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The sensitivity of cyanobacteria to multiple stressors varies with lake type.

Running head: Cyanobacteria and multiple stressors

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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 and temperature and 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 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. However, the sensitivity of cyanobacteria to temperature, retention time and phosphorus differed among types highlighting the complex response of lakes to multiple stressors. The analyses suggested that lake types currently not at risk could be affected by warming in the future, since temperature effects were greatest in lakes at higher latitudes. More work is needed to separate geographical from typological effects in order to provide advice for managers. It is already clear that climate change will need to be accounted for when managing risk of cyanobacteria in lakes and a 'one-size fits-all' approach is not appropriate. Our analysis shows that our understanding is greatly improved by considering how multiple stressors interact in a range of different lake types and that this approach could help better predict responses to future nutrient and climate changes.

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 (Oliver *et al.*, 2017) as human populations grow and become more urbanised, requiring intensive agriculture to expand, while internal cycling of nutrients within lakes occurs as a legacy of past activities (Nürnberg, 2009). 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 *et al.*, 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 generalisable response; others have found that the effect of temperature is dependent on other environmental factors such as trophic setting (Rigosi *et al.*, 2014) or by the mixing state of the lake (Taranu *et al.*, 2012).

Climate change also affects rainfall patterns (Milly *et al.*, 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 *et al.*, 1988, Reichwaldt & Ghadouani, 2012). Studies exploring the effect of changes in 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 *et al.*, 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 generalisable 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 *et al.*, 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 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 *et al.*, 2013). While they all highlight the importance of environmental context, they exclude other key environmental factors that shape community composition; for example, 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). Thus, when exploring how lake type might influence the response of cyanobacteria to multiple stressors such as eutrophication, climatic warming and changing rainfall patterns, including more types is necessary in order 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 hypothesised 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 hypothesised the sensitivity of these response variables to the interactions between multiple stressors would vary among lake types.

Methods

Data

i. *Biological and chemical data*

Data on cyanobacteria biovolume (mm^3 L^{-1}), chlorophyll-*a* concentration (µg L^{-1}), total phosphorus concentration (µg L^{-1}) and lake type variables - altitude, depth, surface area, mixing status, humic content and alkalinity - were extracted from the WISER database (Moe *et al.*, 2013) and supplemented by additional datasets. Total phosphorus was used as 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 strongly positively correlated (R^2 = 0.64, p <0.001). Biological and phosphorus data were summarised as monthly means for July, August and September; a period when cyanobacteria blooms are most reported in temperate, northern latitudes and when biological sampling fortunately is also most intense, thereby maximising data availability. Data were selected between 2000 and 2009 as sampling methods from this period were most standardised. Each lake contributed a variable number of observations; on average six monthly observations from different combinations of years (2000 – 2009) and months (July-September), Table S1 summarises the number lake months for each year, month combination. The hierarchical structure of the statistical models accounts for differences in the number observation per lakes, through the random effect error term.

ii. Catchment data

Catchment data – delineations and percent (%) CORINE land cover – were extracted from the MARS geodatabase (Globevnik *et al.*, 2017).

iii. 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 x 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 of 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 Mircea-Mărgărit (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 of 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 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.

iv. 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 (Fig. S1). Note that any additional lakes without information on these variables were then extracted from the WISER database (2 lakes). Alkalinity also positively co-varied with TP (Fig. S1) but was retained as this relationship showed some non-linearity; in low alkalinity lakes the relationship was not seen yet in these lakes alkalinity and cyanobacteria showed statistically significant positive co-variation ($R^2 = 0.17$, p <0.0001) in the lakes, supplementary material (Fig. S2 and S3), suggesting that alkalinity is an ecologically relevant type variable to include. Furthermore, others (e.g. Carvalho *et al.*, 2011) have 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 *et al.* (2012)) confirmed that these lake types sufficiently explained variation in cyanobacteria (Fig. S4 and Fig. 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^{-1}) as a distinct level, and medium and high alkalinity (>0.2 mEq L^{-1}) 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^{-1}), renaming the level as 'clear', and medium, and high humic (colour > 30 mg Pt L^{-1}) were combined into a new level – 'humic'. 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 than in humic lakes (Ptacnik *et al.*, 2008). Furthermore, clusters formed from the Gower distance analysis also show a tendency for these levels to be grouped together (Fig. S6). The biovolume of cyanobacteria differed statistically significantly between levels of each lake type variable (Fig. S7): alkalinity (low *vs* med-high alkalinity, t = -22.5, df = 1574, p <0.001); humic (clear *vs* humic, t = 7.78, df = 1579.8, 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, Fig. 1a shows the spatial distribution of the 494 lakes by type. A plot of the Silhouette width, Fig. 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 types (Table S3), although differences between polymictic and stratified lakes were less clear when humic type and alkalinity type were taken into account (Fig. 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 (Fig. 1 and Fig. S7).

Table 1. Response and explanatory variables included in the analysis. Means ± standard deviations and minimum and maximum values in parentheses, are summarised 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^{-1})	Chlorophyll-*a* (µg L^{-1})	Mean monthly total phosphorus (µg L^{-1})	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)

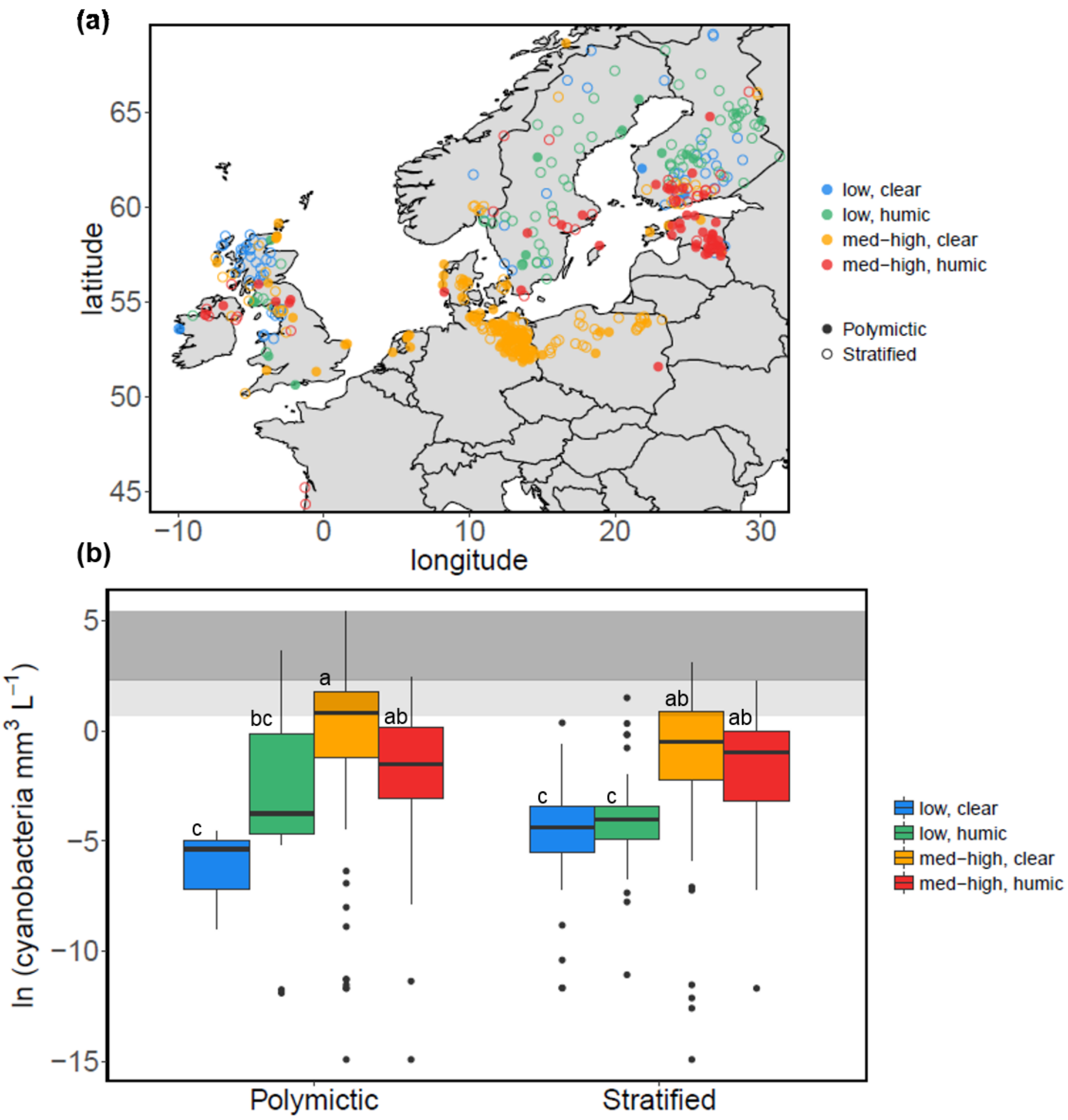

Fig. 1 Distribution of lake location (a) and cyanobacteria biovolume (b) by lake type. Lake types are combinations of: alkalinity, low (<0.2 mEq L-1) and med-high (>0.2 mEq L-1); humic content, clear (colour <30 mg Pt L-1) and humic (colour > 30 mg Pt L-1); and mixing type, stratified and polymictic. In (b) the shaded areas are for exceedance of low, 2 mm^3 L^{-1}, (light grey) and medium, 10 mm^3 L^{-1}, (dark grey) WHO (World Health Organisation) recommended threshold values for drinking and bathing (Chorus & Bartram, 1999). Cyanobacteria biovolume (mm^3 L^{-1}) is log transformed and averaged for each individual lake. Letters (a, ab, bc and c) indicate significant differences (at $p < 0.05$) in mean

cyanobacteria between groupings of lake types, Tukeys test for multiple comparison following an ANOVA (supplementary material). Note that observations of cyanobacteria biovolume in polymictic, low, 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.

Statistical analysis

i. 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 *et al.*, 2015), therefore we chose 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. See '*exploratory analysis*' in the results section for more details.

We found that TP and retention time negatively co-varied (Fig. S1), this relationship was influenced by lakes with very long retention times i.e. greater than a year. To minimise 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 (Fig. S9) while still representing 90% of the data

ii. Lake type models

Linear mixed effects models were fitted using the lme4 package for R statistical software (Bates *et al.*, 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^{-1}), chlorophyll-*a* (µg L^{-1}), retention time (days) and TP (µg L^{-1}) were ln-transformed. All stressor variables were then standardised (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:

<u>*Lake type model e.g. polymictic, medium-high alkalinity, clear lakes*</u>

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

where γ is the log response of interest (cyanobacteria biovolume, mm^3 L^{-1} and chlorophyll-*a,* µg L^{-1}), 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, 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 *et al.*, 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).

Results

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^{-1} and therefore were omitted from the multiple stressor analysis as at high concentrations, TP explained little additional variance in the biovolume of cyanobacteria (Fig. S10). Piecewise regression analysis (Muggeo, 2008) of the data (n = 2900) identified a break point of 4.1 natural log TP, or 60 µg L^{-1} (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^{-1}, 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 *et al.*, 1989, Phillips *et al.*, 2008, Watson *et al.*, 1992). The biovolume of cyanobacteria in these lakes was on average higher (mean 9.3 mm^3 L^{-1}) than in lakes with TP concentrations below 100 µg L^{-1} (mean 1.9 mm^3 L^{-1}); 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^{-1}, while chlorophyll-*a* ranged from 0.2 - 1025 µg L^{-1}. 23% of these lakes had an average cyanobacteria biovolume that exceed the WHO low risk threshold of 2 mm^3 L^{-1} (Chorus & Bartram, 1999). These lakes were predominantly located in central Europe while lakes with lower cyanobacteria biovolume were located in northern regions (Fig. 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 and an increase in percentage forest in the catchment with increasing latitude (Fig. S12).

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, Fig. 5).

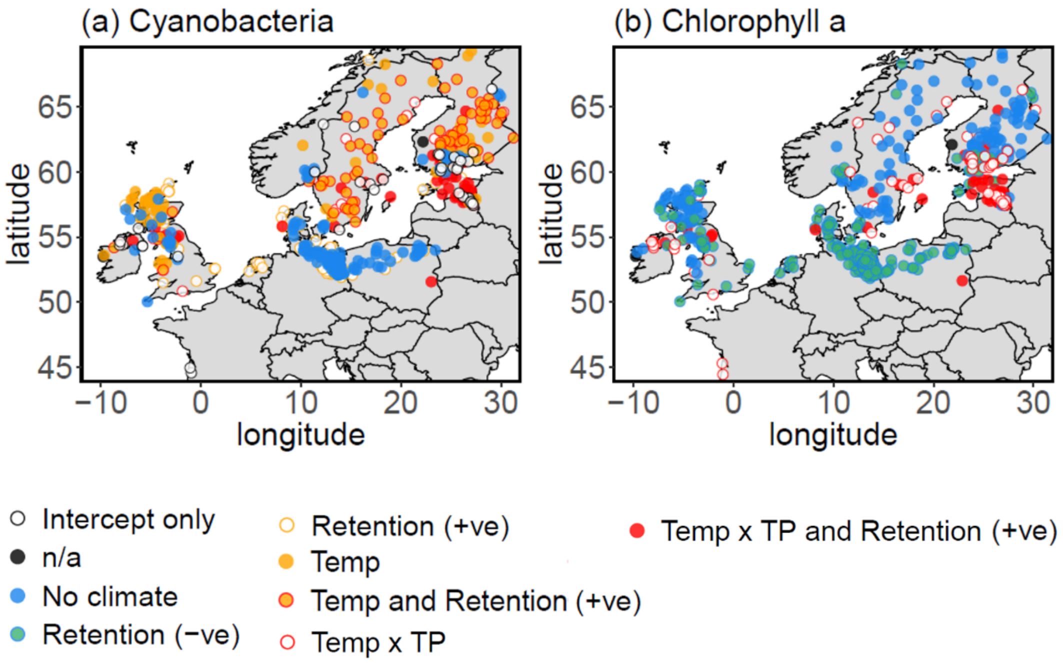

Fig. 2 Model summaries highlighting climate effects (temperature and retention time) for the response of (a) cyanobacteria and (b) chlorophyll-*a*. Each lake (point) is coloured according to statistically significant climate effects estimated for lake type to which the lake belongs. Warmer colours represent 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 Fig. 1 for the spatial distribution of lake types.

We found that temperature and retention time had a stronger effect for cyanobacteria than for chlorophyll-*a* (Table 2, Fig. 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 (Fig. 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 (> 55º N). The temperature gradient above this latitude ranged from 5.3 – 20.4 ºC (mean 14.8 ºC) while the gradient below this latitude ranged from 11.5 – 24 ºC (mean of 17.7 ºC).

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; Fig. 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.

Table 2. Linear regression mixed effect models explaining cyanobacteria biovolume and chlorophyll-*a* concentration. The models explain cyanobacterial biovolume (natural log, mm^3 L^{-1}) and chlorophyll-*a* concentration (natural log, µg L^{-1}) 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^{-1}), mean monthly air temperature (ºC) and monthly retention time (days). TP and retention time are log transformed and all explanatory variables are standardised (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 (standard error)				R^2	
Model	Lakes	Lake Type	TP	Temp	Retention	TP x Temp	Marginal	Conditional
	Cyanobacteria							
1a	3	polymictic, low Alk., clear	*Insufficient data*					
2a	15	polymictic, low Alk., humic	1.25 (0.65)$^{\cdot}$	1.15 (0.58)$^{\cdot}$		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

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; Fig. 3a). The percentage of cyanobacteria biovolume explained by TP concentration and climate effects (temperature and retention time) was less than 7% in all lake types, with the exception of polymictic, medium-high alkalinity, humic lakes in which 16% of variance was explained. The variance of chlorophyll-*a* explained by stressors ranged between 9 – 43%, with most models explaining over 20% of the variance (Fig. 3a).

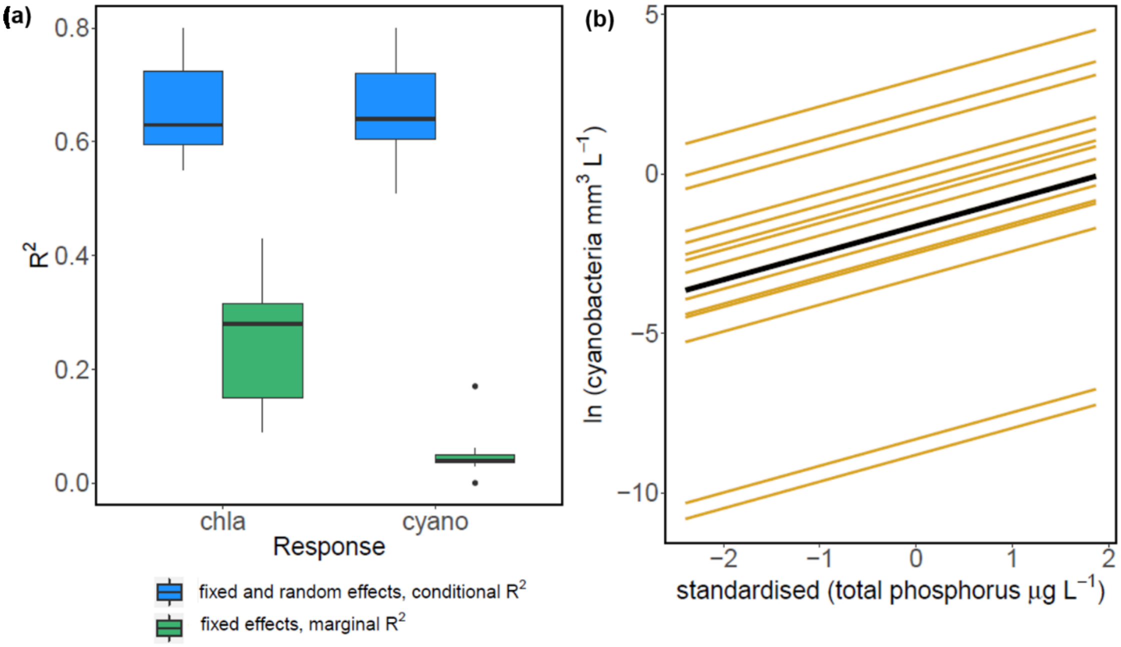

Fig. 3 Marginal and conditional variance explained by the models. (a) Boxplot of conditional R^2 (blue) and marginal R^2 (green) from all lake type models (n = 7 lake types) for chlorophyll-*a* and cyanobacteria responses. (b) Random effect plot of the response of cyanobacteria to TP in polymictic, low 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).

Although significant stressor relationships were detected, the natural variability between lakes was much larger. As an example, Fig. 4b 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 Fig. S15.

Discussion

The sensitivity of cyanobacteria to multiple stressors varies with lake type

Our results are consistent with previous work which suggests that the response of cyanobacteria to environmental change will be shaped by other environmental factors (Beaulieu *et al.*, 2013, Haakonsson *et al.*, 2017, Rigosi *et al.*, 2014, Taranu *et al.*, 2012). Unlike these studies, which mainly focused on one lake type factor, we combined a wider set of lake type variables that are also likely to shape community composition. We found that the sensitivity of cyanobacteria to temperature, retention time and phosphorus varied between lake types, suggesting that these additional lake typology factors are important in shaping the response of cyanobacteria to environmental change and could help better predict responses to future nutrient and climate changes. This is not surprising as the abundance 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 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. 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 eighteen 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, Fig. S11), yet this interaction 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). It should be stressed that these relationships are for the levels of humic substances derived from the WFD European lake types derived from the WFD European lake types, but it should be noted that many studies have demonstrated non-linear effects of colour on total biomass (Seekell *et al.*, 2015) and cyanobacteria/composition (Carvalho *et al.*, 2011, Rasconi *et al.*, 2015, Urrutia-Cordero *et al.*, 2016), adding further complexity. Nevertheless, our results show the importance of colour as a lake type factor and emphasises 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*). The 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 *et al.*, 2010, Kraemer *et al.*, 2017). However, our results show a different picture with greatest effects, particularly for cyanobacteria biovolume, at higher latitudes, which suggests that this is a sensitive part of the temperature gradient for cyanobacteria (ref), or that other latitudinal effects such as longer summer photoperiod at higher latitudes (Nicklisch *et al.*, 2008) or the effect of lake type may enhance the temperature effect. Another potential issue is the co-variation between alkalinity and TP. This co-variation is seen because many medium- high alkalinity lakes are located in central regions where the percentage arable land in the catchment and TP concentrations are higher. At higher latitudes, in contrast, there were a larger number of humic, low alkalinity lakes 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 (Fig. 1b and Fig. 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 both supported in the literature (e.g. Carvalho *et al.*, 2011, Phillips *et al.*, 2008 and Ptacnik *et al.*, 2008) but also from an exploratory analysis of the relationships between alkalinity, cyanobacteria and TP in low *vs* medium-high alkalinity lakes (supporting information).

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 *et al.*, 2001) grazer densities (Jeppesen *et al.*, 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). 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 might also take account of within-year variation as can occur for the presence and duration of stratification (Huber *et al.*, 2012, Jöhnk *et al.*, 2008, Wagner & Adrian, 2009), especially in polymictic lakes (Taranu *et al.*, 2012) but also for colour variation (Lenard & Ejankowski, 2017). Nevertheless, the use of lake types is an efficient means of simplifying statistical models and of providing information for managers on types of lakes at risk of generating algal blooms. It is 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 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.

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 generalisable 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 minimise 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 be emphasised 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 *et al.*, 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 *et al.*, 2017), the effects of which may also depend on ecosystem type. For example, shallow lakes are likely often nitrogen limited during the summer (Dolman *et al.*, 2016, Søndergaard *et al.*, 2017) and so enhanced loading could increase the carrying capacity in lakes with sufficient phosphorus. Furthermore, an increase in nitrogen could trigger a shift from a macrophyte, clear water state to a turbid phytoplankton dominated state (e.g. Olsen *et al*., 2015).

It should be emphasised that this is a broad view of management at a lake type level; the relationships that we present within lake types describe the generalised 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 (Fig. 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 prioritise 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 *et al.*, 2016).

Final remarks

Our results indicate that the response of cyanobacteria to favourable future conditions of enhanced nutrient enrichment, elevated temperatures and prolonged periods of drought may not be the same in all lake types. While other studies have reached similar conclusions, here we provide evidence that these are not just limited to one type factor as has been explored before. We do not conclude that these are definitive ‘end lake types’, however we suggest that our ability to generalise and manage the response of cyanobacteria to multiple stress and future environmental change lies in defining the types of environment in which the risk/sensitivity differs.

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Supplementary material

Supplementary analyses

Relationships between TP, alkalinity and cyanobacteria

Lakes which had numerical alkalinity data were used to explore the relationship between TP, alkalinity and cyanobacteria (number of observations = 1246, number of lakes = 271).

Pairwise plots of alkalinity, TP and cyanobacteria show that they are all positively related (Fig. S1), although most paired relationships show some curvilinear tendency; quantification of these relationships are presented as Pearson correlation coefficients, which assume a linear relationship. It is possible that the relationships between cyanobacteria and alkalinity could be because of the co-variation between TP and alkalinity, in which case there would be a case for removing alkalinity from the types.

However, if we explore relationship between the same variables but split between the two alkalinity types (low and medium-high) used in typology (Fig. S2) we can provide support for the inclusion of alkalinity:

a) The response of cyanobacteria to TP is steeper in medium-high alkalinity lakes over a very similar gradient (Table S2). This suggests that the response of cyanobacteria to TP may depend on alkalinity (Fig. S2a)
b) In low alkalinity lakes there is no longer a relationship between TP and alkalinity ($r = 0.04$, *p* value = >0.05), yet in both low and high alkalinity lakes there's a positive relationship between cyanobacteria and alkalinity (low alkalinity, $r = 0.43$, *p* value = <0.0001; medium-high alkalinity, $r = 0.25$, *p* value = <0.001). This provides further evidence that alkalinity explains variation in cyanobacteria independent of TP and so should be included to categorise lakes into types. Fig S2. b - c.

Gower distance clustering

Gower distance was calculated in R using the daisy function () from the cluster package with ln cyanobacteria as the response and alkalinity (three levels: low, medium and high), humic substances (three levels: low, medium and high) and mixing type (two levels: polymictic and stratified) as the categorical variables for clustering the data. As a visual check, we returned the most and least similar lakes. The two most similar lakes in term of cyanobacteria biovolume were both low alkalinity, medium humic type and stratified, the two least similar lakes were low alkalinity, medium humic and stratified *vs* medium alkalinity, low humic and polymictic. This initial check satisfied a basic expectation that cyanobacteria can be explained in part by combinations of these type variables, and that the most dissimilar values of cyanobacteria were from distinct lake types. We used the PAM algorithm (partitioning around medoids) for clustering and the silhouette width as the metric for helping to choose the number of clusters to be extracted (this is an aggregated measure of how similar an observation is to its own cluster compared to its closest neighbouring cluster, higher values are better). We calculated the silhouette width for clusters ranging from 2 to 30 using the PAM algorithm (Fig. S3) which suggests 17 clusters. These 17 clusters are broadly consistent with clustering cyanobacteria by a three way combination of alkalinity, humic and mixing types i.e. 18 types (Fig. S4). Because of imbalances in the data the 18 types could not be adequately modelled, therefore we further modified these types by combining ecologically similar levels of alkalinity and humic type, *see the manuscript methods*, resulting in 8 types which are broadly consistent with clustering the data by 8 groups using Gower based distance clustering (Fig. S5).

Differences in cyanobacteria among lake types

To test the differences in cyanobacteria biovolume among lake types, an ANOVA (Table S3) was fit with the response of natural log cyanobacteria biovolume (mm^3 L^{-1}) and a factor of 'type' (n=8) which was then followed up with a Tukey test for the differences between each type (using the HSD.test function from the agricolae package in R). As some lakes had multiple data points, and thus violated the assumption of independence, one observation was randomly selected per lake. This random selection of observations was done ten times and the results were compared (Fig. S6). Six of the random draws resulted in the same groupings (Fig. S6 e-j), although there were some broad consistencies between these grouping and the groupings (Fig. S6 a-d) from the other four draws. In the paper we have presented the test based on the average response to complement what is presented.

Supplementary tables

Table S1. Number of monthly lake sample data for each year – month combination

	Month			
Year	**July**	**August**	**September**	**Grand Total**
2000	52	12	3	67
2001	23	58	11	92
2002	49	53	15	117
2003	19	56	14	89
2004	34	56	13	103
2005	32	83	21	136
2006	66	135	61	262
2007	104	153	75	332
2008	130	155	96	381
2009	3	2	3	8
Grand Total	**512**	**763**	**312**	**1587**

Table S2. Model summary for the linear relationship between cyanobacteria and TP in low and medium-high alkalinity lake. The intercept is for medium-high alkalinity lakes.

term	estimate	std.error	statistic	*p* value
(Intercept)	-8.051	0.514	-15.652	<0.001
log(TP)	1.671	0.163	10.263	<0.001
AlkalinityType, low	0.560	0.630	0.889	0.374
log(TP):AlkalinityType, low	-0.762	0.226	-3.369	0.001

ANOVA cyanobacteria by lakes type.

Supplementary figures

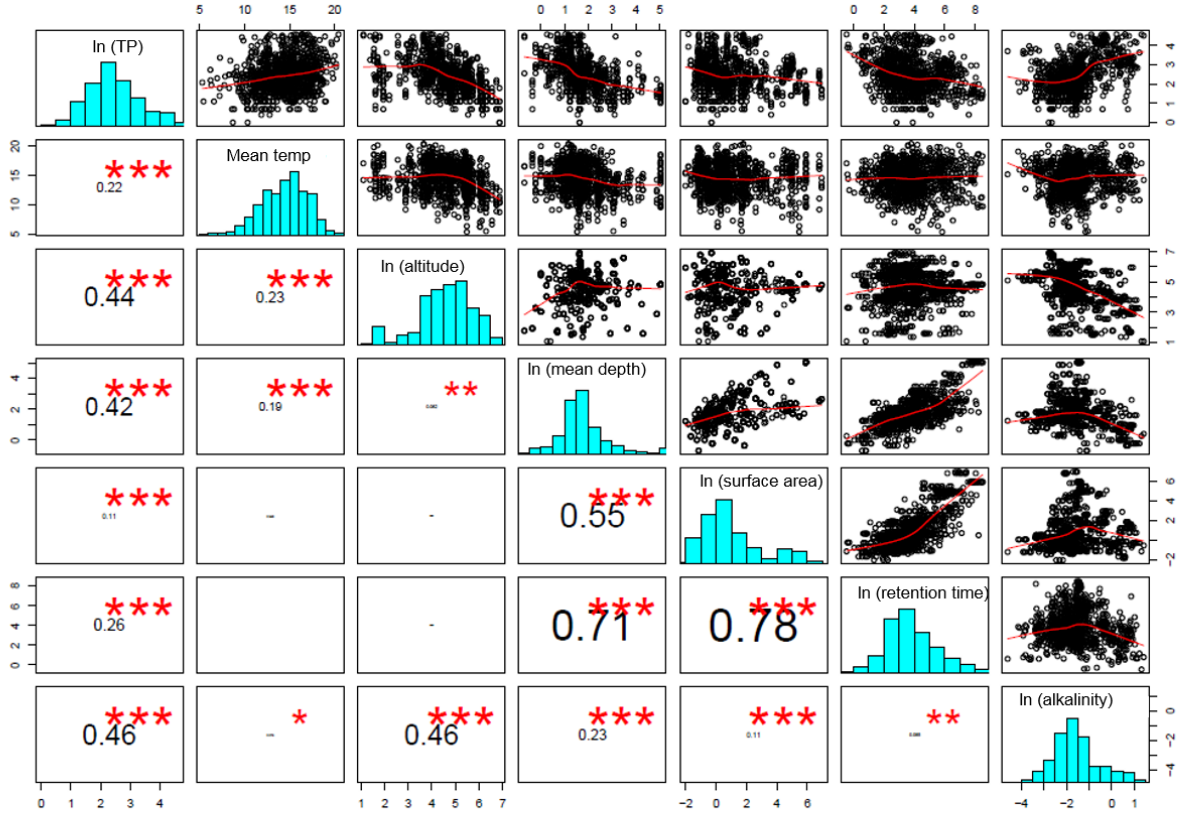


Fig. S1 Pair-wise plots showing the relationships between stressors (TP, temperature and retention time) and lake type variables (alkalinity, surface area, mean depth and altitude). The smooth red line in the upper diagonal panels shows the lowess (locally-weighted polynomial regression) fit, the middle diagonal plot shows a histograms of the distribution of the data and the lower diagonal panels shows the linear Pearson correlation coefficients – the size of the text is relative to the size of the correlation coefficient. Significance is at the 0.05 level is denoted by *, at the 0.01 level by ** and <0.001 by ***. Relationships are for lakes in which TP was ≤ 100 µg L^{-1}. Where appropriate, variables were log transformed to make the distributions more symmetric.

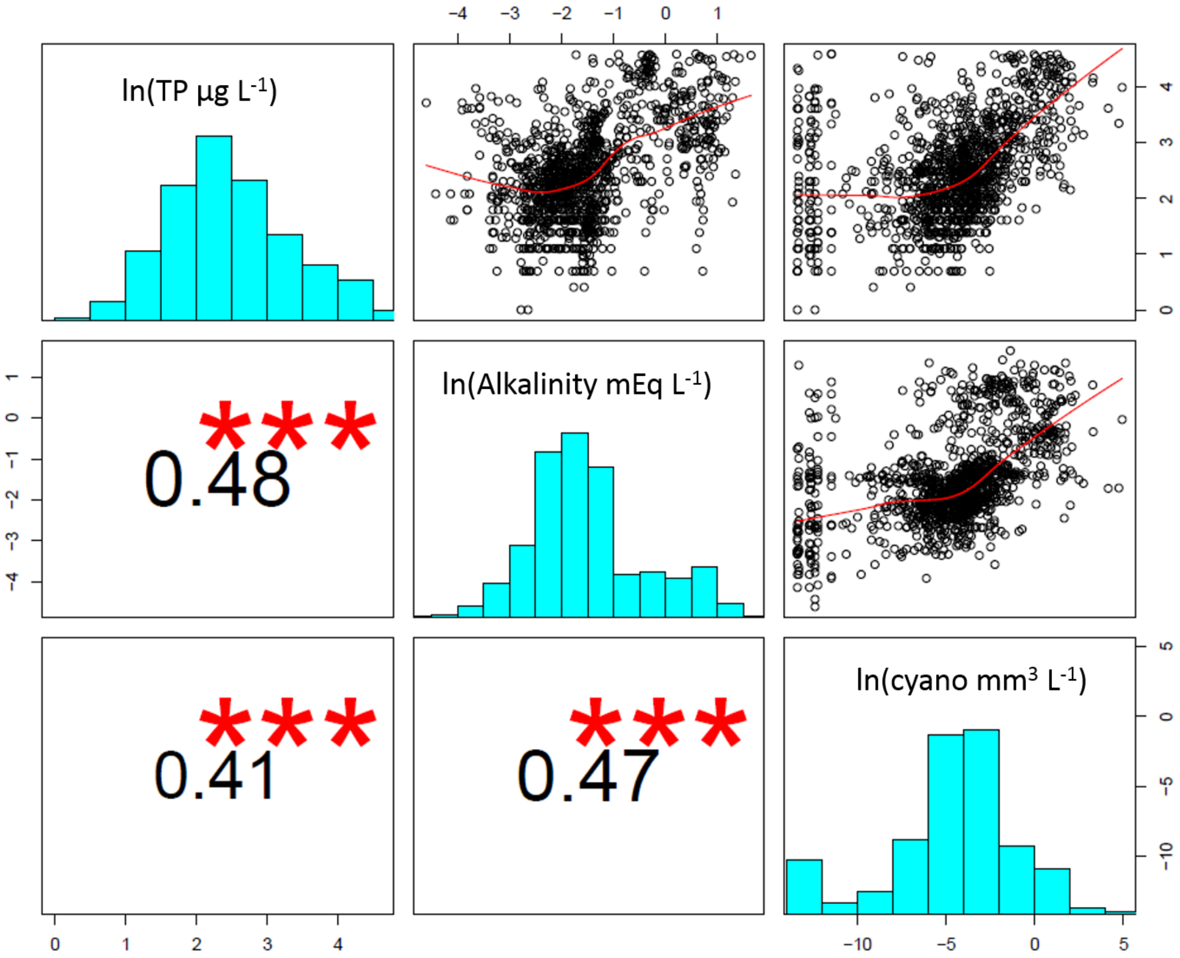


Fig. S2 Pair-wise plots showing the relationships between ln TP (µg L^{-1}), ln Alkalinity (mEq L^{-1}) and ln cyanobacteria (mm3 L^{-1}) (for 271 lakes, 1256 observations). The left horizontal panels show Pearson correlation coefficients and the p value associated with this relationship: ***, <0.001.

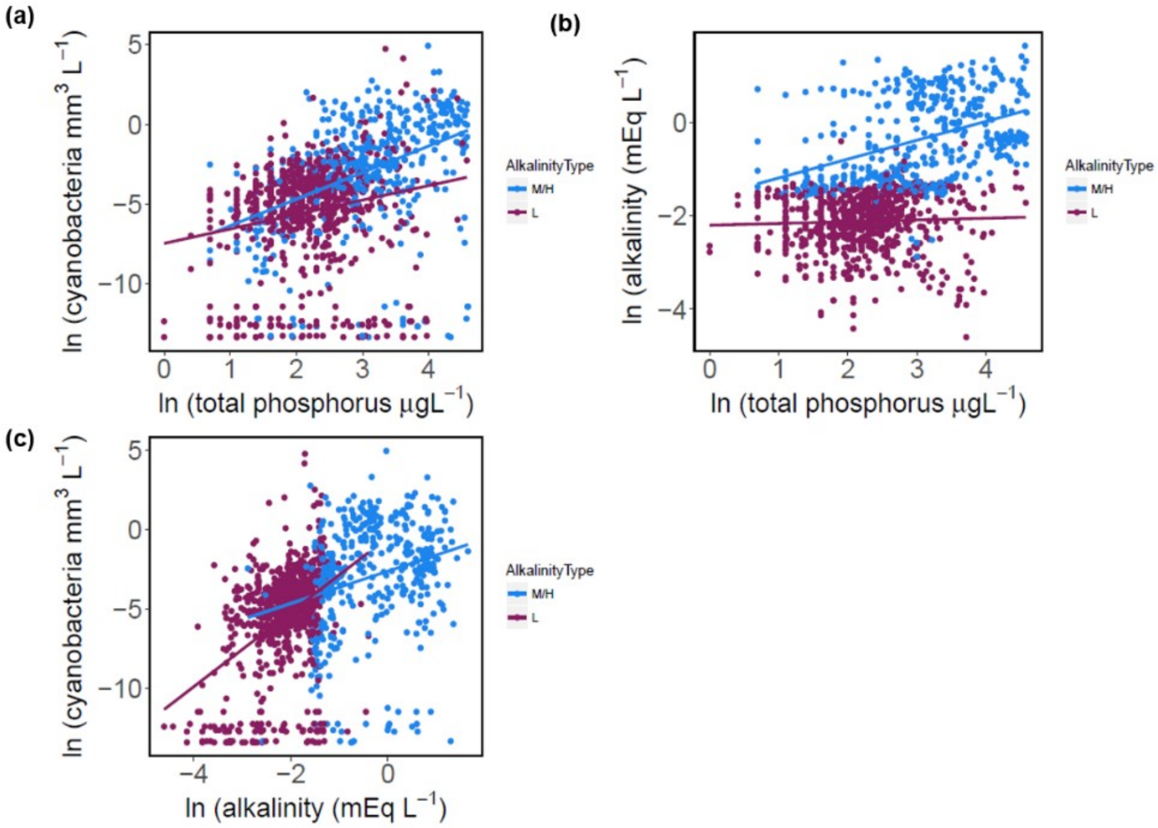


Fig. S3 (a-c). Linear relationships between cyanobacteria, alkalinity and TP in low and medium-high alkalinity lakes. In (c) alkalinity shows some overlap over low and medium-high alkalinity lakes as the types are based on an average state whereas alkalinity is for a sampling date.

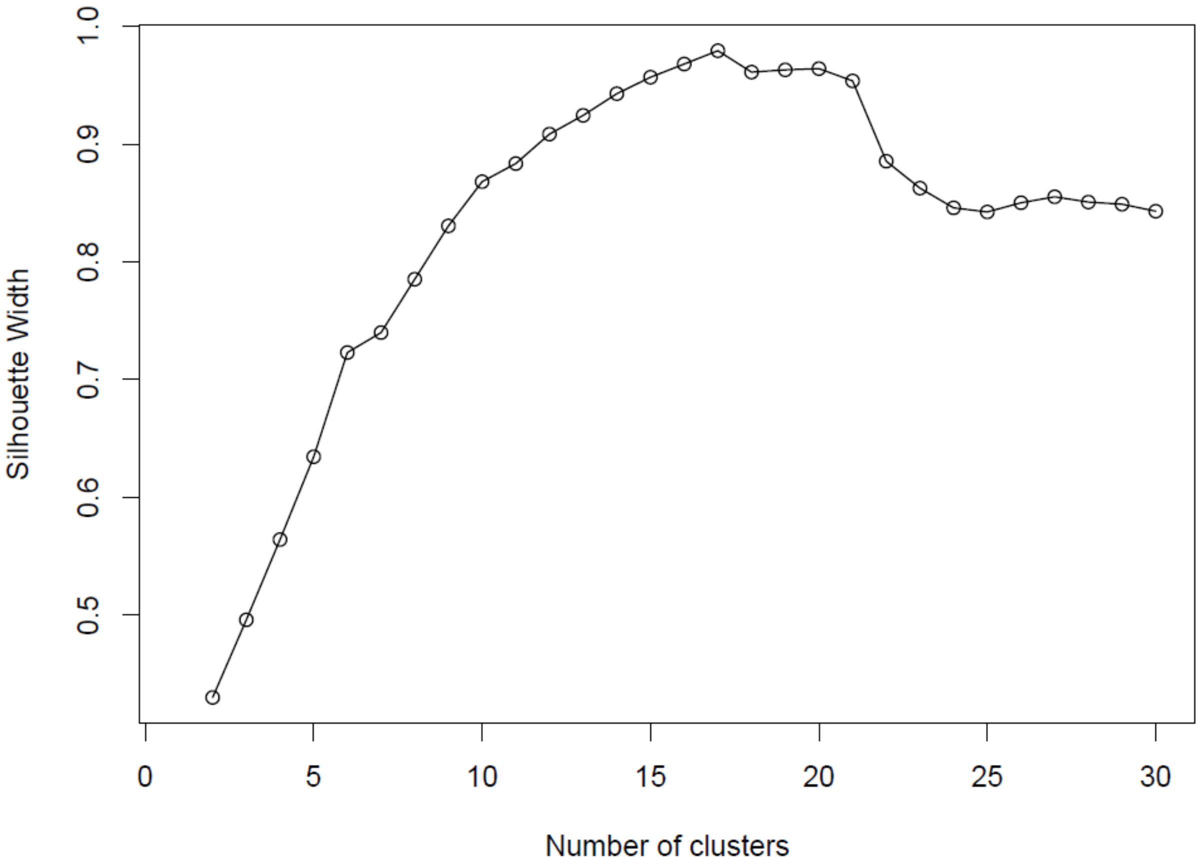
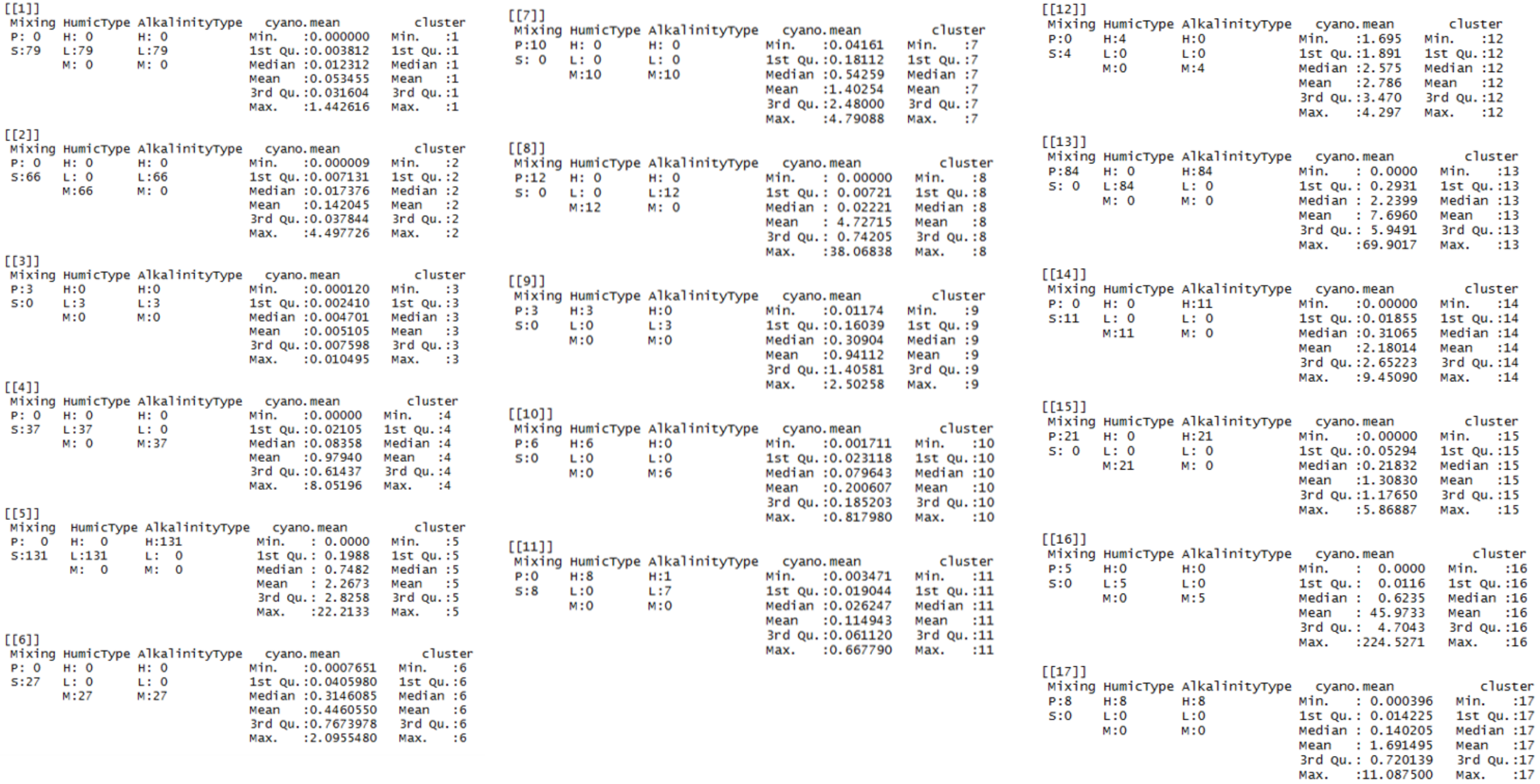


Fig. S4 Sillhoutte width for clusters ranging from 2-30 for the PAM algorithm which suggests 17 clusters, based on the highest value being the best.

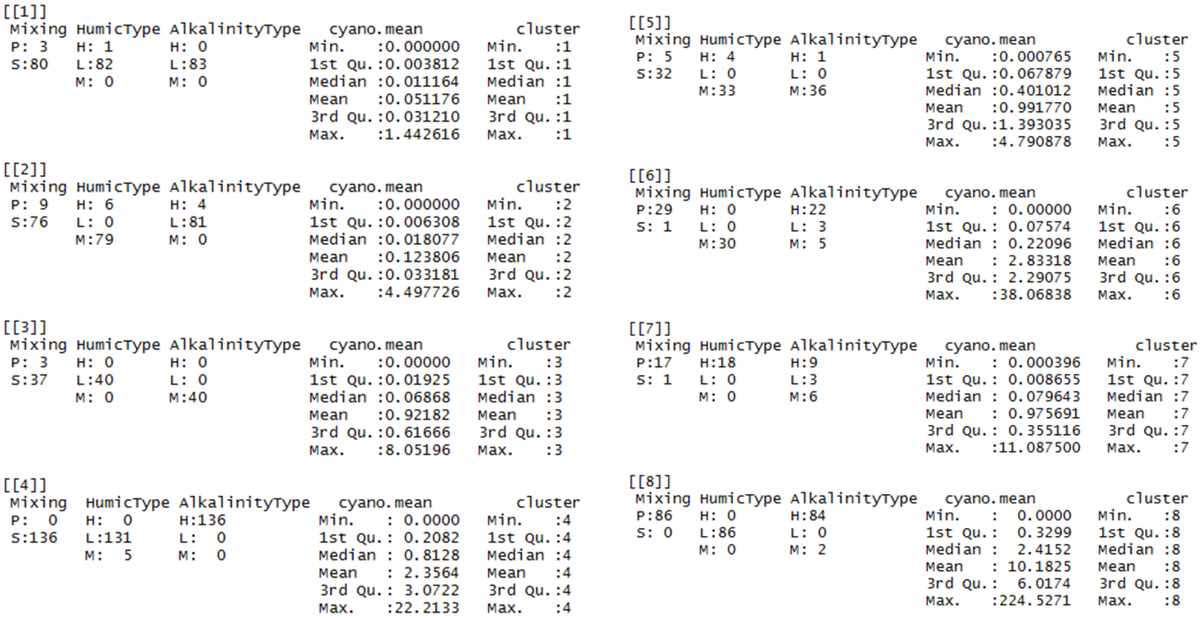


```
[[1]]
 Mixing HumicType AlkalinityType   cyano.mean         cluster
 P: 0   H: 0      H: 0           Min.    :0.000000   Min.    :1
 S:79   L:79      L:79           1st Qu.:0.003812   1st Qu.:1
        M: 0      M: 0           Median :0.012312   Median :1
                                 Mean   :0.053455   Mean   :1
                                 3rd Qu.:0.031604   3rd Qu.:1
                                 Max.   :1.442616   Max.   :1

[[2]]
 Mixing HumicType AlkalinityType   cyano.mean         cluster
 P: 0   H: 0      H: 0           Min.    :0.000009   Min.    :2
 S:66   L: 0      L:66           1st Qu.:0.007131   1st Qu.:2
        M:66      M: 0           Median :0.017376   Median :2
                                 Mean   :0.142045   Mean   :2
                                 3rd Qu.:0.037844   3rd Qu.:2
                                 Max.   :4.497726   Max.   :2

[[3]]
 Mixing HumicType AlkalinityType   cyano.mean         cluster
 P:3    H:0       H:0            Min.    :0.000120   Min.    :3
 S:0    L:3       L:3            1st Qu.:0.002410   1st Qu.:3
        M:0       M:0            Median :0.004701   Median :3
                                 Mean   :0.005105   Mean   :3
                                 3rd Qu.:0.007598   3rd Qu.:3
                                 Max.   :0.010495   Max.   :3

[[4]]
 Mixing HumicType AlkalinityType   cyano.mean        cluster
 P: 0   H: 0      H: 0           Min.    :0.00000   Min.    :4
 S:37   L:37      L: 0           1st Qu.:0.02105   1st Qu.:4
        M: 0      M:37           Median :0.08358   Median :4
                                 Mean   :0.97940   Mean   :4
                                 3rd Qu.:0.61437   3rd Qu.:4
                                 Max.   :8.05196   Max.   :4

[[5]]
 Mixing   HumicType AlkalinityType   cyano.mean         cluster
 P:  0    H:  0     H:131            Min.    : 0.0000   Min.    :5
 S:131    L:131     L:  0            1st Qu.: 0.1988   1st Qu.:5
          M:  0     M:  0            Median : 0.7482   Median :5
                                     Mean   : 2.2673   Mean   :5
                                     3rd Qu.: 2.8258   3rd Qu.:5
                                     Max.   :22.2133   Max.   :5

[[6]]
 Mixing HumicType AlkalinityType   cyano.mean           cluster
 P: 0   H: 0      H: 0           Min.    :0.0007651   Min.    :6
 S:27   L: 0      L: 0           1st Qu.:0.0405980   1st Qu.:6
        M:27      M:27           Median :0.3146085   Median :6
                                 Mean   :0.4460550   Mean   :6
                                 3rd Qu.:0.7673978   3rd Qu.:6
                                 Max.   :2.0955480   Max.   :6
```

```
[[7]]
 Mixing HumicType AlkalinityType   cyano.mean        cluster
 P:10   H: 0      H: 0           Min.    :0.04161   Min.    :7
 S: 0   L: 0      L: 0           1st Qu.:0.18112   1st Qu.:7
        M:10      M:10           Median :0.54259   Median :7
                                 Mean   :1.40254   Mean   :7
                                 3rd Qu.:2.48000   3rd Qu.:7
                                 Max.   :4.79088   Max.   :7

[[8]]
 Mixing HumicType AlkalinityType   cyano.mean          cluster
 P:12   H: 0      H: 0           Min.    : 0.00000   Min.    :8
 S: 0   L: 0      L:12           1st Qu.: 0.00721   1st Qu.:8
        M:12      M: 0           Median : 0.02221   Median :8
                                 Mean   : 4.72715   Mean   :8
                                 3rd Qu.: 0.74205   3rd Qu.:8
                                 Max.   :38.06838   Max.   :8

[[9]]
 Mixing HumicType AlkalinityType   cyano.mean        cluster
 P:3    H:3       H:0            Min.    :0.01174   Min.    :9
 S:0    L:0       L:3            1st Qu.:0.16039   1st Qu.:9
        M:0       M:0            Median :0.30904   Median :9
                                 Mean   :0.94112   Mean   :9
                                 3rd Qu.:1.40581   3rd Qu.:9
                                 Max.   :2.50258   Max.   :9

[[10]]
 Mixing HumicType AlkalinityType   cyano.mean          cluster
 P:6    H:6       H:0            Min.    :0.001711   Min.    :10
 S:0    L:0       L:0            1st Qu.:0.023118   1st Qu.:10
        M:0       M:6            Median :0.079643   Median :10
                                 Mean   :0.200607   Mean   :10
                                 3rd Qu.:0.185203   3rd Qu.:10
                                 Max.   :0.817980   Max.   :10

[[11]]
 Mixing HumicType AlkalinityType   cyano.mean          cluster
 P:0    H:8       H:1            Min.    :0.003471   Min.    :11
 S:8    L:0       L:7            1st Qu.:0.019044   1st Qu.:11
        M:0       M:0            Median :0.026247   Median :11
                                 Mean   :0.114943   Mean   :11
                                 3rd Qu.:0.061120   3rd Qu.:11
                                 Max.   :0.667790   Max.   :11
```

```
[[12]]
 Mixing HumicType AlkalinityType   cyano.mean      cluster
 P:0    H:4       H:0            Min.    :1.695   Min.    :12
 S:4    L:0       L:0            1st Qu.:1.891   1st Qu.:12
        M:0       M:4            Median :2.575   Median :12
                                 Mean   :2.786   Mean   :12
                                 3rd Qu.:3.470   3rd Qu.:12
                                 Max.   :4.297   Max.   :12

[[13]]
 Mixing HumicType AlkalinityType   cyano.mean         cluster
 P:84   H: 0      H:84           Min.    : 0.0000   Min.    :13
 S: 0   L:84      L: 0           1st Qu.: 0.2931   1st Qu.:13
        M: 0      M: 0           Median : 2.2399   Median :13
                                 Mean   : 7.6960   Mean   :13
                                 3rd Qu.: 5.9491   3rd Qu.:13
                                 Max.   :69.9017   Max.   :13

[[14]]
 Mixing HumicType AlkalinityType   cyano.mean         cluster
 P: 0   H: 0      H:11           Min.    :0.00000   Min.    :14
 S:11   L: 0      L: 0           1st Qu.:0.01855   1st Qu.:14
        M:11      M: 0           Median :0.31065   Median :14
                                 Mean   :2.18014   Mean   :14
                                 3rd Qu.:2.65223   3rd Qu.:14
                                 Max.   :9.45090   Max.   :14

[[15]]
 Mixing HumicType AlkalinityType   cyano.mean         cluster
 P:21   H: 0      H:21           Min.    :0.00000   Min.    :15
 S: 0   L: 0      L: 0           1st Qu.:0.05294   1st Qu.:15
        M:21      M: 0           Median :0.21832   Median :15
                                 Mean   :1.30830   Mean   :15
                                 3rd Qu.:1.17650   3rd Qu.:15
                                 Max.   :5.86887   Max.   :15

[[16]]
 Mixing HumicType AlkalinityType   cyano.mean           cluster
 P:5    H:0       H:0            Min.    :  0.0000   Min.    :16
 S:0    L:5       L:0            1st Qu.:  0.0116   1st Qu.:16
        M:0       M:5            Median :  0.6235   Median :16
                                 Mean   : 45.9733   Mean   :16
                                 3rd Qu.:  4.7043   3rd Qu.:16
                                 Max.   :224.5271   Max.   :16

[[17]]
 Mixing HumicType AlkalinityType   cyano.mean            cluster
 P:8    H:8       H:8            Min.    : 0.000396   Min.    :17
 S:0    L:0       L:0            1st Qu.: 0.014225   1st Qu.:17
        M:0       M:0            Median : 0.140205   Median :17
                                 Mean   : 1.691495   Mean   :17
                                 3rd Qu.: 0.720139   3rd Qu.:17
                                 Max.   :11.087500   Max.   :17
```

Fig. S5 Summary of Gower distance clustering based on 17 clusters.



```
[[1]]
 Mixing HumicType AlkalinityType   cyano.mean         cluster
 P: 3   H: 1      H: 0          Min.    :0.000000   Min.    :1
 S:80   L:82      L:83          1st Qu.:0.003812   1st Qu.:1
        M: 0      M: 0          Median :0.011164   Median :1
                                Mean   :0.051176   Mean   :1
                                3rd Qu.:0.031210   3rd Qu.:1
                                Max.   :1.442616   Max.   :1

[[2]]
 Mixing HumicType AlkalinityType   cyano.mean         cluster
 P: 9   H: 6      H: 4          Min.    :0.000000   Min.    :2
 S:76   L: 0      L:81          1st Qu.:0.006308   1st Qu.:2
        M:79      M: 0          Median :0.018077   Median :2
                                Mean   :0.123806   Mean   :2
                                3rd Qu.:0.033181   3rd Qu.:2
                                Max.   :4.497726   Max.   :2

[[3]]
 Mixing HumicType AlkalinityType   cyano.mean        cluster
 P: 3   H: 0      H: 0          Min.    :0.00000   Min.    :3
 S:37   L:40      L: 0          1st Qu.:0.01925   1st Qu.:3
        M: 0      M:40          Median :0.06868   Median :3
                                Mean   :0.92182   Mean   :3
                                3rd Qu.:0.61666   3rd Qu.:3
                                Max.   :8.05196   Max.   :3

[[4]]
 Mixing  HumicType AlkalinityType   cyano.mean         cluster
 P:  0   H:  0     H:136          Min.    : 0.0000   Min.    :4
 S:136   L:131     L:  0          1st Qu.: 0.2082   1st Qu.:4
         M:  5     M:  0          Median : 0.8128   Median :4
                                  Mean   : 2.3564   Mean   :4
                                  3rd Qu.: 3.0722   3rd Qu.:4
                                  Max.   :22.2133   Max.   :4

[[5]]
 Mixing HumicType AlkalinityType   cyano.mean         cluster
 P: 5   H: 4      H: 1          Min.    :0.000765   Min.    :5
 S:32   L: 0      L: 0          1st Qu.:0.067879   1st Qu.:5
        M:33      M:36          Median :0.401012   Median :5
                                Mean   :0.991770   Mean   :5
                                3rd Qu.:1.393035   3rd Qu.:5
                                Max.   :4.790878   Max.   :5

[[6]]
 Mixing HumicType AlkalinityType   cyano.mean         cluster
 P:29   H: 0      H:22          Min.    : 0.00000   Min.    :6
 S: 1   L: 0      L: 3          1st Qu.: 0.07574   1st Qu.:6
        M:30      M: 5          Median : 0.22096   Median :6
                                Mean   : 2.83318   Mean   :6
                                3rd Qu.: 2.29075   3rd Qu.:6
                                Max.   :38.06838   Max.   :6

[[7]]
 Mixing HumicType AlkalinityType   cyano.mean          cluster
 P:17   H:18      H:9           Min.    : 0.000396   Min.    :7
 S: 1   L: 0      L:3           1st Qu.: 0.008655   1st Qu.:7
        M: 0      M:6           Median : 0.079643   Median :7
                                Mean   : 0.975691   Mean   :7
                                3rd Qu.: 0.355116   3rd Qu.:7
                                Max.   :11.087500   Max.   :7

[[8]]
 Mixing HumicType AlkalinityType   cyano.mean         cluster
 P:86   H: 0      H:84          Min.    :  0.0000   Min.    :8
 S: 0   L:86      L: 0          1st Qu.:  0.3299   1st Qu.:8
        M: 0      M: 2          Median :  2.4152   Median :8
                                Mean   : 10.1825   Mean   :8
                                3rd Qu.:  6.0174   3rd Qu.:8
                                Max.   :224.5271   Max.   :8
```

Fig. S6 Summary of Gower distance clustering based on 8 clusters.

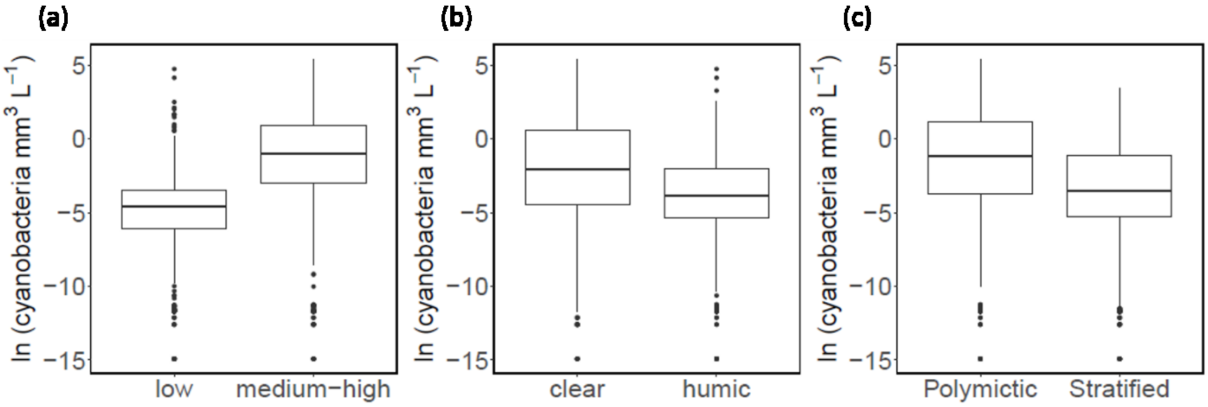
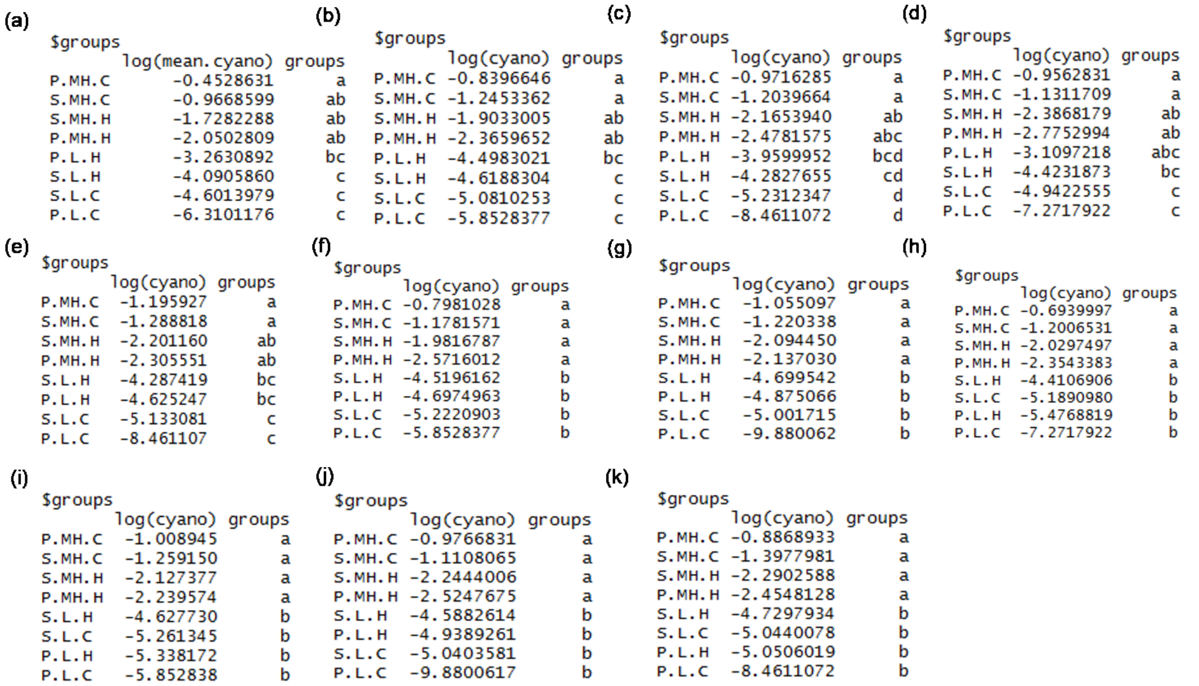


Fig. S7 Natural log cyanobacteria (mm^3 L^{-1}) by lake type variables: (a) alkalinity, low (<0.2 mEq L^{-1}) and med-high (>0.2 mEq L^{-1}); (b) humic content, clear (colour <30 mg Pt L^{-1}) and humic (colour > 30 mg Pt L^{-1}); and (c) mixing type, stratified and polymictic. The biovolume of cyanobacteria was statistically significantly different, between levels of each lake type variable: alkalinity (low *vs* med-high alkalinity, t = -22.5, df = 1574, *p*-value = <0.001); humic (clear *vs* humic, t = 7.78, df = 1579.8, *p*-value = <0.001) and mixing type (stratified *vs* polymictic, t = -7.03, df = 600.97, *p*-value = <0.001).



(a)

```
$groups
       log(mean.cyano) groups
P.MH.C      -0.4528631      a
S.MH.C      -0.9668599     ab
S.MH.H      -1.7282288     ab
P.MH.H      -2.0502809     ab
P.L.H       -3.2630892     bc
S.L.H       -4.0905860      c
S.L.C       -4.6013979      c
P.L.C       -6.3101176      c
```

(b)

```
$groups
        log(cyano) groups
P.MH.C -0.8396646      a
S.MH.C -1.2453362      a
S.MH.H -1.9033005     ab
P.MH.H -2.3659652     ab
P.L.H  -4.4983021     bc
S.L.H  -4.6188304      c
S.L.C  -5.0810253      c
P.L.C  -5.8528377      c
```

(c)

```
$groups
        log(cyano) groups
P.MH.C -0.9716285      a
S.MH.C -1.2039664      a
S.MH.H -2.1653940     ab
P.MH.H -2.4781575    abc
P.L.H  -3.9599952    bcd
S.L.H  -4.2827655     cd
S.L.C  -5.2312347      d
P.L.C  -8.4611072      d
```

(d)

```
$groups
        log(cyano) groups
P.MH.C -0.9562831      a
S.MH.C -1.1311709      a
S.MH.H -2.3868179     ab
P.MH.H -2.7752994     ab
P.L.H  -3.1097218    abc
S.L.H  -4.4231873     bc
S.L.C  -4.9422555      c
P.L.C  -7.2717922      c
```

(e)

```
$groups
       log(cyano) groups
P.MH.C  -1.195927      a
S.MH.C  -1.288818      a
S.MH.H  -2.201160     ab
P.MH.H  -2.305551     ab
S.L.H   -4.287419     bc
P.L.H   -4.625247     bc
S.L.C   -5.133081      c
P.L.C   -8.461107      c
```

(f)

```
$groups
        log(cyano) groups
P.MH.C -0.7981028      a
S.MH.C -1.1781571      a
S.MH.H -1.9816787      a
P.MH.H -2.5716012      a
S.L.H  -4.5196162      b
P.L.H  -4.6974963      b
S.L.C  -5.2220903      b
P.L.C  -5.8528377      b
```

(g)

```
$groups
       log(cyano) groups
P.MH.C  -1.055097      a
S.MH.C  -1.220338      a
S.MH.H  -2.094450      a
P.MH.H  -2.137030      a
S.L.H   -4.699542      b
P.L.H   -4.875066      b
S.L.C   -5.001715      b
P.L.C   -9.880062      b
```

(h)

```
$groups
        log(cyano) groups
P.MH.C -0.6939997      a
S.MH.C -1.2006531      a
S.MH.H -2.0297497      a
P.MH.H -2.3543383      a
S.L.H  -4.4106906      b
S.L.C  -5.1890980      b
P.L.H  -5.4768819      b
P.L.C  -7.2717922      b
```

(i)

```
$groups
       log(cyano) groups
P.MH.C  -1.008945      a
S.MH.C  -1.259150      a
S.MH.H  -2.127377      a
P.MH.H  -2.239574      a
S.L.H   -4.627730      b
S.L.C   -5.261345      b
P.L.H   -5.338172      b
P.L.C   -5.852838      b
```

(j)

```
$groups
        log(cyano) groups
P.MH.C -0.9766831      a
S.MH.C -1.1108065      a
S.MH.H -2.2444006      a
P.MH.H -2.5247675      a
S.L.H  -4.5882614      b
P.L.H  -4.9389261      b
S.L.C  -5.0403581      b
P.L.C  -9.8800617      b
```

(k)

```
$groups
        log(cyano) groups
P.MH.C -0.8868933      a
S.MH.C -1.3977981      a
S.MH.H -2.2902588      a
P.MH.H -2.4548128      a
S.L.H  -4.7297934      b
S.L.C  -5.0440078      b
P.L.H  -5.0506019      b
P.L.C  -8.4611072      b
```

Fig. S8 Similarities in ln cyanobacertia biovolume (mm3 L-1) among lake types. Groupings are from Tukey test's for multiple comparison following an ANOVA (Table S3): (a) are groupings from a comparison of mean cyanobacteria for each lake, (b-k) are groupings based on one observation selected per lake (to meet the assumptions of independence), these were randomly selected 10 times.

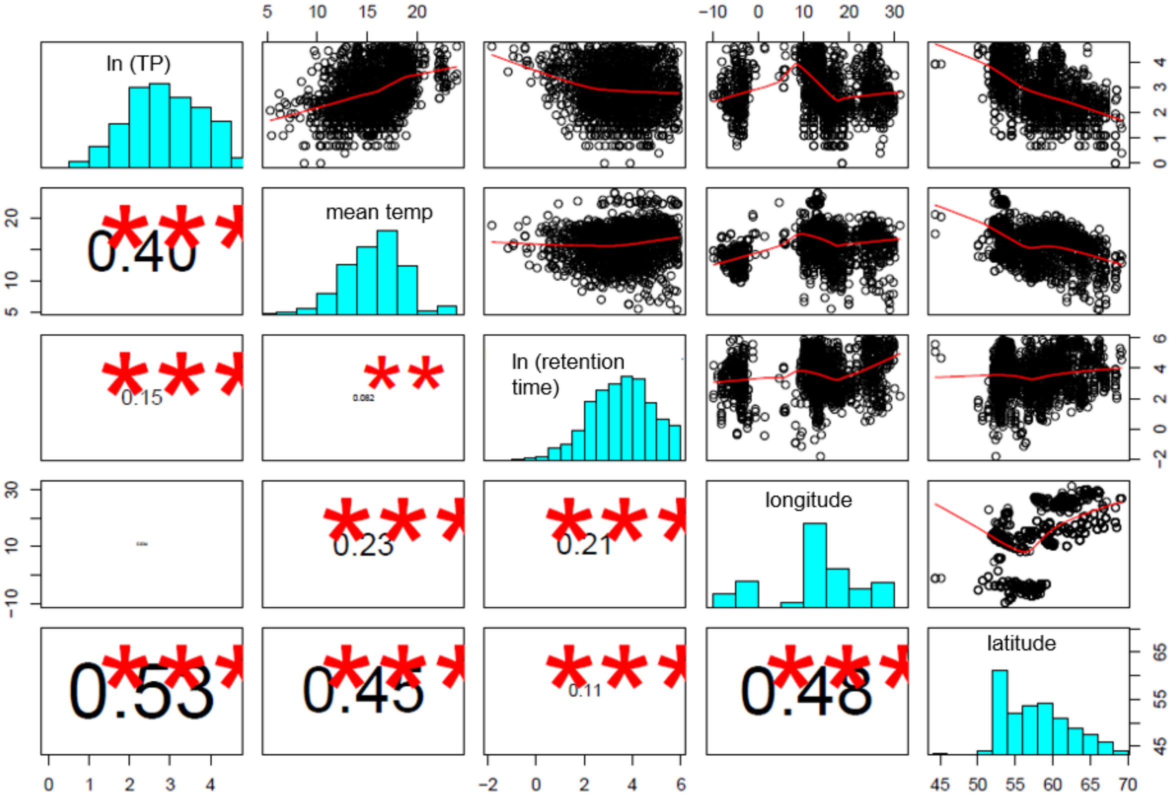


Fig. S9 Relationships between stressors (TP, temperature and retention time), longitude and latitude. The smooth red line in the upper diagonal panels shows the lowess (locally-weighted polynomial regression) fit, the middle diagonal plot shows a histograms of the distribution of the data and the lower diagonal panels shows the linear Pearson correlation coefficients – the size of the text is relative to the size of the correlation coefficient. Significance is at the 0.05 level is denoted by *, at the 0.01 level by ** and <0.001 by ***. Relationships are for lakes in which TP was ≤ 100 μg L^{-1} and retention time was ≤365 days. Where appropriate, variables were log transformed to make the distributions more symmetric. Note that a constant was added to percentage arable land so that the data could be log transformed, as many of the data

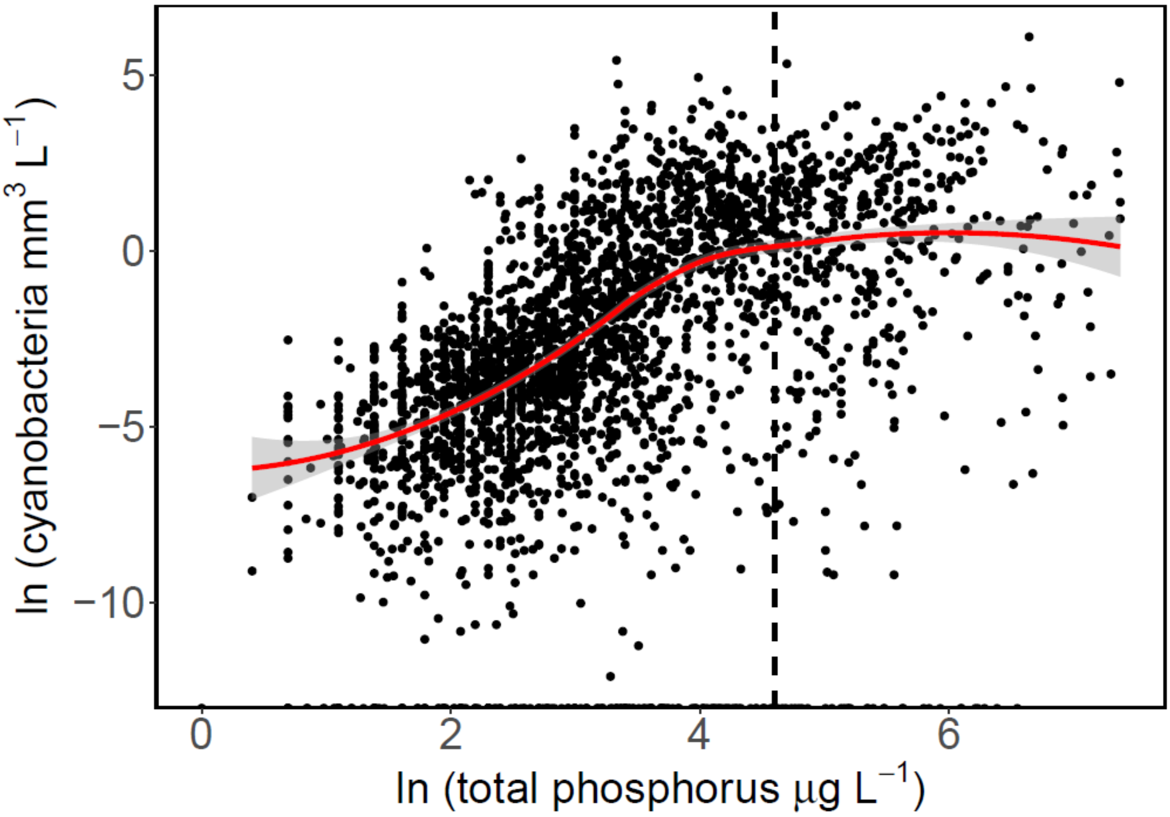


Fig. S10 Relationship between average monthly natural log cyanobacteria biovolume (mm^3 L^{-1}) and average monthly ln total phosphorus (μg L^{-1}) using the global dataset (n = 572 lakes, number of monthly observations = 2900). The red curve shows the smoothed area response of cyanobacteria. Smoothing was fitted using locally weighted polynomial regression (LOESS), the grey shaded area shows 95% confidence intervals. The dashed black line shows the TP concentration which we restricted the regression analysis to (≤100 μg L^{-1}).

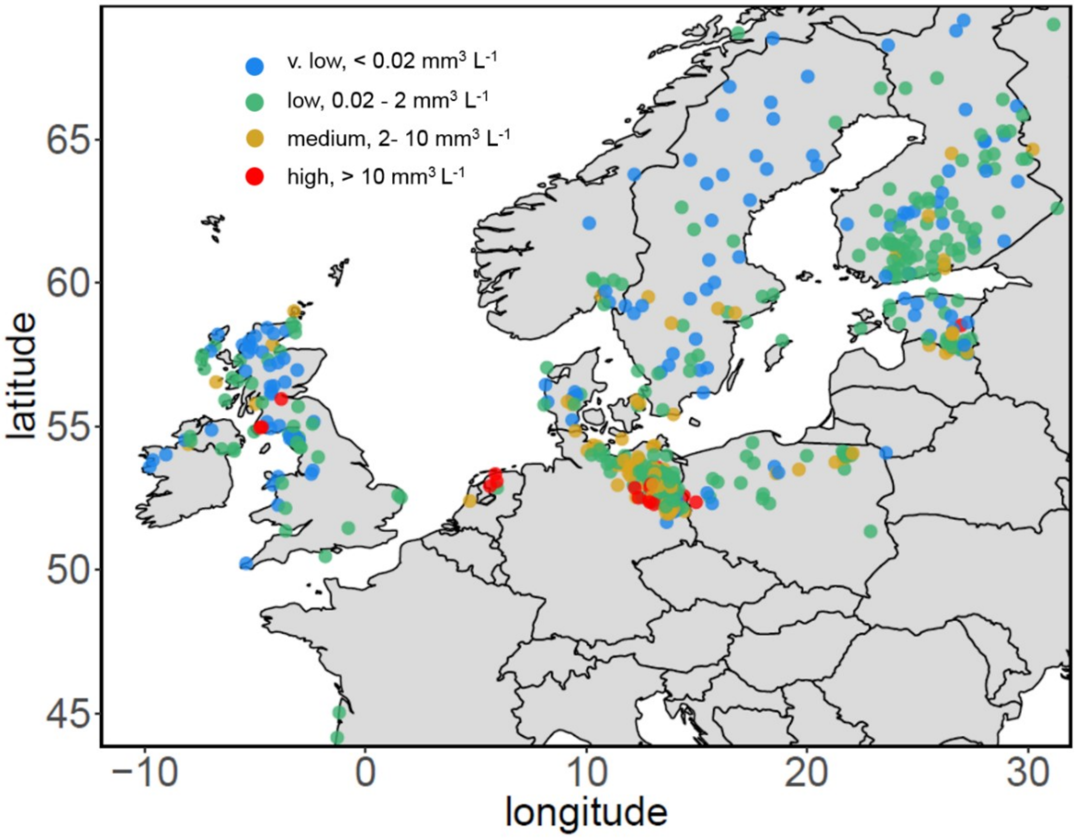


Fig. S11 Categories of average cyanobacteria biovolume (mm^3 L^{-1}) in lakes included in the study (n = 494). Categories are based on World Health Organisation (WHO) recommended threshold values for drinking and bathing (Chorus & Bartram, 1999).

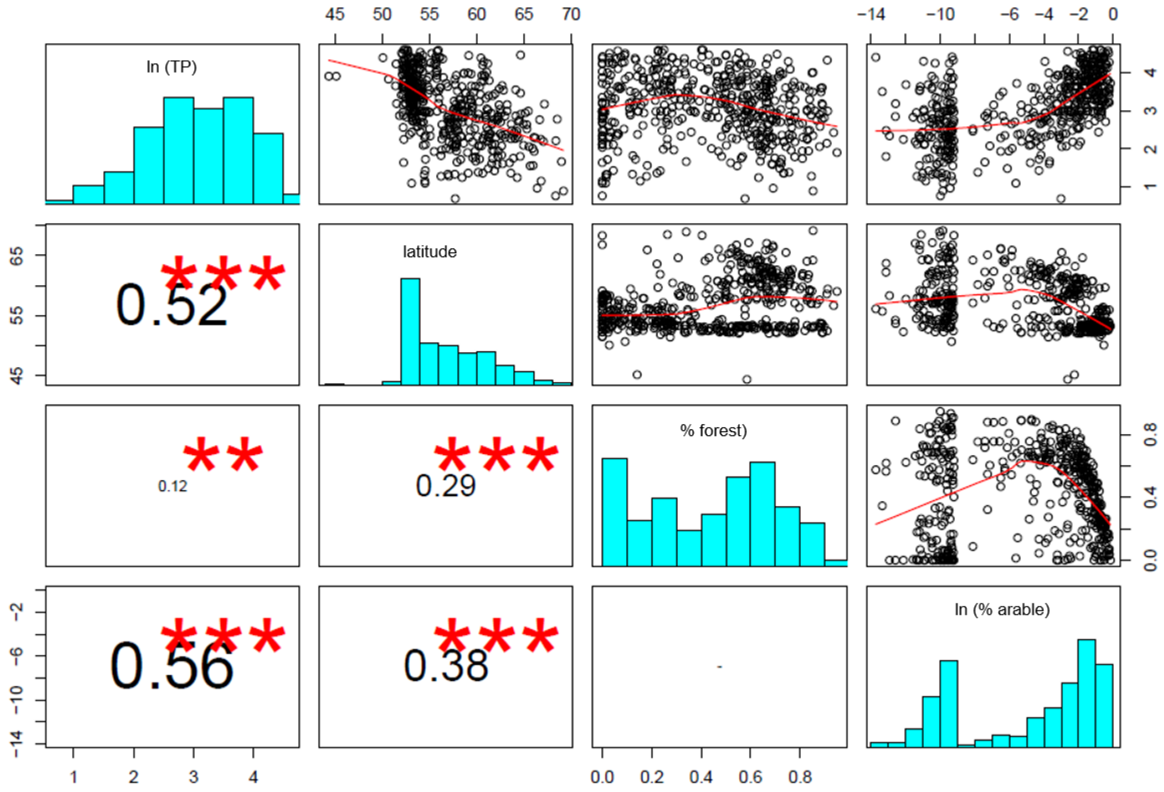


Fig S12. Relationships between TP, latitude, percent catchment forest land cover and percent catchment arable land cover. The smooth red line in the upper diagonal panels shows the lowess (locally-weighted polynomial regression) fit, the middle diagonal plot shows a histograms of the distribution of the data and the lower diagonal panels shows the linear Pearson correlation coefficients – the size of the text is relative to the size of the correlation coefficient. Significance is at the 0.05 level is denoted by *, at the 0.01 level by ** and <0.001 by ***. Relationships are for lakes in which TP was ≤ 100 µg L^{-1} and retention time was ≤365 days. Where appropriate, variables were log transformed to make the distributions more symmetric. Note that a constant was added to percentage arable land so that the data could be log transformed, these were sampled from a random generation of data from the distribution of percentage arable land data.

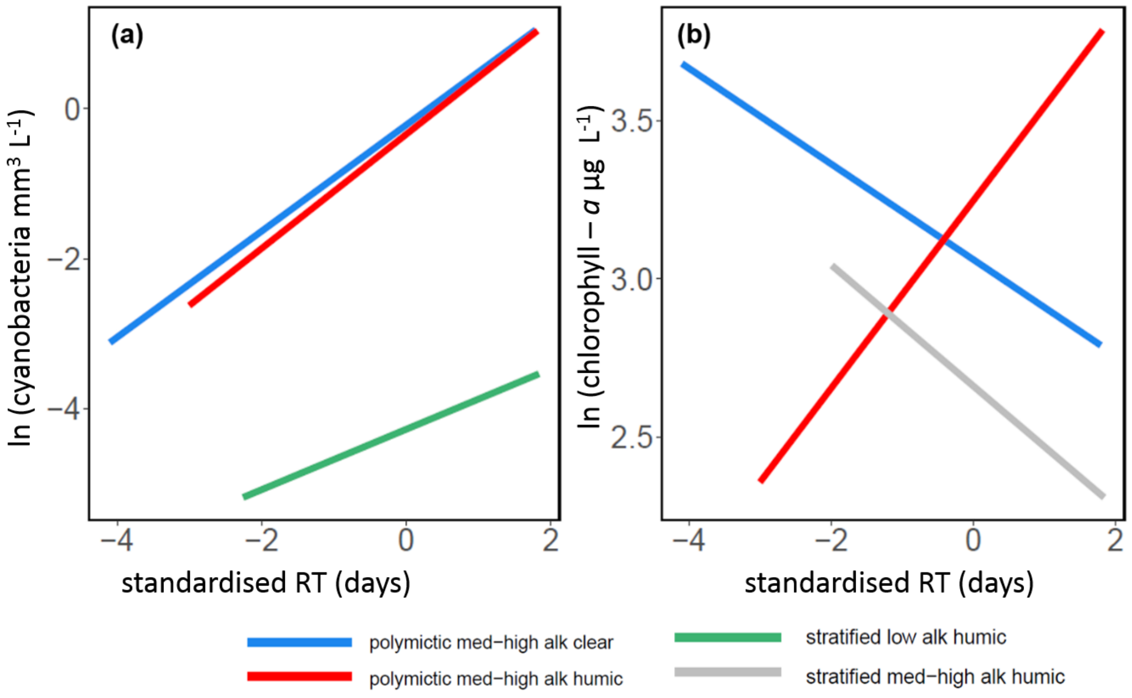
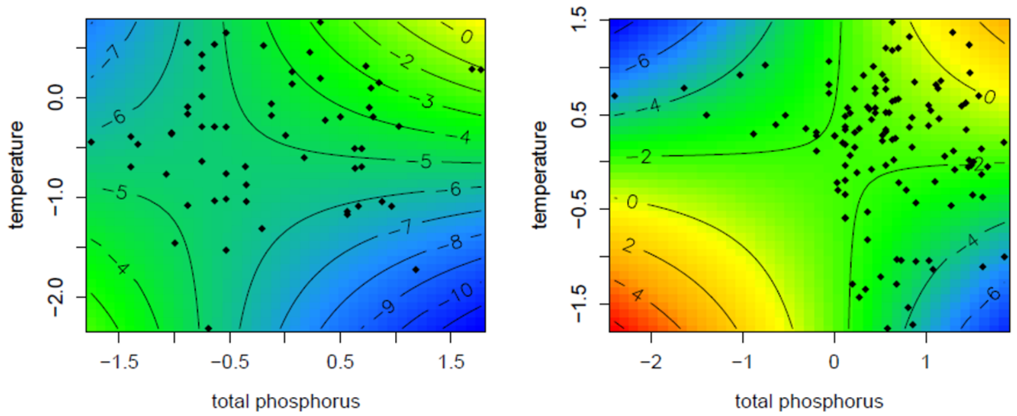
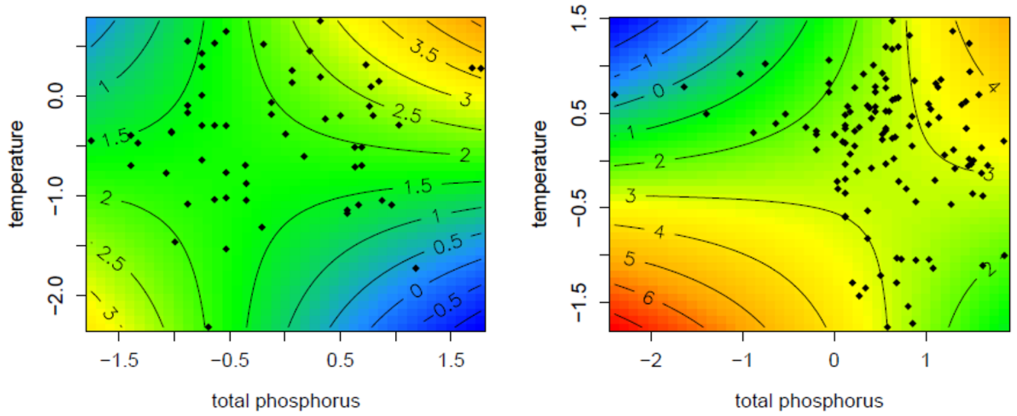


Fig. S13 The effect of retention time on (a) ln cyanobacteria biovolume (mm3 L-1) and (b) ln chlorophyll a (µg L-1) for the lake types which retention time effects were statistically significant. The effects of retention time are fitted from the models presented in Table 2, keeping temperature and TP constant (for models where this applies). Retention time (days) is standardised (mean centred and divided by the standard deviation).



(a) cyanobacteria, low alkalinity

(b) cyanobacteria, med−high alkalinity



(c) chlorophyll, low alkalinity

(d) chlorophyll, med−high alkalinity

Fig. S14 Response of ln cyanobacteria biovolume (mm3 L-1) and ln chlorophyll a (µg L-1) to the interaction between standardised temperature (°C), and standardised total phosphorus (µg L^{-1}) in polymictic, low alkalinity humic lakes (a and c) and polymictic medium-high alkalinity humic lakes (b and d). Temperature and total phosphorus are standardised (mean centred and divided by their standard deviation). Contour lines show the range of the response, colours show comparative differences: cooler colours are lower responses, warmer colours are higher responses. Points show the underlying data driving the model.

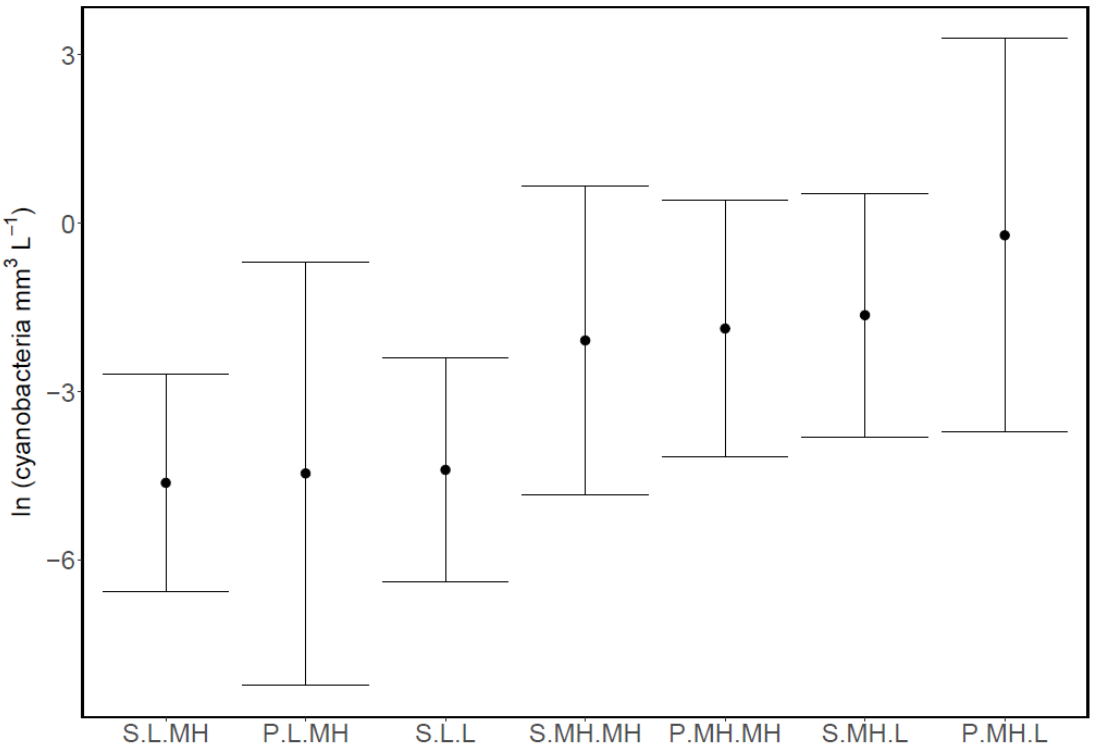


Fig. S15 Variance of the random effect for each lake type model. The point shows the intercept for each model and lake types are ordered from lowest to highest intercept. S.L.MH, stratified, low alkalinity, humic; P.L.MH, polymictic, low alkalinity, humic; S.L.L, stratified, low alkalinity, clear; S.MH.MH, stratified, medium-high alkalinity, humic; P.MH.MH, polymictic, medium-high alkalinity, humic; S.MH.L, stratified, medium-high alkalinity, clear; P.MH.L, polymictic, medium-high alkalinity, clear.

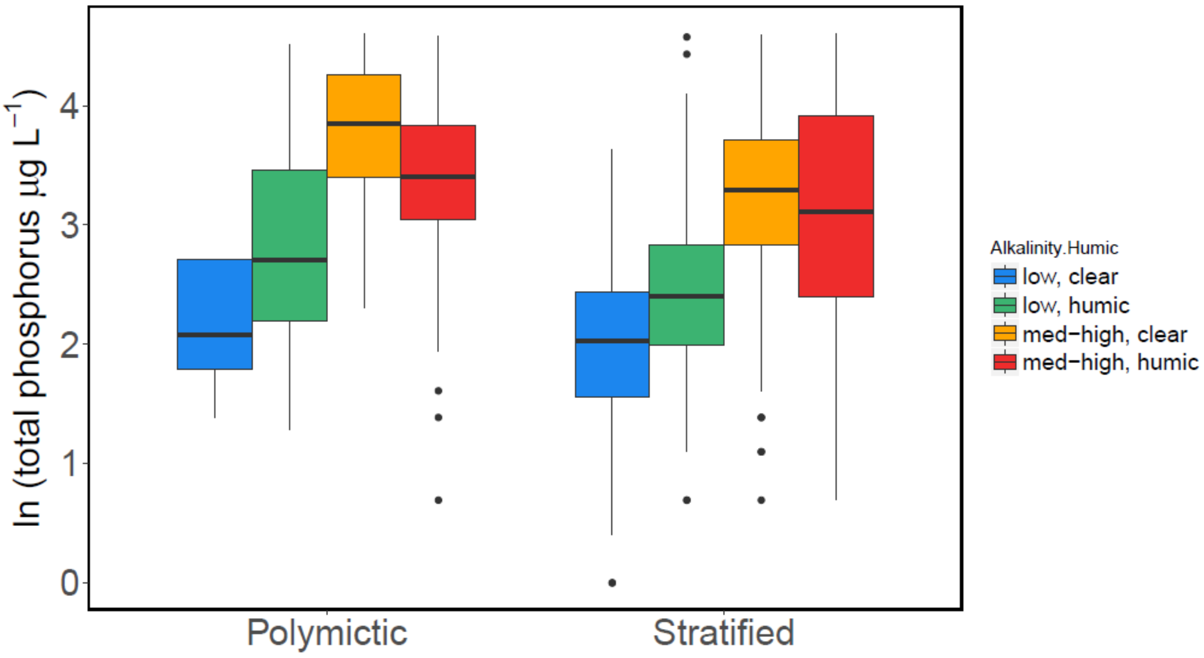


Fig. S16 Natural log total phosphorus (µg L-1) by lake type. Lake type are combinations of: alkalinity, low (<0.2 mEq L-1) and med-high (>0.2 mEq L-1); humic content, clear (colour <30 mg Pt L-1) and humic (colour > 30 mg Pt L-1); and mixing type, stratified and polymictic.