UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL INSTITUTO DE BIOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Dissertação de Mestrado

O PAPEL DO AMBIENTE E DO ESPAÇO SOBRE A COMUNIDADE DE CIANOBACTÉRIAS DE LAGOAS COSTEIRAS DO RIO GRANDE DO SUL

Mariê Mello Cabezudo

Porto Alegre,
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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Mestre em Ecologia.

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Porto Alegre,
Outubro de 2018

“O vento não era o início. O girar da Roda do Tempo não tem inícios nem fins. Mas era um início.”

(Robert Jordan)

AGRADECIMENTOS

Aos meus pais, por todo o apoio que me deram e por não me deixarem desistir;

À minha filha Magnólia, que veio para mudar a forma como eu encaro a vida;

Ao meu companheiro Israel, por sempre me apoiar nas minhas decisões;

À minha família, por todo o amor que me deram e dão sempre;

A todas as minhas amigas e amigos, em especial: Bi, Paulinha, Lagoa e Jordana (que me aguentou durante meu primeiro ano de mestrado inteiro, ainda tenho a chave da Biofísica no meu chaveiro!); Tani, Ane, Gui e Sara (amigos do HT, sempre vou sentir saudades das nossas tardes); Lua (doula querida); Camila Leão (obrigada por me ouvir);

Ao Robert Jordan, por me dar a chance de conhecer outro mundo, e aos amigos que fiz por causa dele;

À prof. Luciane Crossetti, minha querida orientadora, e à Vera Regina Werner, minha coorientadora e mamãe científica;

À Karine, por toda a ajuda que me deu nos 45 do segundo tempo!

À Ju, pelas amostras e por sempre me auxiliar no que eu precisei;

À Capes pela bolsa e ao Programa de Pós-Graduação em Ecologia pela oportunidade.

RESUMO

As cianobactérias são seres procariontes fotossintetizantes responsáveis pela maior parte da produção primária global, sendo de grande importância entender os fatores que influenciam sua distribuição. No presente estudo foi utilizado o particionamento de variação para quantificar a influência relativa de fatores espaciais, ambientais e bióticos (abundância de fitoplâncton eucariótico) na variação da composição taxonômica (a nível de espécies e de ordens) e funcional (grupos de Reynolds e formas de vida) de cianobactérias em lagoas costeiras do sul do Brasil. Em geral, a composição das cianobactérias foi influenciada pelos três fatores, sendo maioritariamente correlacionada com variáveis ambientais. Cada uma das quatro abordagens explicou diferentes quantidades da variação. Cianobactérias classificadas em nível de ordem foram as mais influenciadas pelas condições ambientais, sendo também afetadas pelos fatores bióticos. As classificações por espécies e por grupos funcionais se mostraram influenciadas pelos três fatores, enquanto a classificação por formas de vida foi influenciada apenas por fatores bióticos. Além disso, a comparação de classificações dentro de cada abordagem mostrou que as cianobactérias filamentosas (tanto as heterocitadas quanto as não heterocitadas) foram influenciadas principalmente por variáveis ambientais, enquanto as cianobactérias cocóides, pela fração espacial. Estes resultados demonstram que as características taxonômicas e funcionais das cianobactérias devem ser consideradas em estudos com metacomunidades para melhor compreensão da organização das assembleias de cianobactérias.

Palavras-chave: variação espacial, variação ambiental, traços funcionais, fitoplâncton, abordagem taxonômica

ABSTRACT

Cyanobacteria are photosynthetic prokaryotes responsible for most of the global primary production, being of great importance to understand the factors that influence its distribution. In this study we used variation partitioning to quantify the relative influence of spatial, environmental and biotic (abundance of eukaryotic phytoplankton) factors on the variation in taxonomic (species and order levels) and functional (Reynolds groups and life forms) composition of cyanobacteria in shallow coastal lakes from southern Brazil. Overall, cyanobacteria composition was influenced by the three factors, being mostly correlated with environmental variables. Each of the four approaches explained different amounts of variation. Cyanobacteria classified at the level of order were the most influenced by environmental conditions, in addition to be influenced by biotic factors, while the classifications by species and functional groups showed influence also from spatial factors and classification by life forms was influenced only by biotic factors. Further, the comparison of classifications within each approach showed that filamentous cyanobacteria (both heterocystous and non-heterocystous forming) were mainly influenced by environmental variables, while coccoid cyanobacteria by the spatial fraction. These results demonstrate that taxonomic and functional characteristics of cyanobacteria should be considered in metacommunity studies to better understand the organization of cyanobacteria assemblages.

Keywords variation partitioning, spatial variation, environmental variation, functional traits, phytoplankton

SUMÁRIO

INTRODUÇÃO GERAL

Microrganismos são os seres vivos mais abundantes em nosso planeta e são fundamentais para a emergência e evolução de todos os outros organismos vivos na Terra (Bertrand et al., 2015). Por muito tempo se mantiveram praticamente desconhecidos aos seres humanos, pois um maior entendimento destes seres só foi possível a partir da invenção do microscópio, em meados do século XVII. Os primeiros estudos com estes seres focavam no processo de fermentação e na saúde pública e, mesmo que alguns autores, como Hensen (1887), já se preocupassem com os modos com que microrganismos interagem entre si e com o ambiente, a ecologia destes seres só ganhou força no século XX, principalmente após a década de 1970 (Caumette et al., 2015; Reynolds, 2006). Desde então, esta área se desenvolveu consideravelmente (Caumette et al., 2015), englobando diversas subáreas como a ecologia química e a ecologia de comunidades. Tradicionalmente, estudos ecológicos com comunidades de microrganismos focavam em compreender como estas eram afetadas pelas condições ambientais (Hanson et al., 2012). A ideia de que os microrganismos estão por todo o lugar e o ambiente os seleciona (Baas-Becking, 1934) foi durante muito tempo o grande paradigma da área (Hanson et al., 2012; Padisák et al., 2016). Porém, nos últimos anos, outras visões, como a teoria neutra de Hubbel (2001) e as metacomunidades, e a incorporação de outras áreas de estudo, como a biogeografia, ganharam espaço, e atualmente se busca entender os diferentes padrões e processos que agem na formação destas comunidades (Hanson et al., 2012).

Em comunidades de água doce, algas e as bactérias são seres que desempenham papel fundamental na manutenção da biodiversidade. Algas são os principais organismos envolvidos na conversão da luz em energia, enquanto as bactérias são o grupo de organismos de vida livre mais abundante de toda a biota aquática (Sigee, 2005). Neste contexto, um grupo que se sobressai é o das cianobactérias: por apresentarem características de ambos os grupos, tornam-se ótimos organismos modelo para estudos ecológicos. Cianobactérias, ou algas azuis, são seres procariotos capazes de realizar a fotossíntese a partir da clorofila-a (Whitton & Potts, 2000). São muito reconhecidas pela capacidade de fixar o nitrogênio atmosférico, sendo as mais conhecidas aquelas pertencentes à ordem Nostocales, por possuírem células especializadas (heterocitos) (Komárek, 2013). Além disso, são, em geral, boas competidoras: muitas conseguem regular sua flutuação através de estruturas especializadas, denominadas de aerótopos, conferindo tanto uma vantagem na busca pela luz quanto contra o ressecamento (Whitton & Potts, 2000); algumas também podem formar esporos de resistência (os acinetos), o que gera uma espécie de “banco de sementes”,

mantendo-se dormentes em condições adversas e germinando quando as características do ambiente tornam-se propícias (Sukenik et al., 2012).

Cianobactérias também são reconhecidas pelos danos que podem causar ao ambiente e à saúde pública. Estas são capazes de causar um desequilíbrio ambiental quando há um crescimento desenfreado de uma ou mais espécies, as denominadas florações (Watson et al., 2015). Este fenômeno frequentemente está associado à ação antrópica, que causa a eutrofização das águas através da poluição dos corpos hídricos (O'Neil et al., 2012). Quando ocorre, há diminuição da biodiversidade não só de algas, como também de peixes e de outros animais que habitam ou utilizam o ambiente aquático. Esta mortandade pode estar associada a substâncias com potencial tóxico produzidas por estas cianobactérias (cianotoxinas) (Landsberg, 2002; Zanchett & Oliveira-Filho, 2013). Devido a este potencial danoso que as cianobactérias apresentam, muitos estudos com o grupo se dão em escala local e focam na formação de florações ou trazem questões de saúde pública (Graham et al., 2009). É o caso do ocorrido em 1979 em Palm Island, na Austrália (Byth, 1980), ou em 1996 em Caruaru, PE (Azevedo et al. 2002). Em ambos os casos, um grande número de seres humanos veio a óbito devido às cianotoxinas, o que motivou inúmeras pesquisas através do globo (por exemplo: Bourke et al., 1983; Carmichael et al., 2001; Pádisak, 1997). Por este motivo, pouca atenção é dada à real biodiversidade do grupo (Rejmánková et al., 2004), entretanto, é de suma importância entender melhor os processos que regem a organização das comunidades de cianobactérias, a fim de identificar padrões e evitar futuros danos ambientais (Nabout et al., 2013; Ribeiro et al., 2018). Para tanto, são necessários estudos em escalas maiores, incluindo ambientes heterogêneos, em trabalhos que foquem não só em florações, mas também nas espécies menos abundantes (Ribeiro et al., 2018).

Sendo assim, o presente trabalho trouxe um estudo com 25 lagoas, inseridas na porção sul do sistema do rio Tramandaí, e visou entender os fatores que afetam o arranjo das comunidades de cianobactérias nestes ambientes (ambiente, interação com outras algas e espaço). Estas lagoas possuem grande heterogeneidade ambiental, variando de ambientes oligotróficos a eutróficos, tornando-se uma boa área de estudo para este trabalho, que visou identificar os padrões não só das espécies mais abundantes, mas estudar as comunidades como um todo. Uma das questões centrais do artigo foi verificar se a abordagem utilizada para classificar as cianobactérias, taxonômica ou funcional, interfere nos resultados obtidos. Também foram verificados se existem padrões diferentes entre os grupos de cianobactérias e qual a influência da escala espacial nos resultados.

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Relative importance of environmental, spatial and biotic factors on the organization of cyanobacteria assemblages using taxonomic and functional approaches

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O presente manuscrito será traduzido e submetido à revista Hydrobiologia (fator de impacto 2,165), e está formatado conforme as normas desta revista.

INTRODUCTION

Microbial biogeography is a relatively recent area of research that focuses on distribution patterns of microbial taxa at continental, regional and local scales (Ramette & Tiedje, 2007; Hanson et al., 2012; Padisák et al., 2016). The hypothesis that "everything is everywhere, but the environment selects" (Baas-Becking, 1934) was, for many years, the paradigm of microbial ecology. Hillebrand et al. (2001) were among the first to test this premise and showed that community similarity of microeukaryotes (diatoms and ciliates) decreased with spatial distance, suggesting dispersal limitation. Further empirical studies showed evidence against the hypothesis of distribution based solely on environmental selection. For example, Papke et al. (2003) and Whittaker et al. (2003) demonstrated the role of dispersal limitation and geographic isolation on distribution patterns of prokaryotes from hot springs, resulting in differences in community composition. However, these studies were received with some skepticism, since they analyzed extreme environments and small areas with high degree of isolation, which naturally favor specialization (Fenchel, 2003).

Currently, it is known that microrganisms present biogeographical patterns of distribution, but little is known about the processes that generate such patterns (Hanson et al., 2012). Among the factors affecting microbial distribution, environmental selection, drift, dispersion and mutation are commonly regarded as major drivers (Hanson et al., 2012). These factors can act at different levels of biological organization (genes, individuals and populations) and are not mutually exclusive, being often difficult to dissociate (Hanson et al., 2012). Thus, recent studies are focusing on recognizing and quantifying the relative importance of these processes on the distribution patterns of microrganisms, such as microeukaryotes (Zhang et al., 2018) and archaea (Shi et al., 2016).

The spatial scale is also an important factor determining the biogeographical distribution of microrganisms (Horner-Devine et al., 2004; Martiny et al., 2006). Environmental heterogeneity often increases with increasing area, which usually explains the species-area relationship pattern (Oliver et al., 2010). Also, larger areas offer greater dispersal limitation to species (Horner-Devive et al., 2004). However, since microrganisms are recognized as having higher dispersal capacity and rapid adaptation to environmental changes (Martin et al., 2006; Hanson et al., 2012), it is necessary to further advance in the understanding of how space influences the distribution of microrganisms. For instance, the effect of geographic distance on the distribution of freshwater bacteria was observed only on broader spatial scales (Soininen et al., 2011). Similarly, Ribeiro et al. (2019) observed an increase on the influence of spatial variables with increasing spatial scale in phytoplankton communities, while the influence of environmental variables followed an inverse

pattern. On the other hand, Jones et al. (2012) observed variation in the composition of bacterioplankton at very small spatial scales (only 10 m).

Another important issue that influences the understanding of microbial distribution is the taxonomic resolution used to define a microbial species (Hanson et al., 2012, Dvořák et al., 2015). This is because key concepts studied in biogeography are closely related to the concept of species: habitats are defined as a particular combination of resources and conditions required for a particular species (Tiedje, 1993), and dispersal and drift depend on population sizes (Slatkin, 1987), which depends on the concept of species adopted (Ribeiro et al., 2018). Regarding cyanobacteria, evidence of biogeographic distribution patterns is still scarce. The confusion between botanical and microbiological taxonomic classification systems makes it even more difficult to understand their real biodiversity, impacting the understanding of their distribution and the ecological factors involved (Rejmánková et al., 2004). Many of the well-known species are considered cosmopolitan or sub-cosmopolitan, corroborating the idea of wide dispersal capacity of the group (Padisák et al., 2016; Ribeiro et al., 2018). The most well documented case is the species *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya & Subba Raju (recently proposed to be renamed *Raphidiopsis raciborskii* (Aguilera et al., 2018)). Padisák (1997) traced the history of the geographic expansion of this species, which occurred in less than a century, from the tropics to temperate areas. From this work, several dispersal routes were proposed, and the cause of this expansion was associated to environmental factors, mainly global warming (Ribeiro et al., 2018). Cosmopolitan cyanobacteria species often cause environmental and public health damage due to their high abundance and recurrent ability to form toxic blooms (as is the case of *C. raciborskii*). Therefore, most biogeographic studies with cyanobacteria have focused on these species (e.g. Sukenik et al., 2012; Antunes et al., 2015; Moreira et al., 2015; Cirés & Ballot, 2016; Shirani & Hellweger, 2017), which resulted in a lower understanding of the distribution patterns of rare, endemic, or less harmful species. Studies on other cyanobacterial taxa, however, have already observed evidence of geographic isolation and dispersal limitation (Papke et al., 2003; Ionescu et al., 2010; Gutiérrez-Rodrıguez et al., 2014). Such evidences show that different cyanobacteria may present distinct biogeographic patterns, and that the existence of truly cosmopolitan species does not necessarily imply the absence of species with limited dispersion or endemic distribution resulting not only from environmental factors.

Finally, cyanobacteria are prokaryotes with unique traits in the bacterial world, such as the existence of multicellular groups and the ability to form differentiated cells (Whitton & Potts, 2000). This large morphological variety, which can be observed in optical microscopy, allowed the use of approaches which take into account functional classifications (e.g. Reynolds et al., 2002 and

Kruk et al., 2010) or functional traits (as cell shape and the presence of specialized cells, e.g. Fontes et al., 2013). Thus, cyanobacteria is a good model group to analyze the role of environmental and spatial factors on the distribution of microrganisms from both taxonomic and functional perspectives, an approach often used for macrorganisms, but still poorly explored in the microbial world.

We aimed to quantify the relative influence of spatial, environmental and biotic variables on the variation in taxonomic (species and order levels) and functional (Reynolds functional groups and life forms) composition of cyanobacteria in shallow coastal lakes from southern Brazil. We predicted that (i) the total variance explained and the relative importance of environmental variables will be greater when using functional classifications than taxonomic ones, since functional traits are directly related to the environmental adaptation of species. Similarly, (ii) among taxonomic classifications, those with finer resolution (species level) will be more influenced by environmental variables, since coarser classifications (at the level of order) group many species with different niches. We also expected that species traits are important in determining the effect of environmental and spatial factors, so that (iii) species capable of forming differentiated cells (heterocysts and akinetes, represented by the Nostocales order and the **H1** functional group) will be more influenced by the environment than by space, due to the adaptive advantages that these cells offer.

MATERIAL AND METHODS

Study area

The study was conducted in 25 lakes located in the southern portion of the Tramandaí River system (for a map of the studied area, please refer to Bohnenberger et al., 2018), southern coast of Brazil (29°37’ - 30°30' S, 49°74'- 50°24' W), in February 2014 (austral summer). The Tramandaí river system consists of 41 shallow lakes that have different degrees of connectivity between them and communicate with the Atlantic Ocean through the Tramandaí Estuary. This system is located on a Holocene coastal plain (ca. 5000 BP) formed after a series of marine regressions and transgressions (Schwarzbold & Schafer, 1984; Tomazelli et al., 2000), and is mainly influenced by northeast and south-west winds (Cardoso & Motta Marques, 2004; Bohnenberger et al., 2018), in a humid subtropical climate with hot summers (Cfa; Castro & Mello, 2013). The lakes of the Tramandaí river system are subjected to various anthropogenic uses such as fishing and sewage disposal, among others. In the summer, due to the intensification of tourism, the demand for the use of these lakes increases significantly, intensifying the impacts of human activities (Castro & Mello, 2013). The studied lakes are environmentally and biologically heterogeneous (for more details in the environmental conditions of the studied lakes, please refer to Bohnenberger et al., 2018).

Sampling of biotic and abiotic data

We collected samples for biotic and abiotic analyses in the subsurface of the water column at five sampling points within each lake (pelagic areas, comprising the four cardinal points and the center of each lake), totaling 125 sampling points. We also obtained the geographic coordinates of each of the sampling points using a Garmin Etrex 10 GPS (Material Suplementar, Table S1). For more details on the sampling methods, please refer to Bohnenberger et al. (2018).

The phytoplankton quantification followed the Utermöhl method (1958), using Lund et al. (1958) to estimate the error. We obtained the abundance of the species through the estimation of biovolume ($mm^3.L^{-1}$), accessed from the measurements of 20 individuals in each population and by using geometric solid formulas that are closest to the cellular form (Hillebrand et al., 1999; Sun & Liu, 2003). We used specialized literature to identify cyanobacteria in the lowest taxonomic classification possible (e.g. Komárek & Anagnostidis, 1999, 2005; Komárek, 2013), while the other components of phytoplankton were classified into major groups, according to the classification of van-den-Hoek et al. (1998). We also classified cyanobacteria species according to class (Komárek et al., 2014), functional group (Reynolds et al., 2002) and life form (colonial or filamentous) (Komárek & Anagnostidis, 1999, 2005; Komárek, 2013) (Table 1). In addition to cyanobacteria, the following groups of algae (eukaryotic phytoplankton) were registered: Chlorophyceae, Chrysophyceae, Cryptophyceae, Dinophyceae, Euglenophyceae, Zygnematophyceae and diatoms (Material Suplementar, Table S2).

Data analysis

We first constructed a species matrix using cyanobacteria abundance data from the 125 sampling points. Due to technical limitations, the unidentified coccoid group (UCG) contained all coccoid species with a cell diameter smaller than 2 μm. Moreover, four species of Nostocales remained unidentified because we could not find any specialized cells (heterocysts and akinetes). We then obtained 15 response matrices through the reclassification of the species in other approaches (Table 1). Four of these matrices aimed at comparing taxonomic approaches and were constructed using data on species (SPP), orders (ORD), functional groups (FG) or life forms (FOR). These matrices contained the data of all registered species, and thus the columns were formed by the sum of the abundances of the species belonging to each order, functional group or life form. Further, we deconstructed the species matrices in 11 matrices containing only the species belonging to each classification: Synechococcales (SYN), Chroococcales (CHR), Oscillatoriales (OSC) and Nostocales (NOS) (order level); **H1**, **S1**, **MP**, $\mathbf{L_o}$ and **K** (functional level); coccoid (COC) and

filamentous (FIL) (life form level) (Table 1). Before analyses, abundance data were Hellinger transformed (Legendre & Legendre, 2012) in order to reduce the influence of very common species and to avoid biased data, thus allowing the use of multivariate linear methods (Peres-Neto et al., 2006).

We then constructed three explanatory matrices: one environmental, one biotic and one spatial. All matrices considered the 125 sampling points. The environmental matrix was constructed after eliminating redundant variables through selection procedures based on the variance inflation factor (VIF). Therefore, only variables with VIF value smaller than 5 were used in the analyses (Naimi et al., 2014; Akinwande et al., 2015). The biotic matrix contained the abundance data of the eukaryotic phytoplankton and was also Hellinger transformed. Here, we assumed that the presence of other phytoplankton species reflects a portion of interspecific competition, thus representing a part of the biotic interactions that possibly affect the distribution of cyanobacteria. For the spatial matrix, we used distance-based Moran's Eigenvector Maps (dbMEMs, Dray et al., 2012, Legendre & Legendre, 2012). DbMEMs produce orthogonal eigenvectors used to represent spatial relationships between sampling units in uni- and multivariate data (Dray et al., 2012). Firstly, Euclidean distances among the 125 sampling points were calculated from the geographical coordinates. The distances were based on soil and not on hydrological connections, considering that not all lakes are connected through water and that cyanobacteria exhibit passive dispersal via air (Kristiansen, 1996). We used the minimum truncation distance and selection of all variables with positive spatial autocorrelation using the Moran's I statistic (Legendre & Legendre, 2012), since those with negative values showed no significant relation to the response matrices in previous analyses. The procedure described above produced 36 dbMEMs, which were used on the global analysis. The dbMEM method can also be used to infer the spatial scale in which the effect is perceived since the first eigenvectors usually describe broad spatial structures, while the last eigenvectors (with lower eigenvalues) describe fine spatial structures (Dray et al., 2012; Legendre & Legendre, 2012). Based on this, we also separated the dbMEMs in broad-scale (MEMs 1-18) and fine-scale (MEMs 19-36) matrices, in order to verify whether the influence of the space on the distribution of the cyanobacteria occurred in a more regional or in a more local scale.

After the construction of the explanatory matrices, the explanatory variables were selected separately for each of the 15 response matrices. We followed the forward selection procedure proposed by Blanchet et al. (2008). Therefore, for each explanatory matrix (environmental, biotic and spatial) we performed a redundancy analysis (RDA) using the whole set of variables. This RDA was tested with an ANOVA-like permutation test (Legendre & Legendre, 2012) and the selection of the variables only continued when this global model was significant ($P<0.05$) (Material

Suplementar, Table S3). In the next step, the resulting adjusted R^2 value was used as a threshold for variable selection, associated with the significance level. Thus, a variable was retained in the final model if $P<0.05$ and if the adjusted R^2 value of the reduced model was not higher than the adjusted R^2 calculated using the whole set of variables.

The relative importance of explanatory matrices on the distribution of cyanobacteria was accessed by using partial redundancy analyses (pRDA) in association with variation partitioning procedures (Borcard et al., 1992; Legendre & Legendre, 2012). This approach decomposes the total variation into fractions that indicate the relative importance of the pure environmental (ENV), pure biotic (BIO) and pure spatial (SPA) influence in the abundance of cyanobacteria, as well as the influence of the shared fractions (ENV+BIO, BIO+SPA, ENV+SPA, ENV+BIO+SPA) and the unexplained variation (RES). These procedures were performed separately for each of the 15 response matrices using the selected environmental, biotic and spatial variables. For the matrices in which the spatial factor was significant, we also ran the analysis with the space decomposed in fine-scale and broad-scale dbMEMs (since no fine-scale dbMEMs were selected for SPP and FIL only the broad-scale analysis was performed for those). The portion of the explained variation was estimated using adjusted R^2 values (Peres-Neto et al., 2006) and the significance of the pure fractions was tested through an ANOVA-like permutation test for RDA (Legendre & Legendre, 2012).

All analyses were performed in the R environment (R Core Team, 2018) using the following packages: *adespatial* (Dray et al., 2018), to construct spatial variables (dbMEMs) and to perform the forward selection procedures; *usdm* (Naimi, 2017), to carry out the VIF selection in the environmental variables; *vegan* (Oksanen et al., 2018) for the multivariate analyses; *ggplot2* (Wickham et al., 2018) and *reshape2* (Wickham, 2017) to plot the data.

RESULTS

A total of 21 taxa of cyanobacteria were registered (Table 1; Material Suplementar, Fig. S1), and species richness at each lake ranged from one to nine. The most frequent was *Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerová & Cronberg, present in 84% of the lakes. Despite this fact, the species was not among the most abundant, with *Sphaerospermopsis aphanizomenoides* (Forti) Zapomelová, Jezberová, Hrouzek, Hisem, Reháková & Komárková being the most abundant one, followed by *Chrysosporum ovalisporum* (Forti) E.Zapomelová, O.Skácelová, P.Pumann, R.Kopp & E.Janecek and *Geitlerinema splendidum* (Greville ex Gomont) Anagnostidis (Table 1). In general, the communities were predominantly composed of filamentous species, mainly Nostocales.

We observed a multi-species bloom of *S. aphanizomenoides*, *G. splendidum* and *Cuspidothrix issatschenkoi* (Usachev) Rajaniemi, Komárek, R.Willame, Hrouzek, Kastovská, Hoffmann & Sivonen in Marcelino Lake, and less dense Nostocales blooms in Custódia, Dom Daniel and Lessa lakes.

Variation partitioning

Overall, cyanobacteria composition was influenced by spatial, environmental and biotic factors to a greater or lesser extent depending on the response matrix (Table 2). When comparing approaches (SPP, ORD, FG and FOR), variation in cyanobacteria composition was mostly explained by the environmental fraction, which only showed no significance for the life form (FOR) dataset (Table 2). Regarding the spatial fraction, only SPP and FG had part of the variation explained by this component (Table 2) and it was significant only at broad scales(Fig. 1; Material Suplementar, Tables S4, S5). The biotic fraction explained part of the cyanobacterial variation independently of the approach used (SPP, ORD, FG and FOR) and was most important for explaining variation in life forms (Table 2).

When comparing cyanobacterial orders (SYN, CHR, OSC and NOS), the environmental fraction was also the most important (Table 2), especially for OSC, which did not show any spatial or biotic influence. Variation in species composition of orders NOS and SYN was affected by the three factors, while variation in order CHR was not explained by any factor. Functional groups (H1, S1, L_O, MP and K) varied in their responses, with H1 and S1 being the only groups with significant environmental effects. Variation in group K, which contained mainly small coccoid species, was mostly explained by the spatial fraction, especially by fine-scale dbMEMs (Table 2; Fig. 1; Material Suplementar, Tables S4, S5). Group L_O was only affected by the biotic fraction, while variation in group MP was not explained by any factor. Finally, in relation to life forms (FIL and COC), the two groups differed greatly. Variation in filamentous species (FIL) was mostly explained by environmental factors, while the spatial fraction related to fine-scale dbMEMs explained most of the variation in coccoid species (COC) (Table 2; Fig. 1; Material Suplementar, Tables S4, S5). A great amount of the variation was not explained by any of the explanatory variables (mean of 75% ± 14%), **S1** being the matrix with the most explained variation (43%) (Table 2).

DISCUSSION

Despite the scarcity of studies on the biogeography of cyanobacteria, increasing evidence suggests the importance of both environmental and spatial factors on the organization of these

communities, contrary to the idea that the distribution of microrganisms is determined solely by environmental selection (Ribeiro et al., 2018). In this study, we observed heterogeneity both in relation to the environmental conditions and the biota among the sampling sites, ranging from oligotrophic environments with only one registered species (e.g. das Pombas lake), to lakes with very dense multi-species blooms (e.g. Marcelino lake). Cyanobacteria were influenced by both environmental and spatial variables, depending on the approach used and on the spatial scale. This indicates that, in addition to the environmental filter that has long been known as an important factor influencing the spatial variation of cyanobacteria, other factors may be acting, such as spatial processes related to the dispersal capacity of the group.

Comparison between taxonomic and functional classifications

Comparisons between taxonomic and functional classifications are a common focus of ecological studies, analyzing the responses of distinct classifications on factors that structure communities (e.g. Heino et al., 2007; Algarte et al., 2014; Obertegger & Flaim, 2018). For phytoplankton, recent evidence indicates that functional classifications more accurately describe the responses of these organisms to the environmental conditions (Kruk et al., 2014; Abonyi et al., 2017). Accordingly, we expected that the distribution of cyanobacteria classified through a functional approach would be better explained than when a taxonomic approach is used and would be mostly explained by the variation in environmental conditions. However, our first prediction was not corroborated, since species classification resulted in the highest variance explained. Further, the functional group approach showed similar relative importance of the environmental fraction as species classification, while the life form approach showed the lower environmental relative importance among the four approaches. Similarly, contrary to our second prediction, the importance of environmental factors was greater for the coarser taxonomic resolution of order than for species-level resolution.

Modern taxonomic classification systems for cyanobacteria are complex, and although based in phylogenetic backgrounds, other characteristics, such as cytomorphological features and ecological aspects, are also taken into account (Komárek, 2013). Considering this, one possible explanation for the observed results is that the taxonomic system we used to classify the orders is properly integrating the environmental ecological factors. If this is the case, the phylogenetic traits that separate the orders may be reflecting the morphological adaptations of the group enough that their responses to the environment are perceived even when only traditional (morphological) methods of identification are used. Besides, since the classification by orders was made for cyanobacteria alone and the functional groups approach was thought for the whole phytoplankton, it

is not surprising that the first would reveal more the effects of the environment on cyanobacteria than the second. Furthermore, the classification by species together with the functional groups approach were more successful in unfolding the contribution of spatial factors. The main spatial contribution was observed in broader scales for both approaches (Fig. 1, Material Suplementar, Tables S4, S5), which agrees with a previous work by Ribeiro et al. (2019) in the same region as our study, who observed that the relative influence of environmental variables in the distribution of cyanobacteria increased as the spatial scale decreased, while the spatial factors followed an inverse pattern. Finally, the classification by life form presents the coarser resolution, grouping different species in only two categories. Thus, it may have ignored many niche specificities, oversimplifying and generalizing the analyses (Drakare & Liess, 2010, Östman et al., 2010).

It is important to note that most studies that demonstrate a greater relationship with the environment for functional than taxonomic approaches consider only environmental variables, ignoring the spatial component (e.g. Kruk & Segura, 2012 and Salmaso et al., 2014). Studies that evaluate the spatial factor when comparing different classifications of phytoplankton do not always find a clear pattern. For example, Xiao et al. (2018), studying lakes at different altitudes in China, found greater influence of the environment for phytoplankton functional groups, while the space was significant only when classification by species was used. On the other hand, Algarte et al. (2014) and Huszar et al. (2015) did not find differences between several taxonomic or functional classifications for stream algae. These divergent results may reflect the great diversity found in microalgal groups (Reynolds, 2006). Thus, regarding the present work, the divergences may be related to the ecological differences between total phytoplankton and cyanobacteria, which present very distinct biological characteristics (for example, their prokaryotic nature). In this way, distinct classification approaches are complementary and can show the influence of different processes under different biological perspectives (Heino et al., 2007; Xiao et al., 2018).

Comparison among groups of cyanobacteria within classifications

Comparison among groups showed that, in all classifications, each category responds differently to the ecological factors, which means that cyanobacteria responses to the environment and space are not unique, but depend on the peculiarities of each group. This reinforces the notion of complementarity between taxonomic and functional approaches, as the classifications are not based on the same features and highlight different ecological aspects of the species.

One trait that we expected to be relevant to the response of cyanobacteria to the environment was the presence of specialized cells, which occur in the Nostocales order (also represented by the **H1** functional group - see Table 1). Specialized cells, called heterocysts and akinetes, give

advantage over other species in environments with adverse conditions (Whitton & Potts, 2000; Rejmánková et al., 2004). Heterocysts fix atmospheric nitrogen, an advantage in nitrogen-limited water bodies (Komárek, 2013), while akinetes are resistance spores that are able to survive until environmental conditions become favorable (Sukenik et al., 2012). In addition, many Nostocales observed in the present study (such as *C. ovalisporum*, *C. issatschenkoi*, *Dolichospermum viguierii* (Denis & Frémy) Wacklin, L.Hoffmann & Komárek and *S. aphanizomenoides*) show aerotopes, air vesicles that enable fluctuation (Komárek, 2013). Cyanobacteria possessing these structures remain near the water surface and thus receive higher incidence of sunlight, some of which even regulate their fluctuation to emerge only during part of the day (Whitton & Potts, 2000). All these adaptations confer advantages to this group of cyanobacteria (Sukenik et al., 2012). However, although our third prediction was partly corroborated, since the Nostocales/**H1** groups showed greater environmental than spatial influence, the cyanobacteria which were most influenced by environmental factors were some of the non-heterocystous filamentous species (order Oscillatoriales and functional group **S1**). The Oscillatoriales order comprised only two species, *G. splendidum* and *Phormidium tergestinum* (Rabenhorst ex Gomont) Anagnostidis & Komárek, that presented greater abundances associated with the heterocystous cyanobacteria blooms. Therefore, the bloom-forming species could be altering the environment and thus facilitating the occupation by non-heterocystous species (Whitton & Potts, 2000). Furthermore, it is likely that the main characteristic conferring adaptations to the cyanobacteria in the studied lakes is not the presence or absence of differentiated cells, but the filamentous form (see the discussion about the life forms below). It is also important to note that *C. ovalisporum* and *S. aphanizomenoides*, two of the bloom-forming species observed in this study, are considered invasive in Europe (Sukenik et al., 2012). About 15 years ago, Werner (2002) did not detect such species in the coastal lakes of southern Brazil. In addition, these species are not commonly observed in the American continent, and thus their record in the present study may indicate a recent expansion in their distribution. If this is the case, these two species can reach a cosmopolitan status (Ribeiro et al., 2018). However, additional molecular studies are required to confirm these identifications. In relation to the other taxa, those whose distribution was influenced by neither the environment nor the space are represented by few species with relatively low abundance (Chroococcales, $\mathbf{L_O}$ and **MP**). Thus, these groups may be more influenced by other factors such as ecological drift, which has a greater impact when dispersal is limited and populations are small (Hanson et al., 2012).

As mentioned before, life form was a characteristic of most relevance: while the filamentous species were more influenced by environmental variables, coccoid species had a greater influence of space. The filamentous form is probably one of the main adaptations presented by cyanobacteria

conferring advantage to the environmental conditions in the studied lakes. The filamentous shape increases surface area and confers an efficient light-harvesting antennae (Reynolds, 1997) and a high resistance to sinking (Padisák et al., 2003). It also offers advantages in lakes subjected to frequent or continuous wind mixing (Reynold, 1997), as is the case of the studied lakes (Bohnenberger et al., 2018). On the other hand, the relation of coccoid species with spatial factors can be consequence of the influence of other factors, such as ecological drift and dispersal limitation. In addition, we cannot exclude the possible effect of stochasticity or spatially structured environmental variables not accounted in the present study (Prévost-Bouré et al., 2014). In the latter case, one can mention the strong influence of wind (mainly Northeast) in the studied region, due to its location near the Atlantic Ocean (Schäfer et al., 2014). In this sense, it is possible that coccoid species are more affected by wind conditions, due to their small size, resulting in greater abundance of cells at lake shores downwind and leading to spatial structuring (Zhang et al., 2016; Cyr, 2017). Moreover, very strong or constant winds can disintegrate colonies or transport them to deeper regions where conditions are sub-optimal (Wu et al., 2015). The greater influence of fine-scale spatial variables in the variation of coccoid species is an indicative that this may be the case. It is important to point out that the present comparison between filamentous and coccoid life forms took into account the abundance of each species, while in the previous comparison among functional and taxonomic approaches the life forms matrix contained only two groups (filamentous and coccoids). Therefore, our findings suggest that while the classification of cyanobacteria in only two categories proved to be insufficient, considering the life form of the species (whether coccoid or filamentous) may prove to be of great value, provided the morphotypes are adequately distinguished. This information may be useful for guiding how to classify cyanobacteria in studies that aim to work with the whole phytoplankton.

CONCLUSION

Ecological studies with cyanobacteria are traditionally restricted to environments associated with blooms and concerned only with environmental issues (Padisák et al., 2016). On the other hand, biogeographic studies with this group are still scarce, and are usually based on the discovery of new genera or species (Moreira et al., 2013). Studies that combine environmental and spatial factors repeatedly associate cyanobacteria only with environmental conditions (e.g. Beisner et al. al., 2006; Drakare & Liess, 2010; Branco et al., 2014; Huszar et al., 2015). However, these studies often disregard the particularities of cyanobacteria, treating them as a single group (e.g. Huszar et al., 2015), mixing them to other bacteria or to the total phytoplankton in the analyses (e.g. Beisner et al. al., 2006), or simply not considering the particular traits presented by the species (e.g. Drakare

& Liess, 2010). The results found in the present study demonstrate that each group of cyanobacteria can present marked ecological differences and is influenced by environmental or spatial variables depending on its intrinsic characteristics. Branco et al. (2014) comment that the response of a group as a whole is necessarily influenced by the particular ecology of each subgroup that compose it. Thus, we demonstrated the importance of studying cyanobacteria as a separate entity from the phytoplankton, in order to better understand the ecology and biogeography of these organisms.

The present study evidenced the influence of both spatial and environmental factors on the distribution of cyanobacteria. Differently from what we expected, the approach that showed the greatest influence of environmental factors was not any of the functional ones, but the classification by orders. This result was also contrary to our second prediction, since we expected that the finer the resolution of the identification (at species level), the better the environmental contribution could be detected. Further, we found that the spatial influence was better perceived when the species and the functional groups classifications were used. Therefore, our results highlight that different classification approaches are complementary, since each one shows the influence of different processes under different biological perspectives. Regarding our third prediction, we expected that the relative importance of the environmental fraction would be larger than that of the spatial fraction for heterocystous species such as Nostocales. Despite we found that Nostocales were more influenced by the environment that by space, the relative environmental importance was even greater for non heterocystous-forming filamentous cyanobacteria. Therefore, the filamentous form, not the specialized cells, is likely one of the main adaptations presented by the cyanobacteria conferring a good advantage to the environmental conditions in the studied lakes, probably due to the resistance to wind mixing and the highly efficient light-harvesting antennae which the filamentous shape offers (Reynolds et al. 1997).

Cyanobacteria are an important group for the functioning of aquatic ecosystems, although there is still little knowledge about their biogeography (Ribeiro et al, 2018). The development of molecular techniques has led to greater detail on the taxonomic identification, allowing a deeper understanding about microbial diversity and new look on the biogeography of these organisms (Gutiérrez-Rodríguez et al., 2014; Mazard et al., 2012). Thus, in order to verify if the trends found in this work and in Ribeiro et al. (2019) are maintained, it is essential to carry out similar studies using molecular approaches.

ACKNOWLEDGEMENTS

The first author is supported by a student fellowship by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) - Finance Code 001 (file number 1588368). We thank the

Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the financial support granted to this project (process number 474279 / 2013-8). We also thank the researchers Juliana Elisa Bohnenberger and Marla Sonaira Lima and the technicians from the Instituto de Pesquisas Hidráulicas and the Centro de Estudos Costeiros, Limnológicos e Marinhos (UFRGS) for sampling and laboratory analyses, and Bianca Damacena for the translation of the English version of the text.

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TABELAS

Table 1 Classification, abundance and frequency of the cyanobacteria species recorded in the 25 lakes.

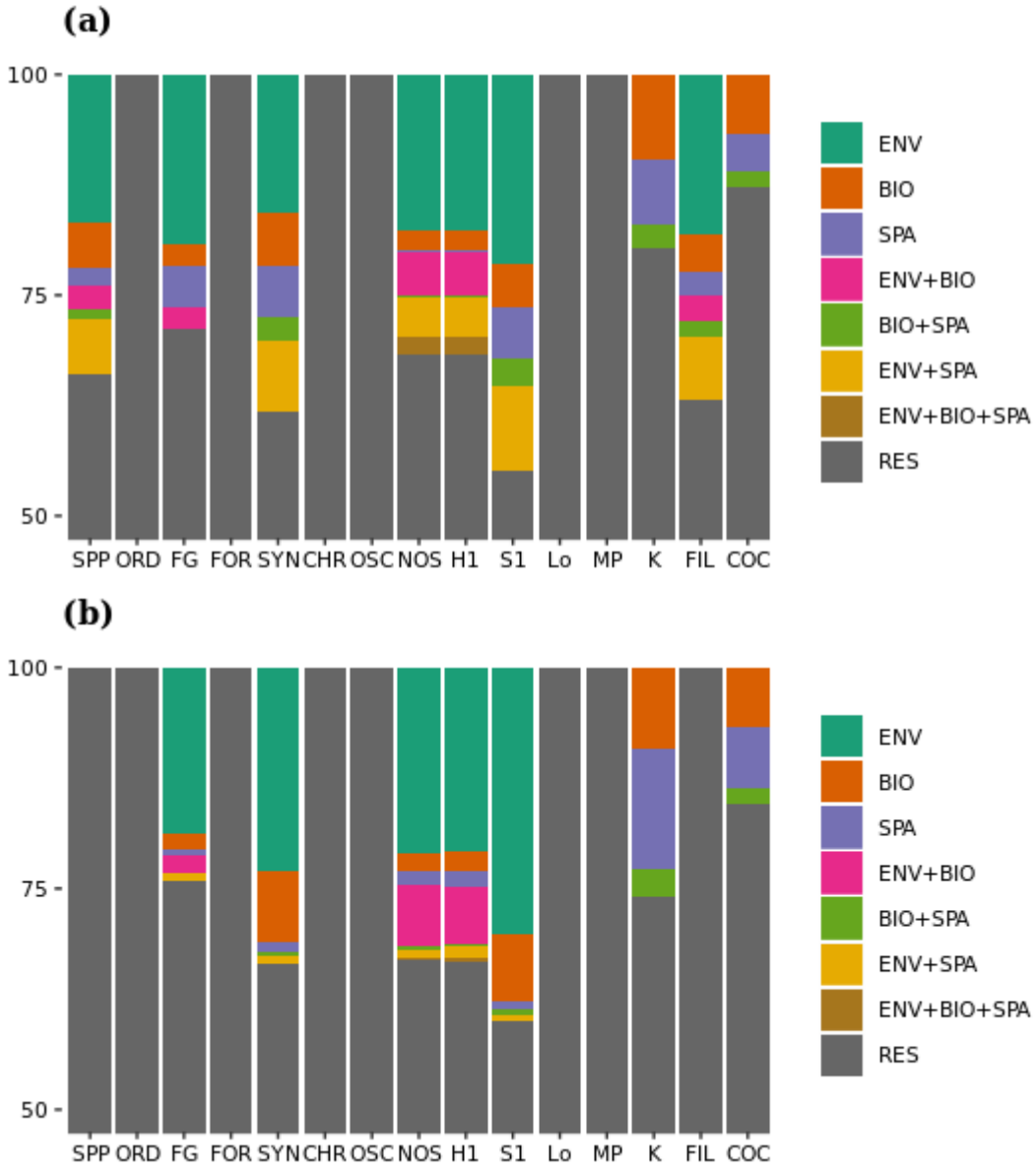
Species	Order (Komárek et. al 2014)	Functional Groups (Reynolds et. al 2002)	Life Form	Total Biovolume ($mm^3.L^{-1}$)	Frequency (% of lakes)
Unidentified coccoid group (UCG)	Synechococcales	**K**	coccoid	0.7836	60
Eucapsis parallelepipedon (Schmidle) Komárek & Hindák 1989	Synechococcales	**L_O**	coccoid	0.8132	12
***Limnococcus* sp.**	Synechococcales	**L_O**	coccoid	0.1267	20
Merismopedia punctata Meyen 1839	Synechococcales	**L_O**	coccoid	0.2089	28
Snowella lacustris (Chodat) Komárek & Hindák 1988	Synechococcales	**L_O**	coccoid	2.2783	36
Planktolyngbya contorta (Lemmermann) Anagnostidis & Komárek 1988	Synechococcales	**S1**	filamentous	2.5953	16
Planktolyngbya limnetica (Lemmermann) Komárková-Legnerová & Cronberg 1992	Synechococcales	**S1**	filamentous	10.9802	84
Chroococcus minutus (Kützing) Nägeli 1849	Chroococcales	**L_O**	coccoid	0.3559	40
Gomphosphaeria aponina Kützing 1836	Chroococcales	**L_O**	coccoid	1.2537	4
Geitlerinema splendidum (Greville ex Gomont) Anagnostidis 1989	Oscillatoriales	**S1**	filamentous	74.0293	20
Phormidium tergestinum (Rabenhorst ex Gomont) Anagnostidis & Komárek 1988	Oscillatoriales	**MP**	filamentous	5.5877	12
Aphanizomenon gracile (Lemmermann) Lemmermann 1907	Nostocales	**H1**	filamentous	10.3819	4
***Anabaenopsis* sp.**	Nostocales	**H1**	filamentous	1.1879	4
Chrysosporum ovalisporum (Forti) Zapomelová et al. 2012	Nostocales	**H1**	filamentous	63.4315	16
Cuspidothrix issatschenkoi (Usachev) Rajaniemi et al. 2005	Nostocales	**H1**	filamentous	30.8646	36
Dolichospermum viguieri (Denis et Frémy) Wacklin et al. 2009	Nostocales	**H1**	filamentous	27.0398	24
Unidentified Nostocales 1	Nostocales	**H1**	filamentous	1.6110	4
Unidentified Nostocales 2	Nostocales	**H1**	filamentous	0.2465	4
Unidentified Nostocales 3	Nostocales	**H1**	filamentous	1.2079	12
Unidentified Nostocales 4	Nostocales	**H1**	filamentous	0.0794	4
Sphaerospermopsis aphanizomenoides (Forti) Zapomelová et al. 2010	Nostocales	**H1**	filamentous	685.9850	40

Table 2 Environmental (ENV), biotic (BIO) and spatial (SPA) variables retained in the final global model and the relative contribution of those components, its shared fractions and the residuals (RES) on the distribution of cyanobacteria. Only significant fractions were used in the final models ($P<0.05$). Order of listing of variables follows their level of importance in the final model.

		Variables retained in final model			Relative contibution (adjusted R^2)							
		ENV	**BIO**	**SPA (MEM)**	**ENV**	**BIO**	**SPA**	**ENV+ BIO**	**BIO+ SPA**	**SPA+ ENV**	**ENV+ BIO+SPA**	**RES**
SPP		Transp, Cond, Temp, Turb, SRSi, DO, DIC, Depth, POC	DINO, ZIGO, CRYP, CRYS, EUGL, CHLO	7, 2, 18, 3, 15	0.1676***	0.0516***	0.0206*	0.0263	0.0123	0.0618	-0.0013	0.6610
ORD		Temp, Turb, Depth, TN	CRYP, DINO	None	0.2159***	0.0332*	-	0.0231	-	-	-	0.7278
	SYN	SRSi, Temp, DO, Turb, POC	ZIGO, DINO	7, 18, 15, 1, 23, 30, 16, 2	0.1527***	0.0595***	0.0772***	-0.0116	0.0298	0.0950	-0.0260	0.6235
	CHR	None	None	None	-	-	-	-	-	-	-	1.0000
	OSC	TDN, SRSi	CHLO	None	0.1966***	-0.0002	-	0.0827	-	-	-	0.7209
	NOS	Cond, Transp, Temp, Turb, Depth, DIC, Color, SRSi	DINO, CRYP, CRYS, ZIGO, EUGL	2, 3, 18, 32, 24, 25	0.1691***	0.0197*	0.0187*	0.0463	0.0043	0.0515	0.0249	0.6653
FG		Depth, Turb, SRSi, DO	CRYP	18, 9, 32	0.1884***	0.0229*	0.0544***	0.0241	-0.0048	0.0070	-0.0028	0.7108
	H1	Cond, Transp, Temp, Turb, Depth, DIC, Color, SRSi	DINO, CRYP, CRYS, ZIGO, EUGL	2, 3, 18, 32, 24, 25, 36	0.1667***	0.0199*	0.0225*	0.0434	0.0041	0.0540	0.0278	0.6616
	S1	SRSi, Temp, Turb, DO, TN	ZIGO	7, 18, 1, 15, 23, 2	0.2164***	0.0475***	0.0710**	-0.0210	0.0387	0.1090	-0.0326	0.5710
	L_o	None	ZIGO, DINO	None	-	0.0485***	-	-	-	-	-	0.9515
	MP	None	None	None	-	-	-	-	-	-	-	1.0000
	K	None	DINO	7, 30, 31, 27, 11, 34, 28	-	0.0683**	0.2190***	-	0.0543	-	-	0.6584
FOR		DO, SRSi	CRYP, DINO	None	0.0110	0.1447***	-	0.0465	-	-	-	0.7978
	FIL	Transp, Cond, Temp, Turb, SRSi, DO, DIC, Depth, TN	CRYP, ZIGO, EUGL, CHLO, CRYS, DINO	7, 2, 18, 3, 15, 1	0.1814***	0.0446***	0.0250**	0.0310	0.0178	0.0720	-0.0065	0.6347
	COC	None	DINO	7, 30, 31, 27, 11, 34	-	0.0513**	0.1171***	-	0.0329	-	-	0.7987

CHLO = Chlorophyceae; CRYP = Chryptophyceae; CRYS = Crysophyceae; DINO = Dinophyceae; EUGL = Euglenophyceae; ZIGO = Zygnematophyceae; SPP = Species; *ORD* = Orders; *SYN* = Synechococcales; *CHR* = Chroococcales; *OSC* = Oscillatoriales; *NOS* = Nostocales; *FG* = Functional Groups; *FOR* = Life form; *FIL* = filamentous; *COC* = coccoid. The significance of the fractions was tested through an analysis of variance (*** P<0.001; ** P<0.01; * P<0.05).

FIGURAS



Biotic matrices: SPP = by species, ORD = by orders, FG = by functional groups and FOR = by life form of the thallus; SYN = Synechococcales, CHR = Chroococcales, OSC = Oscillatoriales and NOS = Nostocales (groupings by order); **H1**, **S1**, **Lo**, **MP**, **K** (groupings by functional group); FIL = filamentous and COC = coccoid (groupings by life form).

Fig. 1 Proportion of the explained variation on the cyanobacteria distribution in the **(a)** broad and **(b)** fine spatial scales, in relation to the environmental (ENV), biotic (BIO) and spatial (SPA) components, its shared fractions and unexplained variation (RES). Gray bars with RES = 100% mean no dbMEMs were selected for that scale. For the significance of the pure fractions, please refer to Tables S4 and S5.

CONSIDERAÇÕES FINAIS

O paradigma de que os microrganismos são onipresentes ainda é muito presente em estudos ecológicos, o que impacta diretamente sobre o conhecimento da biogeografia destes seres (Hanson et al., 2012). Nesse contexto, as cianobactérias são extremamente afetadas, pois há uma crença geral de que estas são influenciadas apenas por filtros ambientais e não sofrem limitações em sua dispersão, ideia corroborada pela existência de várias espécies consideradas cosmopolitas (Padisák et al., 2016). Consequentemente sua biogeografia ainda é muito desconhecida, e estudos com o assunto normalmente estão restritos a descrição de novas espécies ou a registros em novos locais (Moreira et al., 2013; Ribeiro et al., 2018). Este desconhecimento acerca do grupo é grave considerando sua importância: as cianobactérias desempenham um papel ecológico essencial no ciclo dos nutrientes (Whitton & Potts, 2000); além disso, apresentam potenciais riscos tanto ao ambiente quanto à saúde pública, devido ao potencial tóxico e invasor de algumas espécies e à grande resistência a condições adversas que possuem (Whitton & Potts, 2000). Diante disso, estudos que considerem fatores espaciais são de suma importância para que se possa compreender os processos que regem a biodiversidade do grupo (Ribeiro et al., 2018). Deste modo, o presente estudo buscou observar a contribuição relativa de processos espaciais e ambientais sobre a distribuição das cianobactérias. Os resultados obtidos indicam que estas são influenciadas tanto pelo ambiente quanto pelo espaço, sendo os filtros ambientais mais atuantes. Além disso, diferentes grupos taxonômicos e funcionais apresentam respostas distintas sobre estes fatores, portanto classificações diferentes não evidenciarão exatamente os mesmos processos.

Estudos como o aqui apresentado são essenciais para uma melhor compreensão da biogeografia dos microrganismos. A área de estudo considerou lagoas com diferentes condições ambientais e bióticas, onde as comunidades se mostraram bastante heterogêneas. Isto possibilitou uma análise adequada, onde foram contabilizadas não só florações, mas também espécies raras e pouco abundantes. Deste modo, o presente trabalho mostrou que é possível perceber a influência de fatores espaciais sobre a distribuição das cianobactérias mesmo sem a utilização de técnicas moleculares. Este é um dado extremamente importante, considerando que até pouco tempo as cianobactérias eram descritas utilizando apenas caracteres morfológicos, e que muitos estudos com o grupo ainda são publicados sem o auxílio destas técnicas (por exemplo, Branco et al., 2014 e Huszar et al., 2015). Além do mais, diferentes formas de classificação podem ser utilizadas de forma complementar, a fim de melhor compreender os processos que regem sua diversidade. Esta é uma abordagem interessante que deve ser considerada em estudos futuros, mesmo aqueles que

venham a utilizar técnicas moleculares, pois a combinação de classificações taxonômicas e funcionais pode trazer diferentes perspectivas sobre os resultados, além de permitir a comparação com um maior número de trabalhos já realizados.

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MATERIAL SUPLEMENTAR

Table S1 Geographic coordinates of the 125 sampled points.

LAKE	POINT	LATITUDE (S)	LONGITUDE (W)	LAKE	POINT	LATITUDE (S)	LONGITUDE (W)
Cadeia	1	29°54.360'	50°08.462'	**Custódia**	1	30°02.158'	50°10.346'
Cadeia	2	29°54.595'	50°08.482'	**Custódia**	2	30°01.796'	50°11.447'
Cadeia	3	29°54.627'	50°08.682'	**Custódia**	3	30°01.287'	50°11.199'
Cadeia	4	29°54.620'	50°08.844'	**Custódia**	4	30°00.601'	50°10.886'
Cadeia	5	29°54.752'	50°08.719'	**Custódia**	5	30°00.174'	50°11.749'
do Passo	1	29°51.792'	50°05.880'	**Tramandaí**	1	29°58.920'	50°10.741'
do Passo	2	29°51.861'	50°06.491'	**Tramandaí**	2	29°59.824'	50°09.984'
do Passo	3	29°51.244'	50°06.379'	**Tramandaí**	3	29°57.306'	50°09.495'
do Passo	4	29°51.544'	50°07.190'	**Tramandaí**	4	29°57.994'	50°09.466'
do Passo	5	29°52.040'	50°06.710'	**Tramandaí**	5	29°58.397'	50°08.424'
Malva	1	29°48.138'	50°06.508'	**Horácio**	1	29°54.861'	50°13.775'
Malva	2	29°49.576'	50°09.532'	**Horácio**	2	29°54.762'	50°13.935'
Malva	3	29°48.084'	50°10.548'	**Horácio**	3	29°54.884'	50°14.098'
Malva	4	29°47.159'	50°11.031'	**Horácio**	4	29°54.654'	50°14.071'
Malva	5	29°50.436'	50°13.574'	**Horácio**	5	29°54.603'	50°13.713'
Peixoto	1	29°51.706'	50°13.974'	**Caconde**	1	29°51.704'	50°12.928'
Peixoto	2	29°52.170'	50°14.807'	**Caconde**	2	29°51.959'	50°12.361'
Peixoto	3	29°52.285'	50°14.422'	**Caconde**	3	29°52.230'	50°12.333'
Peixoto	4	29°52.378'	50°14.220'	**Caconde**	4	29°52.064'	50°11.726'
Peixoto	5	29°52.644'	50°14.726'	**Caconde**	5	29°51.693'	50°12.032'
Marcelino	1	29°53.118'	50°15.172'	**Traíras**	1	29°52.006'	50°11.169'
Marcelino	2	29°53.219'	50°15.092'	**Traíras**	2	29°51.974'	50°10.928'
Marcelino	3	29°53.240'	50°15.259'	**Traíras**	3	29°52.115'	50°10.623'
Marcelino	4	29°53.111'	50°15.307'	**Traíras**	4	29°51.789'	50°10.678'
Marcelino	5	29°53.193'	50°15.227'	**Traíras**	5	29°51.664'	50°10.906'
Azaléia	1	30°05.657'	50°12.812'	**Lessa**	1	29°49.813'	50°10.596'
Azaléia	2	30°05.683'	50°13.105'	**Lessa**	2	29°50.482'	50°09.922'
Azaléia	3	30°06.102'	50°13.401'	**Lessa**	3	29°50.834'	50°10.045'
Azaléia	4	30°05.634'	50°13.612'	**Lessa**	4	29°51.395'	50°10.226'
Azaléia	5	30°05.567'	50°13.304'	**Lessa**	5	29°51.067'	50°09.163'
Gentil	1	30°04.064'	50°12.501'	**Ramalhete**	1	29°45.383'	50°08.375'
Gentil	2	30°03.249'	50°12.900'	**Ramalhete**	2	29°45.371'	50°07.924'
Gentil	3	30°03.529'	50°12.432'	**Ramalhete**	3	29°44.970'	50°08.293'
Gentil	4	30°03.143'	50°12.152'	**Ramalhete**	4	29°45.270'	50°09.001'
Gentil	5	30°03.429'	50°11.407'	**Ramalhete**	5	29°45.671'	50°09.040'

Table S1 Geographic coordinates of the 125 sampled points. (cont.)

LAKE	POINT	LATITUDE (S)	LONGITUDE (W)	LAKE	POINT	LATITUDE (S)	LONGITUDE (W)
Negra	1	29°46.981'	50°10.313'	**Emboabinha**	1	29°58.095'	50°13.849'
Negra	2	29°46.879'	50°09.895'	**Emboabinha**	2	29°58.054'	50°13.938'
Negra	3	29°47.087'	50°10.199'	**Emboabinha**	3	29°58.134'	50°14.176'
Negra	4	29°47.280'	50°09.982'	**Emboabinha**	4	29°57.942'	50°14.150'
Negra	5	29°47.246'	50°10.263'	**Emboabinha**	5	29°57.976'	50°13.877'
Caieira	1	29°51.943'	50°08.483'	**Suzana**	1	30°08.907'	50°16.204'
Caieira	2	29°51.649'	50°08.505'	**Suzana**	2	30°09.215'	50°15.914'
Caieira	3	29°51.565'	50°08.684'	**Suzana**	3	30°08.945'	50°15.879'
Caieira	4	29°51.197'	50°08.188'	**Suzana**	4	30°08.680'	50°15.765'
Caieira	5	29°51.405'	50°08.027'	**Suzana**	5	30°08.876'	50°15.590'
das Pombas	1	29°54.462'	50°09.867'	**Fortaleza**	1	30°08.273'	50°12.867'
das Pombas	2	29°54.529'	50°10.211'	**Fortaleza**	2	30°06.974'	50°13.749'
das Pombas	3	29°54.012'	50°10.744'	**Fortaleza**	3	30°07.189'	50°15.320'
das Pombas	4	29°54.220'	50°10.970'	**Fortaleza**	4	30°07.848'	50°14.090'
das Pombas	5	29°54.579'	50°09.749'	**Fortaleza**	5	30°09.280'	50°13.991'
Dom Daniel	1	29°57.737'	50°10.957'	**Cidreira**	1	30°09.774'	50°14.744'
Dom Daniel	2	29°57.868'	50°11.475'	**Cidreira**	2	30°11.502'	50°15.568'
Dom Daniel	3	29°57.625'	50°11.674'	**Cidreira**	3	30°12.248'	50°14.348'
Dom Daniel	4	29°57.934'	50°11.353'	**Cidreira**	4	30°12.822'	50°15.367'
Dom Daniel	5	29°58.058'	50°11.477'	**Cidreira**	5	30°13.358'	50°15.358'
Tapera	1	30°03.210'	50°13.571'	**Cerquinha**	1	30°13.680'	50°16.019'
Tapera	2	30°03.365'	50°13.738'	**Cerquinha**	2	30°13.951'	50°15.906'
Tapera	3	30°03.394'	50°13.413'	**Cerquinha**	3	30°14.021'	50°15.727'
Tapera	4	30°03.503'	50°13.837'	**Cerquinha**	4	30°14.266'	50°15.653'
Tapera	5	30°03.274'	50°13.808'	**Cerquinha**	5	30°13.917'	50°15.994'
Emboaba	1	29°58.462'	50°13.208'				
Emboaba	2	29°58.287'	50°13.063'				
Emboaba	3	29°57.941'	50°13.358'				
Emboaba	4	29°58.038'	50°12.904'				
Emboaba	5	29°58.258'	50°12.822'				

Table S2 Total biovolume ($mm^3.L^{-1}$) of the cyanobacteria and the eukaryote phytoplankton in each lake.

Lake	CYAN	CHLO	DIAT	CRYP	ZIGO	DINO	EUGL	CRYS
Cadeia	2.1630	0.4068	1.2034	0.8192	1.3982	0.0229	3.8015	0.0073
do Passo	8.7363	0.3556	1.1343	0.1236	0.0000	0.1441	0.1261	0.3164
Malva	1.8647	0.1382	0.1855	0.4604	0.0125	0.0000	0.0000	0.0000
Peixoto	7.0679	11.8826	38.3105	3.3389	1.0651	0.5591	1.4265	0.0191
Marcelino	741.6714	47.6148	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Azaleia	14.3247	0.9582	2.7353	0.4672	0.8024	0.5658	0.0000	0.4796
Gentil	0.7497	1.3869	0.4616	1.4000	3.0755	0.6693	0.8996	0.0774
Custódia	31.6548	0.9804	3.3239	0.2892	3.7454	0.0678	0.0000	0.0000
Tramandaí	7.5574	0.1162	0.5719	0.2564	0.0909	0.3781	0.0000	0.0000
Horácio	0.0588	0.1126	0.0555	1.8859	0.0000	1.9738	0.0144	0.2229
Caconde	1.0967	5.0296	8.2775	0.5293	9.6253	0.0000	0.0000	0.0000
Traíras	1.6913	1.1557	5.4132	0.2801	5.0323	14.3570	0.1699	0.0000
Lessa	30.0319	1.4760	30.5280	0.6823	24.3894	0.0000	0.0000	0.0000
Ramalhete	0.0063	0.0076	0.1412	0.4962	0.0000	0.0000	0.0000	0.0000
Negra	26.3338	0.4611	0.4284	0.6721	0.0000	1.0974	0.0312	0.0154
Caieira	5.4664	0.1286	1.1755	1.2340	0.0000	0.0000	0.2811	0.0000
das Pombas	0.0100	0.3395	0.3787	0.9929	0.0000	0.2153	0.1022	0.0488
Dom Daniel	32.3378	0.1922	0.4581	0.1033	0.0856	0.4047	0.0000	0.0000
Tapera	0.1037	0.1329	0.0000	1.1709	1.3883	0.1874	0.1198	0.1967
Emboaba	0.4922	0.2550	0.1595	0.2121	0.1063	0.0650	0.0250	0.0000
Emboabinha	0.0674	0.3620	0.2482	0.4212	0.1083	0.0000	0.6767	0.0000
Suzana	0.6661	0.1615	0.0948	0.0609	0.0000	0.0524	0.0000	0.0000
Fortaleza	1.2561	0.1141	1.1074	0.0745	0.1658	0.0229	0.0868	0.0000
Cidreira	0.7089	0.0445	0.0831	0.0934	0.0000	0.0121	0.0000	0.0000
Cerquinha	4.9309	0.0907	0.2495	0.0802	0.0000	0.0000	0.2262	0.0000

CYAN = cianobacteria; *CHLO* = Chlorophyceae; *DIAT* = diatoms, *CRYP* = Chryptophyceae, *ZIGO* = Zygnematophyceae, *DINO* = *Dinophyceae*, *EUGL* = Euglenophyceae, *CRYS* = Crysophyceae.

Table S3 Significance (considered significant at P<0.05) and adjusted R^2 values (R^2 Adj) of the redundancy analysis performed using the whole set of variables. These adjusted R^2 values were used as a threshold for variable selection.

	P-value			R^2 Adj		
	ENV	**BIO**	**SPA**	**ENV**	**BIO**	**SPA**
SPECIES (SPP)	0.001	0.001	0.001	0.258	0.090	0.159
ORDER (ORD)	0.001	0.016	0.056	0.250	0.064	0.116
SYN	0.001	0.004	0.001	0.224	0.069	0.226
CHR	0.858	0.299	0.871	-0.080	0.007	-0.094
OSC	0.027	0.003	0.098	0.293	0.138	0.123
NOS	0.001	0.001	0.005	0.293	0.108	0.110
FUNCTIONAL GROUP (FG)	0.001	0.020	0.021	0.259	0.060	0.118
H1	0.001	0.001	0.003	0.293	0.108	0.110
S1	0.001	0.013	0.001	0.283	0.063	0.237
LO	0.148	0.006	0.818	0.050	0.057	-0.042
MP	0.198	0.524	0.359	0.056	-0.012	0.035
K	0.200	0.010	0.005	0.058	0.125	0.283
LIFE FORM (FOR)	0.021	0.001	0.295	0.111	0.200	0.038
FIL	0.001	0.001	0.001	0.285	0.089	0.158
COC	0.122	0.004	0.015	0.055	0.100	0.163

Table S4 Broad-scale submodel: Relative contribution of the environmental (ENV), biotic (BIO) and spatial (SPA) components, its shared fractions and the residuals (RES) on the distribution of the cyanobacteria. The results are expressed in adjusted R^2 values.

	ENV	BIO	SPA	ENV+ BIO	BIO+ SPA	SPA+ ENV	ENV+ BIO+ SPA	RES
SPECIES (SPP)	0.1676***	0.0516***	0.0206**	0.0263	0.0123	0.0618	-0.0013	0.6610
ORDER (ORD)	-	-	-	-	-	-	-	-
SYN	0.1626***	0.0632***	0.0602***	-0.0139	0.0261	0.0850	-0.0237	0.6404
CHR	-	-	-	-	-	-	-	-
OSC	-	-	-	-	-	-	-	-
NOS	0.1776***	0.0221*	0.0004	0.0511	0.0020	0.0430	0.0202	0.6836
FUNCTIONAL GROUP (FG)	0.1951***	0.0236*	0.0467***	0.0257	-0.0055	0.0003	-0.0044	0.7185
H1	0.1776***	0.0221*	0.0004	0.0511	0.0020	0.0430	0.0202	0.6836
S1	0.2250***	0.0525***	0.0610***	-0.0248	0.0336	0.1005	-0.0288	0.5810
LO	-	-	-	-	-	-	-	-
MP	-	-	-	-	-	-	-	-
K	-	0.0966***	0.0735**	-	0.0260	-	-	0.8039
LIFE FORM (FOR)	-	-	-	-	-	-	-	-
FIL	0.1814***	0.0446***	0.0250**	0.0310	0.0178	0.0720	-0.0065	0.6347
COC	-	0.0672***	0.0428**	-	0.0170	-	-	0.8731

SYN = Synechococcales; *CHR* = Chroococcales; *OSC* = Oscillatoriales; *NOS* = Nostocales; *FIL* = filamentous; *COC* = coccoid.
The significance of the pure fractions was tested through an analysis of variance (*** P<0.001; ** P<0.01; * P<0.05).

Table S5 Fine-scale submodel: Relative contribution of the environmental (ENV), biotic (BIO) and spatial (SPA) components, its shared fractions and the residuals (RES) on the distribution of the cyanobacteria. The results are expressed in adjusted R^2 values.

	ENV	BIO	SPA	ENV+ BIO	BIO+ SPA	SPA+ ENV	ENV+ BIO+ SPA	RES.
SPECIES (SPP)	-	-	-	-	-	-	-	-
ORDER (ORD)	-	-	-	-	-	-	-	-
SYN	0.2380***	0.0850***	0.0117	-0.0365	0.0043	0.0096	-0.0010	0.6890
CHR	-	-	-	-	-	-	-	-
OSC	-	-	-	-	-	-	-	-
NOS	0.2101***	0.0212*	0.0156*	0.0688	0.0029	0.0106	0.0024	0.6685
FUNCTIONAL GROUP (FG)	0.1878***	0.0174*	0.0067	0.0202	0.0007	0.0076	0.0011	0.7585
H1	0.2082***	0.0215*	0.0180*	0.0647	0.0025	0.0125	0.0066	0.6661
S1	0.3186***	0.0798**	0.0087	-0.0494	0.0064	0.0068	-0.0043	0.6333
LO	-	-	-	-	-	-	-	-
MP	-	-	-	-	-	-	-	-
K	-	0.0920***	0.1362***	-	0.0306	-	-	0.7413
LIFE FORM (FOR)	-	-	-	-	-	-	-	-
FIL	-	-	-	-	-	-	-	-
COC	-	0.0671***	0.0697***	-	0.0170	-	-	0.8461

SYN = Synechococcales; *CHR* = Chroococcales; *OSC* = Oscillatoriales; *NOS* = Nostocales; *FIL* = filamentous; *COC* = coccoid.
The significance of the pure fractions was tested through an analysis of variance (** P<0.001; * P<0.01; * P<0.05).

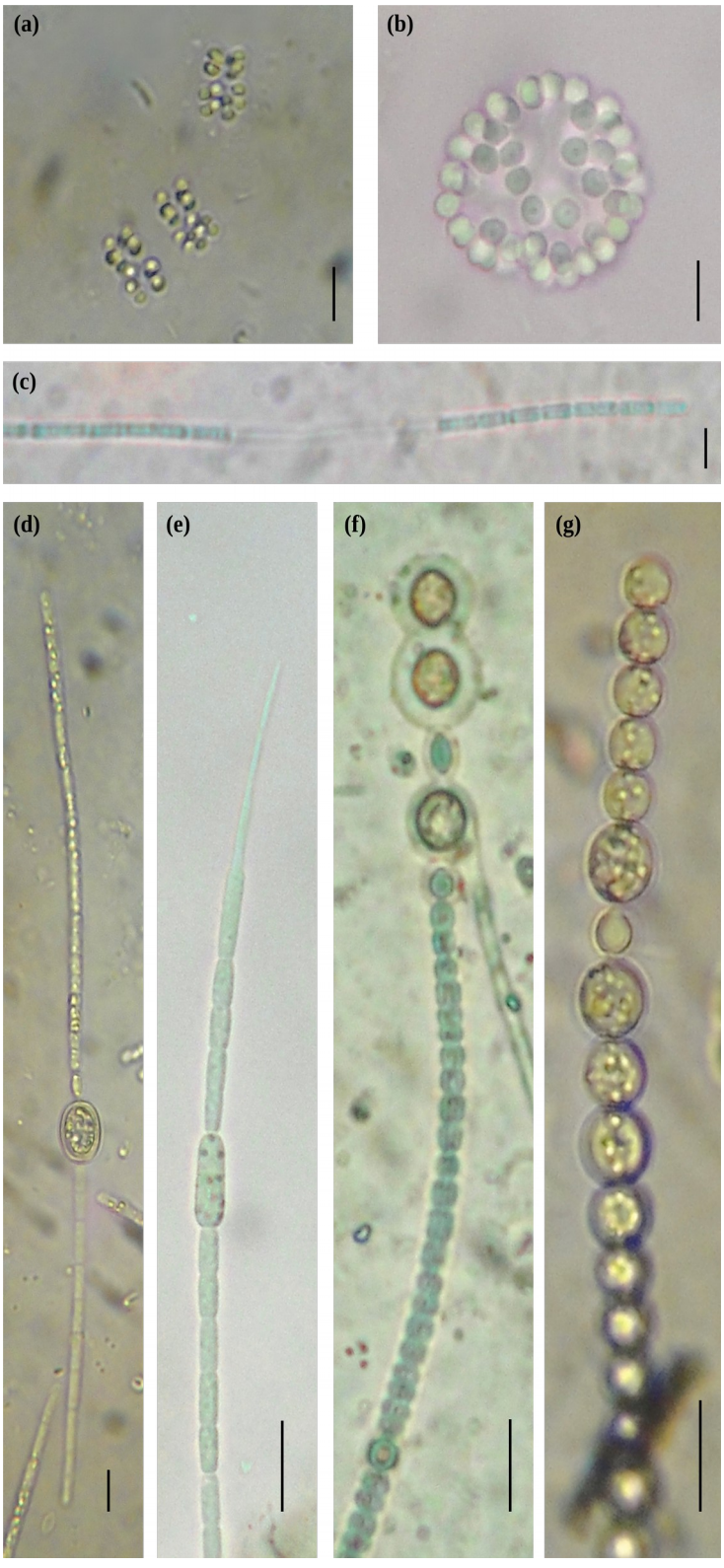

Fig. S1 Some of the main cyanobacteria recorded in the lakes. (a) *Eucapsis parallelepipedon*; (b) *Snowella lacustris*; (c) *Planktolyngbya limnetica*; (d) *Chrysosporum ovalisporum*; (e) *Cuspidothrix issatschenkoi*; (f-g) *Sphaerospermopsis aphanizomenoides*.
Bars: (a-b) = 5 µm; (c-g) = 10 µm.