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Effects of multiple stressors on cyanobacteria abundance vary with lake type

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Abstract

Blooms of cyanobacteria are a current threat to global water security that is expected to increase in the future because of increasing nutrient enrichment, increasing temperature and extreme precipitation in combination with prolonged drought. However, the responses to multiple stressors, such as those above, are often complex and there is contradictory evidence as to how they may interact. Here we used broad scale data from 494 lakes in central and northern Europe, to assess how cyanobacteria respond to nutrients (phosphorus), temperature and water retention time in different types of lakes. Eight lake types were examined based on factorial combinations of major factors that determine phytoplankton composition and sensitivity to nutrients: alkalinity (low and medium-high), colour (clear and humic) and mixing intensity (polymictic and stratified). In line with expectations, cyanobacteria increased with temperature and retention time in five of the eight lake types. Temperature effects were greatest in lake types situated at higher latitudes, suggesting that lakes currently not at risk could be affected by warming in the future. However, the sensitivity of cyanobacteria to temperature, retention time and phosphorus varied among lake types highlighting the complex responses of lakes to multiple stressors. For example, in polymictic, medium-high alkalinity, humic lakes cyanobacteria biovolume was positively explained by retention time and a synergy between TP and temperature, while in polymictic, medium-high alkalinity, clear lakes only retention time was identified as an explanatory variable. These results show that, although climate change will need to be accounted for when managing the risk of cyanobacteria in lakes, a "one-size fits-all" approach is not appropriate. When forecasting the response of cyanobacteria to future environmental change, including changes caused by climate and local management, it will be important to take this differential sensitivity of lakes into account.

KEYWORDS
climate warming, cyanobacteria, eutrophication, global change, lake type, nutrients, retention time, temperature

1 | INTRODUCTION

Blooms of cyanobacteria are becoming an increasing threat to global water security. Through anthropogenic activities we are not only enhancing but also combining some of the optimal conditions for the dominance of cyanobacteria. At the local scale, and despite remediation efforts, nutrient enrichment is hardly abating (Nürnberg, 2009; Oliver et al., 2017). At a global scale, and at the forefront of this paper, is the issue of climate change. In part, the recent rise in cyanobacteria has been attributed to climate warming (Kosten et al., 2012; Paerl & Huisman, 2008). Increases in water temperature (O'Reilly et al., 2015) alongside increases in the duration and strength of thermal stratification (Wagner & Adrian, 2009) create optimal conditions for the physiological and functional traits of many cyanobacteria taxa such as higher temperature growth optima and the ability to regulate buoyancy (Carey, Ibelings, Hoffmann, Hamilton, & Brookes, 2012). In combination with high nutrient concentrations, it is feared that warming will result in the accelerated deterioration of water quality (Jeppesen et al., 2009; Moss et al., 2011; Paerl & Huisman, 2008). This synergism is widely discussed as an important risk factor, however, the evidence so far suggests that this will not be a generalizable response; others have found that the effect of temperature is dependent on other environmental factors such as trophic setting (Rigosi, Carey, Ibelings, & Brookes, 2014) or by the mixing state of the lake (Taranu, Zurawell, Pick, & Gregory-Eaves, 2012).

Climate change also affects rainfall patterns (Milly, Dunne, & Vecchia, 2005). Extreme rainfall events followed by prolonged periods of drought are expected to favour cyanobacteria because of the combined effects of elevated nutrients and stable physical conditions (Paerl & Huisman, 2008). Although, the benefits to cyanobacteria may depend on the frequency, duration, seasonal timing and intensity of rainfall events as well as other factors such as catchment land use and the ratio of catchment area to lake surface area (James et al., 2008; Padisák, Tóth, & Rajczy, 1988; Reichwaldt & Ghadouani, 2012). Studies exploring the effect of changes in hydrologic flow on the abundance of cyanobacteria in combination with other anthropogenic stressors are limited, yet flow dynamics as a driver of the abundance, composition and succession of phytoplankton communities is well documented (e.g. Søballe & Kimmel, 1987; Tolotti, Boscaini, & Salmaso, 2010). In order to understand fully the effects of climate change on water quality in lakes, climate change effects other than that of incremental changes in temperature need to be incorporated. Although more challenging, the effects of extreme rainfall events, heatwave events and prolonged periods of drought need to be understood and quantified in combination with anthropogenic nutrient enrichment (Michalak, 2016).

The evidence so far indicates that the response of cyanobacteria to multiple anthropogenic stress may not be generalizable, i.e. that a “one-size fits-all” approach is not appropriate across all lakes (e.g. Taranu et al., 2012). This is not surprising given that phytoplankton have varying sensitivities and tolerances to their physical and chemical environment (Reynolds, Huszar, Kruk, Naselli-Flores, & Melo, 2002) and so many other factors, aside from temperature, nutrients and flushing rates, are involved in shaping phytoplankton biomass and community structure. Previous analyses have examined the effect of lake type variables on the sensitivity of cyanobacteria to nutrients and temperature in combination, focusing on the effect of trophic type (Rigosi et al., 2014), mixing type (Taranu et al., 2012) and depth x artificial *vs.* natural lakes (Beaulieu, Pick, & Gregory-Eaves, 2013). While they all highlight the importance of environmental context, they exclude other key environmental factors that shape community composition; e.g. alkalinity (Carvalho et al., 2011; Maileht et al., 2013; Ptacnik et al., 2008), pH (Beaulieu et al., 2013; Kosten et al., 2012) and colour (Maileht et al., 2013; Ptacnik et al., 2008). Furthermore, most of these studies exclude the potential for the interactive effect of multiple “type” factors. For the response of phytoplankton to nutrients, the relationships can be improved by grouping the response by “lake types” defined by multiple environmental factors such as depth and alkalinity (Phillips et al., 2008) and colour and alkalinity (Ptacnik et al., 2008). A similar “lake type” approach should be taken to explore the response of cyanobacteria to multiple stressors, testing the effect of key environmental stressors in different lake environments. Identifying the environments in which cyanobacteria will be most problematic under future climate and nutrient scenarios is needed to provide robust information for the effective management of lakes.

Here, we took advantage of existing broad scale data from 494 natural European lakes to test whether eutrophication (phosphorus), temperature, and prolonged periods of drought (retention time) interact to exacerbate the problem of cyanobacteria. We modelled the response of chlorophyll-*a* concentration, as a proxy for total phytoplankton biomass, and cyanobacteria biovolume in eight different lake types which were defined by combinations of alkalinity (low and medium-high alkalinity), colour (clear and humic) and mixing types (polymictic and stratified). These types broadly match the common lake typologies which have been agreed across >25 European countries as part of the European Water Framework Directive (WFD, http://ec.europa.eu/environment/water/water-framework/) in recognition of the differential sensitivity of lakes of different types to environmental stressors. We hypothesized that elevated temperatures and increased retention time would have a greater positive effect on cyanobacteria than on total phytoplankton, and that their effect would be in synergy with phosphorus. We further hypothesized that the sensitivity of these response variables to the interactions between multiple stressors would vary among lake types.

2 | MATERIALS AND METHODS

2.1 | Data

2.1.1 | Biological and chemical data

Data on cyanobacteria biovolume (mm^3/L), chlorophyll-*a* concentration (μg/L), total phosphorus concentration (μg/L) and lake type variables—altitude, depth, surface area, mixing status, humic content

TABLE 1 Response and explanatory variables included in the analysis. Means ± standard deviations and minimum and maximum values in parentheses, are summarized by each lake type. Total number of lakes in the analysis was 494

		Phytoplankton parameters		Stressors		
Lake type	Number of lakes	Total cyanobacterial biovolume (mm^3/L)	Chlorophyll-*a* (μg/L)	Mean monthly total phosphorus (μg/L)	Mean monthly air temperature (°C)	Monthly retention time (days)
Polymictic						
Low alkalinity, clear	3	0.005 ± 0.01 (0–0.02)	3.21 ± 1.8 (1.2–5.6)	9.6 ± 5.1 (4–15)	15.7 ± 1.9 (13.6–18.6)	21.7 ± 22.8 (7.6–61)
Low alkalinity, humic	15	3.1 ± 17 (0–114)	10.1 ± 12.4 (1.2–61)	21.4 ± 17.5 (3.6–91)	14.6 ± 1.9 (9.1–18)	17.3 ± 29.6 (1.7–207.7)
Med-high alkalinity, clear	89	7.9 ± 21 (0–224)	34 ± 33 (2–238)	50.1 ± 25.8 (10–100)	17 ± 2.9 (9.1–24.0)	48 ± 68.6 (0.2–339.7)
Med-high alkalinity, humic	45	1.0 ± 2.0 (0–11)	20.1 ± 22.1 (1–120)	35.8 ± 20.6 (2–98)	16.2 ± 2 (10.6–20)	32.9 ± 53.7 (0.6–351)
Stratified						
Low alkalinity, clear	70	0.05 ± 0.3 (0–5.3)	3.3 ± 2.6 (0.2–21.5)	8.2 ± 4.9 (1–37.6)	14.0 ± 2.6 (6.6–19.9)	82.3 ± 86.6 (2.9–363.2)
Low alkalinity, humic	70	0.17 ± 0.9 (0–12.1)	8 ± 11.8 (0.3–110.3)	14.5 ± 11.8 (2–97)	14.8 ± 2.4 (6.2–20.2)	63.3 ± 74.2 (1.8–359.9)
Med-high alkalinity, clear	163	1.9 ± 3.7 (0–31)	16.5 ± 54 (0.7–1025)	31.7 ± 20.1 (2–99)	17.1 ± 2.7 (5.5–24)	83.0 ± 81.7 (2.5–360)
Med-high alkalinity, humic	39	1.0 ± 2.6 (0–26)	16.0 ± 22.3 (1.4–185.8)	33.2 ± 28.3 (2–100)	15.6 ± 3.0 (5.3–20.6)	82.5 ± 96.6 (3.6–356)

and alkalinity—were extracted from the WISER database (Moe, Schmidt-Kloiber, Dudley, & Hering, 2013) and supplemented by additional datasets. Total phosphorus was used as a measure of nutrient enrichment as it is a robust indicator of eutrophication in freshwater systems (Howarth & Marino, 2006) and was also available for all lakes (whereas total nitrogen was not). Chlorophyll-*a* was used as a proxy for total phytoplankton abundance as this is the most widespread global measure of ecosystem quality used in lake management (OECD, 1982); chlorophyll-*a* and total phytoplankton biovolume were positively correlated (R^2 = 0.64, p < 0.001). Biological and phosphorus data were summarized as monthly means for July, August and September; a period when biological sampling is most intense, thereby maximizing data availability and when in many systems cyanobacterial blooms occur (Reynolds, 2006). Data were selected between 2000 and 2009 as sampling methods from this period were most standardized. Each lake contributed a variable number of observations; on average six monthly observations from different combinations of years (2000–2009) and months (July–September). Supporting Information Table S1 summarizes the number of lake months for each year, month combination. The hierarchical structure of the statistical models accounts for differences in the number of observation per lakes, through the random effect error term.

2.1.2 | Catchment data

Catchment data—delineations and per cent (%) CORINE (coordination of information on the environment) land cover were extracted from the MARS geodatabase (Globevnik, Koprivsek, & Snoj, 2017).

2.1.3 | Climate data

Historical air temperature and effective rainfall data were downloaded from the Agri4Cast Data portal (Toreti, 2014) of the Joint Research Centre (JRC) which contains daily meteorological parameters from weather stations interpolated on a 25 × 25 km grid. Each lake was matched to the JRC square which contained the coordinates of the lake's sampling point. Mean monthly air temperature (°C) was used as a proxy for water temperature. For a subset of 299 lakes which had measurements of epilimnion temperature a significant linear relationship was found between mean monthly air and mean monthly water temperature with a slope of 0.89 ± 0.02

(R^2 = 0.59, $p < 0.001$). Monthly effective rainfall was summed over the area of the catchment (catchment effective rainfall), correcting for the effect of different land cover types on evapotranspiration rates using correction coefficients adapted from Nistor & Porumb (2015). Catchment effective rainfall was then used as an estimate of the volume of water flowing into and out of the lake. To validate this estimate of outflow, measured outflow from a subset of 46 lakes from Norway and the UK were compared to the outflow estimated from effective rainfall. These countries were used as they had national datasets of flow gauge data for lake outflows. A significant positive linear relationship was found between measured and estimated outflow with a slope of 0.69 ± 0.02 (R^2 = 0.56, $p < 0.001$) and this was used to adjust the outflow, estimated from the catchment effective rainfall. Lake volume was estimated by multiplying the mean depth by the area of the lake. The monthly flushing rate of the lake was estimated by dividing the adjusted outflow by the volume of the lake. The retention time, in days, was calculated from the monthly flushing rate divided by 30 days in all cases. Retention time, rather than flushing rate, was used because the expected response of cyanobacteria to all explanatory variables were then in the same direction and because intuitively it is a better representation of prolonged periods of drought.

2.1.4 | Defining lake types

The lake types defined in this study are based on common European typology schemes, used across all European countries in the European Water Framework Directive (WFD) (EC-JRC, 2014; Lyche Solheim et al., 2015). These lake types are based on geology, humic substances, mixing type/depth, altitude, size and region (Mediterranean). Modification to these types were made as some of the factors which define these types—altitude, depth and surface area—co-varied with the stressors (TP, temperature and retention time) and so their influence was retained through these variables (Supporting Information Figure S1). Alkalinity also positively co-varied with TP (Supporting Information Figure S1) but was retained as a type factor because further analysis indicated that the relationship was non-linear (supplementary analysis, Supporting Information Figures S2 and S3). Specifically, in low alkalinity lakes there was no relationship between alkalinity and TP yet cyanobacteria and alkalinity still positively co-varied (R^2 = 0.17, $p < 0.001$) indicating that alkalinity is an ecologically relevant type variable to include. Others (e.g. Carvalho et al., 2011) have also found alkalinity to be an important predictor of cyanobacteria.

Lake types were defined by combining the broad European type levels for alkalinity, humic substances and mixing to give 18 lake types. These lake characteristics are central to the European typology schemes, and have been shown by others (Maileht et al., 2013; Ptacnik et al., 2008) to reflect ecologically meaningful characteristics that explain the distribution of phytoplankton and their response to eutrophication. Gower distance clustering [using the daisy function from the cluster package for R statistical software (Maechler, Rousseeuw, Struyf, Hubert, & Hornik, 2018)] confirmed that these lake types sufficiently explained variation in cyanobacteria (Supporting Information Figures S4 and S5).

Although a large number of lakes were included in the dataset, imbalances in the data meant that 18 types could not be adequately modelled, therefore, we further modified these types by combining ecologically similar levels of alkalinity and humic type. For alkalinity we retained "low alkalinity" (<0.2 mEq/L) as a distinct level, and medium and high alkalinity (>0.2 mEq/L) were combined into a new level—"medium-high alkalinity." For humic type we retained "low humic" as a distinct level (colour <30 mg Pt/L), renaming the level as "clear," and medium and high humic (colour >30 mg Pt/L) were combined into a new level—"humic." For a smaller subset of lakes for which dissolved organic carbon (DOC) concentrations were available, the concentration ranged from 0.4 to 44.6 and 2.9 to 37.1 mg/L in clear and humic lakes respectively. This merging of levels is consistent with the finding that bloom-forming cyanobacteria have a preference for neutral-alkaline lakes (Carvalho et al., 2011; Maileht et al., 2013; Shapiro, 1984), and that cyanobacteria dominate more often in clear lakes than in humic lakes (Ptacnik et al., 2008). Furthermore, clusters formed from the Gower distance analysis also showed a tendency for these levels to be grouped together (Supporting Information Figure S6).

The biovolume of cyanobacteria differed statistically significantly between levels of each lake type variable (Supporting Information Figure S7): alkalinity (low *vs* med-high alkalinity, $t = -22.5$, df = 1574, $p < 0.001$); humic (clear vs humic, $t = 7.78$, df = 1,579.8, $p < 0.001$); and mixing type (stratified vs polymictic, $t = -7.03$, df = 600.97, $p < 0.001$). All combinations of these new levels gave eight types (Table 1). Figure 1a shows the spatial distribution of the 494 lakes by type. A plot of the Silhouette width (Supporting Information Figure S4), used to determine the number of clusters, indicates that most of the differences between clusters are captured within 10 clusters and so reducing the clusters from 17 to 8 can be supported. Variation in cyanobacteria biovolume was explained by the lake types (Supporting Information Table S3), although differences between polymictic and stratified lakes were less clear when humic type and alkalinity type were taken into account (Figure 1b, see also Supporting Information). The clearest difference in cyanobacteria biovolume was seen between levels of alkalinity, both as a single lake type variable but also in combination with other lake type variables (Figure 1b and Supporting Information Figure S7).

2.2 | Statistical analysis

2.2.1 | Relationships between variables

Prior to the analysis, relationships between variables were investigated using pairwise scatterplots, inspecting for co-variation between explanatory variables and also for potentially non-linear responses using LOESS regression (Cleveland & Devlin, 1988). Experimental studies have shown that interactions can change along the stressor gradient when the response to single stressors are non-linear (Piggott, Salis, Lear, Townsend, & Matthaei, 2015), therefore we chose

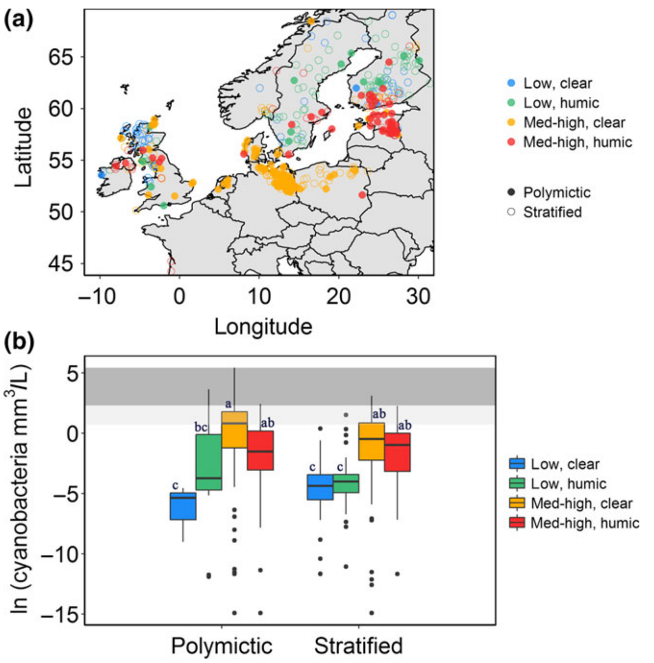

FIGURE 1 Distribution of lake location (a) and cyanobacteria biovolume (b) by lake type. Lake types are combinations of: alkalinity, low (<0.2 mEq/L) and med-high (>0.2 mEq/L); humic content, clear (colour <30 mg Pt/L) and humic (colour >30 mg Pt/L); and mixing type, stratified and polymictic. In (b) the shaded areas are for exceedance of low, 2 mm^3/L, (light grey) and medium, 10 mm^3/L, (dark grey) WHO (World Health Organisation) recommended threshold values for drinking and bathing (Chorus & Bartram, 1999), the conversion of WHO cell number to biovolume was taken from Carvalho et al. (2013). Cyanobacteria biovolume (mm^3/L) is log transformed and averaged for each individual lake. Letters indicate significant differences (at $p < 0.05$) in mean cyanobacteria between groupings of lake types, Tukey's test for multiple comparison following an ANOVA (supplementary material). Note that observations of cyanobacteria biovolume in polymictic, low alkalinity, clear lakes are from three lakes only, this lake type is not subsequently modelled as there is insufficient data for more complex multi variable modelling [Colour figure can be viewed at wileyonline library.com]

to restrict the regression to the range of each stressor where the data were linearly related. This was only relevant for the response to TP in which no relationship was found at high concentrations. Piecewise regression analysis (Muggeo, 2008) of the data (n = 2900) identified a break point of 4.1 natural log TP, or 60 μg/L (standard error = 0.16, R^2 = 0.29). However, to avoid potential biases of the dataset and to limit the number of lakes removed from the analysis, we restricted regression to data where TP ≤ 100 μg/L, which is also a more typical turning point identified in the literature for the widely reported asymptotic behaviours of chlorophyll-*a* and cyanobacteria to TP (Carvalho et al., 2013; Mccauley, Downing, & Watson, 1989; Phillips et al., 2008; Watson, Mccauley, & Downing, 1992).

We found that TP and retention time negatively co-varied (Supporting Information Figure S1). This relationship was influenced by lakes with very long retention times, i.e. greater than a year. To minimize potential issues with this co-variation confounding the response, as well as the potential of outliers skewing the response, we limited the data to lakes with monthly retention times of ≤365 days (1 year). This selection reduced the co-variation between retention time and TP (Supporting Information Figure S9) while still representing 90% of the data.

2.2.2 | Lake type models

Linear mixed effects models were fitted using the lme4 package for R statistical software (Bates, Mächler, Bolker, & Walker, 2015) R, Version 3.4.1 (R Core Team, 2017). To make distributions more symmetric, and assumptions of normality and homoscedasticity for error terms appropriate, cyanobacterial biovolume (mm^3/L), chlorophyll-*a* (μg/L), retention time (days) and TP (μg/L) were ln-transformed. All stressor variables were then standardized (mean centred and divided by the standard deviation) so that the size effect of single stressor effects (when no interaction terms were present) could be compared within models. The potential interactive effects of TP, temperature and retention time on the biovolume of cyanobacteria and the concentration of chlorophyll-*a* were modelled in each lake type separately (seven models for cyanobacteria and seven models for chlorophyll-*a*). For each lake type the following model was fitted:

2.3 | Lake type model, e.g. polymictic, medium-high alkalinity, clear lakes

$$\gamma = \beta_0 + \beta_1 X_{\mathrm{TP}} + \beta_2 X_{\mathrm{Temp}} + \beta_3 X_{\mathrm{Retention}} + \beta_4 X_{\mathrm{TP}\times\mathrm{Temp}} + \beta_5 X_{\mathrm{TP}\times\mathrm{Retention}} + \beta_6 X_{\mathrm{Temp}\times\mathrm{Retention}} + \beta_7 X_{\mathrm{TP}\times\mathrm{Temp}\times\mathrm{Retention}} + \delta_{\mathrm{lakeID}} + \varepsilon,$$
$$\gamma \sim \left(0, \sigma_l^2\right), \quad \varepsilon \sim \left(0, \sigma_r^2\right)$$

where γ is the log response of interest (cyanobacteria biovolume, mm^3/L and chlorophyll-*a*, μg/L), β_0 is the intercept term, β_1, β_2, and β_3 are model parameters for the TP term, temperature term and retention time term, respectively. The model parameters for the interactions are β_4 (TP and temperature), β_5 (TP and retention time), β_6 (temperature and retention time) and β_7 (TP, temperature and retention time). δ is the random effect term for lake ID which allows the response to vary on the intercept for individual lakes and ε is the overall error term, both with a mean of zero and unknown variance. Initially, year and month were also incorporated into the model as random terms to account for sampling within lakes over multiple months and years but this did not explain additional variance so were removed from the final models for parsimony. This model was then simplified by removing higher order interaction terms in turn, comparing simplified and more complex models using AIC and BIC and favouring simpler models when retaining more complex terms did not improve the model. Degrees of freedom and p values were approximated using the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2015). The variance explained by the model is reported as marginal R^2 which describes the proportion of variance explained by the fixed factor(s) alone and conditional R^2 which describes the proportion of variance explained by both the fixed and random factors (Nakagawa & Schielzeth, 2013).

3 | RESULTS

3.1 | Exploratory analysis

Of the 572 lakes initially identified as being suitable for analysis, i.e. lakes with complementary biological, climatic and typology data, 78 had mean monthly TP concentrations which exceeded 100 μg/L and therefore were omitted from the multiple stressor analysis, as at high concentrations, TP explained little additional variation in the biovolume of cyanobacteria (Supporting Information Figure S10). The biovolume of cyanobacteria in these lakes was on average higher (mean 9.3 mm^3/L) than in lakes with TP concentrations below 100 μg/L (mean 1.9 mm^3/L; $t = -4.1$, $df = 277.9$, $p < 0.001$).

In the 494 lakes analysed for the interactive effects of phosphorus, temperature and retention time, the mean monthly biovolume of cyanobacteria ranged from 0 to 225 mm^3/L, while chlorophyll-*a* ranged from 0.2 to 1,025 μg/L. Of these lakes, 23% had an average cyanobacteria biovolume that exceed the WHO low risk threshold of 2 mm^3/L (Chorus & Bartram, 1999). These lakes were predominantly located in central Europe, while lakes with lower cyanobacteria biovolume were located in northern regions (Supporting Information Figure S11). This spatial distribution of cyanobacterial abundance followed a pattern of decreasing temperature and decreasing TP concentrations with increasing latitude ($R^2 = 0.20$, $p < 0.001$ and $R^2 = 0.28$, $p < 0.001$, respectively). Latitudinal patterns in TP concentrations also corresponded to a decrease in percentage arable land in the catchment with increasing latitude (Supporting Information Figure S12).

3.2 | Multiple nutrient and climate effects on the abundance of cyanobacteria and phytoplankton

Climate and phosphorus relationships varied across the different lake types and the response of cyanobacteria and chlorophyll-*a* differed (Table 2, Figure 2).

We found that temperature and retention time had a stronger effect for cyanobacteria than for chlorophyll-*a* (Table 2, Figure 2), being always positive for cyanobacteria, while we found negative retention time effects for chlorophyll-*a* in two of the lake types: polymictic, medium-high alkalinity, clear lakes and stratified, medium-high alkalinity, clear lakes (Supporting Information Figure S13). Total phosphorus was a significant predictor of chlorophyll-*a* in all lake types, while this was not the case for cyanobacteria: in some lake types retention time and temperature were identified as better explanatory variables. Statistically significant effects of temperature showed a spatial pattern, with most temperature effects (independent effects and synergistic interactions with phosphorus) in lakes at Northern latitudes (>55°N). The temperature gradient above this latitude ranged from 5.3 to 20.4°C (mean 14.8°C), while the gradient below this latitude ranged from 11.5 to 24°C (mean of 17.7°C).

There were synergistic interactions between temperature and TP in some lake types. However, unexpectedly, this interaction was not restricted to the response of cyanobacteria: in polymictic humic lakes, warming exacerbated the effect of TP on both the biovolume of cyanobacteria and chlorophyll-*a* concentration (Table 2, models 2 a, b and models 4 a, b; Supporting Information Figure S14). A statistically significant positive interaction was also found in stratified, medium-high alkalinity, humic lakes but this was only significant for the response of chlorophyll-*a* and much smaller in size effect than the interactions found in polymictic, humic lakes (Table 2, model 8b). We did not find statistically significant evidence of interactive effects between retention time and phosphorus, nor between retention time and temperature, in any of the lake types for either response.

The fixed effects of the regression models for chlorophyll-*a* concentration explained more variance than regression models for cyanobacteria biovolume (marginal R^2, i.e. the proportion of variance explained by the fixed factor(s) alone, Table 2, Figure 3a). The percentage of cyanobacteria biovolume explained by TP concentration and climate effects (temperature and retention time) was <7% in all lake types, with the exception of polymictic, medium-high alkalinity, humic lakes in which 16% of the variance was explained. The variance of chlorophyll-*a* explained by stressors ranged between 9% and 43%, with most models explaining over 20% of the variance (Figure 3a).

Although significant stressor relationships were detected, the natural variability between lakes was much larger. As an example, Figure 3b shows that despite the interaction between TP and temperature being the same in all polymictic, low alkalinity humic lakes for any given TP—temperature combination, the average biovolume of cyanobacteria varied among individual lakes. The variance in the random intercept for each lake within each type is shown in Supporting Information Figure S15.

4 | DISCUSSION

4.1 | The sensitivity of cyanobacteria to multiple stressors varies with lake type

We found that the sensitivity of cyanobacteria to temperature, retention time and phosphorus varied among lake types. This indicates that the interactive effects of multiple lake type factors are important in shaping the response of cyanobacteria to multiple stressors and that a lake type analytical approach could help better predict responses to future environmental change. Differences in the response among lake types is not surprising as the biovolume of cyanobacteria is not just affected by factors that affect the amount of phytoplankton such as phosphorus, temperature and retention time but also by factors that shape community composition such as alkalinity, colour and mixing depth (Lenard & Ejankowski, 2017; Maileht et al., 2013; Ptacnik et al., 2008). Our results corroborate other studies that show the importance of allowing for interactions between multiple lake type factors; for example, interactions

TABLE 2 Linear regression mixed effect models explaining cyanobacteria biovolume and chlorophyll-*a* concentration. The models explain cyanobacterial biovolume (natural log, mm^3/L) and chlorophyll-*a* concentration (natural log, μg/L) in different lake types and result from backward stepwise selection, starting with a model with full interactions between the independent variables: mean monthly total phosphorus (TP, μg/L), mean monthly air temperature (°C) and monthly retention time (days). TP and retention time are log transformed and all explanatory variables are standardized (mean centred and divided by the standard deviation) for comparability. Lakes are split into polymictic and stratified lakes (average conditions) and within each mixing regime into a further four types defined by combinations of alkalinity (low, med-high) and colour (clear, humic). Each model has an additional error term which accounts for differences between individual lakes, after accounting for the fixed effects, this is the random intercept term. The variance explained by the models is presented as marginal R^2 which describes the proportion of variance explained by the fixed factor(s) alone and conditional R^2 which describes the proportion of variance explained by both the fixed and random factors. The significance level is denoted as ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$, ·$p < 0.1$

			Model coefficients (*SE*)				R^2	
Model	Lakes	Lake type	TP	Temp	Retention	TP × Temp	Marginal	Conditional
Cyanobacteria								
1a	3	Polymictic, low Alk., clear	*Insufficient data*					
2a	15	Polymictic, low Alk., humic	1.25 (0.65)·	1.15 (0.58)·		1.71 (0.73)*	0.07	0.77
3a	89	Polymictic med-high Alk., clear			0.74 (0.27)**		0.05	0.69
4a	45	Polymictic med-high Alk., humic	−0.05 (0.54)	−0.22 (0.61)	0.78 (0.34)*	1.82 (0.73)*	0.16	0.61
5a	70	Stratified, low Alk., clear	0.54 (0.25)*	0.49 (0.16)**			0.05	0.63
6a	70	Stratified, low Alk., humic		0.29 (0.12)*	0.41 (0.19)*		0.03	0.61
7a	163	Stratified, med-high Alk., clear	0.77 (0.23)***				0.03	0.54
8a	39	Stratified, med-high Alk., humic					0.00	0.80
Chlorophyll-*a*								
1b	3	Polymictic, low Alk., clear	*Insufficient data*					
2b	15	Polymictic, low Alk., humic	0.61 (0.17)***	0.45 (0.16)**		0.84 (0.20)***	0.28	0.61
3b	89	Polymictic med-high Alk., clear	0.70 (0.10)***		−0.15 (0.06)*		0.21	0.78
4b	45	Polymictic med-high Alk., humic	0.32 (0.16)*	−0.71 (0.19)***	0.30 (0.09)**	1.03 (0.22)***	0.43	0.55
5b	70	Stratified, low Alk., clear	0.31 (0.07)***				0.09	0.58
6b	70	Stratified, low Alk., humic	0.35 (0.07)***				0.09	0.67
7b	163	Stratified, med-high Alk., clear	0.65 (0.07)***		−0.19 (0.06)**		0.29	0.63
8b	39	Stratified, med-high Alk., humic	0.51 (0.08)***	0.03 (0.04)		0.08 (0.04)*	0.35	0.81

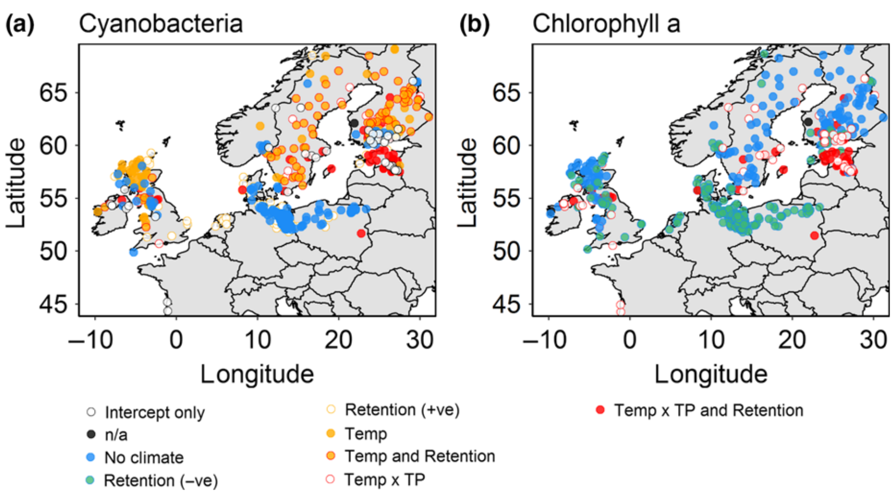

FIGURE 2 Model summaries highlighting climate effects (temperature and retention time) for the response of (a) cyanobacteria and (b) chlorophyll-*a*. Each lake (point) is coloured according to statistically significant climate effects estimated for the lake type to which the lake belongs. Warmer colours represent positive climate effects, cooler colours represent either no climate effect or a negative climate effect (only applicable for retention time in chlorophyll-*a* models). n/a are polymictic, low alkalinity, clear lakes (n = 3) which had insufficient data for analysis. See Figure 1 for the spatial distribution of lake types [Colour figure can be viewed at wileyonlinelibrary.com]

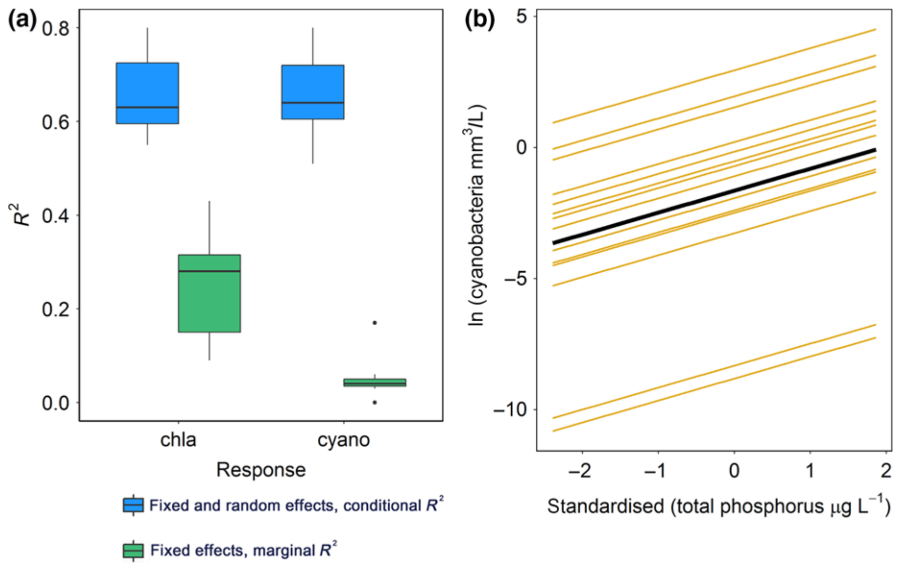

FIGURE 3 Marginal and conditional variance explained by the models. (a) Boxplot of conditional R^2 (blue) and marginal R^2 (green) from all lake type models (n = 7 lake types) for chlorophyll-*a* and cyanobacteria responses. (b) Random effect plot of the response of cyanobacteria to TP in polymictic, low alkalinity, humic lakes (while keeping temperature constant). The fixed response is shown by the bold black line, individual lake responses are shown by the orange lines (i.e. differences in the intercept) [Colour figure can be viewed at wileyonlinelibrary.com]

between mixing regime and colour (Havens & Nürnberg, 2004), alkalinity and colour (Ptacnik et al., 2008), depth and alkalinity (Phillips et al., 2008) have been shown to shape phytoplankton nutrient relationships. A comparison of the sensitivity of chlorophyll-*a* and cyanobacteria to the effects of phosphorus, temperature and retention time among lake types suggests that chlorophyll-*a* may be less influenced by type (the response was similar between some lake types). This is consistent with Phillips et al. (2008) who found that nutrient chlorophyll-*a* relationships could be grouped into fewer groups than the 18 WFD types that they tested, reducing the number of types to three. Our results suggest that more detailed groupings of lake types may be required to capture sensitivities of a community structure response, whereas chlorophyll-*a*, as a proxy for total biomass, appears to be less influenced by these finer details.

Colour as an additional lake type factor is an important inclusion, not only because changes in colour can strongly alter phytoplankton biomass and community structure (e.g. Lenard & Ejankowski, 2017) but also because humic substances have increased in lakes in past decades (Monteith et al., 2007). It is interesting that synergistic effects of temperature and phosphorus were only detected in humic lakes (polymictic, humic types for cyanobacteria and chlorophyll-*a* as well as stratified, medium-high alkalinity and humic type for chlorophyll-*a*). The abundance of cyanobacteria is most often associated with clear lakes (data presented here, and e.g. Carvalho et al., 2011 and Ptacnik et al., 2008); consequently humic lakes are currently the least at risk (do not exceed WHO thresholds, Supporting Information Figure S11). However, the synergistic interaction between temperature and phosphorus indicates that the deterioration of water quality may be accelerated in these lake types. This synergism could be caused by enhanced heat absorption in the lake surface caused by humic substances, a process that also increases thermal stratification (Kirillin & Shatwell, 2016). Since there is evidence of a non-linear relationship between colour and total phytoplankton biomass (Seekell, Lapierre, & Karlsson, 2015) and community composition (Carvalho et al., 2011; Rasconi, Gall, Winter, & Kainz, 2015; Urrutia-Cordero, Ekvall, & Hansson, 2016), the definition of the colour category boundaries might influence the response to multiple stressors, adding further complexity. Nevertheless, our results show the importance of colour as a lake type factor and emphasizes that other environmental factors may alter our expectations of multiple stressor interactions.

There is a risk that co-variation between environmental factors may lead to incorrect attribution of the processes behind a relationship. In particular, the striking spatial pattern of statistically significant temperature effects on cyanobacteria and chlorophyll-*a* in lakes at more northern latitudes coincides with the distribution of polymictic humic lakes (in which interactive temperature effects were found for both cyanobacteria and chlorophyll-*a*). Biological responses to changes in temperature have been shown to be greatest at lower latitudes because of larger shifts in metabolic rate which increases exponentially with temperature (Dillon, Wang, & Huey, 2010; Kraemer, Mehner, & Adrian, 2017). However, our results show a different picture with the greatest temperature effects, particularly for cyanobacteria biovolume, at higher latitudes. This suggests that this is a sensitive part of the temperature gradient for cyanobacteria, or that other latitudinal effects such as longer summer photoperiod at higher latitudes (Nicklisch, Shatwell, & Köhler, 2008) or the effect of lake type may enhance the temperature effect. Another potential issue is the co-variation between alkalinity and TP. This occurs because many medium-high alkalinity lakes are located in central regions where TP concentrations and percentage arable land in the catchment are high. At higher latitudes, in contrast, there were a larger number of humic, low alkalinity lakes in the dataset, reflecting the tendency for acidic, humic and forested catchments in Fenno-Scandian areas (Maileht et al., 2013), in which TP concentrations were lower. Nevertheless, although average differences in the abundance of cyanobacteria among types may be attributed to average differences in TP (Figure 1b and Supporting Information Figure S16), most lakes types were modelled over similar TP gradients, and so differences between lake type models are likely caused by other factors. The use of alkalinity as a type factor is supported both in the literature (e.g. Carvalho et al., 2011; Phillips et al., 2008 and Ptacnik et al., 2008) and also by an exploratory analysis of the relationships between alkalinity, cyanobacteria and TP in low *vs* medium-high alkalinity lakes (supplementary analyses: Supporting Information Figures S2 and S3, Table S2).

Although we found statistically significant stressor relationships within lake types, in many cases the variation these explained was low and the natural variability among lakes within a lake type was much larger than the variance explained by the stressor effects. Phosphorus, temperature and retention time are important drivers, but they are not the only factors which influence phytoplankton biomass. Potential sources of variability can occur because of measurement error or missing covariate information, e.g. other limiting nutrients (e.g. TN, (Dolman et al., 2012; Downing, Watson, & Mccauley, 2001)), grazer densities (Jeppesen, Peder Jensen, Søndergaard, Lauridsen, & Landkildehus, 2000), competition with macrophytes (Phillips, 2005), light climate (Mischke, 2003) and past events such as remediation and associated hysteresis (França et al., 2016; Scheffer, 1998) or recovery from acidification (Battarbee et al., 2014). Furthermore, the use of lake types as categorical variables may have reduced their explanatory power. In the future, it might be possible to incorporate sampling event-specific values that could also account for within-year variation as can occur for the presence and duration of stratification (Huber, Wagner, Gerten, & Adrian, 2012; Jöhnk et al., 2008; Wagner & Adrian, 2009), especially in polymictic lakes (Taranu et al., 2012) but also for variation in colour (Lenard & Ejankowski, 2017). Nevertheless, the use of lake types is an efficient means of simplifying statistical models and of providing information for managers on the types of lakes at risk of generating algal blooms. It is also possible that idiosyncratic responses to environmental change at the individual lake level could arise from interactions with other chemical, physical and biological environmental factors. A way to account for this would be to allow the slopes of individual lakes to vary in the model structure, but due to limited data points within a lake we were unable to do this; further exploration using long-term datasets would be informative.

4.2 | Implications for managing the risk of cyanobacteria in the future

The first take-home message for management is that the sensitivity of cyanobacteria to multiple anthropogenic stressors, and consequently the risk of water quality issues, will not be the same for all lakes. Thus, some lake types may require greater management intervention than others, and lakes that are currently not at risk (i.e. do not exceed WHO guideline thresholds) may develop problems in the future, e.g. polymictic humic lakes. The broad typologies used are similarly adopted (e.g. Havens & Nürnberg, 2004), and relevant, outside of Europe although some regions globally may have additional lake types that would need considering (e.g. endorheic lakes in North America and Africa).

The second take home message, and perhaps a more generalizable outcome, is that our results suggest that in most lake types, management will become increasingly necessary because of the additional effects of climate change (temperature and retention time) on cyanobacterial abundance. As climate effects cannot be locally controlled, this means that existing models detailing phosphorus targets needed to minimize harmful algal blooms (Carvalho et al., 2013) may have to be revised to mitigate these effects (Jeppesen et al., 2009). We do not make any quantitative recommendations here but indicate that this will be a likely management scenario for most lakes.

It should also be emphasized that we make reference here to the effects and control of phosphorus as it is often considered the limiting nutrient in lakes (Phillips et al., 2008; Schindler et al., 2008), however, nitrogen can also play a key role (Beaulieu et al., 2013; Conley et al., 2009; Maberly, King, Dent, Jones, & Gibson, 2002; Paerl et al., 2016). Under projected climate scenarios, it is expected that there will be an increase in nitrogen loading because of enhanced runoff in the north temperate region (Sinha, Michalak, & Balaji, 2017), the effects of which may also depend on ecosystem type. For example, shallow lakes are often nitrogen limited during the summer (Dolman, Mischke, & Wiedner, 2016; Søndergaard, Lauridsen, Johansson, & Jeppesen, 2017) and so enhanced loading could increase the carrying capacity in lakes with sufficient phosphorus. An increase in nitrogen could also trigger a shift from a macrophyte, clear water state to a turbid phytoplankton-dominated state (e.g. Olsen et al., 2015). A lake type approach should also be applied to other important or emerging stressors such as changes in TN.

It should be emphasized that this is a broad view of management at a lake type level; the relationships that we present within lake types describe the generalized response for this population of lakes. However, we found that the natural variability among lakes within a lake type was much larger than the variance explained by the stressor effects. The implications of this are that, for a given value of a stressor (or combination of stressors, depending on the model), the abundance of cyanobacteria may vary considerably among lakes of the same type (Figure 3b). Thus, while these models can be used to assess potential risk across a population of lakes (within a specific lake type), and inform where to prioritize monitoring for risk management, they are not appropriate for decision-making at the individual lake level. This view reflects the perspective which warns of copy and paste management methods for different lakes (Lürling, Mackay, Reitzel, & Spears, 2016).

4.3 | Final remarks

Our results indicate that the response of cyanobacteria to multiple stressors varies greatly with lake type, much more so than chlorophyll-*a*, highlighting the complex nature of biological and community responses to environmental conditions and that a "one-size fits-all" approach is not appropriate in order to understand and manage the risks of harmful algal blooms. Although individual lakes tended to show idiosyncratic responses, the use of lake type categories allows a clear generalization of lake responses that are helpful to lake managers to target measures to minimize risks. In the future, the use of this approach, along with large-scale datasets and rigorous statistical analysis, will improve our ability to forecast responses of cyanobacteria to future environmental changes, including recovery through management and changes in climate.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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