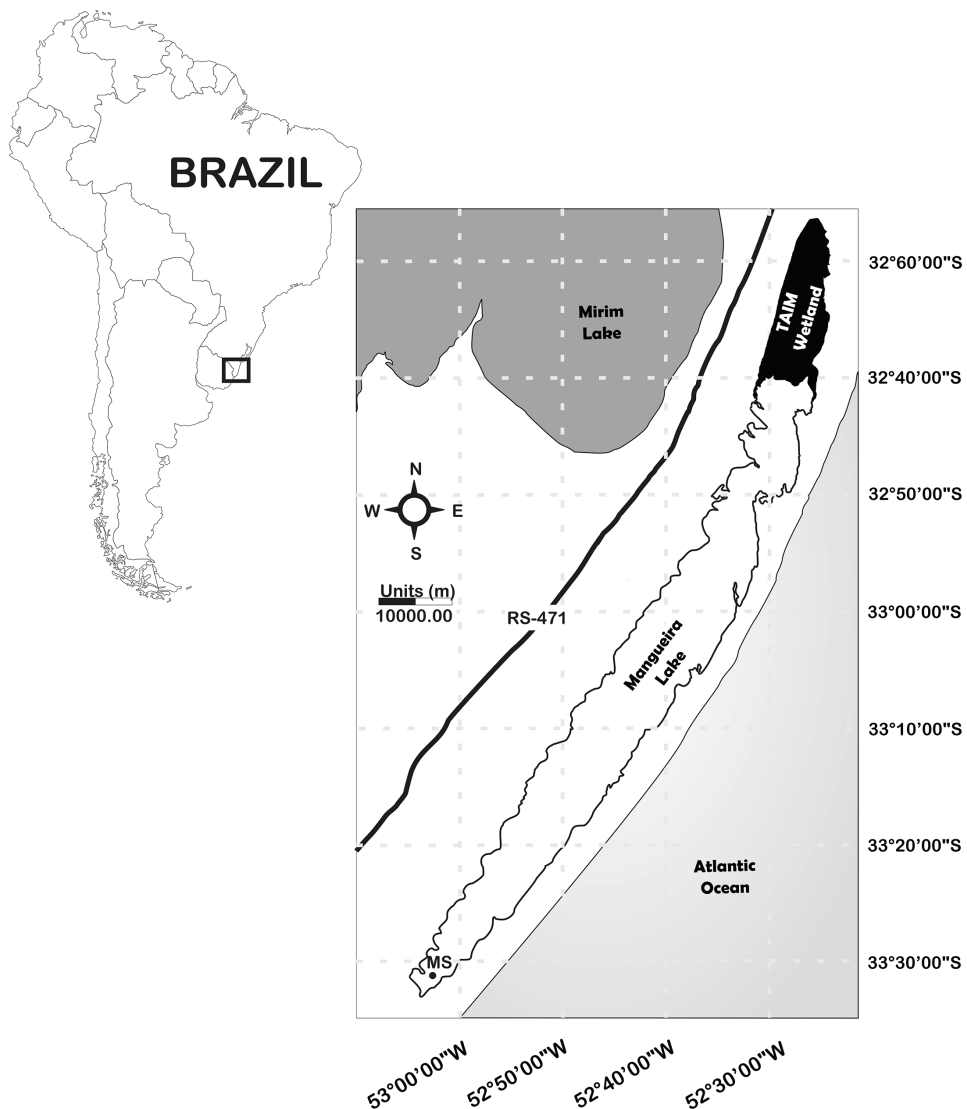
2009; Deng *et al.*, 2016; Gomes *et al.*, 2017). In agricultural catchments, for example, changes in precipitation and organic-matter decomposition may alter mainly the import of nutrients into water bodies (Adrian *et al.*, 2009). On the other hand, during dry periods, increased residence time and nutrient loads are expected, favoring the occurrence of potentially toxic cyanobacteria (Jöhnk *et al.*, 2008; Paerl & Huisman, 2009; Moss, 2011; Newcombe *et al.*, 2012).

Knowledge of the ecology of phytoplankton is a valuable tool for investigating the effects of environmental changes, with results that are applicable to other communities (Reynolds, 1998). Moreover, phytoplankton is an important biological element in the concept of the Water Framework Directive, for the evaluation of lakes, transitional waters and coastal waters (EC Parliament and Council, 2000). Considering the effects of global warming on the phytoplankton, such as increases in total biomass and shifts in the timing and magnitude of spring blooms (Jeppesen *et al.*, 2009), growth of cyanobacteria is among the most frequently cited events (Havens *et al.*, 2016; Richardson *et al.*, 2019). Although many studies have shown higher growth rates and abundance of cyanobacteria as responses to climate change (Weyhenmeyer *et al.*, 2002; Paerl & Huisman, 2008; Adrian *et al.*, 2009; Kosten *et al.*, 2012; Domis *et al.*, 2013; Beaver *et al.*, 2018), other studies have shown that in non-stratified shallow lakes, dominated by macrophytes, the recruitment of cyanobacteria may not occur as expected (Moss *et al.*, 2003; Fragoso *et al.*, 2011). More-recent studies have demonstrated that warmer climates may, in fact, favor cyanobacterial development in shallow lakes (Kosten *et al.*, 2012; Guo *et al.*, 2019); and indeed, that changes

in variables related to climate conditions, such as rainfall regime, may alter lake characteristics such as retention time and water stability, favoring cyanobacterial dominance, particularly in subtropical lakes (Ribeiro *et al.*, 2012; Fuentes & Petrucio, 2015; Havens *et al.*, 2019).

Studying the dynamics of phytoplankton and the effects of temperature increase along with the eutrophication process is essential to initiate the development and planning of management strate-

gies and restoration (Carvalho & Kirika, 2003) of aquatic ecosystems in response to environmental changes. The hypothesis of this study was that the phytoplankton structure might be altered due to variations in temperature (warming) and nutrient concentrations (eutrophication)? Thus, the overall objective of this study was to evaluate the combined effect of temperature and addition of nutrients (N and P) on the phytoplankton community structure in a large shallow polymictic lake



**Figure 1.** Location of Lake Mangueira, state of Rio Grande do Sul, Brazil. Black circle indicates the sampling point. MS = Southern Lake Mangueira. *Localização da Lagoa Mangueira, Estado do Rio Grande do Sul, Brasil. Circulo preto indica o ponto de coleta no sul do lago. MS = Sul da Lagoa Mangueira.*

(Lake Mangueira, southern Brazil), in an *in-situ* experimental approach.

## MATERIALS AND METHODS

### Study area

Lake Mangueira is an oligo-mesotrophic shallow coastal lake (Crossetti *et al.*, 2013) ( $Z_{\text{mean}} = 3$  m;  $Z_{\text{max}} = 9$  m), 90 km long and 3–10 km wide, located in the southern part of the state of Rio Grande do Sul ( $32^{\circ} 20'$  and  $33^{\circ} 00'$  S, and  $52^{\circ} 20'$  and  $52^{\circ} 45'$  W), southern Brazil (Fig. 1). The region has a subtropical climate (type Cfa; Kottek *et al.*, 2006). The lake is drained periodically to irrigate rice fields, which determines its hydroperiod, comprised of low-water (generally in summer) and high-water (generally in winter) periods. The lake is continuous warm polymictic (no seasonal ice cover, stratifying at most a few hours at a time) (Lewis, 1983), with daily mixing due to intense wind action. The lake is connected to wetlands in the north, forming the Taim Hydrological System (THS), a federal conservation unit; in the south, large areas are covered with submerged, free-floating and emergent macrophytes (Rodrigues *et al.*, 2015).

### Experimental design

Water was collected in the pelagic zone (at the sub-surface) of southern Lake Mangueira and placed in barrels, aerated, and taken to the laboratory for an immediate start of the experiment. The individual and combined effects of temperature and nutrient addition were tested. The experimental enrichment consisted of four treatments: control (C), without nutrient addition; addition of phosphorus (P) ( $\text{KH}_2\text{PO}_4$ , Merck PA®); addition of nitrogen (N) ( $\text{NH}_4\text{NO}_3$ , Merck); or combined addition of nitrogen and phosphorus (N and P). The amounts of nutrients added were based on a calculation of four times the mean concentration of orthophosphate and nitrate in the lake in the last five years (historical means 0.13 mgN/L and 0.04 mgP/L). The nutrients were added only on the first day of the experiment, simulating higher nutrient input as a side-effect of climate changes (e.g., input of

allochthonous nutrients or feedback processes).

The water with these treatments was exposed to three scenarios with different temperatures, simulating the predictions of climate change for southern South America described by the IPCC (IPCC, 2007), for winter and summer, as follows:

Scenario 0: control treatment, performed by calculating the mean air temperature over the last five years in the lake area. For the experiment, the control temperatures were 13 °C and 24 °C in winter and summer, respectively.

Scenario 1: followed scenario A2 of the IPCC (2007), which predicts high greenhouse-gas emissions (if emissions continue to increase as in the past decades) on the planet by 2100, when in southern South America a temperature increase of around 4 °C is expected. For the experiment, the temperatures used were 17 °C in winter and 28 °C in summer.

Scenario 2: extrapolation of temperature, simulating increases during heat waves of up to 7 °C. For the experiment, the temperature was 20 °C in winter and 31 °C in summer.

The experiment was conducted in replicated ( $n = 3$ ) microcosms (1.5-L glass aquariums), in climate-controlled chambers (one chamber for each temperature). The water was stirred daily and the photoperiod was 12/12 h. Each experiment lasted 12 days, during which five water samples were taken for analysis of biological and abiotic parameters (on days 1, 3, 6, 9 and 12). The experiments were conducted in the winter of 2011 and the summer of 2012.

At the end of the experiment, on day 12, the mean final concentrations of total nitrogen (TN) for treatment N were 0.12 mg/L in winter and 0.02 mg/L in summer. The mean total phosphorus (TP) concentrations at the end of the experiment were 1.03 in winter and 0.40 mg/L in summer. The mean TN and TP final concentrations in the N and P treatments were 0.07 and 1.02 mg/L in winter, respectively, and 0.02 and 0.54 mg/L in summer.

### Abiotic and biotic variables

The abiotic variables analyzed were temperature, dissolved oxygen, pH (HACH HQd Field - HQ 40d multi HACH), nitrite, nitrate, orthophos-

phate, total nitrogen and total phosphorus (Mackereith *et al.*, 1989).

For phytoplankton quantitative analysis, water aliquots were taken from each microcosm and fixed with 1 % acetic Lugol. Replicate samples were integrated before quantification (Utermöhl, 1958; Lund *et al.*, 1958). Biomass ( $\text{mm}^3/\text{L}$ ) was estimated by species biovolume (Hillebrand *et al.*, 1999). Species that contributed at least 4 % of the total biomass were considered biological descriptors. Species richness was estimated based on the number of taxa and the diversity index (Shannon & Weaver, 1964).

### Data analysis

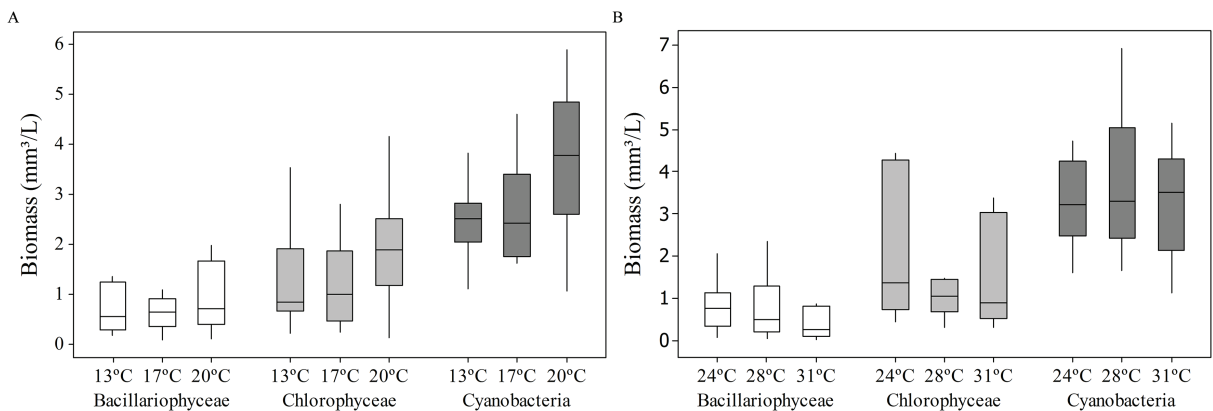
Descriptive statistical analysis was performed for both abiotic and biotic data. One-way blocking analysis of variance (ANOVA) was performed to evaluate the effect of warming (block factor) and nutrient addition on the structure of the phytoplankton community. In all significant cases, Tukey's HSD test was performed. The software used was SYSTAT version 12 (Systat Software).

## RESULTS

Physical and chemical variables of each treatment did not vary significantly among the days of experiment (measured on days 1, 3, 6, 9 and

12), in each treatment. In winter, the mean concentration of total nitrogen was  $0.07 \pm 0.05$  mg/L, total phosphorus  $0.53 \pm 0.51$  mg/L, pH  $8.43 \pm 0.35$  and dissolved oxygen  $9.96 \pm 0.91$  mg/L. In summer, the mean concentration of total nitrogen was  $0.02 \pm 0.01$  mg/L, total phosphorus  $0.28 \pm 0.22$  mg/L, pH  $8.40 \pm 0.31$  and dissolved oxygen  $8.13 \pm 0.85$  mg/L.

One hundred two species were identified, distributed in seven classes of microalgae. In winter, class Chlorophyceae had the highest number of taxa, followed by Cyanobacteria and Bacillariophyceae, in all experimental conditions. In summer, Chlorophyceae and Cyanobacteria had similar numbers of taxa, followed by Bacillariophyceae. Regarding the effects of individual parameters, in winter, Cyanobacteria biomass increased significantly with the increase of temperature, and was highest at 20 °C ( $F = 7.4$ ;  $p = 0.002$ ; Fig. 2A). Total biomass also increased significantly with increasing temperature ( $F = 3.58$ ;  $p = 0.04$ ; Fig. 4A). In summer, temperature manipulation did not result in significant variations in the biomass of the phytoplankton groups ( $F = 0.3$ ;  $p = 0.75$ ; Fig. 2B). The species richness and diversity did not vary significantly with manipulation of temperature alone, either in winter nor in summer (Figs. 4 and 5; Table 1). Addition of nutrients did not result in significant changes during the winter experiment. Neverthe-



**Figure 2.** Boxplot (mean, interquartile ranges,  $n = 20$ ) of Bacillariophyceae, Chlorophyceae and Cyanobacteria biomass in winter (13 °C, 17 °C, 21 °C; (A) and summer (24 °C, 28 °C, 31 °C) (B) experiments. *Boxplot (mediana, intervalos interquartis,  $n = 20$ ) de biomassa de Bacillariophyceae, Chlorophyceae e Cyanobacteria nos experimentos de inverno (13 °C, 17 °C, 21 °C) (A) e verão (24 °C, 28 °C, 31 °C) (B).*

**Table 1.** Relative biomass (%) and total biomass contribution (%) of the phytoplankton descriptor species in all the treatments (C = control, N = N addition, P = P addition and NP = NP addition), in winter (A) and summer (B). *Biomassa relativa (%) e contribuição total de biomassa (%) das espécies descritoras do fitoplâncton em todos os tratamentos (C = controle, N = adição de N, P = adição de P e NP = adição de NP), no inverno (A) e verão (B).*

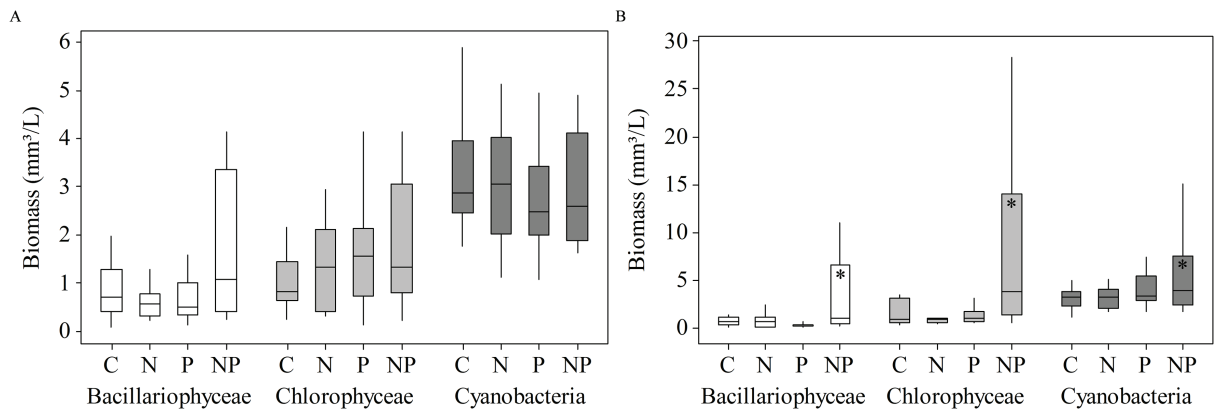
A	13°C				17°C				20°C			
	C	N	P	NP	C	N	P	NP	C	N	P	NP
	Species											
<b>Bacillariophyceae</b>												
<i>Aulacoseira granulata</i> (Ehr.) Simon.	5.2	7.2	2.0	6.1	2.1	4.7	0.6	1.3	5.6	2.7	0.9	0.6
<i>Nitzschia palea</i> (Kütz.) W.Smith	2.2	0.6	0.7	6.8	0.3	0.2	0.6	3.1	0.4	0.8	0.1	11.6
<i>Nitzschia</i> sp.	2.2	0.0	29.2	1.7	0.0	0.0	0.0	0.0	1.6	0.0	3.7	0.0
<i>Punctatriata</i> sp.	2.3	1.4	1.0	1.8	5.2	4.4	6.3	15.3	7.3	3.2	2.9	1.9
<i>Synedra</i> sp.	0.3	0.4	0.2	2.4	0.0	0.0	0.2	0.0	0.1	0.3	0.0	0.1
<b>Chlorophyceae</b>												
<i>Botryococcus</i> sp.	14.0	8.4	6.2	3.8	1.7	6.8	2.3	4.3	2.2	10.0	4.8	0.0
<i>Coelastrum microporum</i> Näg.	0.3	1.4	1.1	3.2	1.0	2.1	0.2	6.5	4.1	0.6	5.5	3.6
<i>Hariotina reticulata</i> Dang.	1.7	9.1	9.6	0.0	8.4	0.0	3.3	1.0	0.0	1.5	0.0	2.6
<i>Pseudopediastrum boryanum</i> (Turp.) E.Hegewald	1.7	2.5	1.9	2.3	1.4	1.8	4.2	2.1	1.6	2.0	3.0	1.7
<i>Scenedesmus ecornis</i> (Ehr.) Chodat	0.1	0.0	1.5	1.6	0.0	0.0	3.3	3.8	0.0	0.0	5.0	9.0
<i>Scenedesmus</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.5	0.0	0.0	0.2	19.6
<b>Cyanobacteria</b>												
<i>Planktolyngbya contorta</i> (Lemm.) Anag. et Kom.	14.0	15.0	8.7	11.5	26.5	22.8	19.7	17.7	16.3	14.9	13.7	7.0
<i>Planktolyngbya limnetica</i> (Lemm.) Kom.-Leg. et Cron.	7.1	7.3	6.4	9.5	15.1	17.2	10.1	9.1	15.9	18.9	19.2	9.3
<i>Pseudanabaena</i> cf. <i>limnetica</i> (Lemm.) Kom.	20.9	27.0	10.4	20.3	12.7	13.1	20.7	9.4	11.9	14.3	11.7	5.8
<i>Snowella lacustris</i> (Chod.) Kom. et Hind.	1.2	0.5	1.1	3.0	1.4	1.3	1.5	1.1	3.0	0.9	3.0	3.3
<b>Zygnemaphyceae</b>												
<i>Staurastrum</i> cf. <i>paradoxum</i> Meyen ex Ralfs	3.5	1.0	4.0	1.3	4.4	1.0	2.6	1.6	2.1	3.1	6.5	0.8
<b>Total Biomass (%)</b>	76.8	81.8	84.1	75.3	80.3	75.3	75.7	76.7	72.2	73.1	80.1	76.9
B												
	24°C				28°C				31°C			
	C	N	P	NP	C	N	P	NP	C	N	P	NP
<b>Bacillariophyceae</b>												
<i>Nitzschia palea</i> (Kütz.) W. Smith	0.0	0.5	0.2	10.0	0.4	0.5	0.1	12.9	0.4	0.8	0.8	9.9
<i>Nitzschia</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	10.4	0.0	0.0	1.2
<i>Synedra</i> sp.	0.7	0.8	0.0	7.7	0.4	0.9	0.3	2.7	0.0	0.2	0.3	0.1
<i>Ulnaria oxyrhynchus</i> (Kütz.) Aboal	9.8	17.8	3.1	5.4	11.5	12.3	3.5	3.0	2.3	3.2	3.7	1.1
<b>Chlorophyceae</b>												
<i>Botryococcus</i> sp.	5.7	0.0	0.0	0.7	9.8	0.0	0.0	1.0	0.0	0.0	0.0	1.4
<i>Coelastrum microporum</i> Näg.	0.4	7.4	1.3	14.6	2.4	0.6	1.7	11.5	0.8	1.7	3.1	9.8
<i>Hariotina reticulata</i> Dang.	0.0	4.8	0.0	4.8	0.0	5.6	0.0	5.6	0.0	0.0	1.1	0.0
<i>Monoraphidium contortum</i> (Thuret) Kom.-Leg.	3.4	3.8	2.5	0.6	5.6	4.1	4.2	1.5	1.5	3.2	1.0	0.9
<i>Mougeotia</i> sp.	37.9	0.0	28.6	23.5	0.0	28.0	0.0	0.0	36.0	0.0	0.0	24.9
<i>Scenedesmus</i> sp.	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.1	0.0	0.0	0.0	5.1
<b>Cyanobacteria</b>												
<i>Planktolyngbya contorta</i> (Lemm.) Anag. et Kom.	7.5	6.2	11.3	0.9	3.1	5.0	12.9	1.5	4.3	7.0	2.3	0.4
<i>Planktolyngbya limnetica</i> (Lemm.) Kom.-Leg. et Cron.	18.6	25.3	28.0	15.3	39.3	20.4	38.1	42.5	17.8	49.9	40.1	26.1
<i>Pseudanabaena</i> cf. <i>limnetica</i> (Lemm.) Kom.	4.8	12.0	6.7	2.1	6.0	7.3	12.7	3.7	8.9	12.7	17.0	3.4
<i>Snowella lacustris</i> (Chod.) Kom. et Hind.	0.0	0.0	0.0	1.4	1.6	0.2	0.5	0.1	0.3	0.0	0.5	0.0
<b>Total Biomass (%)</b>	88.7	78.6	81.7	87.5	80.1	84.9	74.1	87.7	82.5	78.8	70.2	84.3



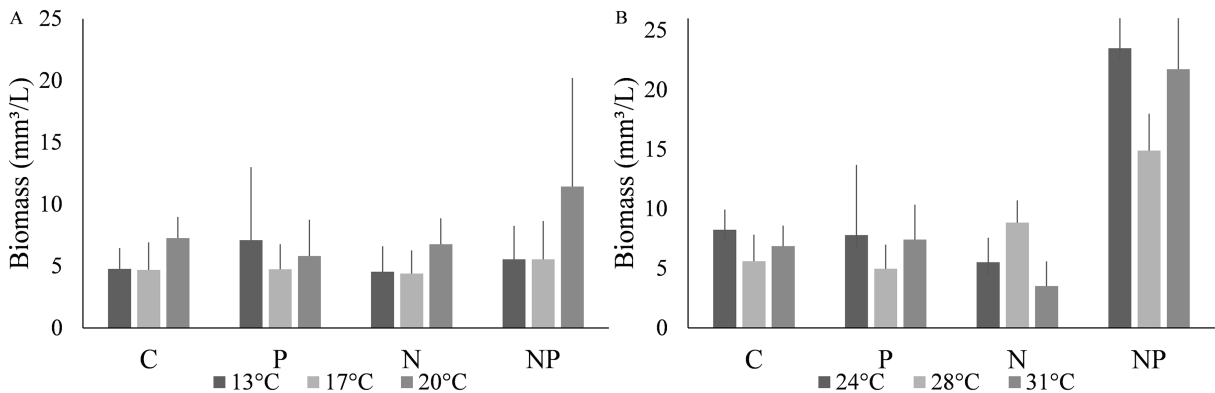
less, the combined addition of N and P resulted in a significant increase in richness ( $F = 9.34$ ;  $p < 0.001$ ; Fig. 5B), total biomass ( $F = 5.35$ ;  $p < 0.005$ ; Fig. 3B), biomass of Bacillariophyceae ( $F = 4.7$ ;  $p = 0.006$ ; Fig. 3B), Chlorophyceae ( $F = 3.55$ ;  $p = 0.02$ ; Fig. 3B) and biomass of Cyanobacteria ( $F = 2.9$ ;  $p = 0.04$ ; Fig. 3B) in the summer experiments.

The interaction between temperature increase and nutrient addition did not significantly affect

the phytoplankton parameters evaluated. Twenty descriptor species were identified in all treatments (winter and summer), contributing about 81 % of the total phytoplankton biomass. Despite the significant increase of Cyanobacteria biomass at 20 °C in the winter experiments (Fig. 2A), the composition of the descriptor species did not change (Table 1A). The biomass of *Planktolyngbya contorta*, *P. limnetica* and *Snowella lacustris* increased slightly when the temperature and



**Figure 3.** Boxplot (mean, interquartile ranges,  $n = 15$ ) of Bacillariophyceae, Chlorophyceae and Cyanobacteria biomass in the treatments with nutrient addition (C = control, P = P addition, N = N addition, NP = NP addition), in winter (A) and summer (B) experiments. \*significant difference from the other treatments. *Boxplot (mediana, intervalos interquartis,  $n = 15$ ) da biomassa de Bacillariophyceae, Chlorophyceae e Cyanobacteria nos tratamentos com adição de nutrientes (C = controle, P = adição de P, N = adição de N, NP = adição de NP), no inverno (A) e no verão (B). \*diferença significativa dos outros tratamentos.*



**Figure 4.** Effect of warming and nutrient enrichment on phytoplankton total biomass ( $\text{mm}^3/\text{L}$ ) in winter (13 °C, 17 °C, 21 °C) (A) and summer (24 °C, 28 °C, 31 °C) (B) experiments, in all treatments (C = control, P = P addition, N = N addition, NP = NP addition) ( $n = 5$ ). *Efeito do aquecimento e enriquecimento de nutrientes na biomassa total do fitoplâncton ( $\text{mm}^3/\text{L}$ ) nos experimentos de inverno (13 °C, 17 °C, 21 °C) (A) e de verão (24 °C, 28 °C, 31 °C) (B), em todos os tratamentos (C = controle, P = adição de P, N = adição de N, NP = adição de NP) ( $n = 5$ ).*

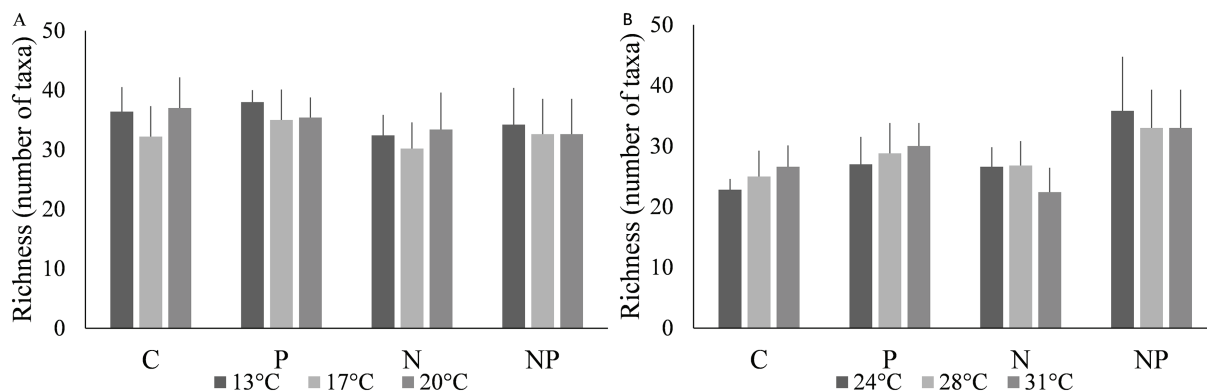
nutrients increased in the winter treatments. In the summer experiments, the descriptor species *Nitzschia palea*, *Coelastrum microporum* and *Planktolyngbya limnetica* mainly contributed to the significant increase in phytoplankton biomass in the N and or P enrichments (Table 1B),

## DISCUSSION

The results showed that in Lake Mangureira, the combined nutrient addition (N and P) was more important in altering the phytoplankton parameters (total biomass, species richness, Bacillariophyceae, Chlorophyceae and Cyanobacteria biomasses) in summer than the temperature increase, which significantly increased the Cyanobacteria biomass in winter. The composition of the descriptor species remained similar following the manipulations. According to some authors, alterations in growth rates, abundance, and species composition of phytoplankton can be considered as indicators of climate changes (Adrian *et al.*, 2009).

Among all the expected side effects of climate change, increasing temperature is one of the most worrying because it directly influences the metabolism of photosynthetic aquatic organisms, increasing their growth rates and biomass accumulation (Padilla-Gamiño & Carpenter, 2007). In shallow lakes, cyanobacteria blooms have

become more common due to the adaptability of this group to extreme conditions, especially in high temperatures (Paerl & Huisman, 2008; Kosten *et al.*, 2012; Winder & Sommer, 2012; Beaver *et al.*, 2018). This adaptability gives cyanobacteria a competitive advantage over other phytoplankton groups such as diatoms and green algae (Reynolds, 2006; Jöhnk *et al.*, 2008). The results of the present study agreed with this statement only in the winter experiments, where the increase in temperature (from 13 °C to 20 °C) led to an increase in cyanobacterial biomass. Although the N and P enrichment also favored the abundance increase of cyanobacteria, in the summer experiments the composition of descriptor species did not change. This outcome contradicts our expectation that potentially bloom-forming species that were previously recorded in high abundance in this lake, such as *Cylindrospermopsis raciborskii* and *Microcystis aeruginosa* (Crossetti *et al.*, 2014), would successfully develop under the experimental conditions; however, in this study both were recorded in low biomasses. The blue-green descriptors found in the present study (*Planktolyngbya contorta*, *Pseudanabaena limnetica* and *Planktolyngbya limnetica*) are usually related to turbid and mixed environments, being tolerant of low light intensities (Reynolds *et al.*, 2002; Padišák *et al.*, 2009).



**Figure 5.** Effect of heating and nutrient enrichment on phytoplankton richness (number of taxa) in winter (13 °C, 17 °C, 21 °C) (A) and summer (24 °C, 28 °C, 31 °C) (B) experiments, in all treatments (C = control, P = P addition, N = N addition, NP = NP addition) ( $n = 5$ ). Efeito do aquecimento e enriquecimento de nutrientes na riqueza fitoplanctônica (número de taxa) nos experimento de inverno (13 °C, 17 °C e 21 °C) (A) e de verão (24 °C, 28 °C, 31 °C) (B), em todos os tratamentos (C = controle, P = adição de P, adição de N = N, NP = adição de NP) ( $n = 5$ ).



Although the vast majority of studies currently seek to demonstrate the drastic effects of global change on aquatic ecosystems and consequently on the structure and dynamics of phytoplankton (Elliott, 2011; Verdonschot *et al.*, 2013; Beaver *et al.*, 2018; Monchamp *et al.*, 2018), some studies have shown that these environments will not always become cyanobacteria monocultures. Moss *et al.* (2003), in a nutrient-addition experiment conducted in mesocosms, found that a rise in temperature (over the year or only in the summer) did not significantly alter the levels of chlorophyll-*a* or the biomass of phytoplankton. Indeed, the results suggesting that in non-stratified shallow lakes dominated by macrophytes, the feared blue-green dominance under global warming may not be as catastrophic as expected. Frago *et al.* (2011), through simulations in a model of ecological dynamics (HPI-TRIM3D-PCLake) in Lake Mangueira, found that the effects of climate change from increasing temperature (according to IPCC, scenario A2) and addition of nutrients (reaching eutrophic levels) were not significantly important for structuring the aquatic communities (phytoplankton, zooplankton, macrophytes, omnivorous and piscivorous fish). These authors showed that the highest nutrient loading negatively affected water transparency, although the changes were relatively small and slow, indicating high resilience of the system, or high inertia of the lake due to its large size.

Lake Mangueira is a large subtropical shallow lake which has been monitored since 2001. Studies of the high spatial and temporal variability of bacterioplankton (Lima *et al.*, 2016), periphyton (Faria *et al.*, 2015), phytoplankton (Crossetti *et al.*, 2014; Freitas-Teixeira *et al.*, 2016), zooplankton (Rosa *et al.*, 2017) and fish (Rodrigues *et al.*, 2014; 2015) have demonstrated that the intense hydrodynamics of Lake Mangueira, influenced by strong winds, is closely related to the structural patterns of these communities. Regime changes in lakes may be related to the inertia of these environments and the intrinsic variability of the ecosystem (Contamin & Ellison, 2009), and should be considered in the context of the expected side effects of climate changes.

For decades, the world has faced the problem of eutrophication of aquatic systems, expanding

scientific efforts aiming at understanding this process and the responses of phytoplankton to nutrient loading. Studies have shown that nitrogen, phosphorus, or the availability of both key nutrients controls phytoplankton growth rates (Smith *et al.*, 1999; Elmgren & Larsson, 2001), biomass (Cloern, 2001; Bledsoe *et al.*, 2004) and species composition (Duarte *et al.*, 2000; Smayda & Reynolds, 2001). From the point of view of global climate change, intensified eutrophication in shallow lakes is expected (Jeppesen *et al.*, 2010; 2011), through both changes in mixing patterns, and altered water regimes that can generate discharges of nutrients from nonpoint sources (Winder & Sommer, 2012). In this study, nutrient enrichment might be indirectly responsible for contributing to the increase in species richness and total phytoplankton, cyanobacteria and diatom biomass in the warm season (summer) regardless of temperature.

A decrease in phytoplankton diversity is also one of the expected effects of climate change, especially due to ecosystem physical and chemical changes and input of nutrients (Winder & Sommer, 2012). In the Lake Mangueira experiment, significant changes in species richness were observed in summer and under N and P enrichment (Fig. 5B). Despite these changes, the diversity of species found in the experiments was not altered, indicating that this increase in species richness did not contribute to the total biomass observed.

## CONCLUSION

In summary, the changes observed in the structure of phytoplankton indicated that the temperature increase alone, in accordance with the IPCC (2007) A2 scenario (+4 °C) and an extreme increase of temperature (+7 °C), was not sufficient to cause structural changes. Addition of key nutrients (N and P combined) proved to be the most significant influence on the phytoplankton parameters, even though turnover of bloom-forming cyanobacteria was not observed. The experimental manipulations in this study are far from representing the actual complexity of the interactions in Lake Mangueira. Further laboratory or *in-situ* studies are still necessary to enable predic-

tions of the influence of global changes on each aquatic ecosystem. Studies emphasizing the resilience of aquatic ecosystems to climate changes may contribute to the conservation and management of these environments.

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