

Nutrients and not temperature are the key drivers for cyanobacterial biomass in the Americas

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ARTICLE INFO

Editor Dr A Willis

Keywords:

Eutrophication
Blooms
Global gradients
Freshwater
Climate change

ABSTRACT

Cyanobacterial blooms imperil the use of freshwater around the globe and present challenges for water management. Studies have suggested that blooms are triggered by high temperatures and nutrient concentrations. While the roles of nitrogen and phosphorus have long been debated, cyanobacterial dominance in phytoplankton has widely been associated with climate warming. However, studies at large geographical scales, covering diverse climate regions and lake depths, are still needed to clarify the drivers of cyanobacterial success. Here, we analyzed data from 464 lakes covering a 14,000 km north-south gradient in the Americas and three lake depth categories. We show that there were no clear trends in cyanobacterial biomass (as biovolume) along latitude or climate gradients, with the exception of lower biomass in polar climates. Phosphorus was the primary resource explaining cyanobacterial biomass in the Americas, while nitrogen was also significant but particularly relevant in very shallow lakes (< 3 m depth). Despite the assessed climatic gradient water temperature was only weakly related to cyanobacterial biomass, suggesting it is overemphasized in current discussions. Depth was critical for predicting cyanobacterial biomass, and shallow lakes proved more vulnerable to eutrophication. Among other variables analyzed, only pH was significantly related to cyanobacteria biomass, likely due to a biologically mediated positive feedback under high nutrient conditions. Solutions toward managing harmful cyanobacteria should thus consider lake morphometric characteristics and emphasize nutrient control, independently of temperature gradients, since local factors are more critical – and more amenable to controls – than global external forces.

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1. Introduction

Over six billion people may face significant limitations in accessing clean water in the next 30 years (Boretti and Rosa 2019). Cyanobacterial blooms and their toxins may compromise drinking water supplies, as well as other water-related economic and recreational human activities in many freshwaters worldwide (Huisman et al., 2018). Increases in the frequency of cyanobacterial blooms suggest interactions between eutrophication, the effects of climate change, geographic location, and individual water body characteristics, generating complex scenarios for management (Ho et al., 2019). Any future changes in the abundance of cyanobacteria will depend on these conditions, their interactions, and how they may vary between climatic regions, thus challenging our ability to forecast and control blooms.

For decades, it has been accepted that nutrient enrichment leads to eutrophication and a consequent increase in cyanobacterial biomass (Schindler 1977; Downing et al., 2001). In this context, the relative roles of phosphorus and nitrogen – the primary limiting nutrients of algal growth – have been the subject of scientific debate (Paerl et al., 2016b; Schindler et al., 2016). Historically, programs seeking to manage nuisance phytoplankton biomass have aimed to control phosphorus alone (the “P-only” paradigm) (Schindler et al., 2008), although other studies have suggested the need to also control nitrogen (dual-nutrient control) (Smith et al., 2016). The rising use of nitrogen-rich fertilizers in recent decades has led to significant increases in nitrogen loading in freshwater ecosystems (Glibert et al., 2014), with an associated increase in total nitrogen/total phosphorus (TN/TP) ratios and consequences for population growth and blooms (Downing and McCauley 1992; Peñuelas et al., 2013; Glibert 2020). Nitrogen and phosphorus dynamics can also vary between broad geographical regions, generating different scenarios for cyanobacteria (Smith 1983; Reichwaldt and Ghadouani 2011). Studies that encompass broad geographic gradients are therefore critical for elucidating the relative roles of each nutrient in controlling the abundance and dominance of cyanobacteria in global freshwaters (Jeppesen et al., 2014).

As anthropogenic global warming has intensified, it has become common to implicate rising temperatures as a cause of increasing cyanobacteria success (Izaguirre et al., 2015; Huisman et al., 2018). While optimal cyanobacterial growth rates are generally found at temperatures above 25 °C (Roberts and Zohary 1987; Reynolds 2006), cyanobacteria may also succeed at low temperatures (< 12 °C) (Konopka and Brock 1978; Ma et al., 2016). In tropical regions, seasonal rain patterns appear to be more critical than temperature as drivers of cyanobacterial abundance (Soares et al., 2008; Castro Medeiros et al. 2015; Giani et al., 2020), while in temperate climates, changes in precipitation regimes may favor shifts from clear to turbid water phases dominated by cyanobacteria (Reichwaldt and Ghadouani 2011). However, even low temperatures in polar climate lakes do not prevent blooms (Taranu et al., 2015; Sivarajah et al., 2021). Despite this, temperature exerts control over the duration of water column stratification and stability in lakes deep enough to stratify, which, in turn, influences light and nutrient availability for phytoplankton growth. Present and future climate change may also favor cyanobacterial blooms in shallow lakes, due to the increase in storm events which accelerate the availability of nutrients from the sediment to the water column, although opposite trends may be expected in deep lakes in certain cases (Chorus et al., 2021). Shifts in precipitation and hydrological regimes, predicted for the future, may affect the physical mixing dynamics generating effects that are largely analogous to nutrient enrichment, thus promoting blooms (Winder 2012; Jeppesen et al., 2014). Moreover, all of these conditions interact, creating complex, challenging scenarios for the prediction of cyanobacterial blooms.

Successful management of harmful cyanobacteria requires improved predictions, for which a greater number of field studies are needed (Mellios et al., 2020). Analyses at broad spatial scales have shown the importance of lake morphometry, type, and climate, as well as their

interactions, for cyanobacterial dynamics (Abell et al., 2010; Kosten et al., 2012). However, with few exceptions, studies have historically focused on the north temperate regions, and our knowledge of bloom processes in warm climates is limited (Kosten et al., 2012; Mowe et al., 2015; Ndlela et al., 2016; Giani et al., 2020). Although by any measure the majority of lakes is found in the north temperate zone (Lehner and Döll 2004), human access to freshwater and threats to its uses are a fundamentally local issue and >71% of the world's population lives in the tropics and subtropics (34°S – 34°N) (Center for International Earth Science Information Network - CIESIN 2018). As such, understanding current processes in warm-climate lakes is highly relevant to protecting the water resources of the majority of Earth's population (Rodell et al., 2018), but also could provide essential insights into future dynamics in temperate regions under warming scenarios. In order to better understand the relative importance of the environmental drivers of cyanobacterial distribution and expansion, there is thus a need for studies at large geographical scales, covering diverse climate regions.

Spanning 14,000 km from north to south and home to a billion inhabitants, the Americas represent 28% of the Earth's land surface and a critical global freshwater reserve (Oki and Kanae 2006). The region, however, is no exception to the multiple challenges related to freshwater quality and cyanobacterial blooms worldwide (Rodell et al., 2018; IANAS 2019). Diverse conditions, including five climate zones from equatorial to polar and trophic status from ultraoligotrophic to hyper-eutrophic, present an excellent opportunity to study conditions affecting water quality at broad spatial scales. We assembled a comprehensive database of 464 lakes with a gradient of over 135° of latitude from Tierra del Fuego, Argentina (54°51'S) to Ellesmere Island, Canada (82°54'N), including very shallow to deep lakes, to examine the role of nutrients, temperature, and other factors (i.e., pH, area, depth and elevation) in the distribution of cyanobacteria at the hemispheric scale.

2. Material and methods

2.1. Data

Since we sought to capture the large-scale forces that influence cyanobacterial biomass distribution, the lakes included in the study cover an extensive range of sizes, depths and elevations, as well as trophic conditions (Table S1). We assembled a database from unpublished and published data and the publicly available USEPA-NLA 2012 field campaign (U.S. Environmental Protection Agency, USEPA; National Lake Assessment, NLA) (Table S2). For each lake, we compiled morphometric data (area and depth), elevation, coordinates (latitude and longitude), origin (natural vs. artificial), and climate type. We selected ecologically relevant and commonly measured limnological variables to maximize geographic diversity in the dataset: water temperature, conductivity, pH, total nitrogen (TN), and total phosphorus (TP). To evaluate cyanobacterial trends, we used biomass (measured as total cyanobacterial biovolume; CYA_{BM}) as the response variable.

Identification, counting, and water chemistry analyses followed standard techniques to assure data quality, including a pronounced emphasis on consistency in sampling and analytical procedures, despite some minor variation among the 13 laboratories involved in the survey (Tables S3 and S4). All samples were taken following routine limnological protocols from the subsurface (about 50 cm depth) of the lake, using an integrating sampler for the euphotic zone (1.5 m long tube) or up to the first 5 m of the water column. Lakes in the United States were sampled once or twice during summer 2012. For the remaining lakes, 40% of the samples were taken in summer, 44% in spring or autumn, and 16% in winter, not including tropical samples where low temperature fluctuation precludes such classification. Tropical lake data were mainly sampled from August to November and in March, including the rainy and the dry seasons. Arctic and Patagonian lakes were sampled in late spring or early summer when water columns were generally well mixed and most warm temperate lakes were sampled over entire annual

cycles. Lakes were sampled between 2000 and 2018, except those from the United States data base (2012, see above) and 7 tropical lakes (sampled from 1995 to 1999). The relationships between the explanatory variables and the response variable are assumed to be independent of the calendar year. In most cases one (68% of the total) or 2 – 8 sampling data per lake were used in the analysis. Phytoplankton samples were identified to the lowest possible taxonomic level (species or genus) using optical microscopes; individuals (cells, filaments, colonies) were counted with routine protocols, and biovolume was calculated based on morphometric measurements of the organisms (cells or individuals) (details in Table S4).

We classified lake climates according to the Köppen-Geiger system (Rubel and Kottek 2010) which identifies five major categories: equatorial (A: tropical, fully humid, summer or winter dry), arid (B: desert and steppe), warm temperate (C: dry to humid, summer hot to cool, coldest average month from 0 to 18 °C), boreal (D: dry to humid, at least one month below 0 °C) and polar (E: including tundra and ice cap climate). To balance the dataset between the continent's five major climates, we randomly subsampled each climatic region in the United States NLA database (Table S5) following Tillé & Matei (2021), thus selecting a total of 237 of the 1050 lakes that this includes (Table S1): warm temperate (150 lakes), boreal (99 lakes), arid (99), equatorial (94) and polar (31). The final database (total $n = 820$ samples), with all selected lakes in the Americas (464 lakes), was distributed almost equally between natural and artificial water bodies (Table S1). Using the average maximum depth of each water body, we classified the lakes in three depth categories following Phillips et al. (2008), named shallow (< 3 m depth), intermediate (Interm., 3 to 15 m) and deep (> 15 m). We used total phosphorus and followed the classification of (Carlson 1977) for discussions of trophic status.

2.2. Statistical analysis

2.2.1. Exploratory analysis

To linearize the relation between variables and to improve model fit, the independent variables (area, elevation, depth, TN and TP) and the response variable CYA_{BM} were ln-transformed ($\ln(x + x_{\min}/2)$ for CYA_{BM}). We constructed conditional inference trees (CIT), a robust exploratory method for observing the association between a single response variable and multiple explanatory variables, to better visualize the main variables explaining cyanobacterial biovolume. We used the environmental variables water temperature, pH, area, depth, elevation, TP and TN, and depth category (Shallow, Interm. and Deep), with CYA_{BM} as the outcome variable.

2.2.2. Linear mixed models

We constructed a series of linear mixed models (LMM) to assess the relative importance of area, elevation, depth category, water temperature, pH, and nutrients (TN, TP) for CYA_{BM} (cyanobacterial biovolume > 0). The variable “lakes” was included as a random effect representing intrinsic between-lake variation not captured by the fixed variables, increasing the model's explanatory power (Harrison et al., 2018). Prior to the analysis, variance inflation factors were tested and all numeric variables were centered and standardized ($x - \text{mean}/\text{sd}$), to make the size effect of each variable comparable within models. LMMs were run following a backward selection for the fixed variables and their interactions according to the starting model:

$$y = \beta_0 + \beta_1 X_{\text{Area}} + \beta_2 X_{\text{Elev}} + \beta_3 X_{\text{depth.category}} + \beta_4 X_{\text{Temp}} + \beta_5 X_{\text{pH}} + \beta_6 X_{\text{Cond}} + \beta_7 X_{\text{Total P}} + \beta_8 X_{\text{Total N}} + \beta_{9-13} X_{\text{(interaction)}} + \delta_{\text{lake}} + \varepsilon$$

$$y \sim (0, \sigma_{21}), \varepsilon \sim (0, \sigma_{21})$$

where y is the transformed response variable (CYA_{BM}); β_0 is the intercept; $\beta_1 - \beta_9$ are the model parameters for the fixed variables (area, elevation, conductivity, TP and TN, which were ln transformed; and

depth category, temperature, and pH to which no transformation was applied). $\beta_9 - \beta_{13}$ are the parameters for the tested interactions (temperature*TP, temperature*TN, pH*TP, pH*TN and TP*TN; nutrients in ln); δ is the random effect (lake), and ε is the model error (δ and ε with unknown variance and mean = 0). Residual distribution and kurtosis were analyzed and the significance of the models tested. Subsequent LMMs were run and compared using the Bayesian information criterion (BIC) until the best model was obtained.

The interaction between variables was tested, and the significance of models with and without interaction was compared. The significance of random effects was also tested. Finally, the proportion of the variance explained by the fixed effects (marginal R^2) and by the fixed and random effects together (conditional R^2) was calculated. Prior tests and evaluation of the models are described in Supplementary Material (Table S5). Since the depth is a relevant factor that can influence the cyanobacterial biomass response to nutrient increase, we further explored the interaction between nutrients (TP and TN) and depth category in two LMMs with two terms, one nutrient (Log TP or Log TN) and one interaction in each model (Depth category*Log TP or Depth category*Log TN, respectively), with the same random effect as previously used.

2.2.3. Piecewise linear regression models

To further explore the cyanobacterial biomass response to nutrients, we fitted a series of linear and piecewise linear regression models between the transformed response variable (Cyanobacterial biovolume) and TP (CYA_{BM}/TP) under two conditions of TN for each lake category (shallow, intermediate and deep). The median TN value of the whole dataset was used to delimit the two TN groups (low $\leq 0.7 \text{ mgL}^{-1}$ > high). The piecewise linear regression was used to detect breakpoints (threshold values where the slope changed) (Davies 1987; Muggeo 2003) in the CYA_{BM}/TP slope (data ln-transformed) according to:

$$y_i = \beta_0 + \beta_1 xTP + \beta_2 (xTP - bp)x_{i2} + \varepsilon_i$$

Where y_i is the ln-transformed response variable (CYA_{BM}) for the depth category i (shallow, intermediate or deep); β_0 is the intercept, β_1 and β_2 are the slopes; x_{i2} is a dummy variable (0, if $xTP < bp$ and 1 if $xTP \geq bp$); bp is the breakpoint defined as the value of the independent variable (TP) where the slope change and ε_i is the independent error. For each lake depth category and TN level the piecewise regression was compared and evaluated to a simple linear regression with r^2 and ANOVA.

All analyses, tables, and figures were carried out or produced in the R programming environment (version 3.5.3). The functions and libraries used for each analysis are shown in Table S5.

3. Results

3.1. General trends in environmental features and cyanobacterial distribution

There were no evident trends in cyanobacterial biomass (CYA_{BM}) with latitude or climate, apart from lower values at both extremes of the latitudinal gradient, particularly at latitudes above 50°N (Figs. 1 and 2). Very high values ($> 500 \text{ mm}^3\text{L}^{-1}$) were found at intermediate latitudes in both the northern and southern hemispheres ($\sim 30 - 40^\circ\text{S}$ and $\sim 40 - 50^\circ\text{N}$) (Fig. 1). Zero values for CYA_{BM} were recorded in only 50 of 820 observations, of which the greatest proportion was from polar climates (28% of polar lake samples). CYA_{BM} was highest in warm-temperate, boreal, and arid climates and lowest in the polar climate (Fig. 2).

Our large-scale dataset encompassed values of environmental variables that often spanned several orders of magnitude, with water temperatures ranging from < 1 to 36 °C and pH from acidic (5.0) to strongly alkaline (10.7). As expected, equatorial lakes had higher temperatures followed by lakes in warm-temperate and arid climates, with boreal and polar climates in the coldest range (Fig. 2). pH was significantly higher in arid climate lakes and significantly lower in equatorial lakes than in

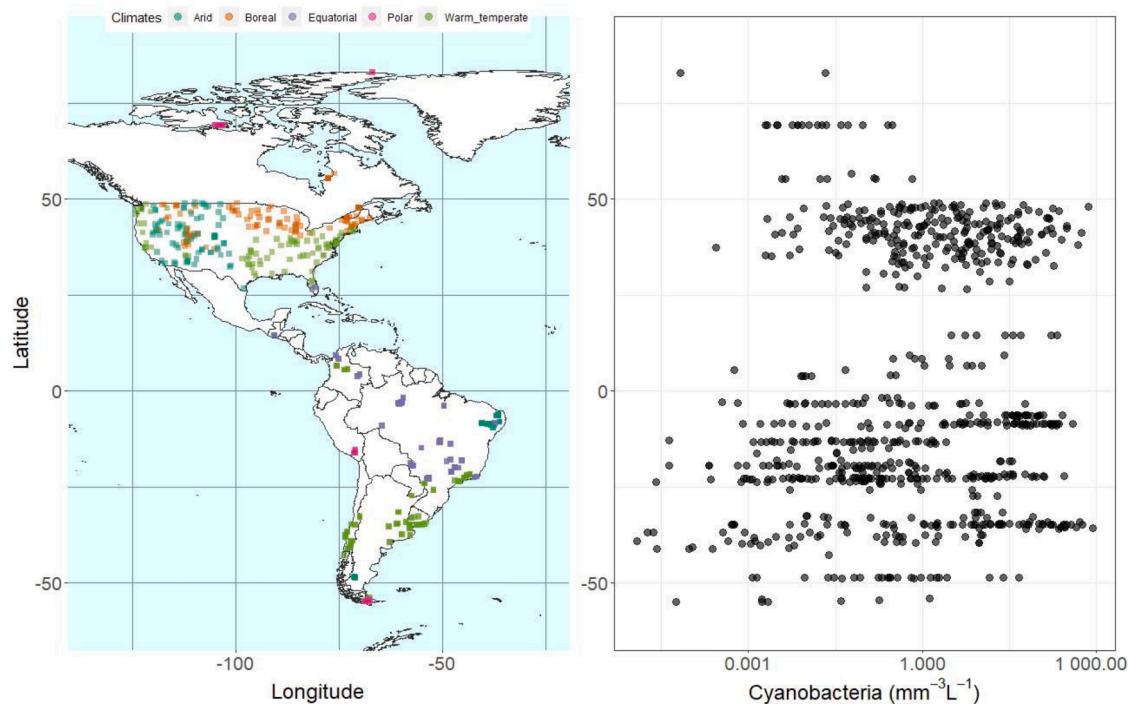


Fig. 1. Left: Location of the studied lakes in the Americas (squares) and right: Distribution of cyanobacterial biovolume along the latitudinal gradient (circles). Colors indicate the five major climates. Polar lakes are located in the extreme Southern and Northern latitudes and at high altitudes in the Andes.

other regions (Fig. 2). TP and TN concentrations varied by 3 and 4 orders of magnitude, respectively, with the overall median TP ($\sim 57 \mu\text{gL}^{-1}$) indicating that more than a half of the lakes had eutrophic conditions. Polar lakes had significantly lower TP than arid, warm-temperate, and equatorial climates; equatorial lakes also had significantly higher TN concentrations than those of the other climates, which showed similar TN (Fig. 2).

With respect to depth categories, shallow lakes had the highest CYA_{BM} , on average, followed by intermediate and then deep lakes, and the maximum CYA_{BM} ($861 \text{ mm}^3 \text{L}^{-1}$) was found in a shallow lake located in the warm temperate region. Shallow lakes had also higher concentrations of total phosphorus and total nitrogen (overall median: $79.7 \mu\text{gL}^{-1}$ and 1.2 mgL^{-1} , phosphorus and nitrogen respectively) in comparison with the other lake depth categories (Fig. S1).

Conditional inference trees indicated that TP was the variable most strongly related to CYA_{BM} (nodes 1 and 2; Fig. 3, Tables S6 and S7). Lower CYA_{BM} was associated with $\text{TP} < 73.4 \mu\text{gL}^{-1}$ (node 1); this threshold further split the data into the lowest biovolume category, driven by $\text{TP} < 10 \mu\text{gL}^{-1}$ (node 2) and $73.4 \mu\text{gL}^{-1} > \text{TP} > 10 \mu\text{gL}^{-1}$ and two groups (node 4; shallow lakes with low biomass and intermediate and deep lakes with higher biomass) (nodes 4–6). pH was significant (> 8.12 ; node 7), but only under conditions of high TP ($> 73.4 \mu\text{gL}^{-1}$). Finally, significant associations between high biomass and total nitrogen concentrations $> 0.29 \text{ mgL}^{-1}$ (node 9) were observed at high levels of TP ($> 73.4 \mu\text{gL}^{-1}$) and high pH > 8.12 (Fig. 3, Tables S6 and S7). The conditional inference tree indicated that temperature and abiotic variables other than nutrients, depth and pH did not significantly influence CYA_{BM} distribution.

3.2. Model results

The best linear CYA_{BM} model included the fixed effects TP, pH, TN and depth category (Figs. 4 and S2). Temperature was not significantly related to CYA_{BM} , either alone or in interaction with any other variable. However, since the model had equal statistical power with or without temperature, and considering its conceptual relevance, we included it in

the final model (Fig. 4 and S2). The fixed effect of the best model explained a high proportion of the CYA_{BM} variance (as measured by marginal $R^2 = 0.302$) which greatly increased when considering the entire model (conditional R^2 , fixed and random effects together = 0.689). Both intermediate and deep lakes showed significantly different intercepts in comparison with shallow lakes (Fig. S2). Further exploration of the interaction between nutrients and depth categories revealed a significant stronger relationship between nutrients and CYA_{BM} in shallow lakes, particularly for TN, than the other two depth categories (Fig. 5, Table S8). CYA_{BM} of deep lakes showed the weakest relationships to TN and TP (Fig. 5). In the two models, the fixed effect explained $\sim 26\%$ of the CYA_{BM} variance, which increased when random effects were included (conditional R^2) (Table S8).

The three type of lakes, defined by their depth, showed different trends in the CYA_{BM} depending on total phosphorus and the level of total nitrogen (threshold $\text{TN} = 0.7 \text{ mgL}^{-1}$), where shallow lakes had the steepest slope between CYA_{BM} and total phosphorus when total nitrogen was higher than 0.7 mgL^{-1} (Fig. 6, Table S9). In shallow lakes, the positive slope of $\text{CYA}_{\text{BM}}/\text{TP}$ suggested strong P-control even when N was low, with no significant breakpoint in this trend (Fig. 6a), while at higher TN concentrations the slope of the TP: CYA_{BM} relationship was steepest up to $144 \mu\text{gL}^{-1}$ TP (breakpoint), after which the influence was still positive but weaker (Fig. 6b). In lakes of intermediate depths, CYA_{BM} responded positively to TP, with a steeper slope at higher TN concentrations, but with no defined breakpoints along the TP gradient (Fig. 6c and d). A different response was found for deep lakes when $\text{TN} < 0.7 \text{ mgL}^{-1}$, with a steep positive $\text{CYA}_{\text{BM}}/\text{TP}$ trend until $76 \mu\text{gL}^{-1}$ TP (breakpoint) (Fig. 6e), while at high TN no significant linear trend was found (Fig. 6f).

4. Discussion

We sought to clarify the roles of nutrients, temperature, and other factors in determining the success of cyanobacteria in freshwaters, and our results provide evidence that phosphorus is the principal driver of planktonic cyanobacterial biomass along the North-South gradient of

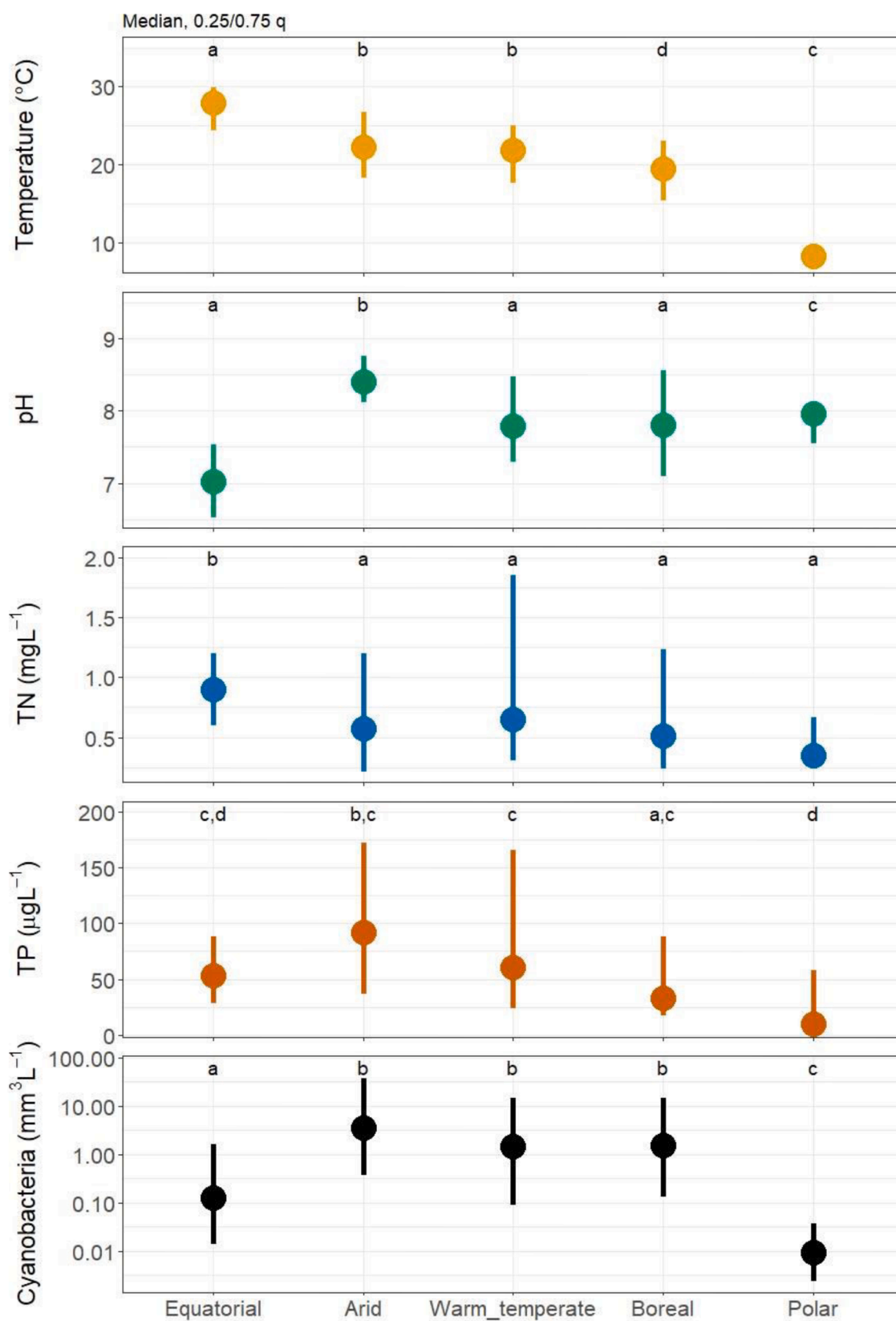


Fig. 2. Temperature, pH, total nitrogen (TN), total phosphorus (TP) and cyanobacterial biomass, median (circle) and quantiles 0.25/0.75 (vertical line) per climate. Cyanobacterial biovolume in log scale. Different letters indicate significant differences between climates (Kruskal-Wallis ANOVA on ranks and all pairwise multiple comparison, Dunn's method).

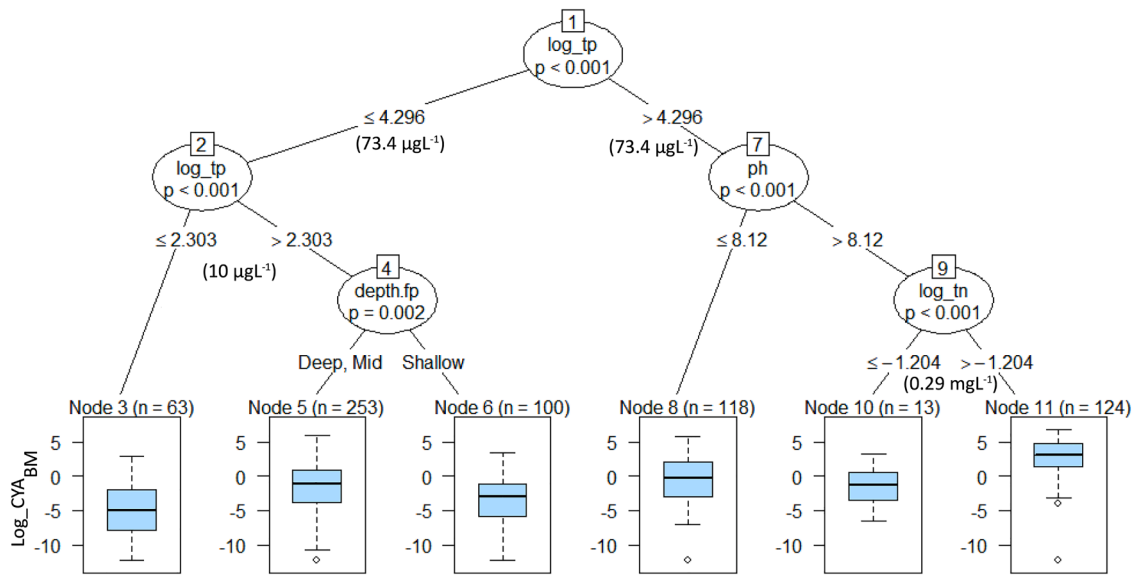


Fig. 3. Regression tree analysis outcome exploring the main factors for cyanobacterial biovolume (mm^3L^{-1}) log transformed ($\text{Log_CYA}_{\text{BM}}$). TP: total phosphorus ($\mu\text{g L}^{-1}$), TN: total nitrogen (mg L^{-1}), Depth.c: Depth category, Intern: Intermediate. Variables not selected by the model: temperature, LogArea and LogAltitude.

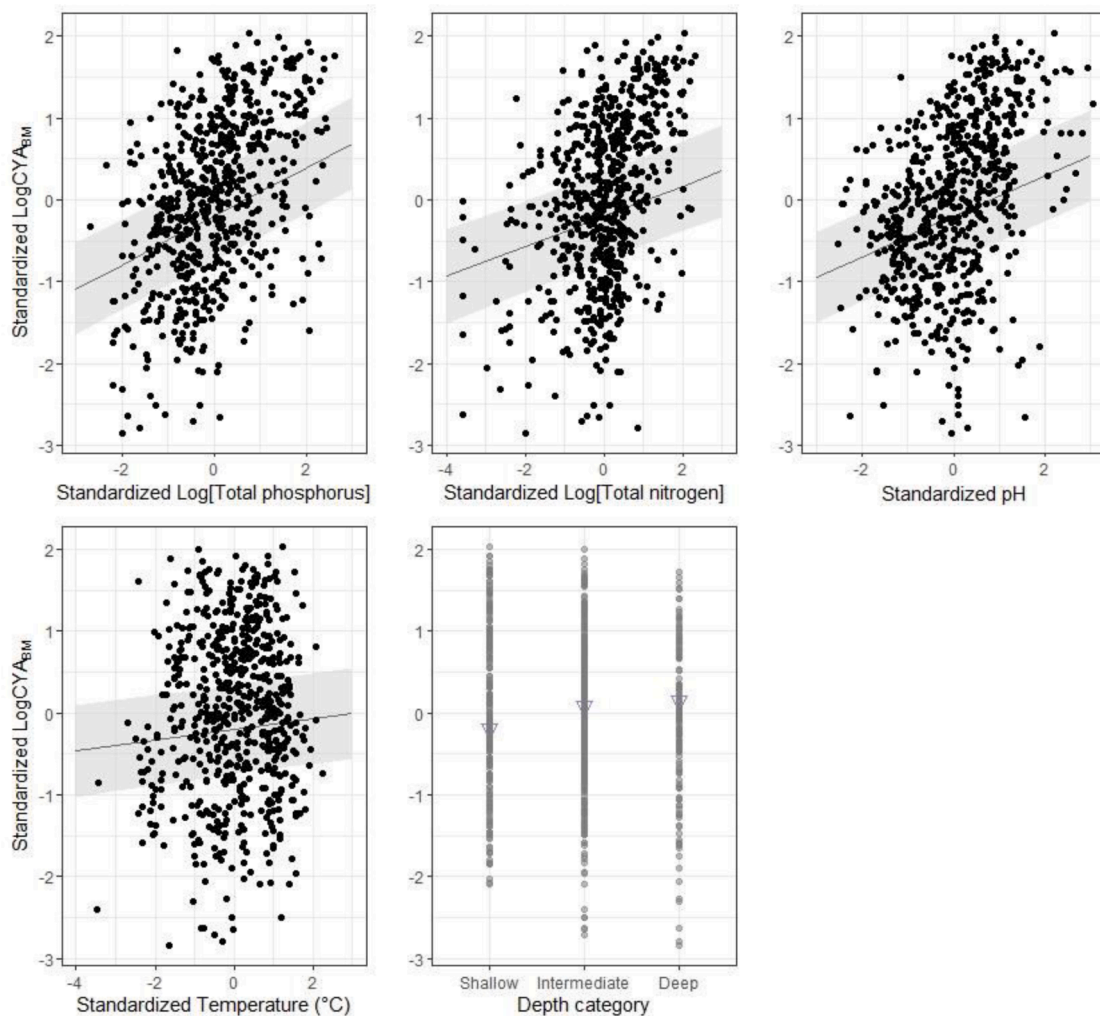


Fig. 4. Output of the linear mixed model (LMM) with random effects (lakes) of the response variable (cyanobacterial biovolume, log transformed, $\text{Log CYA}_{\text{BM}}$) to environmental variables (Temperature, pH, total phosphorus and total nitrogen). Variables were centered and standardized before the analysis. Fit linear regression, confident interval (gray area) and data (black dots) are shown for each fixed explanatory variable (Four first plots from top). Lower right: categorical variable (Depth category), blue diamond, with the distribution of the data (gray dots).

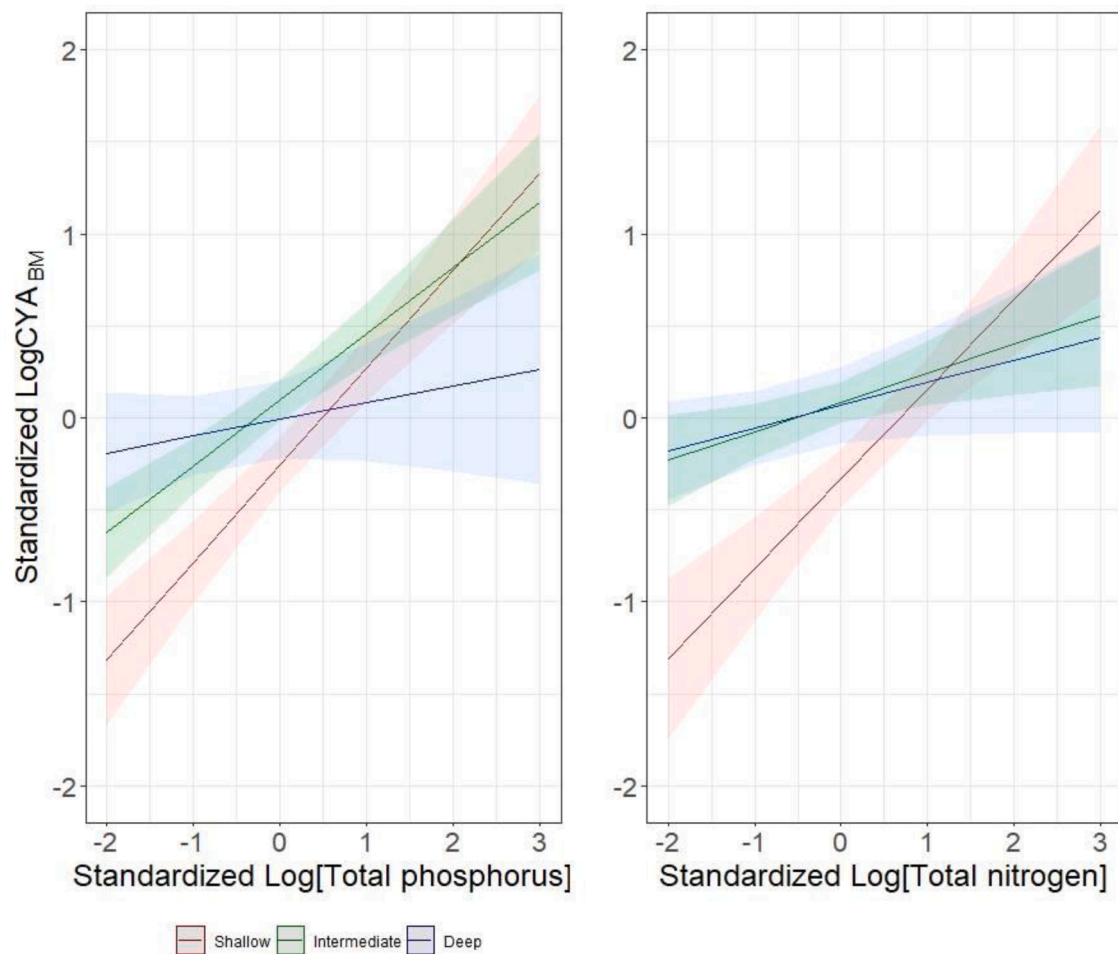


Fig. 5. Output of the linear mixed models (LMMs) with random effects (lakes) for cyanobacteria and the effect of nutrients differentiated by depth (shallow in red, intermediate in green and deep in blue). All variables were centered and standardized before the analysis. The interaction effect between total phosphorus and depth category (model 1, left) and total nitrogen (TN) and depth category (model 2, right) are shown by the three slopes. Shaded areas indicate the confidence interval.

the Americas. No clear climate trends were found in cyanobacterial biomass, indicating that nutrient enrichment (eutrophication) and depth are its principal controls. The further significant effect of pH supports the hypothesis of a positive feedback switch, driven by cyanobacteria, that favors bloom resilience under nutrient-rich conditions.

Total phosphorus was a stronger predictor of cyanobacterial biomass than nitrogen, particularly below hypereutrophic conditions, as demonstrated by the CART node that split hypereutrophic lakes from the others (i.e., $TP \sim 70 \mu\text{gL}^{-1}$) at concentrations consistent with the median TP of widely used trophic classifications (Carlson 1977; Vollenweider and Kerekes 1982). Although regressions between biomass and total nutrients do not necessarily indicate causality (Rousso et al., 2020); the stoichiometry of biomass is a plausible mechanism for limitation by P in this concentration range. Previous studies based on North American lakes have assigned varying degrees of relative importance to P and N as drivers of cyanobacterial biomass (Beaulieu et al., 2013, 2014; Rigosi et al., 2014; Loewen et al., 2020), although the relevance of each nutrient is dependent on its concentration being sufficiently low to limit biomass. A study of European temperate shallow lakes indicated phosphorus to be the principal predictor of cyanobacterial biomass, but, similar to our research, suggested that nitrogen became more relevant towards the eutrophic end of the gradient (Dolman et al., 2012). Despite using large databases, each of these studies was restricted to North American and European lakes, towards which limnological research has shown a historical bias. A survey of 122 south temperate, arid and subtropical lakes ($24^\circ - 45^\circ \text{S}$) found that trophic state and lake type, but

not temperature, explained cyanobacterial abundance (O'Farrell et al., 2019).

Based on observing N-limitation or co-limitation by N and P, some studies have suggested the need to manage both phosphorus and nitrogen, rather than phosphorus alone, to limit the harmful effects of eutrophication (Abell et al., 2010; Bullerjahn et al., 2016; Gobler et al., 2016). The relative importance of phosphorus and nitrogen in explaining cyanobacterial biomass by depth categories as shown in our survey supports the idea that nutrient increases may have different influences on regulating cyanobacterial biomass. At a given TP concentration, waterbody depth influences whether nitrogen (also) limits cyanobacterial biomass. This can be explained by physical mechanisms, such as mixing and turbidity, that influence light availability (Scheffer et al., 1997; Havens et al., 1998; Becker et al., 2009; James et al., 2009). In our study, cyanobacterial biomass in shallow lakes increased most steeply with increasing TP, while biomass in deep lakes showed the weakest relation to TP, and also leveled off at a breakpoint of $76 \mu\text{gL}^{-1}$ at low TN (0.7 mgL^{-1}). High TN levels also help explain the response of cyanobacterial biomass to TP, with higher biomass supported in shallow and intermediate lakes, while there were no clear linear trends in deep lakes, indicating that other factors controlled cyanobacterial biomass.

Our dataset most likely includes cases where the limitation is either by P or N, as well as situations in which the concentrations of both nutrients are low enough to exert growth colimitation. This appears likely for the lakes of intermediate depths at low TN concentrations, for which cyanobacterial biomass showed the least pronounced dependency

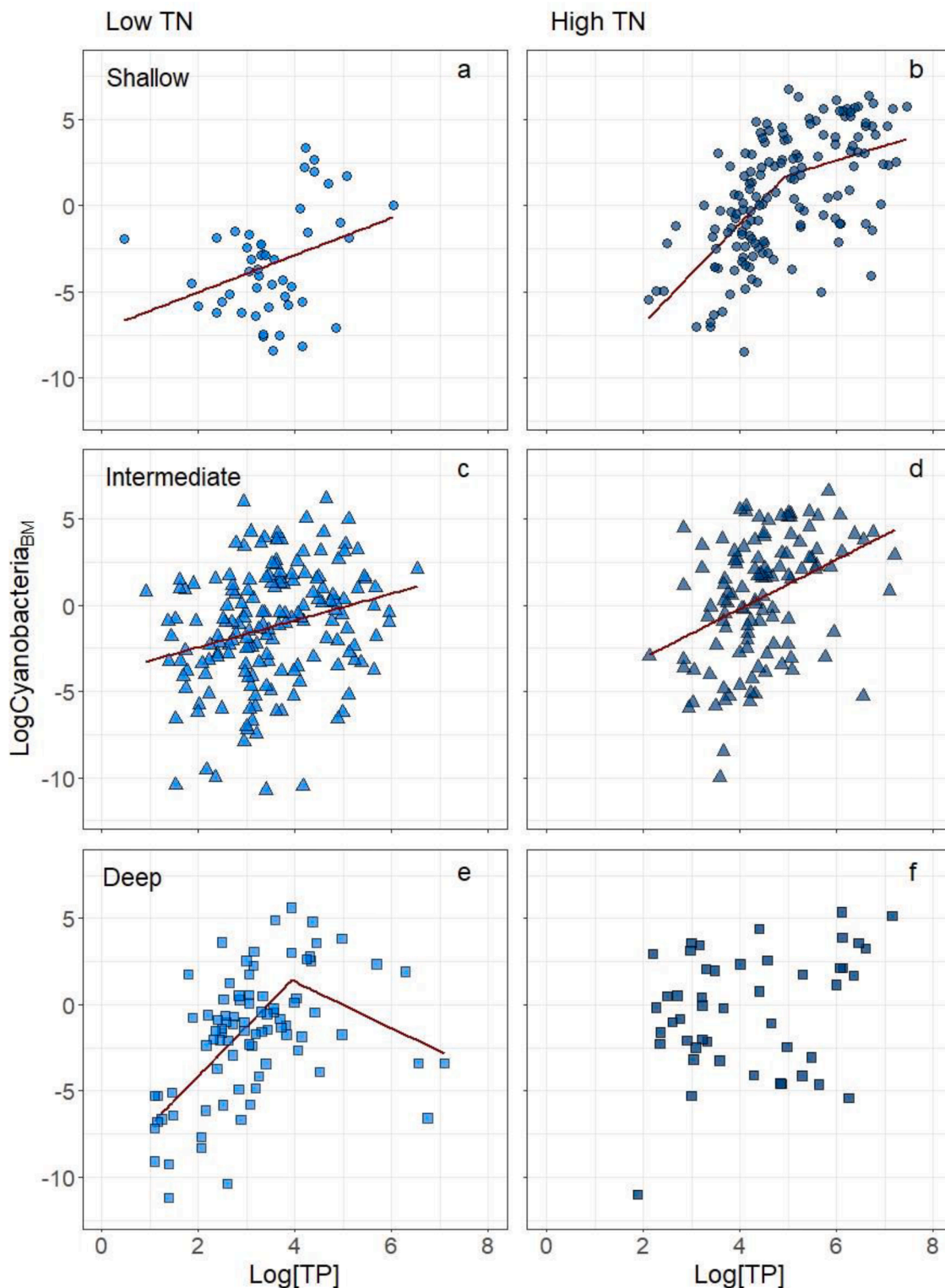


Fig. 6. Output of the linear regressions (simple and piecewise with breakpoints) between log-transformed cyanobacterial biovolume ($\text{Log CYA}_{\text{BM}}$; mm^3L^{-1}) and log-transformed TP in two TN classes: low ($0.01 - 0.7 \text{ mgL}^{-1}$, left panel, light blue symbols) and high ($>0.7 - 10.3 \text{ mgL}^{-1}$, right panels, dark blue symbols) for each depth category. Significant breakpoints were found for shallow lakes in the high TN group and deep lakes in the low TN group (back-transformed TP values: panel *b* = $144 \mu\text{gL}^{-1}$; panel *e* = $76 \mu\text{gL}^{-1}$). No significant relationship was found for deep lakes within high TN (panel *f*). Model estimates and significance of the functions are in Table S9.

on TP (Fig. 6c). In shallow lakes with low TN levels, cyanobacterial biomass showed a positive trend across the entire TP range, when it may have been expected to level off at high TP values in response to nitrogen limitation. The four highest biomass values in Fig. 6a, however, were

from large, shallow eutrophic lagoons, where nitrogen limitation may be less prominent because of multiple effects of wind action (Zhu et al., 2020). The results may also be influenced by the limited number of data points in this category. In shallow lakes with high TN levels, the leveling

off of biomass at high TP is probably due to light limitation effects (Havens et al., 1998; Becker et al., 2009; James et al., 2009). Cyanobacterial biomass in intermediate and deep lakes with high TN levels showed no clear correlation with TP, possibly because most intermediate lakes in the dataset had lower TP concentrations (Fig. 6d). For deep lakes, the data were dispersed, and the lack of data points precluded the detection of trends between biomass and TP at high TN levels (Fig. 6f). In the highest TP range two divergent trends were observed, one with high cyanobacterial biomass in a large, hypereutrophic equatorial lake (Lake Amatitlan) with long records of cyanobacterial blooms (Rejmánková et al., 2011), and another with contrasting low cyanobacterial biomass from a large, turbid Amazonian reservoir (Santo Antonio) (Latrubesse et al., 2017). The inverse trend found for deep lakes at high TP but low TN may be influenced by specific characteristics of the lakes. The three highest TP values (Fig. 6e) were from large, high-altitude reservoirs, located in the polar climate region of Peru and which are highly turbid (Aguada Blanca Reservoir) or may be influenced by the regional ionic composition (Fraysse Reservoir) (McClain and Naiman, 2008), although the specific causes remain unclear.

Based on our results, we suggest that cyanobacteria may better tolerate P-depleted conditions under high N concentrations. Cyanobacterial bloom resilience through P-scavenging down to nanomolar concentrations can be supported by the availability of inorganic N, as cellular mechanisms of P uptake are dependent on N-rich proteins (Aubriot and Bonilla, 2018; Wang et al., 2018). For instance, N-limited cyanobacterial blooms can shift to P deficiency hours after an input of dissolved inorganic nitrogen, which results in a temporary decrease of N limitation and consequent growth (Aubriot 2019). When phosphorus control alone cannot bring concentrations well below $\sim 70 \mu\text{g L}^{-1}$, reducing N to concentrations low enough to stringently limit biomass may be an effective option. This is in line with studies that support the dual-nutrient control approach to minimize eutrophication effects (e.g.: Paerl et al., 2016a; Smith et al., 2016; Newell et al., 2019). Reducing P, however, has been a successful approach to controlling eutrophication and cyanobacteria in many cases (Jeppesen et al., 2005; Fastner et al., 2016; Schindler et al., 2016; Chorus et al., 2021; Molot et al., 2021). The discrepancy between the two positions (P-only versus dual nutrient control) may simply reflect differences in lake-specific characteristics. For instance, many studies include only lakes with P concentrations less than $100 \mu\text{g L}^{-1}$ (e.g.: Schindler et al., 2008; Fastner et al., 2016), a range at which phosphorus is more relevant than nitrogen in controlling cyanobacteria; at higher trophic conditions (hypereutrophic), our data indicate a trend towards nitrogen control. As such, we suggest that the relative importance of N and P, and therefore the emphasis placed upon them for cyanobacterial management, should depend more on the nutrient gradient of the studied sites rather than fixed paradigms.

In our dataset, at high nutrient concentrations higher cyanobacterial biomass was reached in shallow lakes than in intermediate and deep lakes. Mechanisms that may explain this include permanent mixing, sediment-water interactions and P release to the water column (Scheffer 1998; Richardson et al., 2018) or water level changes (Brasil et al., 2016; Yang et al., 2016). Their relevance varies between locations and needs to be assessed site specifically. Shallow lakes are more frequently subjected to nutrient contamination as a result of human population activities than deeper lakes, which are commonly located in less productive and less populated regions (Zhou et al., 2022). We showed that nitrogen is relevant for explaining cyanobacterial biomass especially in shallow lakes, which may be related to the higher denitrification rates due to high sediment area/water volume ratios (Kolzau et al., 2014; Søndergaard et al., 2017). Phytoplankton biomass in shallow lakes, which responds to internal nutrient loads and the lack of light limitation, can increase sharply due to nutrient enrichment (Phillips et al., 2008). In these lakes light may reach the bottom, or they may become highly turbid, depending on the sediment structure and submerged macrophyte development (Scheffer et al., 1993), but even in extreme turbid conditions cyanobacteria can successfully bloom after nutrient enrichment

(Scheffer et al., 1997). Although we do not have data to infer light availability for photosynthesis, we clearly show that nutrients are the major factors explaining cyanobacterial biomass in the studied lakes. Therefore, based on our study, limitation of cyanobacterial blooms is lake specific, driven particularly by lake depth which strongly affects internal P and N loading.

In addition to nutrients, pH was also a significant predictor of cyanobacterial biomass in our dataset. However, this relationship may be both cause and consequence of phytoplankton photosynthetic activity, complicating its interpretation. Different factors may affect the carbonate equilibrium in lakes, including latitudinal gradients and trophic status (Raven et al., 2020), but pH increases as a consequence of photosynthetic activity thus changing the dominant form of inorganic carbon from CO_2 to HCO_3^- . The capacity of cyanobacteria to incorporate carbon at $\text{pH} \geq 8$, where bicarbonate is predominant, exceeds that of eukaryotes due to their highly efficient cellular carbon concentration mechanisms and ability to use urea (Shapiro 1984; Krausfeldt et al., 2019). In eutrophic environments, greater photosynthetic activity and accumulation of phytoplankton biomass results in pH increases that are disadvantageous to eukaryotes (Shapiro 1984; Caraco and Miller 1998). The positive relationship between pH and cyanobacterial biomass in our dataset, particularly at $\text{pH} > 8$ and $\text{TP} > 73.4 \mu\text{g L}^{-1}$, is consistent with this theoretical and empirical evidence. The relationship may reflect a biologically mediated positive feedback switch, whereby increased productivity reinforces the environmental conditions favorable for the group responsible for their production (i.e., cyanobacteria), similar to processes observed in plant communities (Wilson and Agnew 1992). This suggests that eutrophication and the “cause-consequence” of high pH appear to subsidize cyanobacterial blooms and enable their persistence.

Similar to nutrients, temperature is also one of the fundamental factors regulating organism metabolism (Reynolds 2006). It is commonly suggested that high temperatures play a distinctive role in explaining cyanobacteria increases in freshwaters (Paerl and Huisman 2008). Although some previous studies have included large-scale predictive models of cyanobacterial dominance or biomass and suggested significant relationships with temperature, they were restricted to particular lake types (shallow lakes) or geographical regions (Kosten et al., 2012; Beaulieu et al., 2013; Rigosi et al., 2014). Across our broader spatial, climate and lake morphometry gradients, however, temperature was not a significant predictor of cyanobacterial biomass. Cyanobacteria reached high biomass in our dataset across a wide range of temperatures, with the exception of the extreme ranges of the gradient (i.e., < 10 and $> 30^\circ\text{C}$) where the lowest values were observed, in line with other field and laboratory studies (Robarts and Zohary 1987; Bonilla et al., 2016; Ma et al., 2016). While warm conditions favor bloom-forming cyanobacteria when nutrients are available (Jöhnk et al., 2008; Huisman et al., 2018), temperature *per se* does not necessarily confer a competitive advantage to cyanobacteria relative to other groups (Lürling et al., 2013). Although the dominance of phytoplankton by cyanobacteria is more pronounced in warm climates than in other climates, this trend is restricted to shallow lakes (Kosten et al., 2012), and the roles of factors such as predation, hydrology, light penetration, and mixing are not always considered. Cyanobacterial dominance in the phytoplankton is more related to the physical consequences of warm waters (i.e., stratification/mixing, gas diffusion) than to the actual temperature (Huber et al., 2012; Posch et al., 2012; Lürling et al., 2013). In equatorial lakes, the wet/dry season dynamic may explain differing cyanobacterial biomass due to variations in sediment resuspension and internal P loading (Castro Medeiros et al. 2015). The effects of light availability, mediated by turbidity, are often more important than those of temperature for predicting cyanobacterial blooms in subtropical Australian freshwaters and may limit cyanobacterial growth in hyper-eutrophic shallow Pampean lakes despite high summer temperatures (Davis and Koop 2006; Izaguirre et al., 2015).

As expected, polar climate lakes had the lowest cyanobacterial

biomass in our dataset, as such sites are generally highly oligotrophic due to low climate-mediated nutrient loads and limited human impacts. Cold, high-latitude lakes may, however, generate phytoplankton blooms and stimulate cyanobacterial populations if phosphorus increases (Schindler et al., 1974; Przytulska et al., 2017; Ayala-Borda et al., 2021), suggesting that polar lakes may be susceptible to cyanobacterial blooms despite their low temperatures. Moreover, cyanobacteria may be abundant in cold, eutrophic Patagonian lakes (Izaguirre and Saad 2014), and cyanobacterial blooms have been reported in some of the Andean cold, high-altitude (polar climate), eutrophic reservoirs included in our database (Munoz et al., 2020).

Many studies about the role of nutrients have discussed the relative contribution of cyanobacteria to total phytoplankton (cyanobacterial dominance) (e.g.: Downing et al., 2001; Havens et al., 2003; Wagner and Adrian 2009). However, cyanobacterial biomass is a variable of high relevance for water management given that the amount of cyanobacteria in lakes is a greater threat to water quality than their proportion of overall biomass. While high cyanobacterial biomass positively correlates with their dominance in the phytoplankton community, the reverse does not always occur. Cyanobacteria can dominate the phytoplankton of oligo-mesotrophic environments, accumulating a low biomass, without this being in response to eutrophication (Teixeira de Oliveira et al. 2011; Batista and Giani 2019; Reinl et al., 2021). Moreover, most guidance for cyanobacterial risk levels is based on biomass thresholds (Chorus and Welker 2021). The few studies that have used large databases to quantify the relationship between nutrients and cyanobacterial biomass have focused on one or two explanatory variables (e.g., phosphorus only; Carvalho et al., 2013). Our study shows that unwanted cyanobacteria can develop high biomass in any climate if aquatic nutrient concentrations are sufficiently high, and that lake depth is a critical factor for predicting the nutrient-cyanobacteria relationship and the relative importance of nitrogen versus phosphorus.

5. Conclusions

- Eutrophication was a much stronger driver of cyanobacteria than climatic gradients. When considered at a broad spatial scale such as that represented by the Americas, cyanobacterial biomass was not directly controlled by temperature but rather by intrinsic lake conditions.
- Phosphorus was the most important variable explaining cyanobacterial biomass in the Americas.
- Nitrogen was a significant factor explaining cyanobacterial biomass particularly in shallow lakes.
- The relative role of phosphorus and nitrogen for the prediction of cyanobacterial biomass is related to lake characteristics, with shallow lakes being more susceptible than deeper ones to eutrophication.
- pH fuels cyanobacterial abundance under high nutrient conditions through a biologically mediated positive feedback.
- While some studies have found a role of temperature for predicting cyanobacterial biomass, in the broader context of our data across 5 ecoregions, temperature was not significant. The role of temperature in predicting cyanobacteria biomass may thus have been over-emphasized in the literature.
- Rather than pointing to global external causes of cyanobacterial blooms, managing harmful cyanobacteria must therefore control eutrophication with sufficiently efficient measures to reach in-lake concentrations low enough to limit biomass.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

This work was partially financed by the National Agency for Science (ANII, project number FCE_6384) and CSIC ($I + D$ 171) of Uruguay. A. Almanza's participation was supported by CRHIAM Center ANID/FONDAP/15130015. We thank Milla Rautio, Manuel Cano, Anna Przytulska, Warwick Vincent, the Water Quality Agency (Laboratorio Calidad de Agua de AMSA) of Guatemala and the Quebec Ministry of Sustainable Development, Environment, and Fight Against Climate Change (DGSEE, MDDELCC) of Canada for contributing to the dataset. We thank John Smol and two anonymous reviewers for valuable comments.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.hal.2022.102367.

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