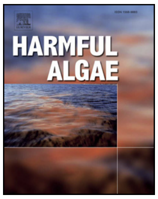
Harmful Algae 97 (2020) 101859

Contents lists available at ScienceDirect

Harmful Algae

journal homepage: www.elsevier.com/locate/hal



Comparing key drivers of cyanobacteria biomass in temperate and tropical systems

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ARTICLE INFO

Keywords:
Predictive models
Cyanobacteria blooms
Global patterns
Eutrophication
Climate change
Hydrology

ABSTRACT

There is growing evidence that cyanobacterial blooms are becoming more common in different parts of the world; within this context, predictive cyanobacteria models have an essential role in lake management. Several models have been successfully used in temperate systems to describe the main drivers of cyanobacterial blooms, but relatively less work has been conducted in the Tropics. We analyzed data from six Brazilian reservoirs and from five Canadian lakes using a combination of regression tree analyses and variation partitioning to evaluate the similarities and differences between regions. Our results, together with a synthesis of the literature from different latitudes, showed that trophic state (i.e. nutrients), climatic variables (e.g., temperature and/or precipitation) and hydrodynamic regimes (i.e. water residence time) are significant drivers of cyanobacteria biomass over several scales. Nutrients came out as the primary predictor in both regions, followed by climate, but when all systems were pooled together, water residence time came out as most important. The consistency in variables identified between regions suggests that these drivers are widely important and cyanobacteria responded quite similarly in different geographical settings and waterbody types (i.e. lakes or reservoirs). However, more work is needed to identify key thresholds across latitudinal gradients. Taken together, these results suggest that multi-region syntheses can help identify drivers that predict broad-scale patterns of cyanobacteria biomass.

1. Introduction

Cyanobacteria are major component of phytoplankton and a group of special concern because several common species produce toxic peptides and alkaloids, like hepatotoxins, neurotoxins, cytotoxins, dermatotoxins, and genotoxins (Carmichael 1994; Buratti et al. 2017). Under favorable environmental conditions, cyanobacteria populations can grow into high-density blooms (Brookes & Carey, 2011; Paerl & Paul 2012; O'Neil et al., 2012). As a result of their potential to produce powerful toxins, cyanobacteria blooms can present a risk to humans and animals through direct contact or the consumption of contaminated water. However, cyanobacterial dominance and bloom occurrence remains highly variable among lakes of the world, and it is still difficult to predict their onset and duration (Carvalho et al., 2011; Cha et al., 2014; Chapra et al., 2017). Predictive modelling efforts also tend to be biased towards temperate ecosystems. Thus, while there has been substantial effort to study cyanobacteria to date, there has been only a limited effort to compare field studies from tropical and temperate ecosystems (see Fig. 1, Table S1).

Analyses of long-term and paleolimnological records (from mostly north temperate and subarctic lakes) have shown that cyanobacteria have become a more dominant portion of the plankton community in many sites around the world in recent decades (Taranu et al. 2015). High-resolution satellite images also showed that peak intensity of summertime algal blooms (many dominated by cyanobacteria) increased in more than two-thirds of freshwater bodies studied from around the world (Ho et al., 2019). The observed rise in cyanobacterial blooms in many waterbodies has been linked to rising nutrients concentrations (Carvalho, et al. 2011; Elliott, 2012), warmer water temperatures (Carey et al 2012; O'Neil et al., 2012), changes in thermal stratification and water-column stability (Wagner & Adrian 2009; Paerl & Paul, 2012), as well as the amount and timing of precipitation and its effect on hydrological patterns and runoff events (Brookes & Carey 2011; Romo et al 2013), which can modify nutrient loading to

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https://doi.org/10.1016/j.hal.2020.101859
Received 18 March 2020; Received in revised form 8 June 2020; Accepted 11 June 2020

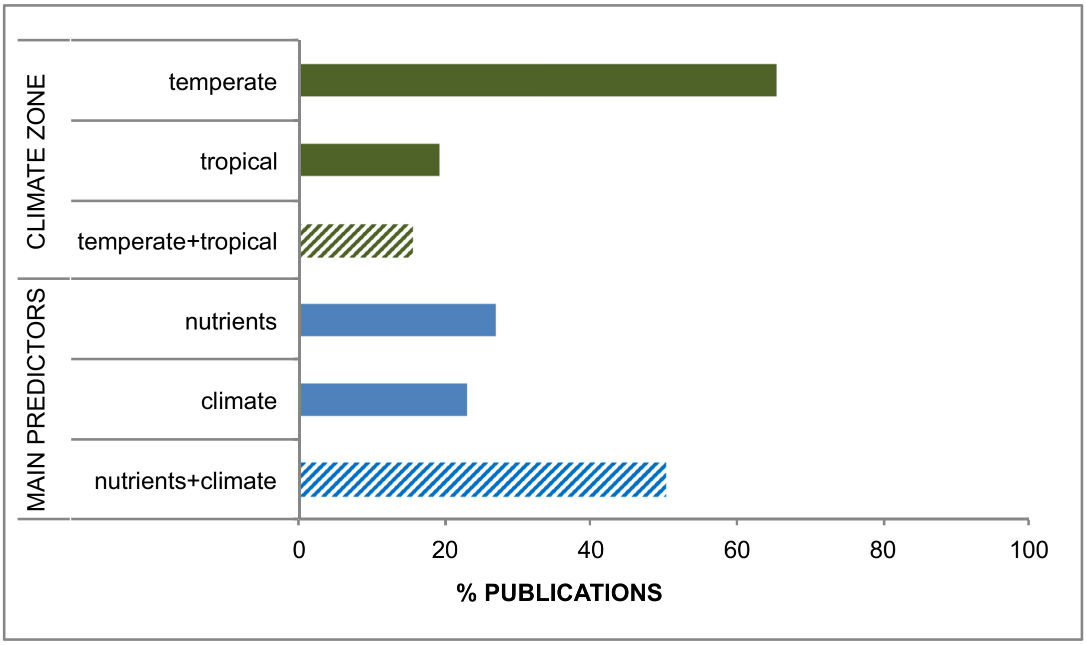

Fig. 1. Publications on predictive cyanobacterial models (cyanobacteria biomass) from 1999 to 2019: Shown are the percentages of publications by climate zone (green) and by main predictors (blue) (see Table S1 for details). Variables that were nested within the category of climate included temperature, precipitation, radiation, water column stability. The nutrients considered were all forms of phosphorus and nitrogen (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

lakes, water residence time and water level fluctuations. Together, these changes are creating opportune conditions for cyanobacterial growth and dominance (Huisman et al., 2018) thanks to several characteristics of their metabolism and physiology. As an example, many cyanobacterial species have the ability to regulate their buoyancy through the formation and control of gas vesicles, which enable them to move within stratified water columns and outcompete other phytoplankton (Walsby 1994; Pfeifer, 2012).

Changes in each of these key drivers will not be isolated, but instead, are expected to interact with unforeseen outcomes. Furthermore, the effect of temperature and nutrients on the phytoplankton community can be additive or even synergistic (Vinebrooke et al 2004; Jackson et al 2016; Taherzadeh et al. 2019). Temperature is known to control metabolic rates and the growth of organisms, which in turn is also dependent on the availability of limiting nutrients. Nutrients are needed for maintenance and reproduction, but temperature will regulate their uptake, storage and use, thus again the interaction of these two factors is evident. Cross et al. (2015) suggested the concepts of metabolic theory in ecology (Brown et al., 2004) and ecological stoichiometry (Sterner & Elser, 2002) as a framework to explore links between temperature and nutrients. This framework can allow us to better understand how organisms and ecosystem function, given that they are based on the thermodynamics and mass balance principles, respectively. Overall, in order to accurately predict community responses to multiple global-change drivers, it is important to consider their interactions and combined effects.

Empirical statistical models have been developed for several aquatic environments to predict cyanobacterial bloom occurrence and to identify the multiple factors that promote their dominance (Downing et al. 2001; Giani et al. 2005; Taranu et al. 2012; Beaulieu et al. 2013, 2014; Pitois et al. 2014). Some studies have also included aquatic systems from different latitudinal regions, with the intent of generalizing patterns over broader geographical areas (Kosten et al. 2012; Mowe et al. 2015; Rigosi et al. 2015; Taranu et al. 2015). However, most of these studies still focus on temperate waterbodies (as summarized in Table S1). Only 19% of studies that adopted empirical models to predict cyanobacterial abundances in the last 20 year were developed in tropical or sub-tropical regions, whereas 65% were based in temperate environments and 15% included both regions (Fig. 1).

To evaluate how comparable temperate lake models are to tropical ones, we conducted a study using data from two groups of freshwater environments: six reservoirs in southeastern Brazil (Minas Gerais state, a tropical region), and four lakes in western Canada (province of Alberta, a temperate region). Because the two regions experience different climatic regimes, we wanted to contrast patterns of cyanobacteria biomass and their potential environmental drivers to recognize differences and similarities in parameter fit. By developing models over a broad geographical range, our objectives were thus to test whether the main drivers of cyanobacterial dominance were similar in temperate and tropical systems. We also evaluated if certain drivers were especially important in only one region. Lastly, given that our study sites covered a broad range of nutrient inputs and hydrodynamic regimes, we aimed to predict cyanobacteria risk in the context of both climate and eutrophication changes.

2. Methodology

2.1. Study sites

We studied six reservoirs located in the state of Minas Gerais (Brazil): São Simão, Emborcação, Furnas, Marimbondo, Volta Grande and Pampulha (Fig. 2). To the exception of Pampulha, which is an urban artificial lake, all reservoirs were built for hydroelectric power generation. Pampulha reservoir was built in 1938 as a water supply for the city of Belo Horizonte, but its use was interrupted in the late 1980s with the first occurrence of cyanobacterial blooms. The six reservoirs cover a gradient from oligotrophic to eutrophic water conditions and are located in three major river basins in the Cerrado biome on Brazil's high central plateau (Rio Grande, Paranaiba and São Francisco rivers), where the largest hydropower generation capacity exists in the country. Because Furnas reservoir is divided in two distinctive branches, receiving water from two different rivers with different trophic status, the branches were analyzed separately (Furnas/Rio Grande river is more

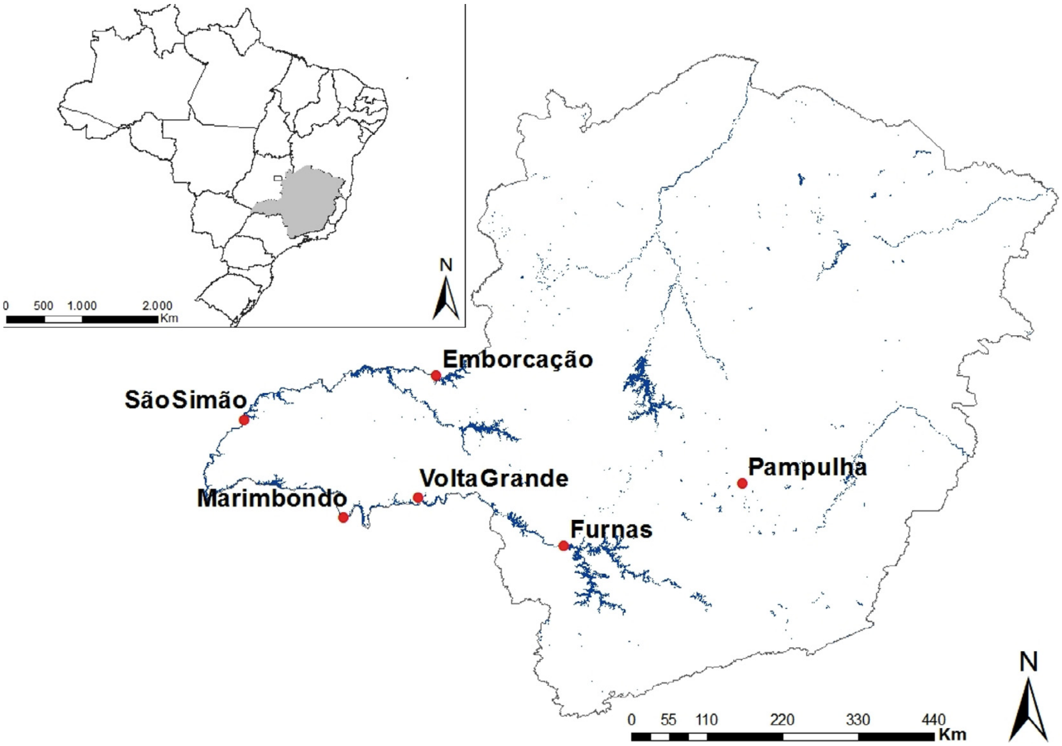

Fig. 2. Location of reservoirs in the state of Minas Gerais (Brazil).

oligotrophic and Furnas/Sapucaí river is more eutrophic). Because of their location in the Tropics, the growing season for phytoplankton in these reservoirs cover the entire year.

The selected lakes from the province of Alberta (Canada) were Ethel, Nakamun, Wabamun and Baptiste (Fig. 3). The lakes are located in the Prairie Parkland region of Alberta that presents rolling hill topography, characterized as a boreal mixed-wood ecoregion. Numerous water bodies in this area are naturally eutrophic as a result of the region's nutrient-rich geology (glacial till or ground moraine surficial deposits). Nonetheless, the four lakes also covered a strong trophic gradient (mesotrophic to hypereutrophic) as a result of distinct land-use histories, morphometry and water residence times. The north and south basins of Baptiste Lake were analyzed separately due to their different morphometry, trophic status and stratification regime (Baptiste North is shallower and weakly stratified whereas Baptiste South is deeper and dimictic). The growing season in the Canadian lakes was six months per year, from May to October.

More details about the two study regions are provided in Supplemental materials.

2.2. Sampling

In the Brazilian reservoirs, samples were taken in several sampling stations every two months in Sao Simão (2005-2006), every four in Emborcação (2005-2006), every three months in Marimbondo (2006-2008), and every month in Furnas (2006-2008), Volta Grande and Pampulha (2009-2011). In the field, temperature profiles were measured by a multiparameter YSI 556 probe (USA) at several stations. Thermal stability of the water column was calculated based on water temperature profiles and converted to density, as described in Wetzel & Likens (2000). Water samples for phytoplankton and chemical analyses were taken at Secchi disk depth by a Van Dorn bottle or alternatively a euphotic zone integrated sample was collected with a vertical silicone tube. The euphotic zone (>1% surface light) was based on transparency measurements by Secchi disc. Sub-samples were stored at -20°C for total phosphorus analysis. Nutrient analyses were performed using spectrophotometric methods according toAPHA – American Public Health Association (2005). For phytoplankton analyses, samples were preserved with Lugol's solution immediately after sampling for subsequent identification and quantification. Cyanobacteria biomass was quantified by the Utermöhl technique (Utermöhl 1958) in a Zeiss Axio Observer D1 inverted microscope. Algae biovolume was calculated from single cells according to Rott (1981) and Hillebrand et al. (1999).

In the Canadian lakes, euphotic-zone integrated water samples were collected for chemical and phytoplankton analyses from each lake basin. Each lake was sampled four to five times during the open water season (May–October). Sampling years were intermittent and varied slightly among basins (Ethel: 1986-1995 (n = 10 yrs), Baptiste: 1985-2005 (n = 7 yrs), Wabamun: 1981-2008 (n = 20 yrs) and Nakamum: 1990-1995 (n = 5 yrs)). Temperature profiles were taken from the deepest point of each lake, or in the case of Baptiste Lake, from each basin. To quantify the thermal stability of the water column at the time of sampling, we converted the temperature profile data to freshwater density (Kalff, 2002), to which we applied the thermal stability index (Wetzel & Likens, 2000). The euphotic depth (>1% ambient surface light) was measured using incident light meters, or more recently, photosynthetically active radiation (PAR) meters. When light meters were not available, euphotic depth was estimated as two times the Secchi disk depth. Phytoplankton samples were preserved in the field with Lugol's solution and stored in amber glass bottles. Phytoplankton enumeration was conducted using Leica DM-IRB inverted microscope and biovolume calculated as described for the Brazilian reservoirs. Total nitrogen (TN) and total phosphorus (TP) were analyzed following the methods described in Prepas & Trew (1983) and Prepas & Rigler (1982), respectively. Phytoplankton enumerations were conducted using Leica DM-IRB inverted microscopes.

2.3. Data analysis

To identify the variables that provided the best dichotomy between low and high cyanobacteria biomass, we used a combination of

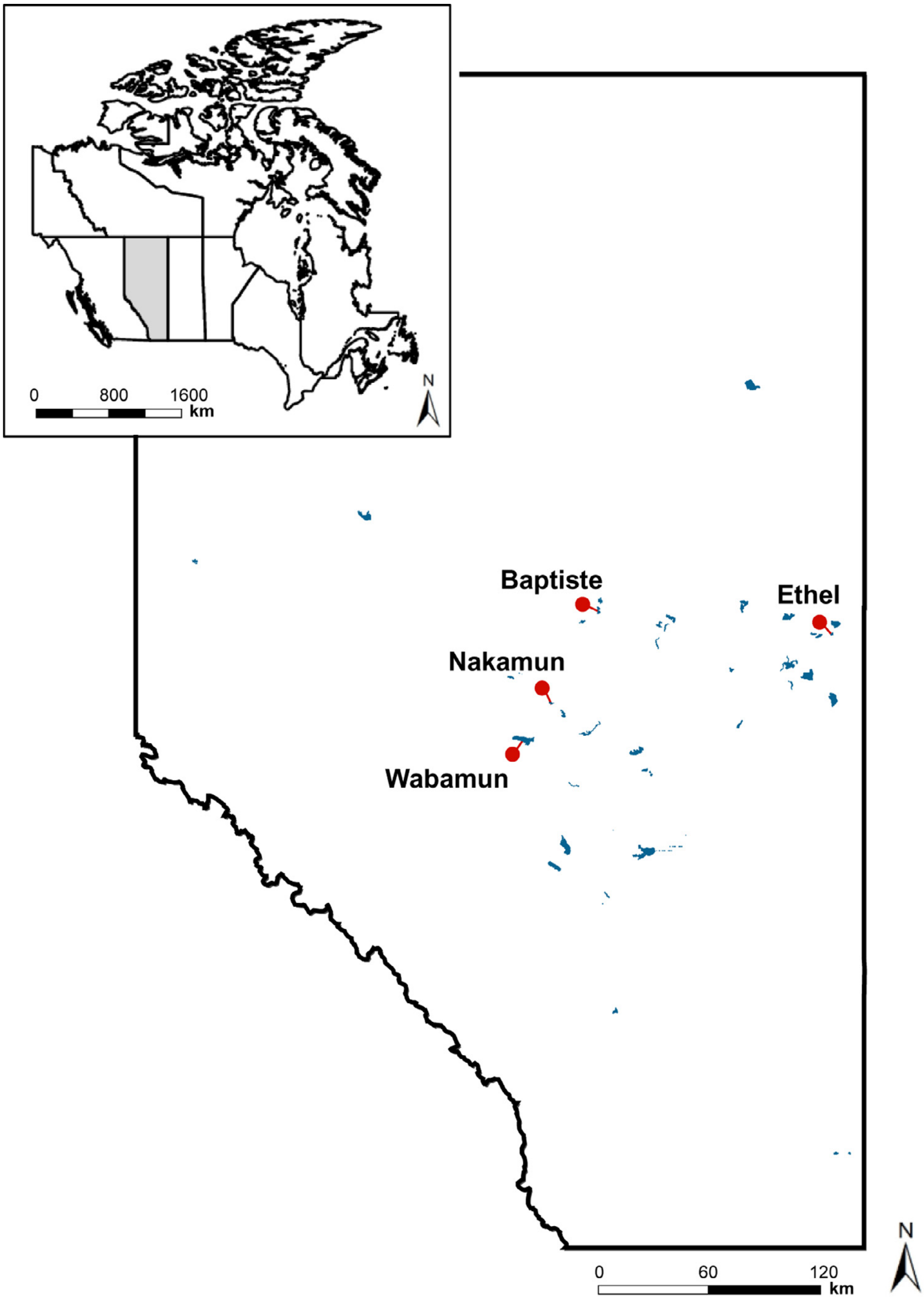

Fig. 3. Location of the lakes in the province of Alberta (Canada).

regression trees and variation partitioning analyses. First, we used LMMT-Linear Mixed Model Trees (glmertree function and package in R; Fokkema et al. 2018). Here, nutrient concentrations, water residence time and climate variables (i.e water temperature and monthly accumulated precipitation from the closest weather station) were used as fixed effects and waterbody ID was used as a random effect (intercepts). We ran LMMTs first on each dataset separately (Brazil reservoirs and Canadian lakes), followed by both regions together to extend the environmental gradients and provide a single model common to our tropical and temperate waterbodies. The LMMTs helped identify threshold response of cyanobacteria to nutrient, climate and water residence time, interactions among these predictors, and among-site variability in baseline cyanobacteria biomass. To build on the LMMTs and identify whether the variation explained by predictors was unique or common, we then ran a variation partitioning analysis (using the varpart function from the vegan package in R; Oksanen et al. 2019). The variation partitioning analysis was used to identify whether two variables (within the context of LMMT results) were independent (i.e., orthogonal), or whether they explained some proportion of shared variation (non-independent).

Lastly, to further characterize the among-site variability in response-driver relationships (random slopes), and build on the LMMTs (where only random intercepts were quantified), we examined how the linear (LMM; using the lme4 package in R; Bates et al. 2015) and non-linear (GAMMs; using the itsadug package in R; van Rij et al. 2017) responses of cyanobacteria biomass to the environmental factors varied among waterbodies.

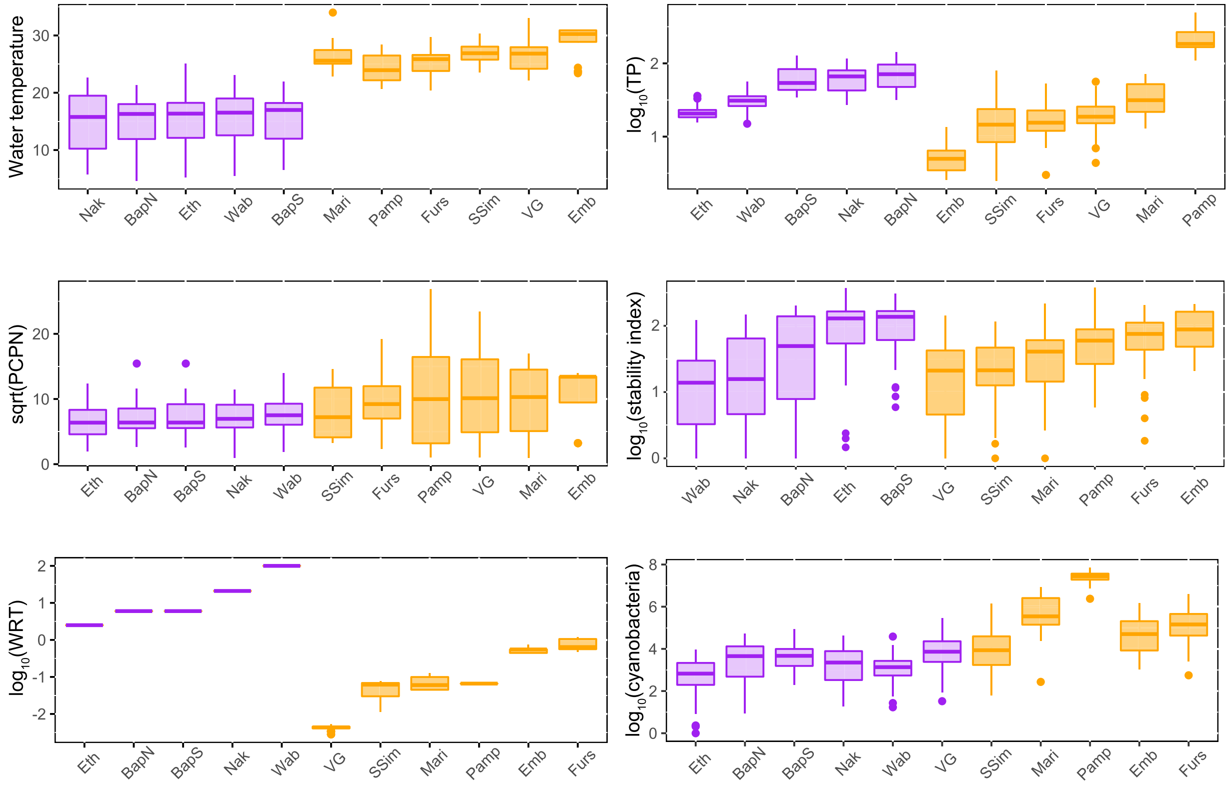

Fig. 4. Box-whisker plots based on individual waterbody data series for water temperature (°C), precipitation (mm/month; PCPN), water retention time (years; WRT), total phosphorus (μg/L; TP), Stability Index (g/cm^3; SI) and cyanobacteria biomass (μm^3/mL). Medians are indicated by central lines and are bounded by the 25th and 75th percentiles. Whiskers show 10th and 90th percentiles. Dots outside boxes and whiskers are extreme values. Purple boxes and points indicate Canadian lakes: BapN (Baptiste North), BapS (Baptiste South), Eth (Ethel), Nak (Nakamun), and Wab (Wabamun). Orange boxes and points indicate Brazilian reservoirs: Furs (Furnas), Mari (Marimbondo), Pamp (Pampulha), SSim (São Simão), and VG (Volta Grande).

3. Results

Temperature clearly distinguished the two sets of waterbodies, as the Brazilian reservoirs were consistently warmer than the Canadian lakes over the growing season (Fig. 4). Regional precipitation was generally more variable in Brazil than in Canada. Measures of water residence time (WRT), defined as the average time spent by the water from time of inflow to that of outflow, were lowest in the Brazilian reservoirs, though within each ecosystem, broad WRT ranges were observed (Fig. 4). The stability of the water column (SI) varied among waterbodies; in general, Canadian lakes had higher average stability than Brazilian reservoirs and the lowest median lake stability corresponded to the average stability observed across all of the reservoirs. In contrast, no clear dichotomy was observed for TP concentration between the two regions, confirming that both temperate and tropical waterbodies covered a wide range of trophic status, from more oligotrophic to eutrophic.

Based on our mixed effect regression tree for Canadian lakes (Fig. 5A), we found that the most important variables to distinguish samples of low vs higher cyanobacteria biomass were TP concentration (node 1; threshold of 86 μg/L), followed by temperature (node 2; threshold of 18.5 °C). This tree clearly shows that cyanobacteria biomass was lowest when nutrients were below 86 μg/L and water temperatures fell below 18.5 °C. In Brazil (Fig. 5C), TP was also the most important variable (node 1; threshold 79 μg/L), followed by WRT (node 2; threshold 14 days per year), and precipitation (node 4; threshold 69 mm per month). In the tropical reservoirs, cyanobacteria biomass was lowest when TP was below 79 μg/L and water residence time was less than 14 days. In contrast, cyanobacteria biomass tended to increase when the waters were very nutrient rich, or when water residence time was greater than 14 days and regional precipitation increased above 69 mm per month (rainy season). The random effects showed important variability among Canadian lakes and Brazilian reservoirs in their baseline cyanobacteria biomass (intercepts); in the Canadian lakes, cyanobacteria biomass was significantly higher than average in Baptiste-South and lower than average in Ethel (Fig. 5B). For the Brazilian reservoirs, Marimbondo and Furnas-2 had higher than average cyanobacteria biomass, while Emborcação, Furnas-1 and São Simão had lower than average means (Fig. 5D).

To extend the environmental gradients and better characterize the interaction between nutrients and temperature, we analyzed the two regions together (Fig. 6). Given the vast differences in cyanobacteria biomass and water residence time between the two datasets (Fig. 4), we observed that WRT was the best explanatory variable to separate high and low cyanobacteria biomass (node 1). For the waterbodies with lower retention time (primarily Brazilian reservoirs), TP was the variable responsible for the second split (node 2; threshold of 79 μg/L), followed by WRT (node 3; threshold of 14 days per year) and precipitation (node 5; 69 mm per month). At higher WRT (primarily Canadian lakes), elevated temperatures (node 9; threshold 12.6 °C) and nutrient concentrations (node 13; threshold 67 μg/L = 10ˆ(1.825)) coincided with an increase in cyanobacteria biomass. The random effects for the joint analysis (Fig. 6B) remained as those observed for individual datasets (Fig. 5B and D), although there was no clear separation between the two regions.

To identify the proportion of variation in cyanobacteria biomass uniquely vs. jointly explained by the environmental variables, we ran a variation partitioning analysis (Fig. 7) constrained by nutrient status (TP), climate (temperature and precipitation) and water retention time (WRT). Interestingly, although nutrients, climate and WRT interacted locally (within tree branches) to promote cyanobacteria biomass (Figs. 5 and 6), they were globally orthogonal variables, each

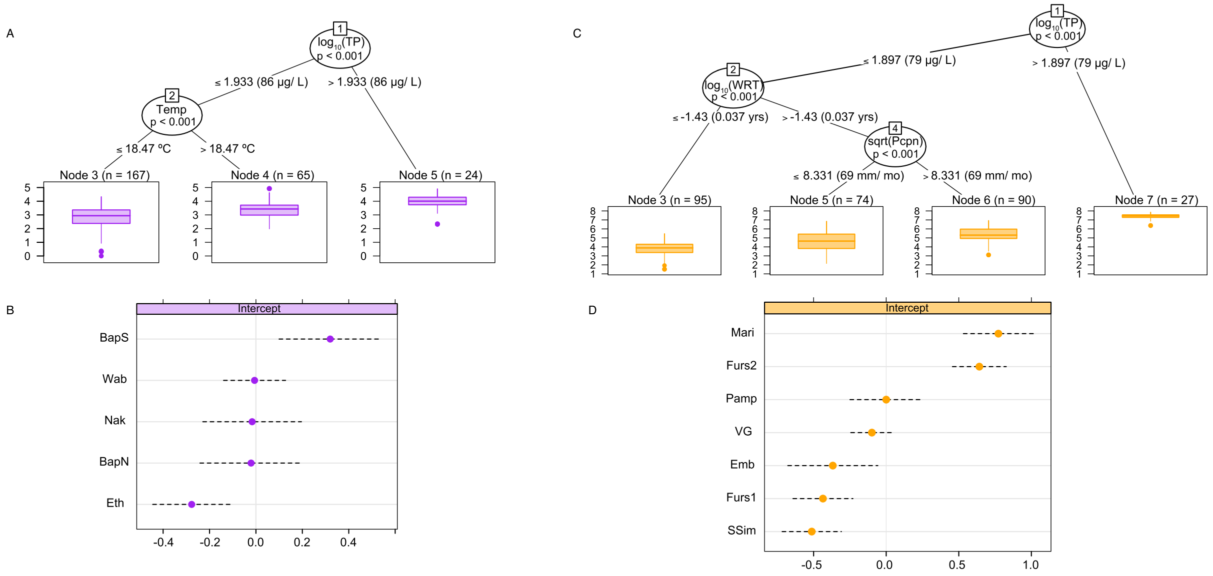

Fig. 5. Regression tree analysis for the Canadian lakes (A, B) and the Brazilian reservoirs (C, D), where random effect intercepts (mean cyanobacteria biomass for each waterbody) are shown in panels B (Canadian) and D (Brazil). Lake and reservoir names in B and D and variable names are as in Fig. 4.

explaining a unique proportion of variation in the response within each region (Fig. 7A, B), to the exception of TP and precipitation in Brazil reservoirs. Nutrients (TP) explained most of the variation in cyanobacteria biomass (17% in Canada and 36% in Brazil), though the proportion of variation explained by temperature was comparable to that of TP in Canadian lakes (15%). As seen with the regression tree analyses, WRT was a key secondary variable in Brazilian reservoirs (24% of variation explained). When we joined both datasets, however,

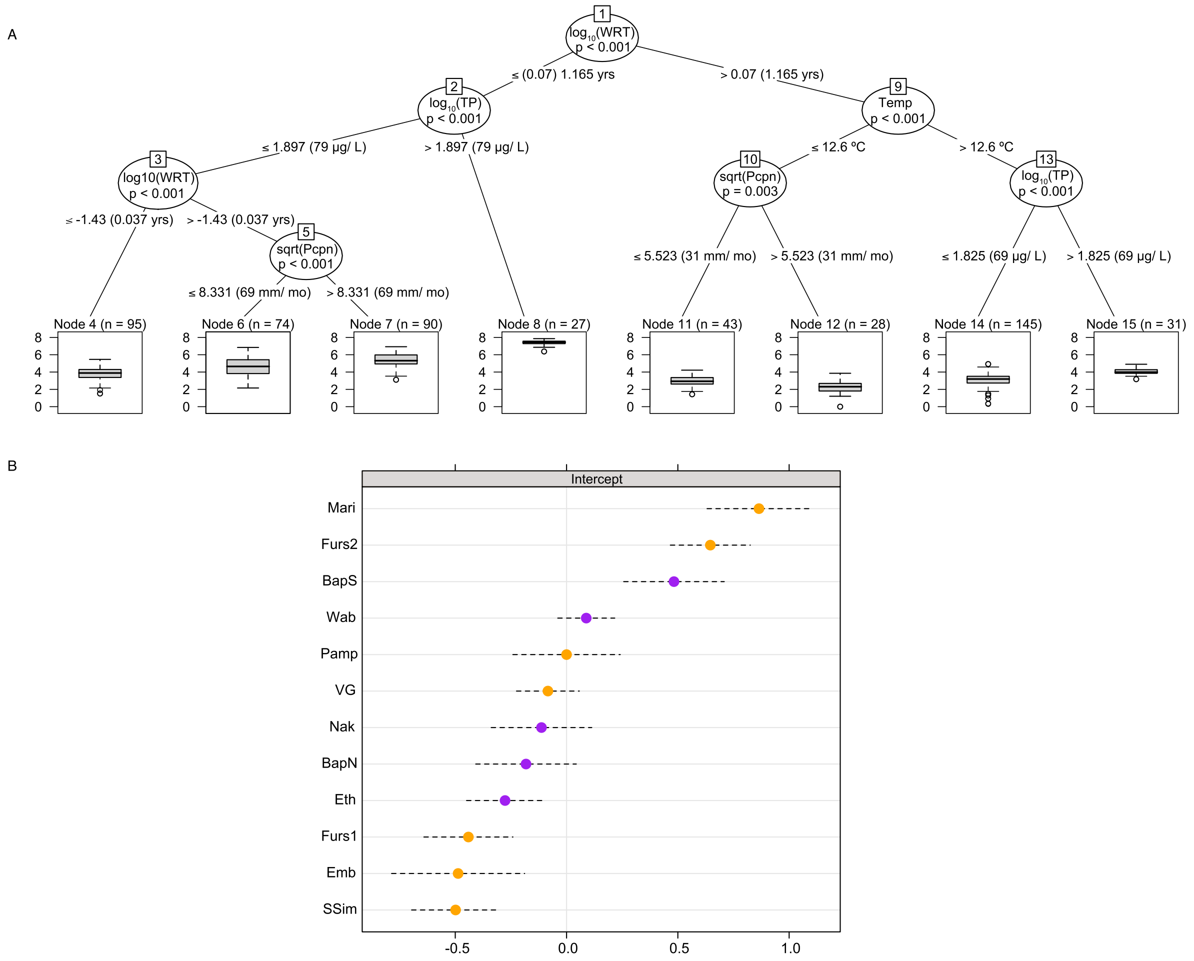

Fig. 6. Regression tree analysis (A) and random effects (B) for the joined data of Canadian and Brazilian waterbodies. Lake and reservoir names in B and variable names are as in Fig. 4.

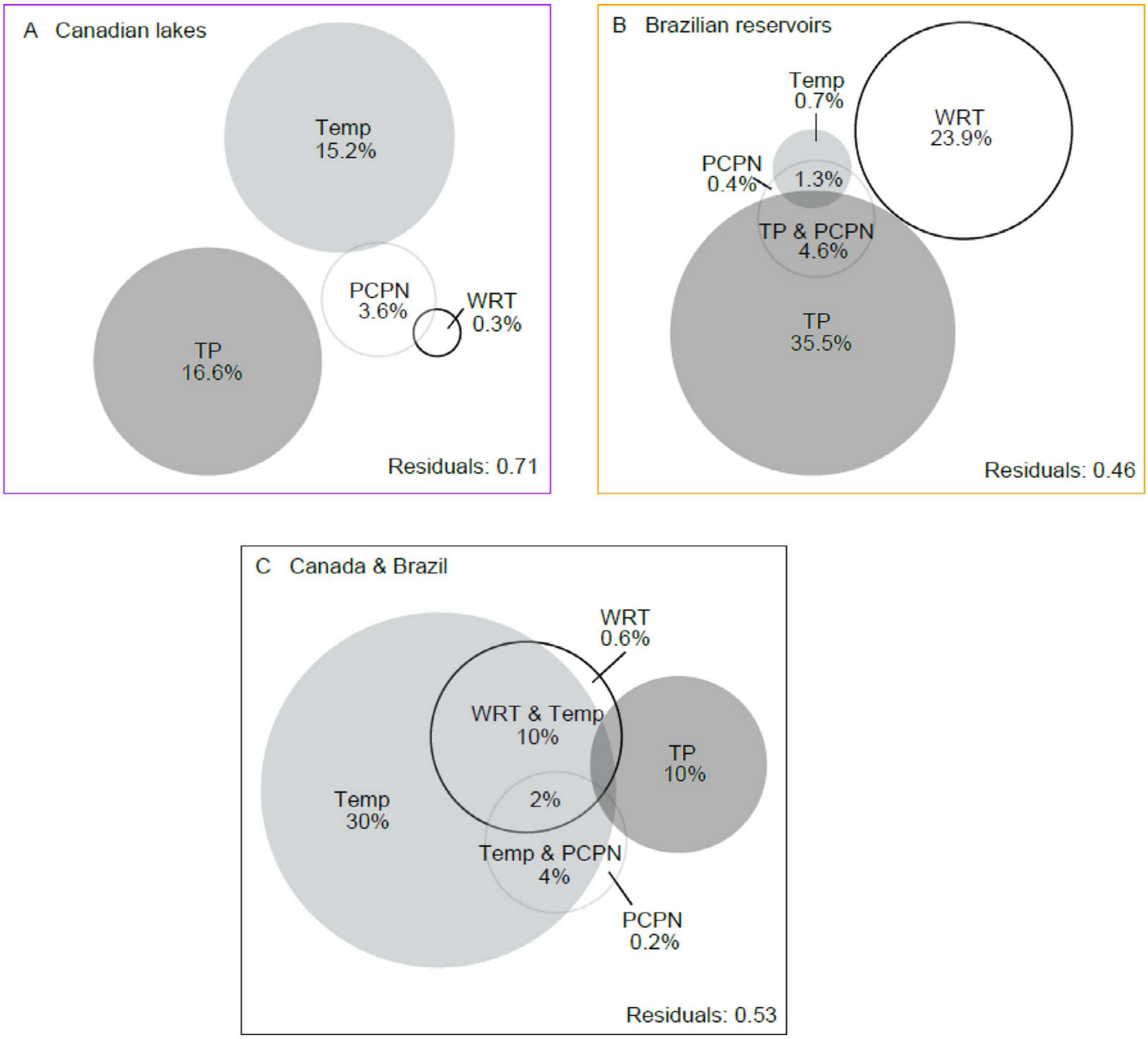

Fig. 7. Variation partitioning of the main explanatory variables represented for Canadian lakes (A), Brazilian reservoirs (B), and for Canadian and Brazil systems together (C). Variable names as in Fig. 4.

temperature and WRT explained higher amounts of the variation in cyanobacteria biomass than TP (Fig. 7). This could be expected since temperature and WRT differ greatly between the two regions. Interestingly, temperature was the most important climate variable for the temperate region (Figs. 5A and 7A) while precipitation was the most important climate variable for the Tropics (Figs. 5C and 7B). These are the main parameters that define seasonal changes in each region. Temperature oscillations are quite small in the Tropics, but rainy and dry seasons are very well delineated (Fig. S1). The importance of WRT in the tropical region is due to the influence of intense rain periods that, by increasing water flows, may reduce WRT. In addition, these reservoirs are artificial systems where both management practices and the original river currents could affect WRT.

Adding TN as explanatory variable (Fig. S2) in the variation partitioning analysis showed similar results to those observed in Fig. 7, where nutrients (as TP and TN) explained a higher proportion of the variation than climate and WRT combined in both region (Fig. S2 A, B). Again, in the aggregated dataset (Fig. S2C), nutrients were less important than climate and WRT. We observed comparable results in the models using TN and TP, but since both variables were collinear, we used TP as main descriptor for nutrients.

When both regions were examined together, the unique effect of TP and temperature on cyanobacteria biomass was clear (Fig. 7C), yet substantial residual variation remained unexplained (53%), possibly due to among site variability in response-driver relationships. We thus applied a linear mixed effect model (LMM) to further characterize how the linear relationship (slopes) among cyanobacteria biomass, phosphorus and temperature varied among waterbodies (Fig. 8). The R^2-adj for this model was 0.77 (i.e. the conditional R^2-adjusted), and both TP and temperature were significant ($p < 0.05$). Interestingly, many of the Brazilian systems had higher intercepts for cyanobacteria biomass. Our results also showed that for a few Brazilian reservoirs, cyanobacteria biomass did not increase as expected with higher TP concentrations (Fig. 8A), which might be due to an interaction with another environmental driver, such as water retention time (WRT; Fig. 7B), that could affect bloom permanence.

Finally, to further examine the divergent importance of TP versus temperature among waterbodies, we used Generalized Additive Mixed Models (GAMMs) to model the non-linear response of cyanobacteria biomass to TP and temperature (Fig. 9). Our GAMM showed that the among-waterbody variability was due in part to how TP and temperature interacted along their gradients. Specifically, the effects of temperature and nutrients were non-linear and additive, with a maximal effect starting at temperatures above 20°C and TP concentrations above 100 μg/L (Fig. S3). Our analysis also shows that higher TP values will generally result in higher cyanobacteria biomass and that the probability of bloom occurrence increases steeply at higher phosphorus concentration (TP values on a log scale in Fig. 9). The effect of water

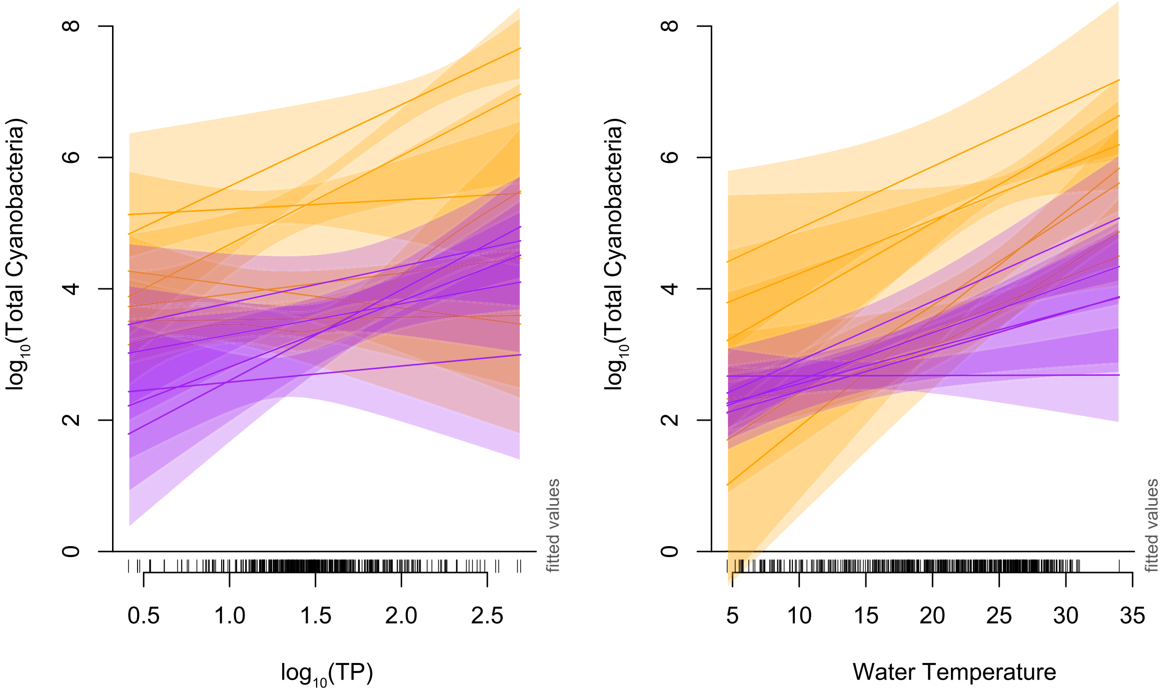

Fig. 8. Linear Mixed effect Models (LMMs) for cyanobacteria biomass versus total phosphorus (TP) (A) and water temperature (B). Lines represent the relationship for each waterbody (orange lines: Brazilian reservoirs; purple lines: Canadian lakes), with their respective confidence intervals. TP and temperature were used in the same model and the fitted lines for each variable were plotted in two separate panels

temperature becomes important at 20°C, also causing a rapid rise of cyanobacteria biomass beyond this temperature point. Since Brazilian reservoirs are located in sites where the average water temperatures are consistently above 20°C, temperature did not play a significant role in explaining among-site variability. However, our LMMTs demonstrates that all waterbodies showed a propensity to increase in cyanobacterial biomass as a function of temperature (Fig. 8).

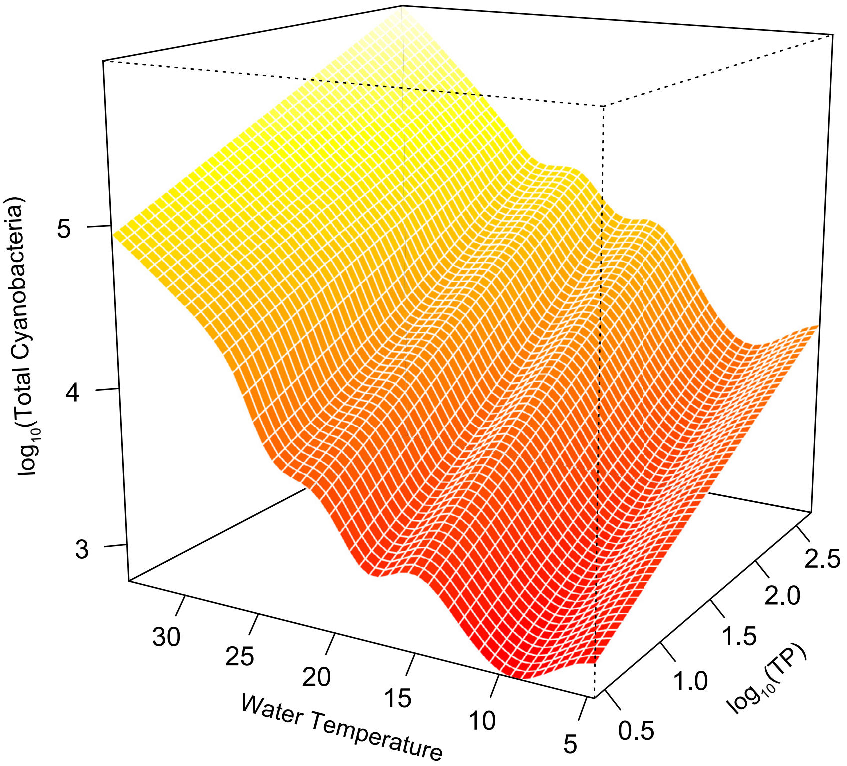

Fig. 9. Three-dimensional representation of the non-linear (GAMM) response of cyanobacteria to total phosphorus (TP) and water surface temperature, for the entire dataset (Brazil and Canada).

4. Discussion

Several models and simulations have been developed to explain and predict the widespread increase of toxic cyanobacteria blooms across different lake types and regions, although few studies have compared regions with a balanced design, giving tropical sites equal weight in model development (see references in Table S1). Our results showed that high nutrient concentration (as TP) was the major driver of elevated cyanobacteria biomass in each region (Figs. 5, 7A and 7B), which is consistent with many previous studies (Graneli et al. 1990; Hallegreff 1993; Stal et al. 1999; Anderson et al., 2002; Downing et al. 2001; Giani et al. 2005; Carpenter 2008; Conley 2009; Heisler et al. 2008; Beaulieu et al. 2014; Figueredo et al. 2016). However, our results also demonstrate that there are numerous secondary variables that can temper the response of cyanobacterial biomass to nutrients, and in the regions studied herein these parameters were water temperature, precipitation and water residence time. Another important finding was that Brazilian reservoirs generally had higher cyanobacteria biomass baselines (intercepts), which may be due to the longer growing season in the tropics.

The ubiquitous nature of nutrients being a primary driver of cyanobacteria blooms, together with intensifying urbanization and fertilizer use in agricultural practices (Carpenter 2008; Conley et al. 2009), could well translate into more cyanobacteria blooms in the future unless strong mitigation measures are put into place. Indeed, several authors showed that at higher phosphorus concentrations, the probability of cyanobacteria dominance over other planktonic species in an aquatic system increases significantly (Downing et al. 2001; Giani et al. 2005; Taranu et al. 2012), and that high cyanobacteria biomass has been identified as a catalyst for the switch to alternate stable states (Cottingham et al. 2015) with limited capacity of recovery, unless conditions of nutrient input change drastically. Our results confirmed that nutrient loading and accumulation in aquatic environments play a major role in cyanobacteria proliferation, independent of latitude.

More recently, bloom development and occurrence has been linked to climate change, in particular changes in temperature, precipitation and water-column stability (Elliott 2012; O'Neil et al. 2012; Taranu et al. 2012; Chapra et al. 2017; Paerl 2017). Our results showed that temperature was related to cyanobacteria biomass in both regions (Fig. 8). Even in the Brazilian reservoirs, where temperature fluctuations are smaller than in temperate lakes (Fig. 4), we noted that temperature interacted with nutrients to promote a rise in cyanobacteria biomass (Figs. 9 and S3). Temperature has a direct effect on cell growth, since cells reproduce faster at higher temperatures. Some debates exist regarding the ability of cyanobacteria to grow faster than other algae under warmer conditions, where some authors report no difference among cyanobacteria and green algae (Lürling et al. 2013). However, the optimal temperature for achieving maximum growth has been repeatedly shown to be higher for prokaryotic cyanobacteria than other algae (Robarts and Zohary 1987; Butterwick et al. 2005; Carey et al. 2012; Nalley et al. 2018), which suggests that cyanobacteria could outcompete other phytoplankton species at higher temperature, promoting an ideal setting for cyanobacteria to thrive.

Interestingly, in analyses where we compared the proportion of variation explained by temperature vs. nutrients in region-specific vs. pooled data (Fig. 7), we found that the temperature effect became more pronounced (variation explained increased to 30%) than that of TP when datasets were pooled (Fig. 7C). This overriding climate signal is likely due to the distinct differences in temperature between the temperate and tropical water bodies. We also noted differences among regions in terms of the relationship between cyanobacteria and temperature (Fig. 8B), with a tendency for steeper slopes in some Brazilian reservoirs than in some Canadian lakes. If we are to expect longer growing seasons with climatic changes, particularly when the average growing season water temperatures rise above 18-20°C, one might expect a significant upsurge of cyanobacteria biomass in temperate environments, as indicated by previous works (Beaulieu et al. 2013; Kosten et al. 2012). Indeed, there is evidence from remote-sensing analyses of 167 inland waterbodies distributed worldwide that lakes at mid and high latitudes are warming the fastest (Schneider & Hook, 2010), and thus these sites could be the most vulnerable to large increases in cyanobacteria. Similar to the non-linear response model we generated (Fig. 9), Kosten et al. (2012) also observed that the percentage of total phytoplankton biomass attributable to cyanobacteria increased markedly with temperature. Likewise, they reported that higher temperatures may lower the nutrient concentration threshold needed for bloom initiation, which agrees with the generally higher intercepts we detected in the cyanobacteria biomass ~ TP model for Brazilian reservoirs (Fig. 8A).

The combined effect of temperature and nutrients observed in the present study, (i.e., pronounced increase in cyanobacteria when temperatures exceeded 20°C and when TP was above 100 μg/L; Fig. 9) is also consistent with the suggested synergy between temperature and nutrient availability on growth rates. Many studies suggest that the influence of nutrient supply on growth rates should increase with temperature to some optimum (maximum growth rates) (Cross et al. 2015). This synergy was described as a “great challenge to water quality” in view of climatic change (Paerl & Paul 2012). Following metabolic theory assumptions, metabolic rates are constrained by temperature through its exponential effect on biochemical reaction rates at the level of organelles (Price et al. 2010). As temperature rises, autotrophs can use nutrients more efficiently (Cross et al. 2015). But, as photosynthesis and growth rates increase, growth will become limited by resource supply that, ultimately, will control the total biomass that a population can attain in a certain environment. Marañón et al. (2018) suggested that the direct, stimulating influence of increasing temperatures on phytoplankton metabolic rates will be confined, in the end, to environments with high availability of nutrients. Metabolic theory assumptions could thus be used to predict organismal response to environmental changes, such as the consequence of climate change (Duarte 2007).

Several authors observed that in warm environments, growth is more sensitive to changes in nutrient supplies than in cold ones, and that the critical nutrient threshold for favorable cyanobacteria growth is lower under warmer water scenarios (Elliott 2012; Kosten et al. 2012; Cross et al. 2015). Additionally, the strength of the response to temperature seems to be highly influenced by the trophic status of the waterbody, i.e., by nutrient concentration (Elliott 2012; Paerl & Paul, 2012; Rigosi et al. 2015). Therefore, controlling nutrient availability in the system would help to minimize the negative outcomes of warming climate and limiting nutrient inputs could help increase the resilience to algal blooms (Brooks & Carey 2011; Rigosi et al. 2015).

With respect to other climatic variables, even though water-column stability has frequently been associated with temperature increases and cyanobacteria blooms (Wagner & Adrian 2009; Carey et al. 2012; O'Neil et al. 2012; Huisman et al. 2018), this variable did not explain the cyanobacterial dynamics observed in our multi-lake dataset. With few exceptions, the average stability index was quite similar among regions (Fig. 4), while at the same time a large variation was observed in the time-series data within a given lake (for example Baptiste North or São Simão). When examining individual lakes or reservoirs, water stability can be an important variable to explain the occurrence of blooms and seasonal changes in any one particular system (Taranu et al. 2012).

Instead, we observed that other climate-related variables helped explain the increase in cyanobacteria biomass, notably water retention time and precipitation in tropical reservoirs (Fig. 5C). Precipitation has also been discussed as an important cyanobacteria bloom promoter and other authors have suggested that rainfall can have major effects on plankton (Havens et al. 2016; Paerl & Paul 2012). Increased precipitation may cause severe runoff, increasing the input of nutrients into waterbodies (Havens et al. 2017; Batista et al. 2018;

Huisman et al. 2018; Silva et al. 2019), as we observed in the Tropics for TP and precipitation (variation co-explained to some degree by both variables; Fig. 7B). If periods of rain are longer, however, they can also have a dilution effect on both the chemical composition of water and the plankton community itself (Reichwaldt & Ghadouani 2012; Rangel et al. 2012; Havens et al. 2017). Therefore, the effect of rain will be seasonally and intensity dependent. In the present study, precipitation was more variable in the Tropics than in temperate lakes (Fig. 4). Since in the tropical region precipitation is used to define dry vs rain season with yearly repeating patterns (Fig. S1) and it is not evenly distributed throughout the year (as seen in temperate systems with precipitation coming in form of rain or snow), it is not surprising that precipitation was observed as a significant predictor of cyanobacteria biomass in this region. Rain in the Tropics is equivalent to temperature in temperate zones, where it is used to demarcate seasons. In fact, we found less variation in temperature in the tropics (Fig. 4).

Water residence time (WRT) was also an important variable in our study. It is one of the key parameters controlling the physical, chemical and biological behavior of the aquatic systems (Rueda et al. 2006). When the tropical reservoirs were examined alone, we found that lower cyanobacteria biomass was related to lower WRT (i.e., faster flushing of the systems; Fig. 5B), suggesting that the very low WRT observed in some reservoirs caused a washout of phytoplankton by internal currents. WRT in these Brazilian reservoirs is also affected by precipitation, since intense rain periods may increase the water flow, thus reducing residence time. Current and future climate change may have an effect on retention times, modifying movements and hydrodynamics of aquatic systems (Elliott et al., 2010; Brookes & Carey 2011; Huisman et al. 2018). Altogether, low flows and high temperatures (Elliott et al., 2010), as well as longer residence time and dry seasons (Elliott 2012; Romo et al. 2013), describe favorable conditions for cyanobacterial growth and accumulation.

When both study regions were analyzed together, WRT became the most important variable in distinguishing sites with high versus low cyanobacteria biomass, or rather, Canadian lakes from Brazilian reservoirs (Fig. 6). Brazilian reservoirs had lower water retention rates than Canadian lakes (Fig. 4), which is typical of reservoirs anywhere. Reservoirs, in general, are an intermediate type of water body between rivers and natural lakes (Thornton et al 1996). However, the large variation in their size, morphometry, hydraulic factors and applications causes considerable differences among them as well. Effects of artificial management control in reservoirs depend on their primary use, as for example flood control, drinking water supply, recreation, and power generation. Four of the five Brazilian reservoirs included in our study were constructed for hydropower generation, and one (Pampulha) was used for flood control. In these reservoirs, flushing pulses can be induced by anthropogenic activity, related to regulation of flood or energy production (Zarfl et al. 2015). We thus expect important and frequent changes in WRT in these systems, and this could help explain why cyanobacteria biomass was sensitive to this driver.

Increasing flushing, and the consequent reduction in water residence time, has been suggested as a management strategy to minimize algal blooms. Havens et al. (2016) observed how flushing variance affected cyanobacteria growth during periods of high rainfall and water discharge by periodically disrupting their growth. They found that at flushing rates sometimes as high as 18% of total lake volume in a month's time, cyanobacterial biomass was noticeably reduced. Paerl et al. (2016) proposed physical-forcing mitigation techniques, such as flushing and artificial mixing, as an alternative method to control cyanobacteria blooms in highly eutrophic systems. The same suggestion was given by Romo et al. (2013) who stated that if retention time and water balance in the watershed could be managed, allowing periodical lake flushing, this could be used as a restoration tool to reduce toxic cyanobacteria growth in waterbodies. In their study of Lake Albufera (Spain), Romo et al. (2013) registered orders of magnitude decreases in *M. aeruginosa* populations when discharge rates were above 10 m^3/s and when water retention time increased by about 45%.

Besides excess nutrients (eutrophication) and climate-related changes, such as temperature increases and thermal stratification, Paerl and Paul (2012) considered reduction in flow regimes and water residence time as one of the main causes for bloom events. Our results are well in agreement with these findings. Systems that had lower than expected cyanobacteria biomass at certain phosphorus concentrations (Fig. 8) were waterbodies with lower WRT, which probably prevented bloom occurrence. To apply our findings to a wider range of lakes, we encourage researchers to expand these models in the future to additional waterbodies, covering more gradients of temperature and water residence time. As such, the thresholds for temperature and water residence time identified in this study should be viewed as preliminary until more data can be added.

Taken together, our modeling approach including both temperate and tropical regions showed that if no effective control is put in place to reduce eutrophication, we can expect cyanobacteria blooms to increase in aquatic ecosystems under future climate change. Temperate systems seem somewhat "protected" from the worst bloom conditions by the arrival of winter and significant temperature drops; in tropical systems, situations of permanent blooms already exist, even though they may benefit from high flushing rates during the rainfall season reducing nutrients and algal biomass. At the ecosystem level, algal blooms imply a significant loss of species and functional diversity (Roelke and Buyukates, 2002; Watson et al. 2015), affecting trophic webs as fewer zooplankton species will be able to feed on cyanobacteria than on other algae (DeMott et al. 2001). The response of organisms or trophic levels to external stressors will scale up to influence the dynamics of the entire ecosystem (Vinebrooke et al. 2004; Cross et al. 2015). Because of their synergy, multiple stressors may increase the size of the environmental response (Scheffer et al. 2001). If the combined effect of several stressors results in severe algal blooms, as we observed in our non-linear additive models based on temperature and TP, it is also possible that the systems will reach a threshold and move toward an alternate stable state, where resilience is lost and the lakes will no longer be able to recover to a previous healthier state (Carpenter et al. 1999; Scheffer et al. 2001; Beisner et al. 2003), therefore making the management and recovery of these waterbodies extremely difficult and costly.

Table 1

Table 1
Limnological characteristics of the Canadian lakes and Brazilian reservoirs (mean values).

	Water Temp °C	PCPN mm/ month	WRT **days/year *** year	TP µg/L	SI g/cm^3	CBB µm^3/mL
Emborcação	28.7	127	201 **	6	102.9	241158
Furnas 01 *	25.3	109	280 **	17	78.9	104447
Furnas 02 *	25.3	109	280 **	23	77.4	801105
Marimbondo	26.2	114	28 **	34	52.4	1773691
Pampulha	24.3	160	24 **	226	71.8	31875049
São Simão	26.9	79	20 **	20	30.0	71470
Volta Grande	26.1	152	2 **	22	25.2	21981
Baptiste North	14.8	57	6 ***	75	76.6	8609
Baptiste South	15.2	59	6 ***	64	123.8	10954
Ethel	15.4	51	2.5 ***	21	123.5	1426
Nakamun	15.4	56	21 ***	66	36.5	5589
Wabamun	15.6	65	100 ***	32	19.2	2475

PCPN: precipitation; WRT: water retention time; TP: total phosphorus; SI: Stability Index; CBB: cyanobacteria biomass
NB: WRT is shown here in days/ year for Brazil reservoirs and years for Canadian lakes, whereas WRT is presented in years for both datasets in all statistical analyses and corresponding figures.
*Furnas 01: branch of Rio Grande river
Furnas 02: branch of Sapucaí river

Acknowledgments

Sampling and samples processing in Brazil were supported by grants from Furnas Centrais Hidroelétrica S.A., Centrais Elétricas de Minas Gerais (CEMIG), Fundação do Amparo a Pesquisa de Minas Gerais (FAPEMIG), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) to AG. A sabbatical visit of AG to the McGill University was supported by a CAPES Senior Fellowship. In Canada, funding was provided from a Natural Science and Engineering Research Council (NSERC) Strategic grant awarded to IGE. We also thank all members of the Phycology laboratory at the Universidade Federal de Minas Gerais UFMG for technical support in sampling and analyses. We are grateful to the help provided by Dr. Ron Zurawell in acquiring all Canadian lakes data, as well as the Alberta Environment and Parks (McIntyre Office) field staff for collecting water samples according to standard water quality sampling field protocols.

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.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.hal.2020.101859.

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