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Global changes may be promoting a rise in select cyanobacteria in nutrient-poor northern lakes

Running title (45 characters): Global changes promote select cyanobacteria

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ABSTRACT

The interacting effects of global changes – including increased temperature, altered precipitation, reduced acidification, and increased dissolved organic matter loads to lakes – are anticipated to create favourable environmental conditions for cyanobacteria in northern lakes. However, responses of cyanobacteria to these global changes are complex, if not contradictory. We

hypothesized that absolute and relative biovolumes of cyanobacteria (both total and specific genera) are increasing in Swedish nutrient-poor lakes and that these increases are associated with global changes. We tested these hypotheses using data from 28 nutrient-poor Swedish lakes over 16 years (1998-2013). Increases in cyanobacteria relative biovolume were identified in 21% of the study sites, primarily in the southeastern region of Sweden, and were composed mostly of increases from three specific genera: *Merismopedia*, *Chroococcus*, and *Dolichospermum*. Taxon specific changes were related to different environmental stressors; i.e., increased surface water temperature favored higher *Merismopedia* relative biovolume in low pH lakes with high nitrogen to phosphorus ratios, whereas acidification recovery was statistically related to increased relative biovolumes of *Chroococcus* and *Dolichospermum*. In addition, enhanced dissolved organic matter loads were identified as potential determinants of *Chroococcus* suppression and *Dolichospermum* promotion. Our findings highlight that specific genera of cyanobacteria benefit from different environmental changes. Our ability to predict the risk of cyanobacteria prevalence requires consideration of the environmental condition of a lake and the sensitivities of the cyanobacteria genera within the lake. Regional patterns may emerge due to spatial autocorrelations with and among lake history, rates and direction of environmental change, and the niche space occupied by specific cyanobacteria.

INTRODUCTION

Northern ecosystems are anticipated to undergo the greatest rates of climate change (Hansen et al., 2006; IPCC, 2007). Climate changes in northern (> 45° North) ecosystems include increasing temperatures (Kirtman et al., 2013; Kjellström et al., 2014), changes to the timing and magnitude of precipitation (Kjellström et al., 2016; Melillo et al., 2014), and altered terrestrial-aquatic linkages (Creed et al., 2015; Senar et al., 2018) that lead to changes in the physical, chemical and biological properties of lakes (e.g., Creed et al., 2018). The integration of these climate changes has manifested in increased lake surface water temperatures (O'Reilly et al., 2015), changes in lake residence time (Schindler & Smol, 2006), and, in combination with other factors, increases in terrestrially-derived dissolved organic matter (DOM) (Finstad et al., 2016; Monteith et al., 2007), a phenomenon referred to as browning (Williamson et al., 2015). In addition to the destabilizing influence of climate change are the long-term impacts of acidification and its recovery. Since peak emissions for sulphur (S) and nitrogen (N) in the 1960s and mid-1980s, respectively, the concentrations of S and N in northern lakes have been in decline (Driscoll et al., 2016; de Wit et al., 2015). Although some lakes have rebounded to near pre-industrial pH levels (Moldan et al., 2013; Skjelkvåle et al., 2001), the recovery of impacted lakes has been slow (Futter, et al, 2014) and interpretation of recovery trends marred by climate change (Holmgren, 2014). The new baseline conditions are thus uncertain but likely to have fundamental consequences for freshwater lake ecological function and associated ecosystem services (Creed et al., 2018).

A better understanding of the cumulative effects of global changes in northern lakes is required to understand how the "re-shuffled deck" of atmospheric conditions – i.e., the return towards baseline atmospheric acidic deposition in the face of altered climate regimes – may influence these lakes in one of the more rapidly changing regions of the planet (Smith et al., 2015). Global changes do not have to be large in magnitude to have a large influence on freshwater ecosystems (e.g., Lehnherr et al., 2018). Phytoplankton communities respond quickly to new environmental conditions due to their rapid growth rates and short life cycles, i.e., they are "harbingers of change" (cf. Huertas et al., 2011). The phytoplankton most associated with freshwater quality problems are the bloom-forming species of cyanobacteria (Huisman et al., 2018; Reid et al., 2018). However, not only bloom-forming species of cyanobacteria reduce water quality; many (and likely most, Calteau et al., 2014;

Rantala et al., 2004) species of cyanobacteria are capable of producing toxic and noxious compounds that degrade water quality and pose a risk to human and aquatic ecosystem health. In addition, cyanobacteria are considered to be a nutritionally poor and often an inadequate food source for zooplankton with cascading effects to higher trophic levels (Bednarska et al., 2014; Creed et al., 2018; von Elert et al., 2003). Food quality is especially important in oligotrophic (total phosphorus (TP) < 25 µgL^{-1}) lakes where food availability already constrains zooplankton growth (Persson et al., 2007). Therefore, changes in the biovolume of cyanobacteria relative to total phytoplankton biovolume can have important implications for trophic transfer and efficiency in northern, oligotrophic lakes.

While generally associated with nutrient-rich lakes, an increasing proportion of cyanobacteria in phytoplankton communities, and occasionally cyanobacteria blooms are now becoming more frequent in nutrient-poor lakes in the north (Callieri et al., 2014; Cottingham et al., 2015; Pick 2015; Przytulska et al., 2017; Winter et al., 2011). However, the factors influencing these increases in cyanobacteria are not well-understood (Creed et al., 2018). There exists a need to revise existing conceptual models traditionally based on nutrient-rich lakes (Paerl & Otten, 2013) to describe the cumulative effects of global changes that may be driving the rise of cyanobacteria in nutrient-poor northern lakes. Specifically, global changes are altering the ecological niches (Hutchinson, 1957)) of northern lakes. Cyanobacteria have unique physiological features compared to their photo-eukaryotic competitors (reviewed in Carey et al., 2012; Dokulil & Teubner, 2000) that may confer a growth advantage in these altered ecological niches. See Table 1 for a review of these global changes and cyanobacteria advantages.

Here, we test the hypothesis that absolute and relative biovolumes of cyanobacteria are increasing in Swedish oligotrophic lakes, and that these increases are associated with global changes. We predict that: (1) increased surface water temperature, especially in the southern region of Sweden where temperatures are already high, results in increased relative abundance of cyanobacteria as a group; (2) recovery from acidification and the ensuing changes in pH result in a decrease in acidophilic genera such as *Merismopedia*; (3) declines in lake water DIN:TP favouring N-fixation result in an increase of N-fixing genera such as *Dolichospermum*; and (4) browning (by providing nutrient subsidies from the catchment with DOM acting as the nutrient vector) results in an increase in cyanobacteria relative biovolume by increasing lake nutrient pools of N and P. These hypotheses were

tested using the Swedish national environmental monitoring program data for 28 minimally impacted (< 5% of non-natural land use) nutrient-poor lakes. Sweden, with its changing climate (Andréasson et al., 2004), recovery from atmospheric acidic deposition (Moldan et al., 2013), changes in lake nutrient stoichiometry (Isles et al., 2018), and browning (de Wit et al., 2016), coupled with long-term lake monitoring program (Fölster et al., 2014), serves as an important case study for examining the potential of cyanobacteria to expand their relative dominance in phytoplankton communities in northern lakes. The Swedish data utilized in this analysis are spatially and temporally extensive, spanning lakes that allow investigation of space and time interactions and the potential formation of phytoplankton niches favourable for cyanobacteria, which may shift in a synchronous manner within geographic regions due to global changes (cf. Isles et al., 2018). The degree of the shift in ecological niches will depend upon the baseline conditions from which the temporal trend in environmental conditions begins. Further, the Swedish data used in this study are not only unmatched in their spatial and temporal extent but also in identification of phytoplankton to the genus level. Therefore, these data provide the opportunity to assess the effects of changing environmental conditions on cyanobacteria in northern, oligotrophic lakes at the genus level and allows for the determination of factors that may contribute to their growth and increasing proportion in phytoplankton communities.

Table 1: A summary of the global changes observed in Sweden, the factors that modulate the global changes, the direct and indirect effects on cyanobacteria dominance (i.e., relative biovolume), and the traits that cyanobacteria possess that may increase their prevalence under global change conditions.

| | | Effects on Cyanobacteria Prevalence | | |
| | | | | Advantageous Traits Contained by Members within the Class *Cyanophyceae* |
Global Change	**Modulating Factors**	**Direct Effects**	**Indirect Effects**	
Higher Water Temperatures[32]	• Humidity, ice-cover, and wind[23] • Lake surface area and depth[24]	• Higher optimal growth temperature (>25°C) than diatoms [1, 2, 3, 4, 5, 6, 7] • Low temperature (<20 °C) growth rate disadvantage compared to chlorophytes reduced/diminished [8]	• Enhanced water column stability[25] • Lower water density • Increase sinking loss of eukaryotic competitors[26]	• Buoyancy (less risk of sinking loss)[12] and access to well-lit surface waters
			• Stronger grazing pressure from *Daphnia* (smaller or absent in warm conditions)[18,19] • Earlier predation of *Daphnia* by fish[20]	• Colony formation[28] • Allelochemical formation[29]
			• Enhanced mineralization[27] • Hypolimnion oxygen depletion (enhanced sediment-nutrient-efflux)[16]	• Rapid nutrient uptake[14] and storage[15] • Buoyancy (access to hypolimnetic nutrient pool)[13]
Changes to Precipitation[31] **(likely increase in Sweden)**[34]	• Amount of rainfall during rainfall events, length of dry preceding and subsequent dry period, hydrology and size of catchment area[30]		• Increased nutrient loading from storm events[33] • Movement of the thermocline by wind and inflow (sediment release of nutrients)[35]	• Rapid nutrient uptake[14] and storage[15] • Buoyancy (access to hypolimnetic nutrient pool)[13]
Acidification	• Extent of historical		• Altered inorganic C availability though	• Cyanobacteria have flexible inorganic

		Effects on Cyanobacteria Prevalence		
Global Change	**Modulating Factors**	**Direct Effects**	**Indirect Effects**	**Advantageous Traits Contained by Members within the Class** *Cyanophyceae*
Recovery (pH)[42]	acidification, catchment geology, sea-salt episodes[43]		pH-dependent change in carbon species (shifts between carbon dioxide, carbonic acid, bicarbonate, and carbonate)[21]	carbon uptake systems[36] compared to other phytoplankton[37] • Cyanobacteria have CO_2 concentrating mechanisms[39] • Cyanobacteria not found in habitats in which the pH is less than 4 or 5[38]
			• Toxic effects of Al lifted	• Release of non-acidophilic cyanobacteria species from Al-toxicity[40]
			• Calcium decline/recovery linked to zooplankton community shifts[22]	
Reduced Atmospheric N deposition[45]		• Shift in nutrient stoichiometry, particularly N:P ratios[41]		• Nitrogen fixation
Browning[46]	• Peatlands and wetlands in catchment area, history of acidification[50], rate of climate warming, tree cover[47], hydrological connectivity[48], lake residence time[49]	• Nutrient delivery to lakes including trace metals[51]		• Cyanobacteria have higher requirements for trace elements compared with eukaryotic phytoplankton[44] • Some cyanobacteria can scavenge nutrients from DOM[53,54] • Some cyanobacteria possess the ability

		Effects on Cyanobacteria Prevalence		Advantageous Traits Contained by Members within the Class *Cyanophyceae*
Global Change	Modulating Factors	Direct Effects	Indirect Effects	
				to assimilate organic C[52]

			• Modifies the physical character of clear lakes by:
			   o Increasing light absorption in surface layers and increasing surface water temperature [10,11]
			   o Reducing depth of the mixed surface layers [10,11]
			   o Increasing the rate of light extinction[9] and therefore regulating phytoplankton habitat depth
			 • Defines different habitat for Zooplankton and fish
				• Cyanobacteria are strong competitors for light due to their accessory pigmentation and the structural organisation of their light-harvesting antenna[17]

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METHODS

Lake selection

The lakes are part of the Swedish National Lake monitoring program for Trend lakes (see http://info1.ma.slu.se/) comprising 106 lakes with surface water chemistry sampled four times per annum (roughly once per season) and phytoplankton biomass and community composition measured at least once per annum, usually in August. All sampling and analytical methods were accredited by Swedac (Acc.No. 1208), which is a formal recognition of competence in accordance with European and International standards (ISO/IEC 17025). A detailed description of the sampling procedure, enumeration procedure, and biovolume calculations are given within the accreditation standards: SS-EN 16698:2015, SS-EN 15204:2006, and SS-EN 16695:2015, respectively.

The criteria for study lake selection were: (1) lakes were sampled for both phytoplankton and chemistry in each year of the study period (the most consistent sampling period was the 16-year period from 1998 to 2013); (2) lakes were sampled in the photic zone (i.e., maximum photic zone depth = Secchi depth × 3 (Holmes, 1970)) for both phytoplankton and chemistry within the same month; (3) lakes had < 5% (as of 2013) human activity-related land use in the contributing catchments (by area), enabling a focus on the effects of global changes rather than land use/land cover changes; and (4) lakes were not part of the Swedish Integrated Liming Effect Studies program.

The 28 lakes that formed the basis of this study were distributed across Sweden spanning latitudinal and longitudinal gradients of 56.6 to 65.8º North and 15.7 to 23.4º East respectively (Figure 1). For details on the contributing catchments and their lake properties see Supplementary Information 1 (S.I.1).

Global change metrics

A list of metrics with ranges for global changes (i.e., climate change, acidification recovery, changes in nutrients and nutrient ratios, and browning) are provided in S.I.2. For each physical, chemical, and phytoplankton variable, annual averages were estimated from monthly means. Water chemistry data were collected using a PVC pipe (Rotter tube) from surface samples (0.5m) at fixed sampling points over the deepest point of the lake. Details on sample collection and analysis can be found at:

https://www.havochvatten.se/download/18.64f5b3211343cffddb280004869/Vattenkemi+i+sj%C3%B

6ar.pdf and https://www.slu.se/institutioner/vatten-miljo/laboratorier/vattenkemiska-laboratoriet/. For lakes with chemical values below the detection limit, the data below the detection limit were replaced with values equal to the detection limit divided by 2, following the guidelines of the US Environmental Protection Agency (EPA, 2000).

Climate change metrics included surface water temperature (ºC) and precipitation (mm). Site specific (i.e., interpolated data at the sampling point) monthly mean precipitation data were extracted from the Swedish Hydrological and Meteorological Institute (SMHI) database (http://luftweb.smhi.se/). Based on the November-October water year, monthly means of precipitation for spring (March-June), summer (July-September), and fall and winter (October-March) were included in the analysis.

Acidification recovery metrics included sulphate (SO_4^{2-}), pH, alkalinity, base cations (calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na^+)), and Al^{3+}. Alkalinity (Henriksen, 1979) was estimated using Acid Neutralizing Capacity (ANC) as well as the ANC adjusted for organic acid acidity (ANCoaa) (S.I.2), both as microequivalents per litre (Reuss & Johnson, 1985). ANC is often more reliable than pH because it is less sensitive to changes in CO_2 concentrations (Stumm & Morgan, 1981). ANCoaa further incorporates the estimated charge associated with organic C that may influence the charge balance of a lake (Lydersen et al., 2004). Major components of the ANC calculations (SO_4^{2-}, Ca^{2+}, Mg^{2+}, Na^+) were also included independently as metrics of acidification recovery. Al^{3+}, which can become mobilized from soils under low pH conditions prompted by acidification (Cronin & Schofield, 1979), was also included as a metric of acidification recovery.

Nutrient metrics included TP, nitrite+nitrate (NO_x), ammonium (NH_4), DIN, and DIN:TP. DIN was estimated as NO_x plus NH_4 and DIN:TP is presented as a molar ratio.

Browning metrics included total organic carbon (TOC), fluorescence properties, and Fe and manganese (Mn). Most of the organic matter in Swedish boreal lakes is in the dissolved state (> 90%,); therefore, there are small differences between dissolved organic carbon (DOC) and TOC (Köhler et al., 2002). The fluorescence properties included DOM absorbance at 420 nm (Abs420); i.e., to elucidate differences in the composition of DOM (Hudson et al., 2007). Lower redox potentials are generally observed in lake systems with both higher concentrations of DOM, Fe and Mn (Allgeier

et al., 1941; Kjemsmo, 1970). Both Fe and Mn also absorb light similarly to DOM and are therefore contributors to browning of surface waters (Kritzberg & Ekström, 2012).

Cyanobacteria metrics

Phytoplankton samples were collected from the epilimnion, as determined by lake temperature profiles. Composite water samples (2 m fixed intervals) representing at least 75% of the epilimnion were taken from five sampling points on a centrally located area of the lake using a Ruttner sampler, or from 0-8 m profiles in the case of non-stratified lakes using a tube sampler. An equal volume of water from each depth was then mixed. Subsamples were taken from the mixed composite and preserved with Lugol's iodine with an addition of acetic acid. Detailed descriptions of the sampling procedures are given in the Swedish accreditation standards for quantitative and qualitative sampling of phytoplankton in inland waters (SS-EN 16698:2015), and in the guidelines from the Swedish Agency of Marine and Water Agency (Havoch Vattenmyndigheten, 2016b, and references therein).

Phytoplankton were identified using an inverted light microscope and the modified Utermöhl technique (Olrik *et al.,* 1989), following the Swedish accreditation standards on the enumeration of phytoplankton using inverted microscopy (SS-EN 15204:2006), and were identified to species-resolution when possible. Phytoplankton biovolume was identified for single cells and then summed following the Swedish accreditation standards: Water quality – guidance on the estimation on phytoplankton biovolume (SS-EN 16695:2015). Picophytoplankton are counted when they exist in colonies (like *Merismopedia*); solitary picophytoplankton are not counted. A detailed description of the methods can be found at https://www.havochvatten.se/download/18.64f5b3211343cffddb280004877/V%C3%A4xtplankton+i +sj%C3%B6ar.pdf (ed. 2010-02-18) and https://www.slu.se/institutioner/vatten-miljo/laboratorier/biologiska-laboratoriet/vaxtplankton/.

Phytoplankton data were downloaded as species-specific biovolume (mm^3 L^{-1}) per lake per sampling date. Species data were then merged into genus as most of the phytoplankton were identified to this taxonomic level. Non-detects (i.e., when a phytoplankton species was not observed) were given a value of 0 for the biovolume in that lake. The maximum summer (July-September) genus-specific biovolume (mm^3 L^{-1}) for each year was taken to represent the lake, with most samples collected in August.

Two metrics were utilized in order to assess cyanobacteria change. The first metric was the absolute biovolume which refers to the sum of the total biovolume of each cyanobacteria species within a genus or cyanobacteria as a group (mm^3 L^{-1}). The second metric was the relative biovolume which refers to the proportion of cyanobacteria in the total phytoplankton biovolume. The two metrics and their ranges are provided in S.I.3.

Statistical analyses

The statistical approaches used to (a) detect trends in global change metrics and the absolute and relative biovolume of cyanobacteria, and (b) detect relationships between global change metrics and the proportion of cyanobacteria are described below and in Figure 2.

Trend analyses: Temporal trends in the global changes and phytoplankton community responses were statistically tested for monotonic trends using the Kendall's rank correlation coefficient (τ) (Kendall, 1975; Mann, 1945). The Theil-Sen estimator (Sen, 1968; Theil, 1950) was then used to compute the slopes of the significant ($p < 0.05$) monotonic time-series trends (unit yr^{-1}) for each lake. The Theil-Sen slope for the period from 1998 to 2013 was divided by the mean value for the same period to estimate percentage change over the 16 years as was performed in a Sweden-wide study of time series data of air temperature, precipitation, and atmospheric N deposition in Isles et al. (2018). The Theil-Sen slope and the time period change were averaged for all lakes with significant monotonic trends to summarize Sweden-wide trends. The Kendall τ and Theil-Sen slope calculations were performed in Python v 3.6.3 (Python Software Foundation, https://www.python.org/) using the 'Scipy' package (Jones et al., 2001).

Spatial trends in the selected global change metrics and phytoplankton community metrics were assessed using the Moran's Index (MI) (Moran, 1950). MI measures the global (i.e., Sweden-wide) spatial autocorrelation in an attribute *y* measured over *n* spatial units. MI ranges between +1 to -1; positive MI values suggest a spatial clustering behavior (i.e., high values attract other high values), whereas negative MI values suggest a spatial dispersing behavior (i.e., high values repel other high values). MI was calculated using the log-transformed values of the first and last five-year means of each variable under consideration using the inverse Euclidean distance as the spatial weights matrix. The MI for the Theil-Sen slope was used to understand spatial patterns in the rates of change. Two-tailed pseudo-p values were derived by mimicking the null hypothesis using a random re-labelling

scheme with 10,000 permutations. The pseudo-p value is the ratio of the number of times that a value was obtained that is equal to or more extreme than the one observed in the data. Pseudo p-values allow comparison of the MI that we obtain from our data to a reference distribution, and if the MI is extreme, the null hypothesis is rejected (i.e., there is spatial correlation). The MI and Theil-Sen slope calculations were performed in Python v 3.6.3 (Python Software Foundation, https://www.python.org/) using the 'PySAL' package (Rey & Anselin, 2007). Spatial autocorrelation was visualized over the surface of Sweden by generating maps employing the empirical Bayesian kriging interpolation method in ArcGIS v 10.5.1 (ESRI, 2016; Krivoruchko & Gribov, 2014). This method was selected because it is more accurate than other kriging methods for smaller datasets (Krivoruchko & Gribov, 2014). All maps were generated using the Power Semivariogram model.

Links between global change and cyanobacteria metrics: A canonical correspondence analysis (CCA) was used to assess the relationship between environmental conditions and the structure of cyanobacteria genera using the 'scikit-bio' package (https://github.com/biocore/scikit-bio) in Python v 3.6.3 (Python Software Foundation, https://www.python.org/). The global change metrics formed the "explanatory matrix" and (all non-zero values of) the relative biovolume of different cyanobacteria genera for the 16 years for each lake formed the response matrix. Collinearity in the global change metrics was reduced prior to input in the CCA model using the variance inflation factor (VIF) to quantify multicollinearity; a VIF of 10 was used as the acceptable limit (Hair et al., 1995). Global change metrics with VIF > 10 were collapsed into categories with similar metrics (e.g., Fe and Abs420 into 'browning'). Cyanobacteria genus data were normalized using $\log10(c+1)$, where c is each data point, and the explanatory metrics were z-score standardized. Scaling (type 2) was used to emphasize the relationship among species, where the distances among species approximate their chi-square distances (Legendre & Legendre, 2012). Statistical tests for the ordination and the significance of each axis of the ordination were based on permutation-based p-values. The function 'anova' from the 'vegan' package (Oksanen et al., 2018) in R v 3.5 (R Core Team, 2013) was used to perform the permutations (n = 10,000).

A linear mixed effects model was used to identify the global change metrics with the strongest association with increases in relative biovolume of cyanobacteria (R script can be found in S.I.7). To select the random effects structure, a "beyond optimal" model with all the selected global change

metrics as fixed effects was created (after Diggle et al., 2002; Finstad et al., 2016). The relative biovolumes of cyanobacteria genera with significant temporal trends were used as the dependent variables. The global change metrics were pre-processed using a z-score standardization by lake. The restricted maximum likelihood estimation (REML) was used to compare the different models, with the Akaike Information Criteria (AIC) serving as the basis for the selection. The following models were compared: (1) a generalized least squares model with no fixed structure; (2) lake-ID included as a random intercept; (3) year nested within lake-ID as a random slope; (4) year nested within lake-ID as a random slope and a one-year-lag temporal autocorrelation structure; and (5) lake-ID as a random intercept with a one-year-lag temporal autocorrelation. Once the optimal random structure was selected for each cyanobacteria genera, the optimal fixed structure was selected using the maximum likelihood to compare models. All possible combinations of global change metrics (fixed effects) were assessed as inputs to the model, and then ranked according to AIC. Since there was no clear top-ranked model, an Akaike weight (wi)-based model averaging of models (cumulative AIC weights of models = 0.95) was applied to estimate average coefficients for the best candidate models as well as their 95% confidence intervals. The relative influence of each metric, defined as the sum of all wi across the models containing the variable, was included. Final model selection and model averaging on fixed effect structure were done by model comparison using the MuMIn library (Grueber et al., 2011), and the nlme library was used to select random effect structure (nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.5; Pinheiro et al., 2012).

RESULTS

Global change metrics

Temporal trends:

The global change metrics assessed showed variable temporal trends (Figure 3). Global changes over the 16-year period across Sweden were characterized by acidification recovery, a lowering of DIN:TP, and an increase in browning, rather than climate changes.

Climate metrics showed few temporal trends (i.e., where $p < 0.05$). Annual surface water temperature had no temporal trend, and seasonal precipitation showed trends in only 7% (2/28) of lakes in spring (mean Theil-Sen slope = -1.19 mm yr^{-1}) and no trends in precipitation in the remaining seasons. Acidification recovery metrics showed that all lakes included in this study experienced

significant decreases in SO_4^{2-} concentrations (mean Theil-Sen slope = -3.0×10^{-3} meq L^{-1} yr^{-1}), while 68% (19/28) of the lakes experienced significant decreases in Ca (mean Theil-Sen slope = -2.0×10^{-3} meq L^{-1} yr^{-1}) and Mg concentrations (mean Theil-Sen slope = -1.1×10^{-3} meq L^{-1} yr^{-1}). Only one lake experienced significant decreases in Al concentrations. Nutrient metrics showed that 32% (9/28) of lakes experienced decreases in the ratio of DIN:TP (Theil-Sen slope = -3.3 yr^{-1}), driven primarily by decreases in NO_x (mean Theil-Sen slope = -0.2 µg L^{-1} yr^{-1}) but also decreases in NH_4 (mean Theil-Sen slope = -0.5 µg L^{-1} yr^{-1}). Browning metrics (TOC and Abs420) showed that lakes experienced increases in browning in 21% (6/28, mean Theil-Sen slope = 0.1 mg L^{-1} yr^{-1}) and 18% (5/28, mean Theil-Sen slope = 7.1×10^{-4} absorbance units) of lakes, respectively. Trace metals associated with browning trended in opposite directions. Fe increased in 11% of lakes (3/28, Theil-Sen slope = 5.9 µg L^{-1}), but also decreased in one (1/28, Theil-Sen slope = -0.77 µg L^{-1}), while Mn decreased in 11% of lakes (3/28, Theil-Sen slope = -1.5 µg L^{-1}).

Spatial trends:

The global change metrics assessed had spatial trends that varied along north-to-south gradients, both for mean concentration values as well as the rates of change of the metrics over the 16-year time period (S.I.9.1, S.I.9.2). The most significant global changes were seen in southern lakes that were warmer (and in drier conditions in the southeast compared to the southwest), with higher acidity but greater rates of acidification recovery, with more rapid decreases in DIN:TP, and with more rapid increases in browning in northern lakes.

For the climate metrics, annual maximum summer surface water temperature averages formed a north-to-south (cool-to-warm) gradient (ranging from 12°C in the north to 21°C in the south (S.I.9.1)) with MI = 0.35 (S.I.9.2). Annual and seasonal precipitation, however, formed a west- to-east (wet- to-dry) gradient (mean annual and seasonal precipitation ranged from 50 and 38-56 mm in the east to 96 and 78-130 mm in the east (S.I.9.1)), with MI = 0.19 in the west and 0.23 in the west (S.I.9.2).

Acidification recovery metrics also formed a north-to-south gradient, with southern lakes having higher SO_4^{2-} concentrations (mean 0.03 meqL^{-1}), lower pH (mean 6.1) and ANC (mean 110 µeqL^{-1}), and lower base cation concentrations (with means for Ca, Mg, Na ranging from 0.04 to 0.08 µeqL^{-1} (S.I.9.2)). Most lakes experienced decreases in SO_4^{2-} and base cation concentrations (Figure 3).

However, southern lakes experienced greater rates of decline, but little change in pH and ANC (S.I.9.3).

Nutrient metrics also formed a north-to-south gradient, with southern lakes having higher concentrations of nutrients (TP, NO_x, NH_4, see S.I.9.2) and higher rates of decrease in the DIN:TP ratio (MI = 0.11) (S.I.9.3).

Mn was the sole browning metric that showed a significant north-to-south gradient in concentrations (ranging from a mean of 11 μgL^{-1} in the north to 74 μgL^{-1} in the south, MI = 0.14); although TOC, Abs420, and Fe also demonstrated, on average, higher mean concentrations in southern lakes (12 mgL^{-1}, 0.06 absorbance units, and 1500 μgL^{-1}, respectively) (S.I.9.2). The rate of change in concentrations of browning metrics over the study period showed a north-to-south gradient in TOC only (MI of Theil-Sen slope = 0.06); TOC ranged on average from 5 mgL^{-1} in the north to 12 mgL^{-1} in the south, and the rates of TOC change were lowest (or no change) in northern lakes and highest and positive in southern lakes (MI of Theil-Sen slope = 0.22) (S.I.9.3).

Cyanobacteria metrics

Cyanobacteria metrics showed high variability in terms of magnitude and trends in both time and space (Figure 4, S.I.4, S.I.10). Temporal trends in the relative biovolume of cyanobacteria in many lakes were close to zero, with occasional high values.

In 32% (9/28) of lakes, the relative biovolume of cyanobacteria was above 25% in at least one year. In 21% (6/28) of lakes, the relative biovolume of cyanobacteria had significant (p < 0.05) increasing trends, with Theil-Sen slope ranging from 0.02 to 0.26% yr^{-1} (Figure 4). Lakes with both the largest relative biovolume of cyanobacteria (median of 17% for the period 2009-2013) and the largest rates of change in relative biovolume of cyanobacteria (mean Theil-Sen slope = 0.24% yr^{-1}) were in the southeast (Figure 4). Further, 50% (14/28) and 61% (17/28) of lakes had significant trends in the relative and absolute biovolumes, respectively, of one or more cyanobacteria genera (Figure 5). Southeast Sweden exhibited the majority of these positive trends (Figure 4). In total (including multiple trends per lake), there were 24 significant trends in relative biovolume and 22 significant trends in absolute biovolume of cyanobacteria. This is for a possible 16 cyanobacteria genera present in the 28 lakes (i.e., from a possible 448 trends if every cyanobacteria genus was present and changing in every lake). Among these trends, 68% (16/24) were positive for relative biovolume and 55%

(12/22) were positive for absolute biovolume (Figure 5). Most of the lakes with positive trends were in the southeast (Figure 4).

Spatial trends in the species composition of cyanobacteria in the lakes were variable. In southeast lakes, the area that corresponded to the greatest percent change in cyanobacteria (mean Theil-Sen slope = 0.26% yr^{-1}, Figure 4b), the positive temporal trends in relative and absolute biovolume were composed of *Dolichospermum spp.* (*D. lemmermanii* and *D. crassum*), *Chroococcus spp.* and *Merismopedia tenuissima*.

In southwest lakes, there were no clear overall trends in cyanobacteria genera. Here, *Merismopedia tenuissima* was the most variable, with both increases and decreases in relative and absolute biovolume. In northern lakes, there were negative temporal trends in relative and absolute biovolume for *Dolichospermum lemmermanii* and *Merismopedia tenuissima*, but positive temporal trends for *Chroococcus spp.* and *Snowella atomus*, although the magnitudes of these changes were relatively low (Figure 4b, Figure 5).

Links between global changes and cyanobacteria

Niche determination:

The first two canonical axes together account for 17% of the variation in the cyanobacteria species data (p = 0.001 after 10,000 permutations) (Figure 6). The two genera with the greatest changes in both relative and absolute biovolume (*Merismopedia* and *Dolichospermum*) were split along the primary axis CCA1. This axis was primarily characterized by factors related to acidification, with lower pH, lower acid neutralizing capacities, lower Ca (and higher Al) favouring *Merismopedia*, and higher acid neutralizing capacities associated with the other genera, including *Dolichospermum* and *Chroococcus*. The primary axis also demonstrated strong canonical correlation to DIN:TP, with *Merismopedia* positively associated with higher DIN:TP, and *Dolichospermum* negatively associated with higher DIN:TP. The canonical relationship between the selected global change metrics and cyanobacteria genera was significant (pseudo F = 8.98, p = 0.001, max VIF = 7.1).

The genera of cyanobacteria that showed the largest increases in the Swedish lakes were significantly related to different global change metrics (Table 2). *Merismopedia* had the highest explained variance (R^2 = 0.62) and was best explained by increases in temperature (model coefficient estimate (Est) = 0.042, p < 0.05), with a Relative Index (RI) = 1.00. *Chroococcus* had the lowest

explained variance of the three focal genera ($R^2 = 0.31$) and was best explained by decreases in $SO_4{}^{2-}$ (model coefficient estimate (Est) = -0.043, $p < 0.05$) and TOC (Est = -0.043, $p < 0.05$), with RI = 0.88 and 0.86, respectively. *Dolichospermum* ($R^2 = 0.38$) was best explained by decreases in Ca (Est = -6.7 × 10^{-2}, $p < 0.02$) (RI = 0.92) and increases in Mn (Est = 4.3 × 10^{-2}, $p < 0.04$) (RI = 0.82).

Table 2: Mixed linear effects models explaining the relative biovolume of increasing cyanobacteria genera: *Merismopedia*, *Chroococcus*, and *Dolichospermum*. Model coefficient estimates (Est) from model averaging are provided below along with the standard error (SE), z-score (z), p-value (p) and relative influence of the selected variables (RI). The variance explained by the models is presented as a conditional variance (R^2) which describes the proportion of variance explained by fixed and random factors. The cells for predictors with p < 0.05 are highlighted in **red**.

	Merismopedia (R^2= 0.62)					*Chroococcus* (R^2= 0.31)					*Dolichospermum* (R^2= 0.38)				
	Est	SE	z	p	RI	Est	SE	z	p	RI	Est	SE	z	p	RI
(Intercept)	0.27	0.07	4.17	<.0001		0.18	0.04	4.99	<.0001		0.25	0.05	4.99	<.0001	
Temperature	0.042	0.01	3.54	<.0001	1.0	0.009	0.02	0.58	0.56	0.30	0.019	0.02	1.13	0.26	0.41
Summer Precipitation	-0.0013	0.01	0.10	0.92	0.26	-0.012	0.02	0.72	0.47	0.32	-1.6×10^{-4}	0.02	0.01	0.99	0.27
Winter Precipitation	-0.0068	0.01	0.56	0.58	0.29	0.0047	0.02	0.28	0.78	0.27	-0.013	0.02	0.71	0.48	0.32
Spring Precipitation	0.0065	0.01	0.52	0.60	0.29	0.013	0.02	0.79	0.43	0.33	0.013	0.02	0.70	0.48	0.32
TOC	-0.013	0.02	0.87	0.38	0.36	**-0.043**	**0.02**	**2.32**	**0.02**	**0.88**	-0.018	0.02	0.89	0.37	0.35
Abs420	-0.024	0.02	1.42	0.16	0.53	-0.015	0.02	0.64	0.52	0.33	-0.011	0.02	0.43	0.66	0.30
Fe	0.0047	0.01	0.31	0.75	0.28	-0.001	0.02	0.05	0.96	0.27	-0.038	0.02	1.69	0.09	0.63
Mn	0.0052	0.01	0.41	0.68	0.28	-0.011	0.02	0.74	0.46	0.32	**0.043**	**0.02**	**2.10**	**0.04**	**0.82**
TP	0.0021	0.01	0.16	0.88	0.27	0.0029	0.02	0.17	0.86	0.27	0.011	0.02	0.63	0.53	0.30
DIN:TP$_{molar}$	-0.019	0.01	1.25	0.21	0.47	-0.0068	0.02	0.29	0.77	0.30	0.011	0.02	0.48	0.63	0.30
NO$_x$	0.0019	0.01	0.14	0.89	0.27	0.028	0.02	1.71	0.09	0.64	0.0066	0.02	0.37	0.71	0.28
NH$_4$	-0.011	0.01	0.77	0.44	0.36	4.6×10^{-4}	0.02	0.02	0.98	0.27	0.013	0.02	0.66	0.51	0.32
SO$_4^{2-}$	0.029	0.02	1.50	0.13	0.56	**-0.043**	**0.02**	**2.21**	**0.03**	**0.86**	6.6×10^{-4}	0.03	0.03	0.98	0.28
Ca	-0.011	0.02	0.55	0.58	0.31	-0.0097	0.02	0.42	0.68	0.31	**-0.067**	**0.03**	**2.27**	**0.02**	**0.92**
Mg	-0.0052	0.02	0.28	0.78	0.28	-0.0024	0.02	0.12	0.91	0.28	0.035	0.03	1.28	0.20	0.63
Na	0.023	0.02	1.09	0.28	0.42	-0.004	0.02	0.17	0.86	0.29	-0.024	0.03	0.83	0.41	0.36
ANCoaa	-0.018	0.02	0.91	0.36	0.39	-0.019	0.03	0.74	0.46	0.37	0.015	0.03	0.57	0.57	0.31
pH	-0.0061	0.01	0.43	0.67	0.29	0.0019	0.02	0.11	0.92	0.27	0.013	0.02	0.70	0.48	0.32
Al	-0.019	0.02	1.23	0.22	0.46	-0.029	0.02	1.65	0.10	0.61	-0.022	0.02	1.08	0.28	0.40

DISCUSSION

Global changes have the potential to enhance the growth of potentially harmful cyanobacteria (Creed et al., 2018). However, cyanobacteria are a diverse phytoplankton group containing, by best estimates, more than 3,330 species (Guiry, 2012), with differing environmental optima, physiology, and competition strategies. Here, we demonstrate the need to move away from the view of cyanobacteria as a monolith (typically of bloom forming genera such as *Microcystis* in eutrophic lakes) towards a more nuanced view that considers genus-specific environmental tolerances and adaptations that may help to understand better the cumulative effects of global changes on cyanobacteria prevalence and relative biovolume in northern lakes. In addition, we demonstrate that the complex interactions among global changes are re-shuffling the deck of environmental conditions, effectively shifting the baseline environmental conditions in northern lakes and redefining the niches of different cyanobacteria genera. In addition, we demonstrate that, because the interaction between baseline environmental conditions and the differences in global changes over time has an inherent spatial component, the responses in cyanobacteria genera also displayed differences among the lakes.

We tested the hypothesis that both the direct and indirect effects of climate change and acidification recovery are associated with increases in cyanobacteria prevalence (Figure 7). We found that in 21% (6/28) of lakes, the relative biovolume of cyanobacteria had significantly increased. Cyanobacteria, however, did not respond as an aggregate group. Instead, changes in their absolute and relative biovolume were driven by a small number of genera with diverse morphologies, primarily the N-fixing filamentous *Dolichospermum*, the few-celled *Chroococcus*, and the colonial *Merismopedia*. Lake-specific differences in global changes were found to be associated with the presence or absence of these specific genera, which, in turn, was related to the magnitude and direction of the cyanobacteria response.

Significant temporal and spatial trends in the hypothesized controls of cyanobacteria were observed. The most dynamic global change metrics over the 16-year period were the recovery from acidification (as reflected in SO_4^{2-}, Ca^{2+}, Mg^{2+}, and Na^+ concentration changes) and reduction in DIN:TP (driven by NO_x and NH_4 declines). The highest rates of change in these metrics occurred in relatively warm regions of Sweden (i.e., the southeast). Lakes with both the largest relative biovolume

of cyanobacteria and the largest rates of change in relative biovolume of cyanobacteria were also in the southeast (Figure 4).

Hypothesized vs. actual cyanobacteria responses

    (a) Climate warming

        Rising surface water temperatures are known to favour cyanobacteria (Paerl & Huisman, 2008). In northern lakes, correlative niche models for cyanobacteria have related the prevalence of cyanobacteria in a phytoplankton community to periods of relatively high temperatures (Watson et al., 1997). Therefore, it was predicted that both high and increasing surface water temperatures would lead to high and increasing relative biovolume of cyanobacteria. Specifically, it was predicted that southern lakes where surface water temperatures were highest would have the highest cyanobacteria relative biovolume, but that northern lakes where rates of change in surface water temperatures were highest would experience the greatest relative increase in the relative biovolume of cyanobacteria.

        The region that had lakes with the highest relative biovolume of cyanobacteria (the southeast) was also the region with the highest mean annual surface water temperature. *Dolichospermum*, *Chroococcus*, and *Merismopedia* experienced increases in lakes within this region. However, there was a significant correlation between temperature and relative biovolume for *Merismopedia* only. *Merismopedia,* though a colony former, is a small-celled species of coccoid cyanobacteria with individual cell sizes within the picophytoplankton size range (0.2 to 2.0 µm) (Bell & Kalff, 2001). Picophytoplankton have amongst the largest growth responses to temperature and obtain higher photosynthesis per unit biomass than any other size group of phytoplankton (Andersson et al., 1994). While *Merismopedia* showed a significant relationship with increasing surface water temperature over time, the lack of association with the relative biovolume of other cyanobacteria genera was not anticipated. One possible explanation is that the cyanobacteria are in competition with other phytoplankton that may also have a strong temperature response. For example, the bloom forming nuisance alga *Gonyostomum semen* is thought to be stimulated by higher temperatures in Swedish lakes and may outcompete cyanobacteria in warmer waters (Rengefors et al., 2012). Further, other climate warming-associated factors may be influencing cyanobacteria. For example, there may have been a link between the disproportionately earlier ice-off and longer growing seasons in the south (Weyhenmeyer et al., 2004) and *Dolichospermum*. Longer growing seasons are well-suited to the

filamentous N-fixer, *Dolichospermum*, as they provide *Dolichospermum* with time to increase their length sufficiently to produce specialized N-fixing cells (heterocysts) (Chan et al., 2006; Leblanc et al., 2008). The alignment between the effects of climate changes and the ecological niches of *Merismopedia* and *Dolichospermum* makes these two genera difficult to ignore when considering the phytoplankton communities of the future.

(b) Acidification recovery

Most cyanobacteria have a low tolerance to low pH waters (Findlay et al., 1999; Schindler et al., 1990; Vinebrooke et al., 2002). *Merismopedia* is an exception and is common in acidified lakes (Andersson et al., 1989; Molot et al., 1990). We predicted acidification recovery would have resulted in a shift in cyanobacteria genera from acidophilic genera such as *Merismopedia* to alkaliphilic genera such as *Dolichospermum* (Willén & Mattsson, 1997). We did not observe a relationship between declines in SO_4^{2-}, the major acidifying agent, and a reduction in *Merismopedia* relative biovolume. Despite, SO_4^{2-} declines occurring in all sampled lakes, lakes exhibited only small increases in pH and ANC; base cations decreased less rapidly than SO_4^{2-}, and decreases were not as wide-spread. This slow rate of acidification recovery suggests that only a small number of lakes may have experienced transitions from acidophilic to alkaliphilic conditions during the 16-year study time period. However, we did find an inverse relationship between SO_4^{2-} and *Chroococcus* relative biovolume. Findlay et al. (1999) observed decreases in *Chroococcus* when an experimental lake was acidified from pH 6.7 to pH 5.8. This suggests that within-lake changes in *Chroococcus* may be in response to changes in strong acid anion concentrations itself, while their presence or absence within a lake is related to pH that will change only over longer time periods. Thus, the 16-year period appears to be too short to observe a pH change large enough to result in community shifts; however, the results suggest that community shifts are a possibility in the future.

(c) Nutrients

We predicted that declines in DIN:TP in lake waters would result in a shift in cyanobacteria genera to N-fixing genera such as *Dolichospermum* and an increase in cyanobacteria prevalence. DIN:TP was related to the prevalence of cyanobacteria genera, where higher DIN:TP favored *Merismopedia*, and lower DIN:TP was more closely associated with *Chroococcus* and *Dolichospermum*. High P and low N is known to support N-fixing filamentous cyanobacteria such as

Dolichospermum (Schindler et al., 2008). Although not a known N-fixer, *Chroococcus* have also been observed to be associated with low N:P ratios (Taylor et al., 1979). However, the physiological explanation for this association is not well understood. Contrary to what was predicted, change in DIN:TP or concentrations of either N form were not related to the relative biovolume of cyanobacteria in these lakes. A recent N enrichment experiment performed in six unproductive Swedish lakes demonstrated that increasing N concentrations increased phytoplankton biovolume, but the composition of the phytoplankton within the community remained unchanged (Deininger et al., 2017). If N acts solely as a modulator of phytoplankton quantity and not community constituents, it would follow that reductions in N would not influence the relative biovolume of cyanobacteria until a critical niche threshold is passed. However, if current trends continue in tandem with an increase in the length of the growing season, the ability to fix N would become increasingly important.

(d) Browning

We predicted that increases in lake browning would result in an increase in cyanobacteria prevalence. This prediction was not supported. *Chroococcus* was the genus with the highest increase of all genera and was the sole genus where higher relative biovolume was related to TOC; however, it was an inverse relationship with an increase in relative biovolume as TOC declined. Prokhotskaya & Steinberg (2007) found that when two coccoid phytoplankton, *Desmodesmus communis* (a green alga) and *Chroococcus minutus*, were exposed to natural organic matter, the yields of both primary producers were reduced, but the reductions were greater for C. *minutus*. This suggests a particular sensitivity of *Chroococcus* to browning, potentially related to light limitation (Bergström & Karlsson, 2019).

Both trace metals related to browning (Fe and Mn) had the highest concentrations in southern Sweden. Two processes influence Fe and Mn availability in freshwaters. The first is bottom water anoxia and the subsequent release of Fe and Mn from sediments (Mortimer, 1941). Although, bottom water anoxia was not measured as part of the Swedish long-term monitoring program, there are several known mechanistic connections between rising DOC concentrations and subsequent declines of oxygen (Knoll et al., 2018; Solomon et al., 2015; Tanentzap et al., 2008). The second is the DOM-associated delivery of Fe and Mn to lakes from the surrounding landscape. DOM forms stable complexes with Fe^{3+} and Mn^{2+} (Ekström et al., 2016; Zajicek & Pojasek, 1976). This terrestrial source

of Fe and Mn may provide an explanation for the increase in the relative biovolume of *Dolichospermum* in southeastern lakes. *Dolichospermum*, a cyanobacteria known to produce specialized iron-binding ligands termed siderophores (Wilhelm & Trick, 1994), may be able to utilize Fe from DOM (Sorichetti et al., 2014), thereby reducing the available pool of Fe, leaving Mn in solution. If Fe, which is required for N-fixation (Berman-Frank et al., 2007), is only available through a highly specialized mechanism, this allows *Dolichospermum* to unlock a nutrient source that allows them to outcompete other phytoplankton. Recent experimental work performed on the prominent marine filamentous N_2-fixing cyanobacterium *Trichodesmium* serves as a useful analog for understanding this advantage. Hong et al. (2017) found that increasing oceanic CO_2 concentrations did not increase phytoplankton productivity (as might be predicted) because the resulting lowered pH coupled with low ambient Fe availability inhibited N-fixation (with a deleterious effect on productivity). In Swedish freshwaters, if the results of acidification on pH and Fe concentrations are reversed, the growth of N_2-fixing cyanobacteria may no longer be suppressed, perhaps stimulated by increased nitrogenase, as in the marine *Trichodesmium* (Luo et al., 2019).

What the future may bring

Cyanobacteria genera respond differently to global changes based on the set of starting environmental conditions in lakes (Figure 7). The relative biovolume of specific cyanobacteria genera (*Merismopedia*, *Chroococcus*, and *Dolichospermum*) could be predicted based on: (a) if that genus was present within a lake at the beginning of the time period (which is a function of the environmental suitability of the lake); and (b) the magnitude, direction, and interactive effects of these atmospheric changes on the environmental suitability of the lake.

Merismopedia was associated predominantly with more acidic lakes with low DIN:TP, with higher relative dominance of *Merismopedia* within those lakes with higher surface water temperatures. Given the expectation that temperatures will continue to rise in Sweden (SMHI, 2018), acidic lakes with *Merismopedia* might be expected to see increases in cyanobacteria relative biovolume. *Merismopedia* rarely produce dense blooms (Vincent, 2009); however, they are known to produce toxins (Furtado et al., 2009), and therefore may pose challenges to aquatic ecosystems.

Chroococcus was associated predominantly with lakes that had reductions in SO_4^{2-}, but without browning. This suggests potential trade-offs among global changes, as decreases in SO_4^{2-}

deposition have been linked to increases in browning (Monteith et al., 2007). The positive effect of reduced SO_4^{2-} for *Chroococcus* might, therefore, be suppressed by browning in lakes where both changes are coinciding. However, since browning occurred in a relatively small proportion of lakes (primarily in the south), it is possible that *Chroococcus* growth was not suppressed in our study lakes over the 16 years, consistent with their increasing relative biovolume. It is unclear if more lakes will undergo the process of browning as acidification recovery progresses, and if so, if this will suppress *Chrooccocus* in the future.

Dolichospermum was associated predominantly with lower precipitation (i.e., drier conditions promoting longer lake water retention times, higher pH, and lower DIN:TP). Unlike the other two genera, the global changes associated with increased *Dolichospermum* relative biovolume are not only projected to become more pronounced in the future but also to have the potential for synergistic effects (Futter et al., 2014; Weyhenmeyer et al., 2016). This is a potential widespread concern, as the presence of *Dolichospermum* is: common throughout northern latitudes (Sivonen et al., 1990; Skulberg et al., 1994; Willén & Mattsson, 1997; Winter et al., 2011); on the rise in some northern lakes (Winter et al., 2011; Pick 2015); and known to produce blooms as well as hepatotoxins and neurotoxins (Rapala et al., 1993; Willén & Mattsson, 1997; Sivonen & Jones, 1999; Dittmann et al., 2013).

Greater relative biovolumes of cyanobacteria in northern lakes have potential food web implications. Cyanobacteria, compared to their eukaryotic competitors, generally do not contain long-chain poly-unsaturated fatty acids (Buse et al., 2013; Senar et al., 2019), do not produce sterols (Volkman, 2003), and are an insufficient source of vitamin B_{12} (Helliwell, 2016). In freshwater ecosystems, cyanobacteria blooms are known to reduce resource quality of the food base (cf. Ruess & Müller-Navarra., 2019) suggesting that shifts to larger relative biovolumes of cyanobacteria over longer periods could have similar consequences. This would be an interesting avenue for future research, particularly by examining zooplankton and fish communities present in the region and lakes within Sweden where cyanobacteria relative biovolumes have increased.

Future global changes are anticipated to have antagonistic effects for *Chrooccocus*, and potentially for *Merismopedia* if recovery from acidification increases pH and lowers DIN:TP further. Therefore, the increase in these genera could potentially be a short-lived artefact of the legacy effects

of previous atmospheric changes. Conversely, future global changes promoting longer lake water retention times, higher pH, and N-limitation are anticipated to promote *Dolichospermum* (Sharma et al., 2019). Further, it is possible that the simulatenous progression of global changes favouring *Dolichospermum* environmental will promote a rapid response in *Dolichospermum* prevalence, as has been described for Baltic Sea N$_2$-fixing cyanobacteria (Hense et al., 2013).

Establishing links between global changes and phytoplankton assemblages is challenging, as phytoplankton have been shown to exhibit orders-of-magnitude variation over seasonal, inter-annual, and decadal time scales (Cottingham et al., 1998; Cottingham & Carpenter, 1998). In particular, the realized niches (i.e., the set of *actual* conditions utilized by phytoplankton to produce biomass) are extremely difficult to constrain given the knowledge gaps that exists within grazing (Beckett & Weitz, 2017), parasitism (Sime-Ngando, 2012), competition (Grognard et al., 2015), and the general scarcity of available data. The combined variance that could be explained by the models utilized in this investigation accounted for a relatively small fraction of the overall variance (Figure 6). Nonetheless, given the limitations of the sampling frequency and the complexity of the temporal and spatial factors, the results provide promising a direction for future work.

This investigation illustrates how global-change driven alterations to physical and chemical conditions may result in increases to particular cyanobacteria relative biovolumes in lakes in northern latitudes. While the interplay between climate changes, changing trends and histories of atmospheric acidic deposition, and browning have been observed in northern lakes (Meyer-Jacob et al., 2019), the highest rates of atmospheric S and N deposition on earth occur in parts of Asia (Vet et al., 2014) with increased rates occurring in southern latitudes (Kuylenstierna et al., 2001). This suggests that lakes in southern latitudes could experience an analogous re-shuffling of the deck of environmental conditions with potential implications for aquatic resource quality and stability.

CONCLUSION

The vast majority of broad-scale analyses lump cyanobacteria into one single group, often due to data availability constraints. When species or genera-specific data are provided, they most often focus on common bloom-forming species, such as *Microcysti*s, which is rarely generalizable. We provided novel insights by focusing on genera-specific data for cyanobacteria in northern lakes with a temporally and spatially extensive Swedish dataset. We found that the relative biovolume of

cyanobacteria showed high variability in terms of trends in both time and space but are on the rise in southeastern Sweden. The rise in cyanobacteria was driven primarily by a small number of cyanobacteria genera: *Merismopedia*, *Chroococcus*, and *Dolichospermum*. The increased prevalence of these three genera was associated with global changes – including the interactive effects of climate change and acidification recovery – but the starting conditions and the rate of global changes varied across the country creating environmental niches that favor different cyanobacteria genera. These starting conditions likely played an important role in determining the initial phytoplankton community and the presence of a particular genus, which then may have decided, depending on their unique adaptations, their response to changing global conditions. Research on how landscape controls determine the baseline conditions within lakes and how global changes may be shifting these baselines would provide advancement. Further, more research is needed to constrain better the niche of the cyanobacteria genera observed in this study, including their interactions with other members of aquatic food webs for which the changes observed over the 16 years could have implications.

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DATA SHARING AND DATACCESSIBILITY

The original data are available from the Swedish National Lake monitoring program for Trend lakes (see http://info1.ma.slu.se/). The processed data are available by contacting the corresponding author.

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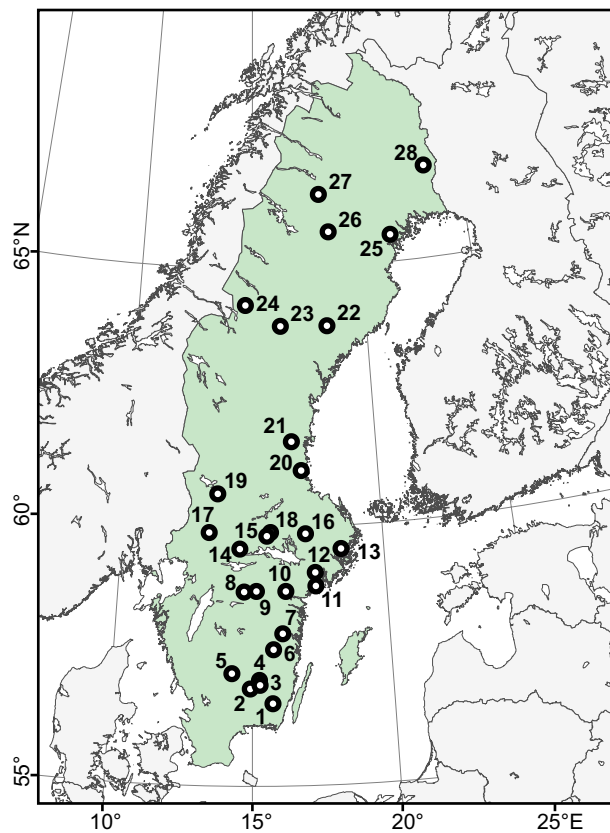
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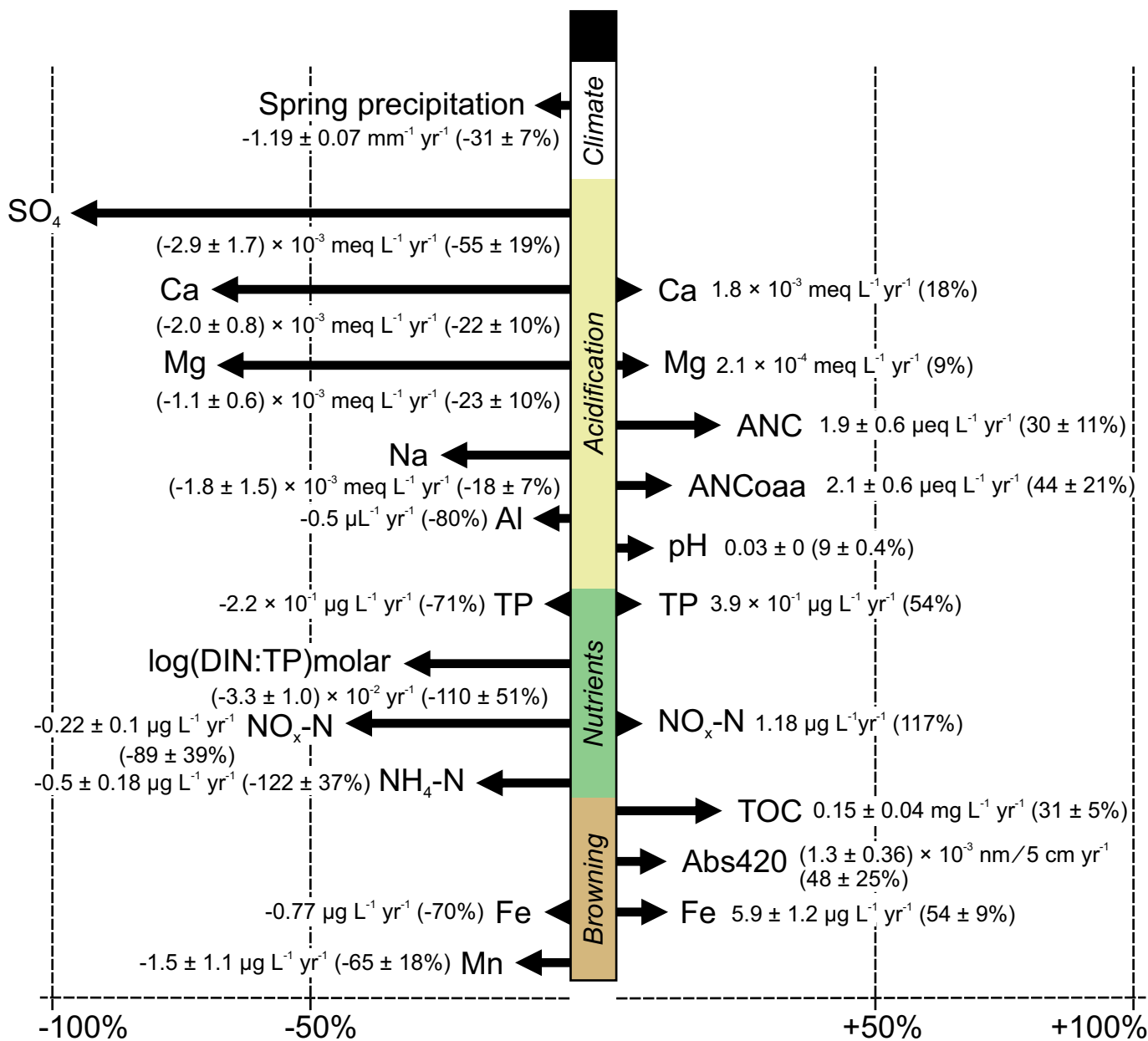
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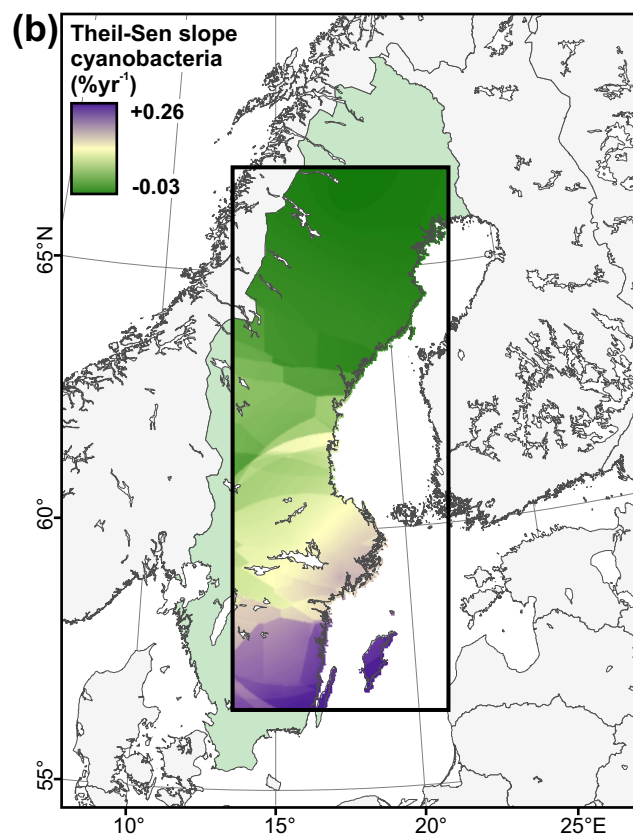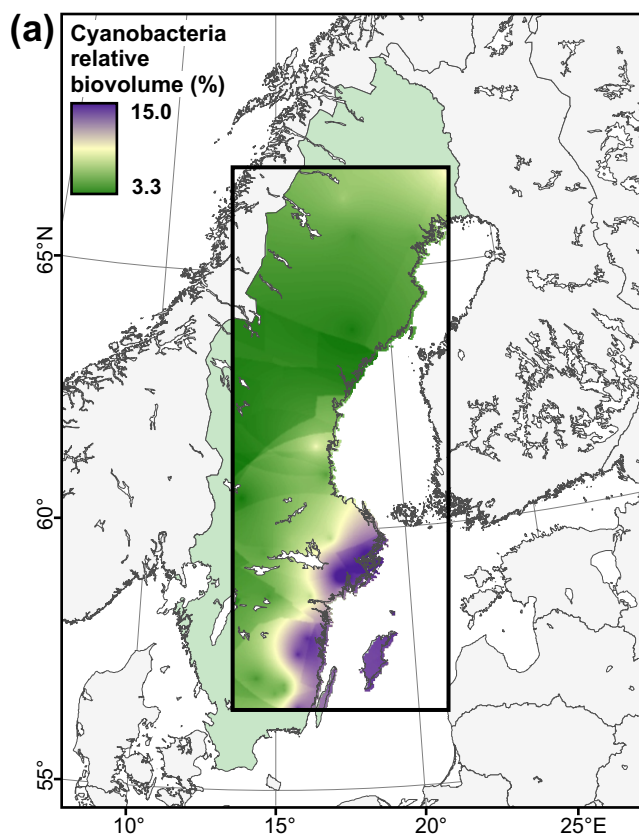
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1	Brunnsjön	10	Skärgölen	19 Gipsjön
2	Hinnasjön	11	Björken	20 Gosjön
3	Storasjö	12	Stora Envättern	21 Stensjön
4	Hjärtsjön	13	Tärnan	22 Remmarsjön
5	Älgarydssjön	14	Limmingsjön	23 Degervattnet
6	Hökesjön	15	Övre Skärsjön	24 Dunnervattnet
7	Allgjuttern	16	Ekholmssjön	25 Brännträsket
8	Fagertärn	17	Översjön	26 Vuolgamjaure
9	Grissjön	18	Dagarn	27 Louvvajaure
				28 Pahajärvi

	Statistical analysis	Predictor metric(s)	Response metric(s)
Q1. Are there trends with time? What are the rates of change? (Figures 3 and 5)			
	Kendall τ & Theil-Sen Slope	Time	Global change metrics, cyanobacteria absolute biovolume, cyanobacteria relative biovolume
Q2. Are like values clustered? Are there spatial trends? (Figures 4a)			
	Moran's Index & Kriging	X,Y coordinates	Global change metrics, cyanobacteria relative biovolume
Q3. Are there spatial trends in rates of change? (Figure 4b)			
	Moran's Index of Theil-Sen Slope & Kriging	X,Y coordinates	Δglobal change metrics, Δcyanobacteria relative biovolume
Q4. Are the different cyanobacteria genera associated with different environmental optima? (Figure 6, Table 2)			
	Canonical Correspondence Analysis (CCA)	Driver metrics (each lake, each year)	Cyanobacteria genus relative biovolume
Q5. Within lakes, what are the driver metrics that predict greater cyanobacteria dominance?			
	Generalized Mixed Effects Models (GLMM)	Driver metrics (each lake, each year)	Standardized cyanobacteria genus relative biovolume

Space-time trends
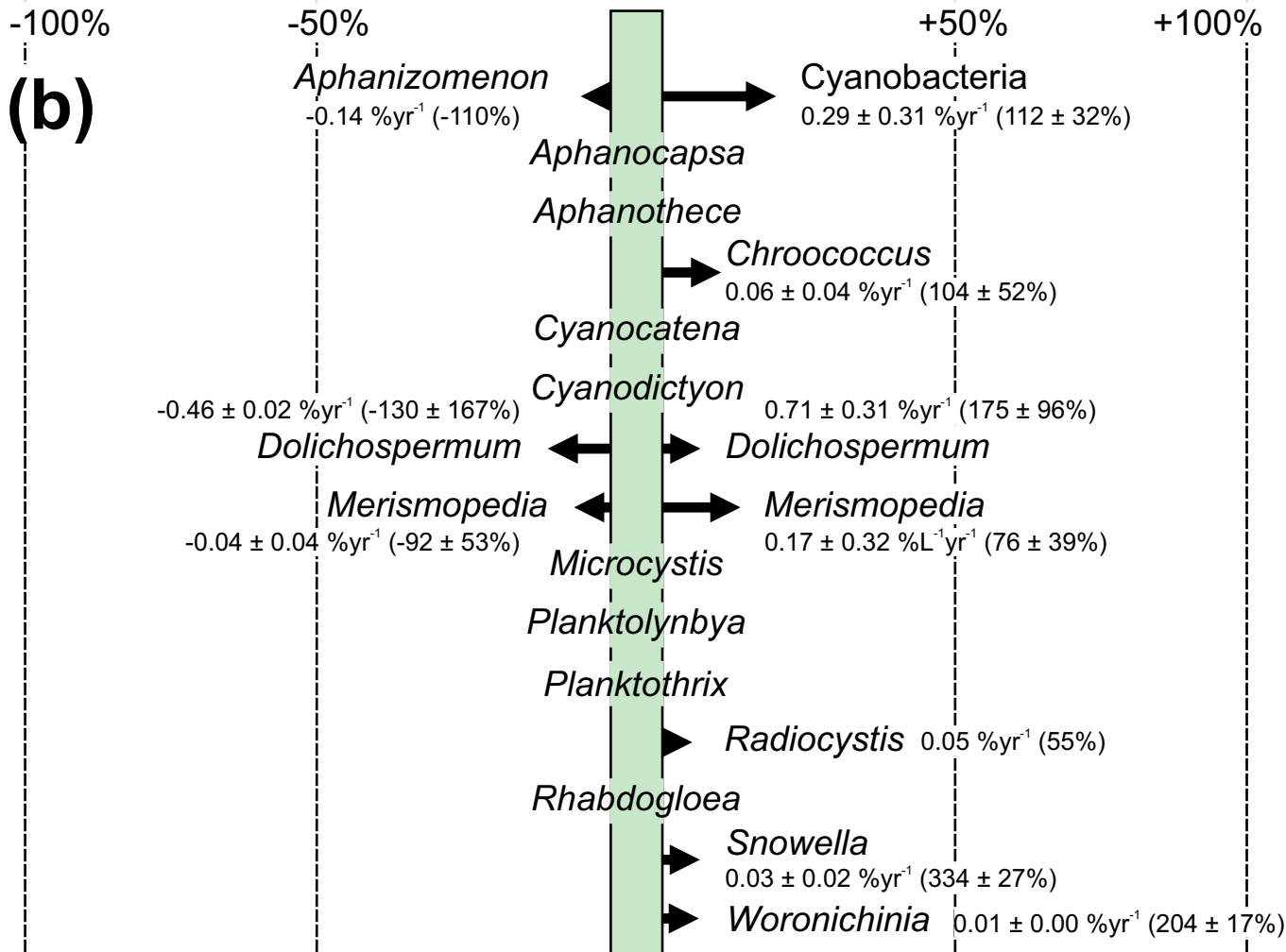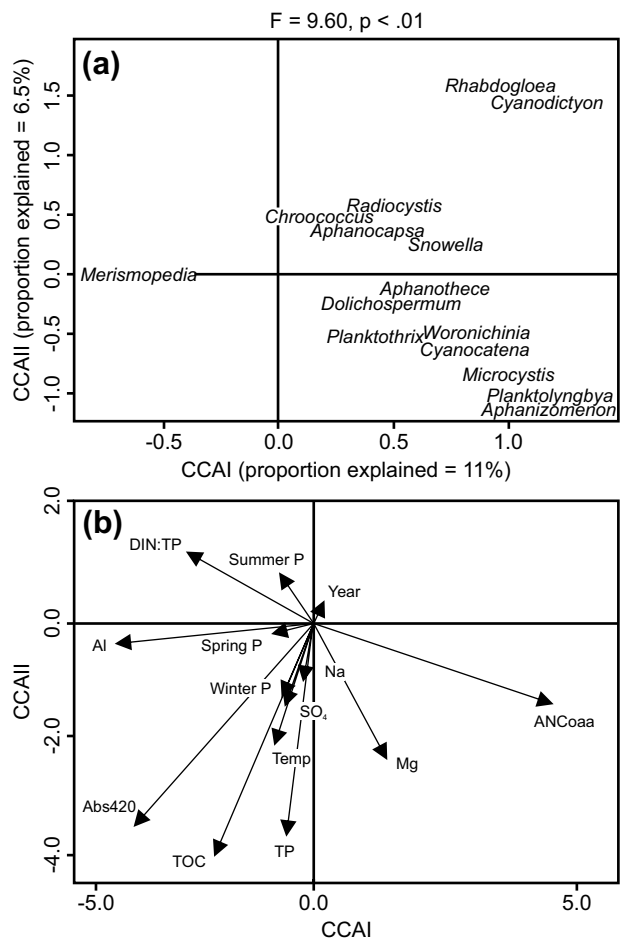
Cyanobacteria as response metric

Climate

Spring precipitation ← -1.19 ± 0.07 mm^{-1} yr^{-1} ($-31 \pm 7\%$)

Acidification

SO$_4$ ← $(-2.9 \pm 1.7) \times 10^{-3}$ meq L^{-1} yr^{-1} ($-55 \pm 19\%$)

Ca ← $(-2.0 \pm 0.8) \times 10^{-3}$ meq L^{-1} yr^{-1} ($-22 \pm 10\%$)   Ca 1.8×10^{-3} meq L^{-1} yr^{-1} (18%)

Mg ← $(-1.1 \pm 0.6) \times 10^{-3}$ meq L^{-1} yr^{-1} ($-23 \pm 10\%$)   Mg 2.1×10^{-4} meq L^{-1} yr^{-1} (9%)

ANC → 1.9 ± 0.6 µeq L^{-1} yr^{-1} ($30 \pm 11\%$)

Na ← $(-1.8 \pm 1.5) \times 10^{-3}$ meq L^{-1} yr^{-1} ($-18 \pm 7\%$)   ANCoaa → 2.1 ± 0.6 µeq L^{-1} yr^{-1} ($44 \pm 21\%$)

-0.5 µL^{-1} yr^{-1} (-80%) Al ←   pH → 0.03 ± 0 ($9 \pm 0.4\%$)

Nutrients

-2.2×10^{-1} µg L^{-1} yr^{-1} (-71%) TP ←   TP → 3.9×10^{-1} µg L^{-1} yr^{-1} (54%)

log(DIN:TP)molar ← $(-3.3 \pm 1.0) \times 10^{-2}$ yr^{-1} ($-110 \pm 51\%$)

-0.22 ± 0.1 µg L^{-1} yr^{-1} NO$_x$-N ← ($-89 \pm 39\%$)   NO$_x$-N → 1.18 µg L^{-1} yr^{-1} (117%)

-0.5 ± 0.18 µg L^{-1} yr^{-1} ($-122 \pm 37\%$) NH$_4$-N ←

Browning

TOC → 0.15 ± 0.04 mg L^{-1} yr^{-1} ($31 \pm 5\%$)

Abs420 → $(1.3 \pm 0.36) \times 10^{-3}$ nm/5 cm yr^{-1} ($48 \pm 25\%$)

-0.77 µg L^{-1} yr^{-1} (-70%) Fe ←   Fe → 5.9 ± 1.2 µg L^{-1} yr^{-1} ($54 \pm 9\%$)

-1.5 ± 1.1 µg L^{-1} yr^{-1} ($-65 \pm 18\%$) Mn ←

-100% -50% $+50\%$ $+100\%$

(a) Cyanobacteria relative biovolume (%)

15.0

3.3

(b) Theil-Sen slope cyanobacteria (%yr^{-1})

+0.26

-0.03

(a)

Aphanizomenon
-1.1 × 10^{-3} mm^{3}L^{-1}yr^{-1} (-154%)

Cyanobacteria
(1.1 ± 1.4) × 10^{-3} mm^{3}L^{-1}yr^{-1} (138 ± 31%)

Aphanocapsa

Aphanothece

Chroococcus
(1.8 ± 2.5) × 10^{-3} mm^{3}L^{-1}yr^{-1} (95 ± 55%)

Cyanocatena

Cyanodictyon

(-1.8 ± 1.2) × 10^{-4} mm^{3}L^{-1}yr^{-1} (-192 ± 103%)

(3.8 ± 2.3) × 10^{-3} mm^{3}L^{-1}yr^{-1} (170 ± 90%)

Dolichospermum   *Dolichospermum*

Merismopedia   *Merismopedia*

(-1.1 ± 1.5) × 10^{-4} mm^{3}L^{-1}yr^{-1} (-80 ± 30%)

(1.3 ± 0.6) × 10^{-4} mm^{3}L^{-1}yr^{-1} (79 ± 50%)

Microcystis

Planktolynbya

Planktothrix

Radiocystis   1.8 × 10^{-4} mm^{3}L^{-1}yr^{-1} (38%)

Rhabdogloea
(-1.8 ± 1.6) × 10^{-5} mm^{3}L^{-1}yr^{-1} (-58 ± 39%)

Snowella
(1.1 ± 1.6) × 10^{-4} mm^{3}L^{-1}yr^{-1} (103 ± 28%)

Woronichinia   2.0 × 10^{-5} mm^{3}L^{-1}yr^{-1} (170%)

-100%   -50%   +50%   +100%

(b)

Aphanizomenon
-0.14 %yr^{-1} (-110%)

Cyanobacteria
0.29 ± 0.31 %yr^{-1} (112 ± 32%)

Aphanocapsa

Aphanothece

Chroococcus
0.06 ± 0.04 %yr^{-1} (104 ± 52%)

Cyanocatena

Cyanodictyon

-0.46 ± 0.02 %yr^{-1} (-130 ± 167%)

0.71 ± 0.31 %yr^{-1} (175 ± 96%)

Dolichospermum   *Dolichospermum*

Merismopedia   *Merismopedia*

-0.04 ± 0.04 %yr^{-1} (-92 ± 53%)

0.17 ± 0.32 %L^{-1}yr^{-1} (76 ± 39%)

Microcystis

Planktolynbya

Planktothrix

Radiocystis   0.05 %yr^{-1} (55%)

Rhabdogloea

Snowella
0.03 ± 0.02 %yr^{-1} (334 ± 27%)

Woronichinia   0.01 ± 0.00 %yr^{-1} (204 ± 17%)

F = 9.60, p < .01

Global change driver	Predicted cyanobacteria response	Actual cyanobacteria response

1 Climate change

↑ water temperature

↑ cyanobacteria

↑ increase in *Merismopedia* only

2 Acidification recovery

↓ acidity

shift from acid-tolerant (*Merismopedia*) to acid-intolerant (*Dolichospermum*)

Merismopedia in low pH only
Dolichospermum in high pH and declining Ca only
Chroococcus increasing as SO$_4$ decreases

3 Reduced N deposition

↓ DIN:TP

↑ *Dolichospermum*

Dolichospermum in low DIN:TP only **BUT** no change because change in DIN:TP not large enough

4 Browning

↑ TOC

↑ cyanobacteria

↑ *Dolichospermum*

↓ *Chroococcus*