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El Niño and La Niña events shape distinct phytoplankton dynamics in a subtropical shallow lake

Eventos de El Niño e La Niña moldam de forma distinta a estrutura e dinâmica do fitoplâncton em um lago raso subtropical

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Abstract: Aim: This study aimed to evaluate the effects of El Niño Southern Oscillation (ENSO) on the structure and dynamics of the phytoplankton community of an extensive subtropical shallow lake in southern Brasil (Lagoa Mangueira, RS). **Methods:** Phytoplankton and environmental variables were collected twice per year at three different sites in the pelagic region of the lake, between 2001 and 2013, totaling 6 samples per year. Meteorological variables such as rainfall, radiation, wind speed and direction, as well as limnological variables such as total phosphorus, total nitrogen, dissolved total nitrogen, among others, were also used to compose the analyses. To assess the phytoplankton community's response to environmental variability during El Niño and La Niña periods, and the regular year, we analyzed the species richness, diversity, evenness, dominance, species composition, and biomass. The correlation among meteorological and limnological data was verified using a Principal Component Analysis (PCA). To verify the relationship between the descriptor species and the environmental data, a Redundancy Analysis (RDA) was performed. **Results:** We identified 188 taxa distributed in 9 classes, of which Chlorophyceae, Cyanobacteria and Bacillariophyceae were the most representative. Among the analyzed groups, Cyanobacteria and Raphidophyceae showed significant variations between ENSO periods. The results showed statistically different environmental scenarios between ENSO periods, mainly with regard to total suspended solids, reactive soluble silica, total phosphorus, total nitrogen, total dissolved nitrogen, conductivity, dissolved oxygen, alkalinity, ammonia and wind speed. Phytoplanktonic biomass was significantly higher in La Niña years. No differences were observed in richness, dominance, diversity and evenness between the periods studied. However the descriptor species reflected the environmental differences of each observed scenario. **Conclusions:** The study demonstrated the occurrence of different ecological species grouping of phytoplanktonic species in the El Niño and La Niña periods, associated with the different environmental scenarios of each ENSO event.

Keywords: cyanobacteria; monitoring; ENSO; oligotrophic; extreme climatic events.

Resumo: Objetivo: Este estudo objetivou avaliar os efeitos do El Niño Oscilação Sul (ENOS) na estrutura e dinâmica da comunidade fitoplanctônica de uma extensa lagoa rasa subtropical no sul do Brasil (Lagoa Mangueira, RS). **Métodos:** O fitoplâncton e as variáveis ambientais foram coletadas duas vezes ao ano na região pelágica da lagoa, entre 2001 e 2013. As variáveis meteorológicas como precipitação, radiação, velocidade e direção do vento também foram utilizadas para compor as análises. A riqueza, diversidade, equitabilidade, dominância, espécies descritoras e a biomassa da comunidade fitoplanctônica foram utilizadas como resposta à variabilidade ambiental dos períodos de El Niño, La Niña e ano regular. A Análise de Componentes Principais (ACP) foi realizada para avaliar as tendências das variáveis meteorológicas e limnológicas. Para verificar a relação entre as espécies descritoras e os dados ambientais foi realizada uma Análise de Redundância (RDA). **Resultados:** Identificamos 188 táxons distribuídos em 9 classes, dos quais Chlorophyceae, Cyanobacteria e Bacillariophyceae foram os mais representativos. As análises evidenciaram cenários ambientais diferentes estatisticamente entre os períodos de ENOS, principalmente no que se refere aos sólidos suspensos totais, sílica solúvel reativa, fósforo total, nitrogênio total, nitrogênio dissolvido total, condutividade, oxigênio dissolvido, alcalinidade, amônia e velocidade do vento. A biomassa fitoplanctônica foi significativamente maior em períodos de La Niña. Não foram observadas diferenças na riqueza, dominância, diversidade e equitabilidade ente os períodos estudados. No entanto, as espécies descritoras refletiram as diferenças ambientais de cada cenário observado. **Conclusões:** O estudo demonstrou a ocorrência de diferentes grupos de espécies fitoplanctônicas nos períodos El Niño e La Niña, associadas aos diferentes cenários ambientais de cada evento ENOS.

Palavras-chave: cianobactérias; monitoramento; ENOS; oligotrófico; eventos climáticos extremos.

1. Introduction

In April-May 2024, the state of Rio Grande do Sul, located in the subtropical zone of southern Brazil, experienced the most severe climate-related disaster in its recorded history. Rainfall levels far exceeded historical averages – in some regions reaching up to five times the expected monthly total - affecting multiple municipalities across the state and impacting over two million people (Rio Grande do Sul, 2024a, b).

Previous climatic events — such as extratropical cyclones, increased rainfall, and local or regional flooding episodes, including those recorded in 1941, 1959, 1967, 2010, and 2023 (Marengo et al., 2024) — had already indicated the region's vulnerability to the increasingly frequent occurrence of extreme climate events. The observed climatic disaster seen in April-May 2024 stems from the interaction between the intensification of extreme rainfall events, largely influenced by El Niño events, and changes in regional atmospheric circulation patterns (Marengo et al., 2024). In southern Brazil, evidence indicates that episodes of intense rainfall have been increasing in both frequency and severity since the 1950s, and projections for the coming decades underscore the urgent need for attention and preparedness in the face of this emerging climatic scenario (Marengo et al., 2024).

Given the increasing incidence of extreme climatic events and their consequences for the dynamics and functioning of aquatic ecosystems, understanding how communities are shaped under these new scenarios is of high ecological importance. El Niño Southern Oscillation (ENSO) refers to situations in which the Equatorial Pacific Ocean is warmer (El Niño) or colder (La Niña) than the historical average. The change in the temperature of the Equatorial Pacific Ocean has global effects on temperature and rainfall (Grimm et al, 1998; Cera & Ferraz, 2015). The El Niño Southern Oscillation (ENSO) phenomenon exerts a significant influence on Brazil's climate, with impacts that vary across regions. In the Southern Region, these effects are particularly pronounced: during the warm phase (El Niño), rainfall increases substantially, often exceeding climatological averages, which heightens the risk of flooding and soil erosion (Grimm et al., 1998; Cera & Ferraz, 2015). Conversely, the cold phase (La Niña) tends to cause prolonged droughts, compromising water availability and agricultural productivity (Grimm et al., 1998). These changes affect not only agriculture but also aquatic ecosystems, altering the physical, chemical, and biological properties of water bodies, with consequences for phytoplankton biomass, species composition, and primary productivity (Tuvikene et al., 2011; Morales & Anabalón, 2012). In other Brazilian regions, ENSO impacts are also significant: El Niño typically intensifies droughts in the North and Northeast and reduces rainfall in the Central-West and Southeast, whereas La Niña generally leads to above-average rainfall in these areas, modifying agricultural and hydrological patterns. Given the Southern Region's reliance on rain-fed agriculture and surface water systems, understanding these variations is essential for regional adaptation and mitigation strategies.

Shallow lakes are vulnerable to stochastic events such as windstorms that directly influence sediment resuspension, floods and droughts, which, for instance, substantially alter the lake's water volume (Scheffer et al., 1993; Havens et al., 2007). Hydrodynamics acts as a force that governs these environments (Legendre & Demers, 1984), being able to model the structure and productivity of communities (Frenette et al., 1996). Shallow lakes are considered effective ecological models for investigating environmental and climatic changes, particularly in subtropical regions, where elevated temperatures allow these systems to sustain primary production throughout the year. This continuous productivity distinguishes them from temperate lakes, where biological activity is typically restricted to spring and summer (Talling, 1992; Cunha et al., 2013, Díaz Torres et al., 2021).

Phytoplankton community in shallow lakes is influenced by weather events (Chen et al., 2003; Zhang et al., 2018; Deng et al., 2019). The study of Deng et al. (2019) showed that, besides nutrients, climatic variables were import drivers of the functional structuring of phytoplankton in a large shallow subtropical lake, with it varying significantly among seasons, evidencing the importance of temporal variability of weather conditions in determining the environmental scenario of shallow lakes. Recently, significant higher phytoplankton biomass on ENSO periods (especifically on La Niña periods) were found in a subtropical shallow lake in Brazil compared to regular years (Wieliczko et al., 2021), and other study has demonstrated the relationship between cyanobacteria bloom recruitment and limnological changes in a subtropical urban shallow lake under a La Niña event (Ribeiro et al., 2012). ENSO influences on the limnological scenario was also related to the recruitment of different functional assemblages of phytoplankton in a subtropical shallow lake (Wieliczko et al., unpublished data). In this context, integrative investigations of phytoplankton community structure and spatiotemporal dynamics remain necessary to clarify response patterns and mechanistic pathways under ENSO variability.

Assuming that ENSO influences the limnology of shallow lakes by modifying habitats, environmental conditions and resources for phytoplankton, the objective of this study was to evaluate the influence of ENSO on the structure (species richness, diversity, equitability, dominance, descriptor species and biomass) and dynamics of phytoplankton over 12 years (2001-2013) in a shallow large subtropical lake (Lake Mangueira, southern Brazil). Our results contribute to understanding anomalous climatic scenarios effects on the ecology of inland aquatic ecosystems and communities, given the projected increase in frequency and intensity of such events in the state of Rio Grande do Sul.

2. Material and Methods

2.1. Study site

Lake Mangueira is a large subtropical shallow lake (90 km long, 3-10 km wide), oligo-mesotropic and polymictic (Crossetti et al., 2013; Figure 1)

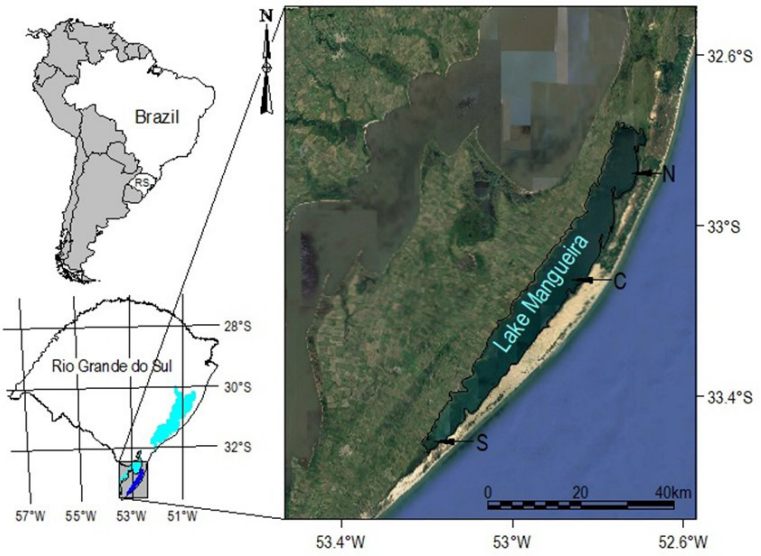

Figure 1. Location of Lake Mangueira, state of Rio Grande do Sul, Brazil. Letters N (North), C (Center) and S (South) are the sampling points.

located in the southern state of Rio Grande do Sul, Brazil, a subtropical climate region with a mean annual temperature of 16 °C and annual rainfall between 1,800 and 2,200 mm (Cfa type; Kottek et al., 2006). The region of Lake Mangueira is strongly influenced by the ENSO phenomenon and experiences high rainfall during El Niño phases and drought during La Niña (Grimm et al., 1998). The lake has a northeast-southwest orientation and an elongated morphology. This configuration aligns with the prevailing wind direction in the region, resulting in a high fetch and enhancing wind-driven dynamics along the lake's main axis. The north of the lake is influenced by a connection with wetlands while the south is influenced by dense banks of submerged, free and emerging floating macrophytes (Crossetti et al., 2014; Rodrigues et al., 2015; Ferreira et al., 2018). The lake undergoes seasonal water withdrawal to irrigate rice fields, which determines its hydroperiod comprised of low-water (generally in summer) and high-water (generally in winter) periods.

2.2. Sampling methodology

For abiotic and biological analysis, sampling was carried out twice a year, during cold (comprising the months of May, June, July, August, September or October) and warm (November, December, January, February, March or April) periods, from 2001 to 2013. Samples were collected from subsurface water at three points of the lake (north, center and south) in the pelagic region (Figure 1). Water transparency (SECCHI), dissolved oxygen (DO), water temperature (WT), electrical conductivity (COND), hydrogen ionic potential (PH) and turbidity (TURB) were measured in the field with a multi-parameter probe (Yellow Spring Model 6920, YSI, Ohio, USA). Alkalinity (ALKA), water color (WC), total suspended solids (TSS), soluble reactive phosphorus (SRP), total phosphorus (TP), total nitrogen (TN), total dissolved nitrogen (TDN), total ammoniacal nitrogen (TAN), soluble reactive silica (SRSi) were analyzed in the laboratory according to MacKereth et al. (1979) and APHA (2012). A volume of 500 mL was filtered for chlorophyll a (Chl a) analysis. Chl a was extracted from a glass microfiber filter (GF/F) into cold 90% ethanol (Jespersen & Christoffersen 1987) and measured in a spectrophotometer (APHA 2012), with values corrected for phaeopigments.

Meteorological data rainfall (PREC), air temperature (AT), wind direction (WD) and wind velocity (WV) were acquired from INMET (2025). The meteorological station was Santa Vitória do Palmar (33°51' S, 53°35' W), located 23 Km from the south end of Lake Mangueira. Each meteorological variable was averaged daily using three individual hourly measurements (at 00:00, 12:00, and 18:00), except for rainfall, which was considered as the accumulated total for the seven days prior to the sampling date. Radiation was obtained through data and remote sensing processing using the CERES/NASA product. The CERES data sets were downloaded through the web interface (NASA, 2025). Photosynthetically active radiation (direct and diffuse surface flux; PAR), and ultraviolet radiation (UVA and UVB) were selected from the product CERES_SYN1deg_Ed4A. "SYN" (Synoptic Radiative Fluxes and Clouds) means that this version provides radiation data under clear conditions and all sky conditions, "1deg" means that it has a spatial resolution of 1 degree, and "Ed4A" is the number of the version. CERES products consist of hourly data (UTC time), based on MODIS (Moderate Resolution Imaging Spectroradiometer) (CERES Science Team, 2017). Data sets were downloaded for the period 2001-2013 with an hourly frequency. CERES products were processed and analyzed using a routine in MATLAB®.

The variability of the El Niño Southern Oscillation (ENSO) during the study period was assessed using the Oceanic Niño Index (ONI; three month running mean of ERSST.v5 SST anomalies in the Niño 3.4 region). These data (2001-2013) were obtained from the National Oceanographic and Atmospheric Administration (NOAA, 2025) website. Identification of the climate anomalies of El Niño and La Niña and their periods and intensities (weak, moderate and strong) were done using reports of the Center of Weather Prediction and Climate Studies (Centro de Previsão de Tempo e Estudos Climáticos) (CPTEC, 2025). Following the methodology of Trenberth (1997), the years in which the intensity of a phenomenon was considered strong were those in which the sea surface temperature anomaly was greater than 1.5 °C in any of the months belonging to the series, whereas episodes of moderate intensity were between 1.0 and 1.5 °C, and episodes of low intensity between 0.5 and 1.0 °C. The La Niña periods comprised the years 2001, 2007, 2008, 2011 and 2012, the El Niño periods comprised the years 2002 to 2006, 2009 and 2010, while the regular year corresponded to the year 2013.

For the quantitative analysis of phytoplankton, samples were preserved with 1% acetic Lugol, following the methods of Utermöhl (1958).

Sedimentation time, as well as quantification accuracy, followed Lund et al. (1958) while density was expressed in individuals mL^{-1}. Phytoplankton biomass ($mm3\ L^{-1}$) was estimated from the product of the biovolume of the species (μm^3) and their densities (individuals mL^{-1}) (Hillebrand et al., 1999; Reynolds, 2006). In general, 30 individuals of each species were measured. Species volume was estimated by calculating the volume of the geometric shape most similar to each cell form (Hillebrand et al 1999). The descriptor species were identified separately for each year in which El Niño, La Niña, or the regular year occurred, by selecting those species that contributed with, at least 2%, of the total biomass as representatives of the community structure during that specific period. Diversity index followed Shannon & Weaver (1964); evenness, Lloyd & Ghelardi (1964) and the dominance index, Simpson (1949).

2.3. Statistical analysis

Kruskal-Wallis nonparametric tests were performed to assess significant diferences between the structure of the phytoplankton community and different ENSO periods. This test was also carried out to verify differences in physical, chemical and meteorological characteristics between the different ENSO periods. Prior to analysis, data normality was tested using the Shapiro–Wilk test, confirming non-normal distribution. The post hoc analysis for the Kruskal-Wallis test was performed using the Mann-Whitney test with Bonferroni correction. This analysis was performed using SPSS v.16.0 software (SPSS Inc. 2007).

Meteorological and limnological data were assessed and summarized by correlation-based principal components analysis (PCA), exclusively considering La Niña and El Niño years. Detrended correspondence analysis (DCA) was employed to decide between unimodal and linear-based methods; the gradient length (<1) indicated the suitability of a linear method. Redundancy analysis (RDA) was performed to identify the environmental and meteorological variables most closely associated with the descriptor species of phytoplankton during different ENSO years. The significance of the constrained axes was statistically tested by the Monte Carlo Permutation test (999 permutations). The abiotic datasets were normalized by range and the biomass of phytoplankton was transformed by log x+1. The RDA was performed with PC-ORD v.6 software (McCune & Mefford 2011). A complete list of species names and their corresponding acronyms is provided in Table 1.

Table 1. List of indicator species used in the redundancy analysis and their respective acronyms.

Group	Species	Acronyns
CYA	*Anathece smithii* (Komárková-Legnerová & Cronberg) Komárek, Kastovsky & Jezberová	Asmi
CYA	*Aphanocapsa conferta* (West & G.S.West) Komárková-Legnerová & Cronberg 1994	Aconf
CYA	*Aphanocapsa delicatissima* West & G.S.West 1912	Adeli
CYA	*Aphanocapsa elachista* West & G.S.West 1894	Aela
CYA	*Aphanocapsa incerta* (Lemmermann) G.Cronberg & Komárek	Ainc
CYA	*Aphanothece stagnina* (Sprengel) A.Braun	Asta
BAC	*Coscinodiscus* Ehrenberg, 1839	Cosci
BAC	*Cyclotella meneghiniana* Kützing 1844	Cmen
CHL	*Desmodesmus armatus var. longispina* (Chodat) E.Hegewald 2000	Darm
CHL	*Desmodesmus denticulatus* (Lagerheim) S.S.An, T.Friedl & E.Hegewald 1999	Dden
CHL	*Desmodesmus opoliensis* (P.G.Richter) E.Hegewald 2000	Dopo
BAC	*Gyrosigma acuminatum* (Kützing) Rabenhorst 1853	Gacu
CHL	*Hariotina reticulata* P.A.Dangeard 1889	Hret
CYA	*Limnococcus limneticus* (Lemmermann) Komárková, Jezberová, O.Komárek & Zapomelová	Llim
CYA	*Microcystis aeruginosa* (Kützing) Kützing 1846	Maer
CHL	*Mougeotia* sp. C.Agardh, 1824	Moug
CHL	*Oocystis lacustris* Chodat 1897	Olac
CYA	*Planktolyngbya contorta* (Lemmermann) Anagnostidis & Komárek 1988	Pcon
CYA	*Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerová & Cronberg 1992	Plim
CHL	*Pleurotaenium* sp. Nägeli, 1849	Pleu
CYA	*Radiocystis fernandoi* Komárek & Komárková-Legnerová 1993	Rfern
CHL	*Scenedesmus* cf. *caribeanus* Komárek 1983	Scar
CHL	*Scenedesmus obtusus* Meyen 1829	Sobt
CYA	*Snowella lacustris* (Chodat) Komárek & Hindák 1988	Slac
ZYG	*Spondylosium* sp. Brébisson ex Kützing	Spon
CYA	*Synechococcus nidulans* (Pringsheim) Komárek 1970	Snid
BAC	*Tabellaria flocculosa* (Roth) Kützing 1844	Tflo
CHL	*Treubaria* sp. C.Bernard, 1908	Treub
BAC	*Ulnaria acus* (Kützing) Aboal 2003	Uacu

Legend: CYA = Cyanobacteria; CHL = Chlorophyceae; BAC = Bacillariophyceae; ZYG = Zygnemaphyceae.

3. Results

Between 2001 and 2013, seven El Niño years, five La Niña years, and one regular year were identified. Significant differences were observed in meteorological and limnological variables, including TSS, SRSi, TP, TN, TDN, COND, DO, ALKA, TAN, and WV (Table 2). These results indicate variations in nutrient dynamics, physico-chemical properties of the water, and atmospheric conditions associated with distinct climatic regimes. Overall, the regular year exhibited higher concentrations of nutrients and parameters related to ALKA and COND, whereas El Niño years were characterized by greater availability of DO and SRSi, and La Niña years by increased wind velocity. Although only one regular year was present in the time series, its inclusion provides a unique reference for assessing phytoplankton dynamics under conditions not influenced by ENSO. This limitation necessitates cautious interpretation of the results. Nevertheless, the analysis of this regular year is essential for elucidating ecological responses under scenarios of increased climatic stability. DO was significantly higher during El Niño years compared to La Niña, whereas SRSi was greater in El Niño than in both La Niña and the regular year. ALKA, COND, TN, TDN, and TAN were higher in regular years compared to El Niño and La Niña. For TP and TB, El Niño years differed significantly from the others, showing lower values. WV was greater in La Niña compared to El Niño and the regular year. These differences reflect shifts in physicochemical patterns and nutrient availability associated with ENSO periods.

The PCA performed with environmental and meteorological variables for the different ENSO periods explained 52.5% ($p<0.01$) of the variability in La Niña years with the first three axes (Figure 2). Regardless of the intensity of the event (weak or moderate), a separation was observed in relation to years without the event. Most years of weak and moderate La Niña events were ordered on Axis 1 with high values for ALKA (r = -0.77), TN (r = -0.62), TDN (r = -0.62), TAN (r = -0.55), COND (r = -0.52), UVA (r = 0.79), UVB (r = 0.78) and PAR (r = 0.78). Regular years were ordered by Axis 2, with higher values of DO (r = –0.45), PREC (r = –0.40), SRSi (r = 0.67), WT (r = 0.62), UVB (r = 0.57), COND (r = 0.56), TDN (r = 0.52) and TN (r = 0.51). The positive side of Axis 3 ordered regular year with higher values of TP (r = 0.85) and SRP (r = 0.78), as well as most years of weak La Niña events with higher values of PREC (r = - 0.80).

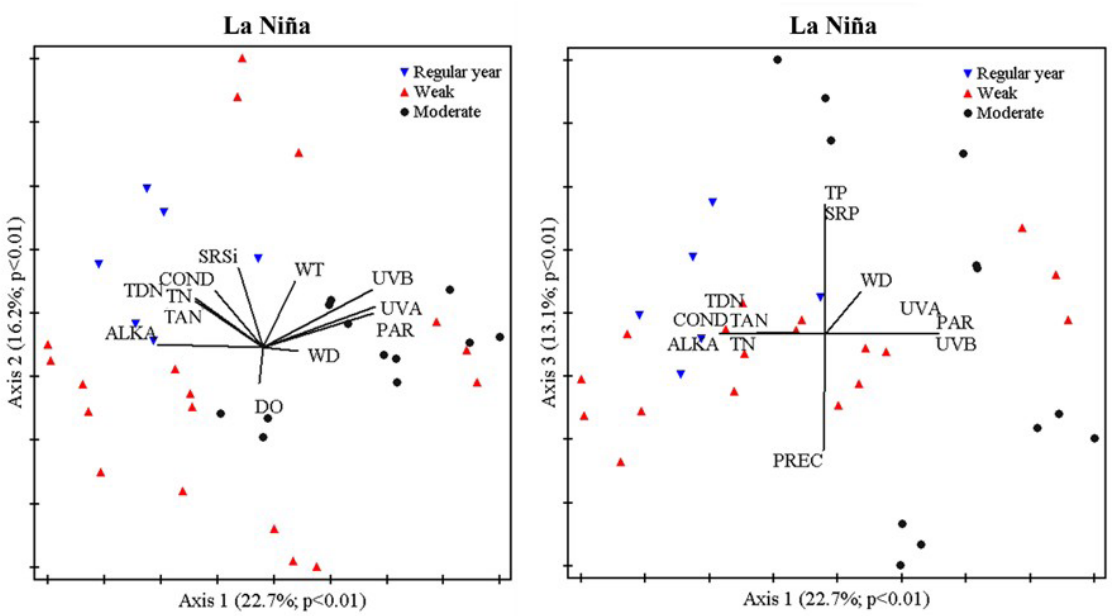

Figure 2. Biplot of axes 1 and 2, and axis 1 and 3 of the principal component analysis (PCA) of environmental variability of samples from La Niña years and one regular year (moderate) in Lake Mangueira from 2001 to 2013. TP = total phosphorus; SRP = soluble reactive phosphorus; TN = total nitrogen; TDN = total dissolved nitrogen; SECCHI = water transparency; COND = conductivity; DO = dissolved oxygen; SRSi = soluble reactive silica; AT = air temperature; WT = water temperature; WV = wind velocity; ONI = Oceanic Niño Index; TAN = total ammoniacal nitrogen.

Table 2. Variation of environmental and biological variables, including mean, minimum (Min), maximum (Max), standard deviation (SD), and results of the Kruskal–Wallis nonparametric test comparing El Niño, La Niña, and the regular year periods (N = 78, $p < 0.05$).

Environmental and biological variables	EL NIÑO YEARS				LA NIÑA YEARS				REGULAR YEAR				*p* value
	Mean	Min	Max	SD	Mean	Min	Max	SD	Mean	Min	Max	SD	
Water temperature (°C)	18.85	11.21	25.50	3.83	20.09	10.43	27.50	4.66	20.61	18.83	21.79	0.97	0.25
Condutivity (mS cm^{-1})	0.28 a	0.19	0.39	0.06	0.35[b]	0.27	0.48	0.06	0.39[b]	0.35	0.44	0.04	**0.00**
Dissolved oxygen (mg L^{-1} O_2)	9.52 a	7.66	12.12	1.04	8.62[b]	5.68	10.90	1.30	9.04[ab]	8.02	9.41	0.56	**0.03**
pH	8.07	6.76	8.81	0.48	8.16	7.02	8.73	0.44	8.18	7.90	8.47	0.26	0.43
Depth (m)	2.40	0.80	4.30	0.71	2.08	0.53	5.50	1.09	2.73	0.70	6.31	2.50	0.17
Secchi (m)	0.86	0.16	2.00	0.41	0.85	0.50	1.54	0.21	0.81	0.65	1.06	0.16	0.75
Alkalinity (mg L^{-1} $CaCO_3$)	60.78 a	43.80	76.56	9.77	65.16[ab]	18.93	93.75	20.83	81.84[b]	67.58	87.67	7.48	**0.00**
Water colour (mg L^{-1} PtCo)	4.10	0.00	15.00	4.29	5.44	0.70	40.00	8.67	4.07	2.50	7.80	2.00	0.40
Soluble reactive silica (mg L^{-1})	3.70 a	1.44	7.80	1.75	2.59[b]	1.10	4.08	0.78	3.65 a	2.85	5.75	1.06	0.01
Total suspended solids (mg L^{-1})	19.82 a	1.00	72.00	14.75	19.23 a	6.00	45.00	9.37	49.67[b]	20.00	120.00	35.47	**0.01**
Total phosphorus (mg L^{-1} P)	0.04 a	0.01	0.16	0.03	0.07[b]	0.02	0.24	0.06	0.07[b]	0.05	0.10	0.02	**0.00**
Soluble reactive phosphorus (mg L^{-1})	0.02	0.00	0.16	0.03	0.03	0.00	0.11	0.03	0.03	0.01	0.05	0.02	0.24
Total nitrogen (mg L^{-1})	0.25 a	0.03	0.78	0.17	0.26 a[b]	0.02	0.62	0.17	0.44[b]	0.39	0.62	0.09	**0.01**
Total Dissolved Nitrogen (mg L^{-1})	0.13 a	0.01	0.37	0.11	0.19 a[b]	0.01	0.52	0.15	0.34[b]	0.31	0.40	0.05	**0.00**
Total amoniacal nitrogen (mg L^{-1})	0.12 a	0.01	2.00	0.32	0.08 a[b]	0.01	0.21	0.06	0.19[b]	0.03	0.43	0.13	**0.01**
CoeK	2.18	0.72	9.00	1.44	1.79	0.94	2.88	0.45	1.83	1.36	2.22	0.33	0.75
Zeu/Zmax	0.97	0.21	3.33	0.60	1.22	0.35	5.13	1.03	1.27	0.32	2.94	0.96	0.75
Chlorophyll *a* (µg L^{-1})	7.54	0.20	34.08	8.02	11.61	0.19	63.30	15.55	3.75	2.87	5.05	0.95	0.22
Air temperature (°C)	17.87	8.57	25.50	4.13	18.03	8.60	26.27	4.93	18.53	17.33	19.20	0.86	0.94
Rainfall (mm)	27.28	0.00	116.20	29.03	25.83	0.00	57.10	18.66	10.80	2.10	19.50	9.53	0.22
Wind velocity (m s^{-1})	3.25[a]	1.33	6.33	1.52	4.21[b]	1.00	8.00	1.67	3.05[ab]	1.67	3.77	0.89	**0.04**
Wind direction	18.31	5.00	36.00	8.70	15.80	0.00	32.00	10.32	13.17	0.00	23.00	7.39	0.22
Radiation UVA (W m^{-2})	18.47	3.00	32.83	8.37	18.22	4.87	29.09	7.84	17.36	11.86	24.39	6.09	0.90
Radiation UVB (W m^{-2})	0.44	0.06	0.92	0.25	0.45	0.08	0.76	0.23	0.47	0.37	0.63	0.11	0.90
Radiation PAR (W m^{-2})	141.46	20.38	253.63	65.31	138.74	32.43	224.09	61.84	128.34	79.85	189.78	53.66	0.91
ONI	0.27[a]	-1.70	1.30	0.78	-0.60[b]	-1.50	0.20	0.54	-0.20[ab]	-0.20	-0.20	0.00	**0.00**
Bacillariophyceae (mm^3 L^{-1})	0.51	0.00	3.01	0.70	0.45	0.00	3.54	0.75	1.07	0.00	4.38	1.74	0.65
Chrysophyceae (mm^3 L^{-1})	0.01	0.00	0.22	0.04	0.00	0.00	0.04	0.01	0.00	0.00	0.00	0.00	0.73
Chlorophyceae (mm^3 L^{-1})	0.77	0.01	4.03	0.84	1.00	0.00	4.31	0.88	1.49	0.00	3.89	1.68	0.36
Cryptophyceae (mm^3 L^{-1})	0.01	0.00	0.14	0.03	0.01	0.00	0.14	0.03	0.01	0.00	0.06	0.02	0.72
Cyanobacteria (mm^3 L^{-1})	1.95[a]	0.19	12.95	2.78	3.72[b]	0.47	11.96	2.94	5.91[b]	4.55	7.07	1.00	**0.00**
Dinophyceae (mm^3 L^{-1})	0.00	0.00	0.07	0.01	0.00	0.00	0.04	0.01	0.00	0.00	0.00	0.00	0.80
Euglenophyceae (mm^3 L^{-1})	0.01	0.00	0.12	0.03	0.03	0.00	0.30	0.08	0.01	0.00	0.05	0.02	0.77
Raphidophyceae (mm^3 L^{-1})	0.00[a]	0.00	0.00	0.00	0.00[a]	0.00	0.00	0.00	0.39[b]	0.00	1.33	0.62	**0.00**
Zygnemaphyceae (mm^3 L^{-1})	0.19	0.00	6.24	0.96	0.05	0.00	0.48	0.11	0.01	0.00	0.08	0.03	0.65
Total Biomass (mm^3 L^{-1})	3.45[a]	0.57	13.05	3.27	5.26[b]	0.48	13.22	3.45	8.89	5.86[b]	11.76	2.25	**0.00**
Richness (number of species)	18.29	7.00	31.00	5.54	20.03	4.00	35.00	6.24	17.17	5.00	30.00	11.20	0.43
Dominance (D)	0.22	0.09	0.98	0.16	0.22	0.08	0.62	0.13	0.31	0.12	0.65	0.22	0.50
Shannon index (H)	2.06	0.07	2.67	0.49	2.04	0.75	2.88	0.46	1.76	0.70	2.48	0.79	0.70
Evenness (e^H/S)	0.49	0.15	0.75	0.16	0.44	0.16	0.87	0.15	0.44	0.34	0.51	0.06	0.12

Bold values indicate significant differences. Means followed by different superscript letters differ significantly from one another ($p < 0.05$), according to Mann-Whitney post hoc tests with Bonferroni correction performed after the Kruskal-Wallis test.

The PCA performed with El Niño years explained 50% ($p < 0.01$) of the data variability with its first three axes (Figure 3). Biplot analysis showed the separation of most El Niño years from regular year, regardless of the intensity of the events. For Axis 1, El Niño years were mainly associated with higher values of WT (r = 0.85), UVB (r = 0.80), UVA (r = 0.78), PAR (r = 0.75), DO (r = 0.50) and ONI (r = 0.50). The positive side of Axis 2 separated the sample units of the year without the event, showing the highest relationship with TDN (r = 0.72) and ALKA (r = 0.70), and on the negative side of the axis the association with UVA (r = -0.56), UVB (r = -0.56), PAR (-0.55), PREC (r = -0.53) and WV (r = -0.50). For Axis 3, the regular year was associated with higher SRP (r = 0.89) and TP (r = 0.80) values.

A total of 188 species distributed in 8 phytoplanktonic groups were recorded, with Chlorophyceae (80 species), Cyanobacteria (39 species), Bacillariophyceae (36 species) and Zygnemaphyceae (14 species) had the highest species richness values. A total of 106 species were found in La Niña periods (total biomass of 157.84 $mm^3\ L^{-1}$) and 109 (144.93 $mm^3\ L^{-1}$) and 57 (53.3 $mm^3\ L^{-1}$) in El Niño periods and the regular year, respectively. A significant difference was observed for phytoplankton biomass among El Niño, La Niña and the regular year (Table 3). During La Niña, phytoplankton biomass was higher (mean of 5.26 $mm^3\ L^{-1}$), driven by increased WV (mean of 4.21 $m\ s^{-1}$), elevated concentrations of TP (mean of 0.07 $mg\ L^{-1}$) and TN (mean of 0.26 $mg\ L^{-1}$), which favored cyanobacteria growth (mean of 3.72 $mm^3\ L^{-1}$) and contributed to the overall increase in total biomass. Among the registered groups, Cyanobacteria and Raphidophyceae showed a significant difference in biomass between the periods (Table 3). During El Niño, cyanobacterial biomass was low (mean of 1.95 $mm^3\ L^{-1}$), likely related to reduced nutrient concentrations, such as TP (mean of 0.04 $mg\ L^{-1}$) and TN (mean of 0.25 $mg\ L^{-1}$), in addition to lower ALKA and COND. In the regular year, the occurrence of Raphidophyceae (0.39 $mm^3\ L^{-1}$) was associated with environmental conditions characterized by higher COND (mean of 0.39 $mS\ cm^{-1}$) and ALKA (mean of 81.84 $mg\ L^{-1}\ CaCO_3$). Additionally, higher concentrations of TN (mean of 0.44 $mg\ L^{-1}$), TDN (mean of 0.34 $mg\ L^{-1}$), and TAN (mean of 0.19 $mg\ L^{-1}$) were recorded, providing essential nutrients for the growth of this group. The lower WV (mean of 3.05 $m\ s^{-1}$) also favored the development of Raphidophyceae by creating a less turbulent environment. The analysis of phytoplankton community diversity index, species richness, dominance and evenness did not show significant differences between ENSO and the regular year periods (Table 2; Figure 4).

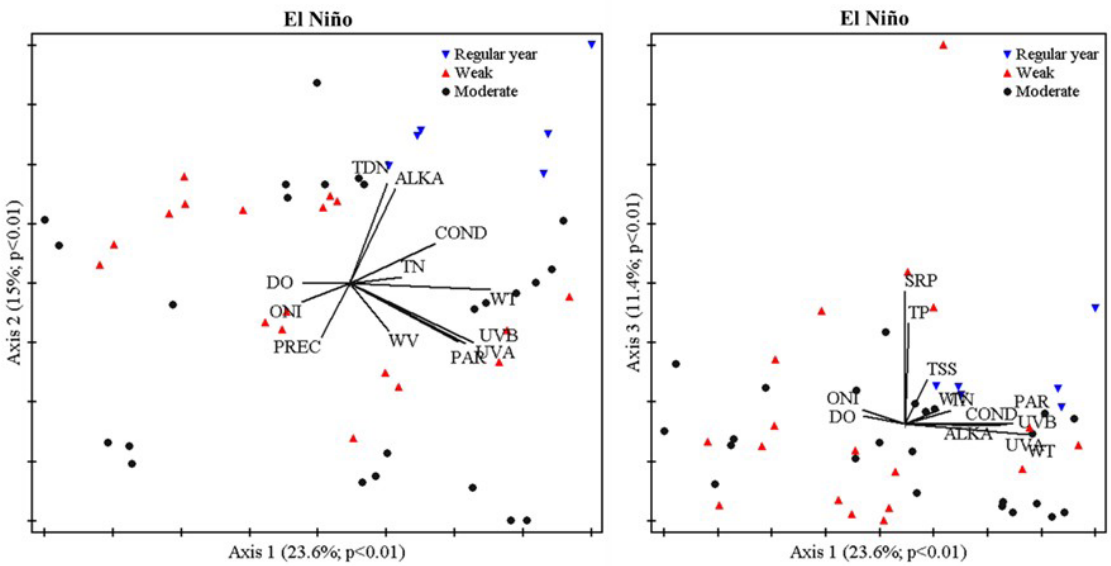

Figure 3. Biplot of axes 1 and 2, and axis 1 and 3 of the principal component analysis (PCA) of environmental variability of sampled from El Niño years and one regular year (moderate) in Lake Mangueira from 2001 to 2013. TSS = total suspended solids; TP = total phosphorus; SRP = soluble reactive phosphorus; TN = total nitrogen; TDN = total dissolved nitrogen; COND = conductivity; DO = dissolved oxygen; WT = water temperature; WV = wind velocity; ONI = Oceanic Niño Index; PAR = Photosynthetically active radiation; UVA and UVB = ultraviolet radiation.

Table 3. Percentage (%) of contribution biomass of descriptor algal species (> 2%) to total algal biomass during the years of La Niña occurrence (N=30).

Descriptor species of La Niña periods						
Group	**Species**	**2001**	**2007**	**2008**	**2011**	**2012**
BAC	Coscinodiscus Ehrenberg, 1839	5.9	-	-	-	-
BAC	*Tabellaria flocculosa* (Roth) Kützing 1844	12.0	6.5	-	-	4.6
BAC	*Ulnaria acus* (Kützing) Aboal 2003	-	-	-	-	2.3
CHL	*Desmodesmus denticulatus* (Lagerheim) S.S.An, T.Friedl & E.Hegewald 1999	-	-	-	6.1	-
CHL	*Desmodesmus opoliensis* (P.G.Richter) E.Hegewald 2000	-	-	-	7.2	-
CHL	*Hariotina reticulata* P.A.Dangeard 1889	3.8	-	-	-	-
CHL	*Mougeotia* sp. C.Agardh, 1824	5.5	3.2	2.3	-	-
CHL	*Oocystis lacustris* Chodat 1897	7.2	4.9	10.1	9.4	7.8
CHL	*Pleurotaenium* sp. Nägeli, 1849	-	-	10.0	-	-
CHL	*Scenedesmus ecornis* (Ehrenberg) Chodat 1926	2.1	-	-	-	-
CHL	*Stauridium tetras* (Ehrenberg) E.Hegewald 2005	-	-	-	2.5	-
CHL	*Tetraëdron triangulare* Korshikov 1953	-	-	-	2.2	-
CYA	*Anathece smithii* (Komárková-Legnerová & Cronberg) Komárek, Kastovsky & Jezberová	-	4.3	4.0	3.4	10.8
CYA	*Aphanocapsa conferta* (West & G.S.West) Komárková-Legnerová & Cronberg 1994	9.9	29.5	44.1	6.8	34.9
CYA	*Aphanocapsa delicatissima* West & G.S.West 1912	2.6	2.0	-	4.4	3.1
CYA	*Aphanocapsa incerta* (Lemmermann) G.Cronberg & Komárek	-	14.9	6.5	15.9	6.9
CYA	*Aphanothece stagnina* (Sprengel) A.Braun	-	-	-	2.2	-
CYA	*Limnococcus limneticus* (Lemmermann) Komárková, Jezberová, O.Komárek & Zapomelová	-	2.2	-	6.6	2.4
CYA	*Microcystis aeruginosa* (Kützing) Kützing 1846	-	10.2	-	-	-
CYA	*Planktolyngbya contorta* (Lemmermann) Anagnostidis & Komárek 1988	9.4	3.6	10.5	12.5	8.6
CYA	*Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerová & Cronberg 1992	5.1	-	-	3.3	2.7
CYA	*Pseudanabaena catenata* Lauterborn 1915	-	-	-	2.8	-
CYA	*Radiocystis fernandoi* Komárek & Komárková-Legnerová 1993	12.6	-	-	-	-
CYA	*Radiocystis geminata* Skuja 1948	2.3	-	-	-	-
CYA	*Snowella lacustris* (Chodat) Komárek & Hindák 1988	-	4.1	-	-	4.0
Total biomass (%)		**78.1**	**85.4**	**87.6**	**85.1**	**88.2**

Legend: CYA = cyanobacteria; CHL = chlorophyceae; BAC = bacillariophyceae; ZYG = zygnemaphyceae; - = zero.

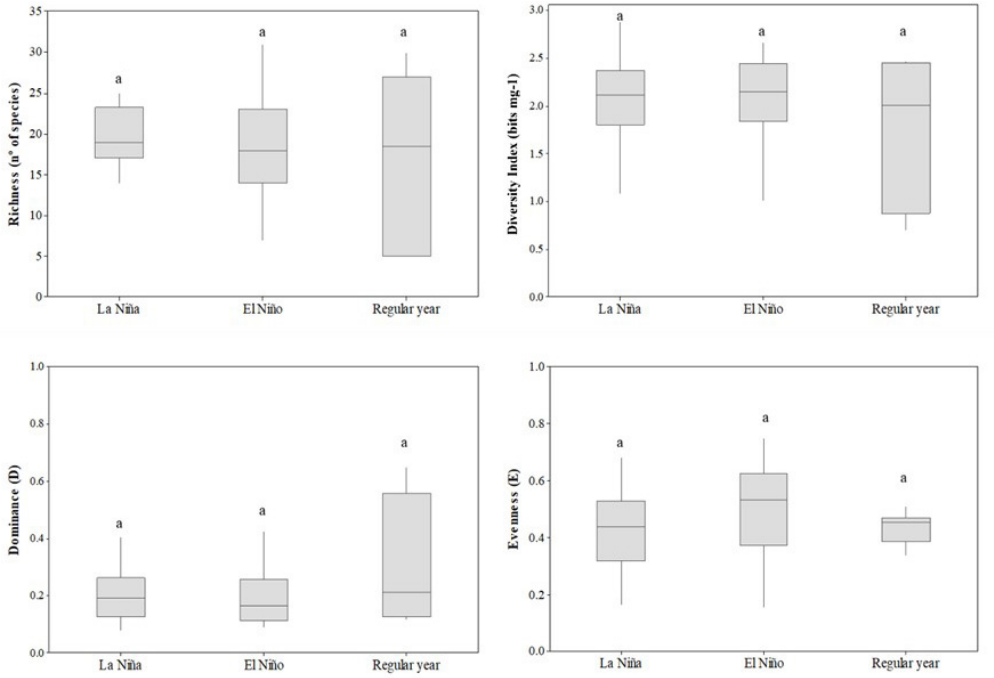

Figure 4. Boxplot (median, interquartile ranges, n = 78) of dominance (D), Evenness (E), Richness (nº of species) and Diversity index (bits mg^{-1}). Different letters above the boxes indicate statistically significant differences among periods.

For the La Niña years, 25 descriptor species were identified, 13 species belonging to the Cyanobacteria group, 9 species belonging to the Chlorophyceae group and 3 species of Bacillariophyceae (Table 3). For the El Niño years, 33 descriptor species were recorded, being 17 species of Cyanobacteria, 9 species of Chlorophyceae, 5 species of Bacillariophyceae and 2 Zygnemaphyceae (Table 4). For the regular year, 12 descriptor species were identified, 7 species of Cyanobacteria, 2 species of Chlorophyceae, 2 species of Bacillariophyceae and 1 of Raphidophyceae (Table 5). In general, the Cyanobacteria group was represented by *Aphanocapsa conferta, Microcystis aeruginosa*, *Planktolyngbya contorta* and *Anathece smithii*. The representatives of Chlorophyceae were *Oocystis lacustris* and Bacillariophyceae *Tabellaria flocculosa*. Among the periods studied, La Niña events showed higher biomass of CYA and EUG than the other periods, as well as El Niño events recorded higher biomass of CHL, BAC, ZYG, CRY and CHR (Figure 5). On the other hand, regular year was the only period in which RAP were recorded.

Table 4. Percentage (%) of contribution biomass of descriptor algal species (> 2%) to total algal biomass during the years of El Niño occurrence (N=42).

Descriptor species of El Niño periods								
Group	**Species**	**2002**	**2003**	**2004**	**2005**	**2006**	**2009**	**2010**
BAC	*Cyclotella meneghiniana* Kützing 1844	2.8	4.0	-	-	11.9	2.0	-
BAC	*Gomphonema parvulum* (Kützing) Kützing 1849	-	3.1	-	-	-	-	-
BAC	*Navicula cryptocephala* Kützing 1844	-	-	-	4.2	-	-	-
BAC	*Tabellaria flocculosa* (Roth) Kützing 1844	16.6	4.4	5.5	8.4	15.0	-	-
BAC	*Ulnaria acus* (Kützing) Aboal 2003	3.0	-	-	-	-	-	9.4
CHL	*Desmodesmus armatus* var. *longispina* (Chodat) E.Hegewald 2000	-	-	-	-	-	-	8.5
CHL	*Hariotina reticulata* P.A.Dangeard 1889	-	5.7	-	-	-	-	-
CHL	*Oocystis lacustris* Chodat 1897	3.7	5.5	2.2	-	3.1	18.2	7.8
CHL	*Oocystis parva* West & G.S.West 1898	-	-	-	-	-	-	3.8
CHL	*Pseudopediastrum boryanum* (Turpin) E.Hegewald 2005	-	-	-	4.9	3.1	2.2	-
CHL	*Scenedesmus* cf. *caribeanus* Komárek 1983	-	-	-	2.2	7.5	-	-
CHL	*Scenedesmus obtusus* Meyen 1829	-	-	-	24.4	-	-	-
CHL	*Tetraëdron minimum* (A.Braun) Hansgirg 1889	-	-	-	2.0	-	-	-
CHL	*Treubaria* sp. 2 C.Bernard. 1908	-	-	6.7	-	-	-	-
CYA	*Anathece smithii* (Komárková-Legnerová & Cronberg) Komárek. Kastovsky & Jezberová	2.1	-	-	-	-	6.4	2.9
CYA	*Aphanocapsa conferta* (West & G.S.West) Komárková-Legnerová & Cronberg 1994	-	-	-	-	-	11.7	-
CYA	*Aphanocapsa delicatissima* West & G.S.West 1912	8.9	2.6	4.8	8.7	4.7	4.7	7.6
CYA	*Aphanocapsa elachista* West & G.S.West 1894	-	-	-	-	-	-	6.8
CYA	*Aphanocapsa incerta* (Lemmermann) G.Cronberg & Komárek	-	-	-	-	-	18.4	-
CYA	*Chroococcus dispersus* (Keissler) Lemmermann	-	-	-	-	-	2.6	-
CYA	*Coelomoron* sp. H.F.Buell, 1938	-	-	-	-	-	-	2.8
CYA	*Eucapsis* sp. F.E.Clements & H.L.Shantz, 1909	2.9	-	-	3.1	-	-	-
CYA	*Gloeocapsa* sp. Kützing, 1843	-	-	-	-	-	2.4	-
CYA	*Limnococcus limneticus* (Lemmermann) Komárková, Jezberová, O.Komárek & Zapomelová	-	-	-	-	-	-	9.3
CYA	*Microcystis aeruginosa* (Kützing) Kützing 1846	-	38.1	-	-	-	-	-
CYA	*Planktolyngbya contorta* (Lemmermann) Anagnostidis & Komárek 1988	22.8	4.3	3.0	10.5	6.4	10.2	10.2
CYA	*Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerová & Cronberg 1992	3.3	-	-	2.4	-	-	7.2
CYA	*Radiocystis fernandoi* Komárek & Komárková-Legnerová 1993	-	14.6	-	-	-	-	-
CYA	*Snowella lacustris* (Chodat) Komárek & Hindák 1988	10.1	2.7	-	11.0	3.5	2.3	-
CYA	*Synechococcus nidulans* (Pringsheim) Komárek 1970	-	-	63.2	-	-	-	-
CYA	*Synechocystis aquatilis* Sauvageau 1892	-	-	-	2.0	-	-	-
ZYG	*Closterium kuetzingii* Brébisson	-	-	-	-	-	-	4.0
ZYG	*Spondylosium* sp. Brébisson ex Kützing	-	-	-	-	28.2	-	-
Total biomass (%)		**76.1**	**85.0**	**85.5**	**83.7**	**83.6**	**81.0**	**80.2**

Legend: CYA = cyanobacteria; CHL = chlorophyceae; BAC = bacillariophyceae; ZYG = zygnemaphyceae; - = zero.

Table 5. Percentage (%) of contribution biomass of descriptor algal species (> 2%) to total algal biomass for the regular year (N=6).

Descriptor species of Regular year		
Group	**Species**	**2013**
BAC	*Coscinodiscus* Ehrenberg, 1839	2.1
BAC	*Gyrosigma acuminatum* (Kützing) Rabenhorst 1853	8.2
CHL	*Desmodesmus armatus* var. *longispina* (Chodat) E.Hegewald 2000	3.2
CHL	*Oocystis lacustris* Chodat 1897	3.6
CYA	*Anathece smithii* (Komárková-Legnerová & Cronberg) Komárek, Kastovsky & Jezberová	15.5
CYA	*Aphanocapsa incerta* (Lemmermann) G.Cronberg & Komárek	3.0
CYA	*Chroococcus dispersus* (Keissler) Lemmermann	3.3
CYA	*Microcystis aeruginosa* (Kützing) Kützing 1846	25.8
CYA	*Planktolyngbya contorta* (Lemmermann) Anagnostidis & Komárek 1988	4.6
CYA	*Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerová & Cronberg 1992	4.0
CYA	*Snowella lacustris* (Chodat) Komárek & Hindák 1988	8.0
RAP	*Vacuolaria* sp. 2 Cienkowski, 1870	2.5
Total biomass (%)		**83.9**

Legend: BAC = bacillariophyceae; CHL = chlorophyceae; CYA = cyanobacteria; RAP = Raphidophyceae.

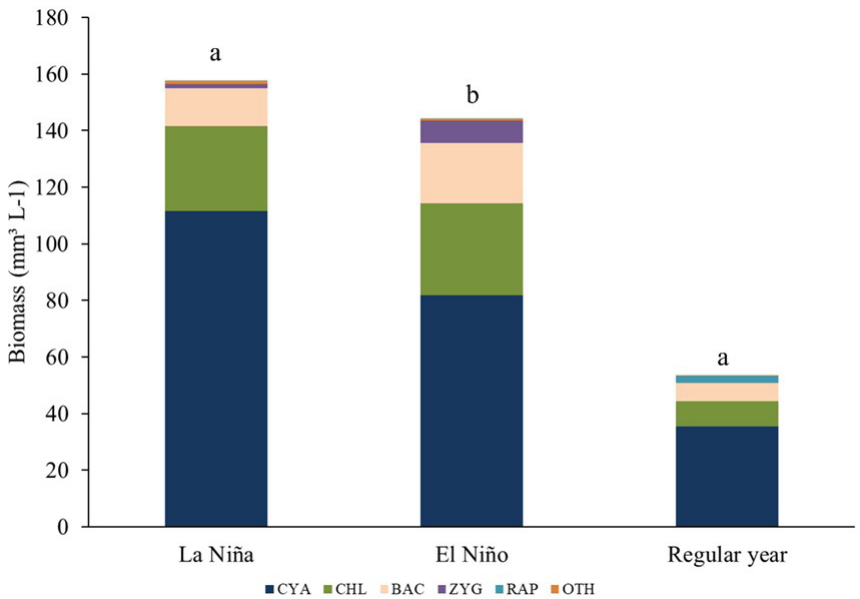

Figure 5. Phytoplankton classes biomass contribution in Lake Mangueira from 2001 to 2013 (n=78).
Legend: CYA = cyanobacteria; CHL = chlorophyceae; BAC = bacillariophyceae; ZYG = zygnemaphyceae; RAP = Raphidophyceae and OTH = others. Different letters above the boxes indicate statistically significant differences among periods.

Redundancy analysis (RDA) allowed exploring the relationship between the main descriptor species and environmental variables (meteorological and limnological) considering the biomass of the species over the period studied (2001 – 2013). This integrated analysis indicated the significant ordination of the first three axes ($p < 0.05$). Axis 1 was mainly correlated with COND (r = 0.38), WV (r = 0.14), WT (r = 0.13), UVB (r = 0.1), DO (r = -0.54), SRSi (r = -0.40), Ainc (r = 0.55), Aconf (r = 0.54), Pcon (r = 0.50), Olac (r= 0.47), Asmi (r = 0.40), Treub (r = -3.22), Tflo (r = -0.23) e Scar (-0.29). Axis 2 was mainly correlated with SECCHI (r = -0.28) and PREC (r = 0.33) and Axis 3 was correlated with TSS (r = 0.48), SRSi (r = 0.40), WT (r = 0.40), COND (r = 0.36), DEP (r = 0.35), UVB (r = 0.34), TN (r = 0.33), Asmi (r = 0.45), Maer (r= 0.40), Llim (r = -0.15) e Moug (-0.17). Axis 1 separated, mostly, El Niño in negative side and La Niña periods and the regular year on the positive side (Figure 6) Axis 1 ordination showed, on its negative side, species as Scar (r = -0.29), Tflo (r = -0.23) and

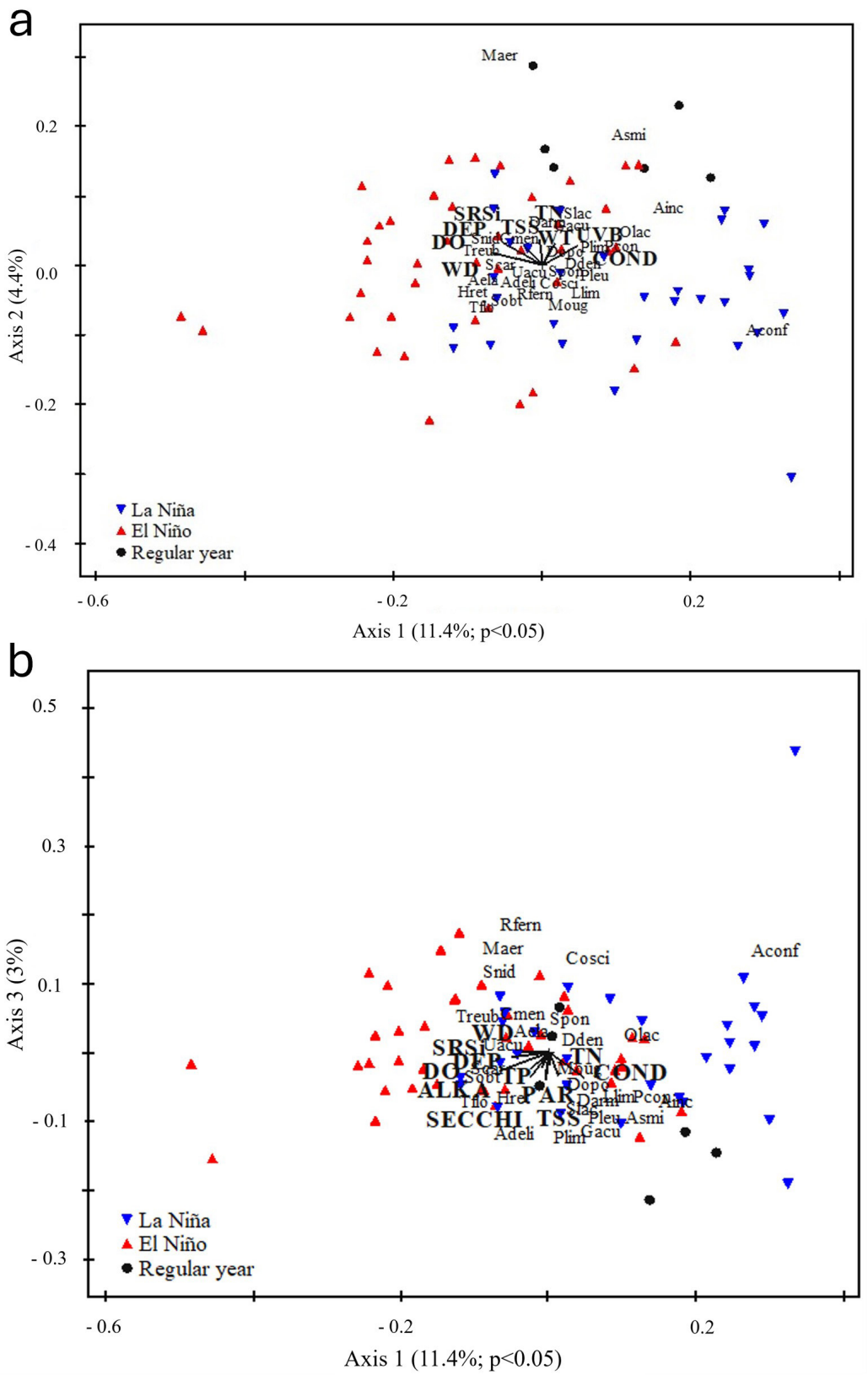

Figure 6. RDA ordination (axis 1 and 2; a; axis 1 and 3, b) of the descriptor species according to abiotic variables in El Niño periods, La Niña periods and Regular year, in Lake Mangueira from 2001 to 2013. ALKA = alkalinity; TSS = total suspended solids; TP = total phosphorus; SRP = soluble reactive phosphorus; TN = total nitrogen; TDN = total dissolved nitrogen; SECCHI = water transparency; COND = conductivity; DO = dissolved oxygen; SRSi = soluble reactive silica; AT = air temperature; WT = water temperature; WV = wind velocity; ONI = Oceanic Niño Index.

Treub (r = -0.22) mostly ordinated with El Niño periods, associated with the higher values of DO, SRSi, DEP and TSS. On the positive side of Axis 1, the species Ainc (r = 0.55), Aconf (r = 0.54), Pcon (r = 0.50), Olac (r= 0.47), Asmi (r = 0.40) and Lilim (r = 0.34) associated with higher values of COND, WV, WT and UVB. Axis 2 ordination showed, on its negative side, especially Moug (r = -0.17) and Llim (r = -0.15) associated with higher values of PREC and SECCH and on its positive side Asmi (r = 0.45) and Maer (r = 0.40) ordinated with higher values TSS, SRSi, WT, COND, DEP, UVB and TN (Figure 6). Axis 3 ordination showed, on its negative side, Plim (r = -0.44), Gacu (r = -0.23), Pleu (r = -0.24) and Asmi (r = -0.22) associated with ALKA, SECCHI, COND and TN, and on its positive side, Cosci (r = 0.47) and Rfern (r = 0.38) ordinated with higher values PREC and WD. In summary, this analysis made it possible to identify the clear separation between the ENSO periods, as well as to visualize the similarities between the La Niña period and the regular year.

4. Discussion

The results of this study indicate that El Niño and La Niña events did not significantly affect the species richness, diversity, dominance, or evenness of the phytoplankton community in Lake Mangueira. However, total phytoplankton biomass was notably higher during La Niña years, which coincided with drought conditions. Similarly, the integrated analysis of environmental variables and indicator species using Redundancy Analysis (RDA) revealed a significant ordination of sets of species exhibiting similar ecological response to the environmental conditions characterizing each period. Moreover, phytoplankton groups were also influenced by the ENSO phenomenon; for example, cyanobacteria exhibited lower biomass values during El Niño years.

In southern Brazil, particularly in the region where Lake Mangueira is located, rainfall patterns are influenced by various climate indices, including both direct and indirect effects of interannual phenomena such as El Niño and La Niña, as well as the Pacific Decadal Oscillation (PDO), during both dry and wet periods (Motta Marques et al., 2013). This region typically exhibits well-distributed rainfall throughout the year (Rao & Hada, 1990) and is affected by frontal systems, cyclones, cold fronts, atmospheric blocking events, and mesoscale convective systems. Nevertheless, several studies have reported the occurrence of extreme rainfall events during El Niño years (Rao & Hada, 1990; Grimm et al., 1998; Grimm & Pscheidt, 2001; Haylock et al., 2006). These climatic influences contribute to Lake Mangueira being a highly hydrodynamic system, with limnological characteristics that are strongly shaped by regional atmospheric processes (Wieliczko et al., 2021).

In light of the limnological conditions associated with ENSO events in Lake Mangueira, the RDA analysis revealed a clear separation between the El Niño and La Niña periods based on the distribution of phytoplankton species. In the El Niño period, a group formed mainly by *Treubaria* sp., *Tabellaria flocculosa* and *Scenedesmus* cf. *caribeanus* was ordered to the highest concentrations of DO and SRSi, suggesting a preference for more oxygenated and silica-rich environments conditions that favor diatoms and chlorophytes adapted to well-oxygenated waters (Costa et al., 2021). During La Niña period a set of species formed mainly by *Aphanocapsa incerta*, *Aphanocapsa conferta*, *Planktolyngbya contorta*, *Oocystis lacustris*, *Anathece smithii* and *Limnococcus limneticus* was associated with higher values of COND, WV, WT and UVB indicating mixed and nutrient-enriched environments that favor the development of colonial and filamentous cyanobacteria (Burford et al., 2023). Variations in species contributions were evident across ENSO events, although such changes were not reflected in aggregated community-level metrics. Thus, the observed responses indicate distinct adaptive strategies to hydrological and nutritional oscillations imposed by ENSO, highlighting that the functional structure of phytoplankton can undergo subtle and specific reorganization even when traditional community indicators remain stable.

The descriptor species are those that contribute to the highest biomass of the phytoplankton community by optimizing resources more efficiently and overcoming loss processes, such as predation and competition. Among the 25 La Niña period descriptor species, 10 occurred exclusively in this period (Table 3). For the El Niño period, 33 descriptor species were counted, 17 of which were exclusive (Table 3). Fourteen species were common in both ENSO periods. Other studies demonstrate the relationship between phytoplankton species composition and environmental changes related to ENSO events. For example, Pineda et al. (2019) demonstrated that environmental factors varied among seasons and ENSO events, explaining changes in phytoplankton composition of connected shallow lakes of a subtropical floodplain.

Sathicq et al. (2015), in Río de la Plata estuary, registered the composition shift from green algae in La Niña periods to diatoms during El Niño, identifying higher values of turbidity and conductivity in La Niña and higher rainfall in during El Niño events. These examples, added to the findings of our study, allow us to infer that species composition cannot be neglected in the investigation of environmental changes arising from climatic events, despite the several phytoplankton metrics that exists, species are still good indicators of temporal macroscale environmental shifts.

Considering the monitoring of the present study, 2013 was the only year without the occurrence of ENSO. In an updated conference to the CPTEC database, in the following years (between 2014 and 2018), only 2014 was considered a regular year. This indicates that in the period of 18 years (2001 to 2018), Lake Mangueira was only two years without the influence of ENSO events. The absence of ENSO in 2013 offers a unique opportunity to examine phytoplankton dynamics under relatively stable climatic conditions in subtropical lakes. Several renowned authors in phytoplankton ecology emphasize that single sampling events, when properly contextualized and interpreted with caution, can provide valuable insights into ecological patterns and community responses to environmental variation, especially in systems subject to extreme events or rapid changes. However, it is essential to acknowledge methodological limitations and avoid excessive generalizations (Reynolds, 2006; Huszar et al., 2011; Padisák et al., 2015).

In light of Hutchinson's (1961) phytoplankton paradox, our findings provide an intriguing perspective on community dynamics in a system historically characterized by climatic variability. During the monitoring period, 2013 was the only year without ENSO occurrence, representing a condition of relative stability in an environment where El Niño and La Niña events predominate. This absence of disturbance can be interpreted as a new type of selective pressure, requiring functional reorganization of the community, as suggested by Margalef (1978) and Reynolds (2006), who emphasize that phytoplankton diversity and structure are shaped by disturbance regimes. We observed that, although traditional metrics such as richness and diversity remained stable, the functional composition showed adjustments, indicating that stability does not imply the absence of stress but rather the action of a distinct environmental filter that reorganizes the community's functional structure. This interpretation reinforces the central premise of the paradox: phytoplankton coexistence and diversity depend on variability, and its interruption can trigger ecological responses as significant as those caused by extreme events.

Redundancy analysis (RDA) positioned the year 2013 close to La Niña events, indicating that local hydrological processes may reproduce conditions typically associated with ENSO events, even in the absence of the phenomenon. The dominance of a group of species composed of *Anathece smithii*, *Aphanocapsa incerta*, and *Microcystis aeruginosa*, correlated with higher COND, WT, UVB radiation, and TN, reinforces the role of nutrient enrichment and thermal conditions in promoting cyanobacterial prevalence (Beaulieu et al., 2013; Vanderley et al., 2022). Such patterns are consistent with findings from other subtropical systems, where nitrogen and temperature are key predictors of cyanobacterial biomass and bloom persistence (Paerl & Otten, 2013; Lefler et al., 2023). Moreover, the exclusive occurrence of Raphidophyceae in 2013 may indicate niche exploitation under specific physicochemical conditions. These observations highlight that, even in years without large-scale climatic anomalies, local environmental variability can drive community structures resembling those observed during ENSO-related disturbances, supporting the notion that both regional climate oscillations and local factors interact to shape phytoplankton functional organization (Pineda et al., 2019; Wieliczko et al., 2021).

Another phytoplankton group that registered a significant difference between the years studied was cyanobacteria, with the El Niño period being different from the others. This period presented the occurrence of the lowest values of cyanobacterial biomass when compared to the years of La Niña and the regular year. The cyanobacterial species exclusive to El Niño were species such as *Aphanocapsa elachista*, *Coelomoron* sp., *Eucapsis* sp., *Gloeocapsa* sp., *Synechococcus nidulans* and *Synechocystis aquatilis*. During these periods, higher values of DEP, SECCHI and PREC, were associated with dilution effects and reduced nutrient concentrations (TDN, PT, SRP), which likely contributed to the lower phytoplankton biomass observed in this group. There is a wide scientific concern reagarding cyanobacterial recruitment and climate change-induced shifts in lakes (Tilahun & Kifle, 2019; Deng et al, 2019). If, on one hand, the La Niña drought scenarios may recruit cyanobacteria through, for example, internal feedback processes, high rainfall scenarios predicted for the Lake Mangueira region may recruit cyanobacteria through processes of allochthonous nutrient inputs and reduced internal transparency

(Wieliczko et al., 2020). Besides, there is evidence that interannual variability associated with ENSO phases modulates hydrological processes that, in turn, regulate the magnitude of cyanobacterial blooms (Havens et al., 2019).

Phytoplankton is an important primary producer of aquatic ecosystems and its structure and dynamics are vulnerable to changes in these environments in a climate changing world. There is now evidence that the frequency of ENSO phenomena will increase with global warming as a result of ongoing emissions of greenhouse gases (Cai et al., 2015). In this respect, species richness, diversity, dominance and evenness did not evidence the environmental changes between El Niño and La Niña years. Nevertheless, our study demonstrated distinct set of phytoplankton species during El Niño and in La Niña years, associated to the different environmental scenario of each ENSO event.

It is undeniable that critical ecosystem services provided by freshwater ecosystems are at risk under projected climate scenarios, and understanding these systems is essential in this context. Although the presence of only one regular year in the time series represents a limitation for broader extrapolations, this period served as a unique reference for evaluating phytoplankton community responses under relatively stable climatic conditions. Our findings highlight that phytoplankton dynamics of Lake Mangueira is significantly influenced by climatic events, reinforcing the importance of incorporating climate data into ecological studies of aquatic communities. Furthermore, there is a clear need to systematically explore the ecological consequences of extreme events on ecosystems and biological communities. In summary, our findings highlight the vulnerability of aquatic ecosystems to climatic fluctuations and underscore the relevance of long-term monitoring to unravel the complex interactions between regional climate oscillations and local environmental factors in subtropical lakes.

Data availability

Research data analyzed in this study is not publicly available by any mean.

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