Acta Limnologica Brasiliensia



# Evaluating the growth potential of harmful cyanobacteria in aquatic environments under climate change scenarios

Avaliando o potencial de crescimento de cianobactérias nocivas em ambientes aquáticos em cenários de mudanças climáticas

Ariane Guimarães<sup>1\*</sup> (D), Pablo Silva<sup>2</sup> (D) and Daniel Paiva Silva<sup>3</sup> (D)

<sup>1</sup>Programa de Pós-graduação em Recursos Naturais do Cerrado, Universidade Estadual de Goiás, Fazenda Barreiro do Meio, BR 153, nº 3.105, 75132-903, Anápolis, GO, Brasil

<sup>2</sup>Programa de Pós-graduação em Ecologia e Evolução, Universidade Federal de Goiás, Avenida Esperança, Térreo bloco ICB5, s/n, 74690-900, Goiânia, GO, Brasil

<sup>3</sup>Departamento de Ciências Biológicas, Instituto Federal Goiano, Rodovia Geraldo Silva Nascimento, Km 2,5, s/n, 75790-000, Urutaí, GO, Brasil \*e-mail: arianeifgoiano@gmail.com

**Cite as:** Guimaráes, A., Silva, P. and Silva, D.P. Evaluating the growth potential of harmful cyanobacteria in aquatic environments under climate change scenarios. *Acta Limnologica Brasiliensia*, 2025, vol. 37, e5. https://doi.org/10.1590/S2179-975X0424

Abstract: Aim: Neotropical freshwater environments face severe threats from climate change, posing significant risks to global water security. Extreme hydrological events, such as torrential rains and prolonged droughts, are expected to become more frequent and intense. These conditions increase the residence time of nutrients, especially phosphorus and nitrogen, favoring the proliferation of harmful cyanobacteria (cyanoHABs). Furthermore, cyanobacteria are competitive in environments with few nutrients and high CO<sub>2</sub> concentrations. This feature exacerbates ecological and public health challenges, as these cyanobacteria can cause harmful algal blooms that contaminate water supplies and disrupt aquatic ecosystems. We aimed to evaluate the growth of cyanobacteria in specific regions concerning the prevalence of three representative species of cyanoHABs. Methods: We used ecological niche modeling tools (ENMs) based on occurrence records from available databases to predict the distribution of the three most frequently representative species of cyanoHABs. We employed three different modeling methods: generalized linear models (GLM), Gaussian models (GAU), and maximum entropy (MXS). Results: The potential distributions for the current scenario were consistent with known distributions for the modeled cyanoHABs in the ENMs results. Still, we identified new areas of research for future scenarios. Conclusions: The variations we observed indicate that the impacts of climate change vary regionally, affecting the future fitness of cyanobacteria. In the short term, they may maintain stable fitness, but a significant reduction is expected in the long term due to high temperatures. This result highlights the urgent need for mitigating actions to protect aquatic ecosystems.

**Keywords**: ecological niche model; cyanoHABs; *Microcystis aeruginosa*; *Planktothrix agardhii*; *Raphidiopsis raciborskii*; toxins.



#### **Graphical Abstract**



Resumo: Objetivo: Os ambientes neotropicais de água doce enfrentam graves ameaças das mudanças climáticas, representando riscos significativos para a segurança hídrica global. Espera-se que eventos hidrológicos extremos, como chuvas torrenciais e secas prolongadas, se tornem mais frequentes e intensos. Essas condições aumentam o tempo de residência dos nutrientes, principalmente fósforo e nitrogênio, favorecendo a proliferação de cianobactérias nocivas (cianoHABs). Além disso, as cianobactérias são competitivas em ambientes com poucos nutrientes e altas concentrações de CO2. Esta característica agrava os desafios ecológicos e de saúde pública, uma vez que estas cianobactérias podem causar proliferação de algas nocivas que contaminam o abastecimento de água e perturbam os ecossistemas aquáticos. Nosso objetivo foi avaliar o crescimento de cianobactérias em regiões específicas quanto à prevalência de três espécies representativas de cianoHABs. Métodos: Utilizamos ferramentas de modelagem de nicho ecológico (ENMs) baseadas em registros de ocorrência de bancos de dados disponíveis para prever a distribuição das três espécies mais frequentemente representativas de cianoHABs. Empregamos três métodos de modelagem diferentes: modelos lineares generalizados (GLM), modelos gaussianos (GAU) e entropia máxima (MXS). Resultados: As distribuições potenciais para o cenário atual foram consistentes com as distribuições conhecidas para os cianoHABs modelados nos resultados dos ENMs. Ainda assim, identificamos novas áreas de pesquisa para cenários futuros. Conclusões: As variações que observamos indicam que os impactos das mudanças climáticas variam regionalmente, afetando a aptidão futura das cianobactérias. No curto prazo, podem manter a aptidão estável, mas espera-se uma redução significativa no longo prazo devido às altas temperaturas. Este resultado destaca a necessidade urgente de ações mitigadoras para proteger os ecossistemas aquáticos.

Palavras-chave: modelo de nicho ecológico; cyanoHABs; *Microcystis aeruginosa*; *Planktothrix agardhii; Raphidiopsis raciborskii*; toxinas.

#### 1. Introduction

Climate change fundamentally impacts the frequency and global distribution of harmful blooms in aquatic environments (Meriggi et al., 2022; Prakash et al., 2024) with the predicted increase in extreme weather events due to climate change (Tuchyňa & Haas, 2025), an increase in shortterm hydrodynamic fluctuations is expected, which favor the proliferation of harmful cyanobacteria (CyanoHABs) (Marrone et al., 2024). These climate patterns include episodic hydrological events, such as droughts (Kimambo et al., 2019) and flooding (Stockwell et al., 2020), which alter the residence time of nutrients, particularly phosphorus and nitrogen (Igwaran et al., 2024). Furthermore, harmful cyanobacterial blooms can occur in environments with low nutrient levels and high  $CO_2$  concentrations (Ma & Wang, 2021), highlighting the ability of these species to adapt to adverse environmental conditions (Cameron et al., 2024).

Considering the results of the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), which suggests a greater than 50% probability of global temperatures exceeding the limit of 1.5°C by 2040 (Intergovernamental Panel on Climate Change, 2022), the spread and permanence of cyanobacteria forming of harmful blooms in water reservoirs can become a significant problem (Kimambo et al., 2019). Harmful algal blooms cyanobacteria are known for their ability to produce cyanotoxins and hypoxic conditions, resulting in the death of fish and other aquatic species (Kimambo et al., 2022). They also disrupt the food chain, impacting biodiversity levels and aquatic ecosystems. Investigations into this subject reveal that spatial and temporal changes in CyanoHABs events in lentic systems, including artificial reservoirs, are influenced by climatic variables such as solar radiation, temperature, and precipitation (Chapra et al., 2017). The filamentous cyanobacteria Planktothrix agardhii (Gomont) Anagnostidis & Komárek 1988 (order Oscillatoriales) and Raphidiopsis raciborskii (Woloszynska) Aguilera, Berrendero Gómez, Kastovsky, Echenique, and Salerno 2018 (order Nostocales), and the colonial species Microcystis aeruginosa (Kützing) Kützing (order Chroococcales), are the most successful bloom-forming organisms in shallow lakes (Mantzouki et al., 2018). Considering these species, understanding the impact of climate change on their distributions and persistence in water reservoirs is crucial to assessing their growth potential in aquatic environments. In particular, we chose cyanobacterium M. aeruginosa, a temperaturesensitive species (Huisman et al., 2018). The species P. agardhii forms large, perennial populations in shallow, eutrophic reservoirs worldwide (Padisák et al., 2016), posing a significant problem in countries with inadequate water treatment. Microcystis aerugionosa produces Microcystin-LR (Huisman et al., 2018). Finally, the cyanobacterium R. raciborskii thrives by forming toxic blooms in reservoirs, lakes, and rivers worldwide (Yang et al., 2018) and producing various types of toxins, including cylindrospermopsin and saxitoxin (Poniedziałek et al., 2012). We chose these three species are our model organisms in this study.

One of the commonly used methods for predicting species distributions and understanding their environmental requirements is ecological niche modeling (ENM). Such methods estimate the suitability of species based on their environmental requirements. Previous research has already used ENMs to estimate the distribution of toxic cyanobacteria (Goncharenko et al., 2021; Guimaráes et al., 2020; Meriggi et al., 2022). We assume that climate change will increase the suitability areas of the chosen species, allowing us to assess the growth potential of specific regions to the prevalence of three cyanoHABs representative species.

We adopted a higher taxon approach, modeling their niche as a species assemblage, as they share similar ecological requirements due to the limited number of records available. By employing this approach, we generated present and future suitability maps to evaluate the geographical impact of climate change on suitability patterns in Brazil. These maps serve as valuable tools for monitoring water reservoirs throughout Brazil. We focused on the main Brazilian water reservoirs to identify areas highly susceptible to cyanobacterial blooms. For each location, we investigated whether there was an increase in suitability, aiming to elucidate the relationship between climate change and the heightened susceptibility to blooms. Furthermore, we proposed a hypothesis stating that the correlation between present and future suitability in water reservoirs exhibits a positive trend, indicating an expansion of suitable areas and, consequently, creating favorable conditions for the proliferation of cyanoHABs.

#### 2. Material and Methods

# 2.1. Database of the occurrence of cyanobacteria in freshwater environments

We searched for occurrences of these species on a global scale using the Global Biological Information Facility (GBIF, 2023), to assess the growth potential of specific regions for the prevalence of three representative species of harmful cyanobacteria. We chose to use records of cyanobacteria species occurrences on a global scale, as these species are widely distributed globally. Therefore, using data only for Brazil and confirmed bloom events would leave an incomplete model. Under these conditions, we would not capture the entire realized niche of the species, biasing the model. We know that the evidence in Brazil highlights a great sampling effort in the Atlantic Forest region. In contrast, only a few areas were sampled in the Amazon Forest region. The northern portion of Brazil, which still has a lower suitability for bloom events compared to other areas with a large concentration of urban centers and population, requires more precise sampling (Guimarães et al., 2020).

Based on the taxonomic change of R. raciborskii, we also performed the search considering its previous name, Cylindrospermopsis raciborskii, to ensure that we were describing its niche. We initially obtained 789 records for R. raciborskii, 8,207 for P. agardhii, and 1,089 for M. aeruginosa. We applied several criteria often used in ENMs to improve the quality of data and correct potential problems associated with this database, such as: (1) we fixed possible exchanges between longitude and latitude, (2) we removed records that did not contain geographic coordinates and duplicates, and (3) we did not consider occurrences in marine environments. We chose to use occurrence records on a global scale, as the cyanobacteria species are globally distributed, and therefore, using data only for Brazil would leave the model incomplete. In such conditions, we would not capture the complete realized niche of the species, biasing the model.

We thought a higher taxon approach would be necessary to estimate climate suitability, including all records for modeling procedures to describe the cyanoHABs, as these three species share the same ecological requirements and represent the same bloom risks. This solution can enhance the fit of our models, thereby avoiding problems associated with Wallacean and Hutchinsonian shortfalls that may lead to overprediction and underprediction in niche modeling. Ultimately, we had only 440 records considering these three species.

# 2.2. Environmental variables

Since cyanobacteria are prokaryotes, and their growth rates are optimized at high temperatures (Paerl & Paul, 2012), we chose the temperature variables, considering that climate variations on large geographic scales can modify community structures in freshwater ecosystems (Domisch et al., 2015). The temperature at which cyanobacteria exhibit the highest growth rate varies depending on the specific cyanobacterial species. It can vary from 20 °C for the species P. agardhii to 28 °C for M. aeruginosa. In particular, the cyanobacteria M. aeruginosa is a temperature-sensitive species, and environmental variables are known to play an important role in its initiation of colony formation (Huisman et al., 2018). Raphidiopsis raciborskii causes blooms at temperatures ranging from 20 °C to 35 °C. Such a wide temperature range has allowed this species to invade temperate zones (Hong et al., 2006). In temperate regions, the species is found during the summer, when temperatures are around 26 °C (Hamilton, 2018), and exhibits permanent

blooms in tropical lakes throughout the year. In subtropical lakes, however, they are restricted to the summer (Vieira et al., 2018). We also chose the variable precipitation because, during the rainy season, there is a greater transport of nutrients to aquatic ecosystems, with an increase in the density of cyanobacteria being observed. Another factor is that extreme precipitation in a reservoir causes an increase in nutrient concentration (Simić et al., 2017). We also consider that aquatic chemical environments are and will continue to be influenced by increases in  $CO_2$  concentration in the atmosphere, whether through changes in pH or declines in carbonate ion concentrations (Meriggi et al., 2022; Paerl & Huisman, 2009).

The 19 bioclimatic variables, a crucial component of our study, were sourced from WorldClim version 2.1. These variables were instrumental in our models, aiding in the estimation of climate suitability for cHBAs in both present and future scenarios. The data were generated from interpolations of climate conditions collected between 1970 and 2000 and represent a set of primary conditions that assist in estimating the ecological niche (Fick & Hijmans, 2017). We considered six Global Atmosphere-Ocean Circulation Models, with projections for the climate to 2040, 2060, 2080, and 2100, which were BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, IPSL-CM6A-LR, MIROC-ES2L, and MIROC6. All six models belonged to the CPMI6 approach, representing an improvement since the last version of these climate projections. Within our niche modeling, we focused on the ssp585 scenario, which represented the most pessimistic outlook. Given their high dispersion rates, we considered the grid cell resolution of 10 arc-min (~18.5 km at the Equator) to model these cyanoHABs globally. Thus, large cells could show a more significant effect of climate on the distribution of the species.

Given the multicollinearity among the bioclimatic variables, we performed a principal component analysis (PCA) to reduce the number of predictor variables and create new orthogonal principal components for predicting species distribution using the new environmental variables. We projected the PCA linear coefficients of the current scenario into future scenarios and performed a PCA on those climate projections. The selected orthogonal components accounted for 95% of the original variation in climate. This treatment simplifies the algorithms used for model fitting, thereby ensuring more accurate and realistic predictions. Also, there is evidence that this method has increased the accuracy of ENM (De Marco & Nóbrega, 2018).

# 2.3. Modeling procedures

The ENM method, a cornerstone in our research, is based on models that use species tolerance limits to project suitability in geographic space according to environmental conditions. In ENMs, the ecological niche of a species is fully known and conserved over time, depending on the distribution pattern of the occurrence records (Peterson, 2011). Consequently, the estimation of species distribution derives from the niche concept. The theory describes the niche as a biotic-abioticmigration (BAM) diagram, composed of three essential elements that consider the occurrence of species, with their distribution represented by the intersection (Soberón, 2007). Overall, these elements can be summarized by the biological interactions necessary to maintain ecological functions (B), suitable environmental conditions for species survival (A), and the ability to disperse and occupy suitable regions (M). For cyanobacteria, the accessible region is wide, with practically no geographic restrictions affecting their occurrence (Padisák et al., 2016). Still, these species require a dispersal agent (e.g., rivers, air, animals, humans) and travel conditions that meet their transport tolerance (Padisák & Naselli-Flores, 2021). Given the lack of restrictions on dispersal, mobility has an exceptionally low or even nonexistent effect. Therefore, the set of environmental conditions can be significantly representative of these organisms' geographic distribution.

We considered algorithms with different methods of fitting to predict climate suitability for the cyanoHABs: (i) based only on actual presences, (ii) presences and background, and (iii) presences and absences. Thus, we selected the Generalized Linear Model (GLM) (Guisan et al., 2002), the Gaussian Model (GAU; (Vanhatalo et al., 2012), and the Maximum Entropy (MXS) (Phillips et al., 2006; Phillips & Dudík, 2008). We created pseudoabsences to meet algorithm requirements, as data on absence in nature are difficult to obtain. Based on this, we used bioclimatic envelopes similar to the BioClim algorithm (Booth et al., 2014). This procedure constrained the occurrence points of the taxa in the geographical space using a bioclimatic envelope (Lobo & Tognelli, 2011; VanDerWal et al., 2009). Therefore, we allocated pseudo-absences in external areas considered unsuitable for species occurrence at a ratio of 1:1. We focused the evaluation metrics on three components of the confusion matrix: true positives, false positives, and false negatives. We sought to maximize true positives and minimize false positives and false negatives relative to true positives.

The Jaccard metric, a key tool in our evaluation process, measures the similarity between predictions and observations. A value of 1 indicates that the forecasts perfectly match the observations without any false positives or false negatives. In contrast, a value of 0 indicated that none of the forecasts corresponded to the observation. The lower the similarity value, the greater the number of false positives and false negatives concerning the number of true ones (Leroy et al., 2018). The predictions are assumed to be acceptable in reaching values close to 0.7, while "excellent" projections reach values closer to 0.9. We performed all modeling procedures in R software version 4.0.3 using the ENMTML Package (Andrade et al., 2020). We represented the final distributions using consensus maps to reduce the uncertainties associated with each algorithm (Araújo & New, 2007) and ensure a high quality of the models. We made the consensus maps using the mean of the models that presented Jaccard values above the mean. The mean was 0.945, meaning the GLM method was not used in the ensemble. The idea of consensus models considers that different errors can affect the final result (e.g., model sensitivity and the lack of true absences). For this reason, the literature has argued that using consensus maps as final distribution models can reduce the number of errors (Diniz Filho et al., 2010). This method produces ecological niche models from the most accurate algorithms, resulting in potentially more realistic predictions.

# 2.4 Analytical procedures

We produced suitability maps for cyanoHABs for the present and the four future projections (e.g., 2040, 2060, 2080, and 2100). For this reason, we restricted the presentation to Brazilian territory, as we aimed to focus on the water reservoirs distributed across this geographical area. These maps can support the monitoring of water reservoirs, identifying areas of high suitability that require attention. Each map presents the consensus among the algorithms used for modeling this group. We used data from water reservoirs distributed throughout the Brazilian territory to evaluate the growth potential of harmful cyanobacteria in lentic environments, with a focus on three representative CyanoHAB species. The data were downloaded on June 28, 2023, and are available at Sistema de Acompanhamento de Reservatórios (SAR, 2023). These data are part of the Sistema de Acompanhamento de Reservatórios, officially launched in 2014. SAR consists of a web platform that enables the monitoring of the main reservoirs in Brazil, providing access to the geographical coordinates of these reservoirs. Altogether, we considered only 70 occurrences of reservoirs with dams after removing 92 pumping power plants without dams. For each water reservoir coordinate, we extracted suitability values from the current and future models to evaluate assumptions about the growth potential of harmful cyanobacteria.

We employed two distinct methodologies to comprehend the suitability of the alteration in the context of climate change scenarios. We assessed whether there were any modifications in the suitability of the climate projections for the future in the initial approach. To accomplish this, we subtracted the values of future suitability from the present. We created a forest plot chart to visualize the changes using the average value and a 95% confidence interval, distinguishing between water reservoirs that increase and decrease their suitability under climate change scenarios. However, this methodology does not provide evidence of the real suitability value but highlights the water reservoirs impacted by climate. Based on this, we applied a second approach using a dispersion chart, and to further improve our understanding of the impact of climate change, we included a line that cut the y-axis at 0, indicating no change. We developed all analytical procedures in the software R version 4.3.1.

# 3. Results

We observed an excellent assessment of our niche model, except for the GLM algorithm, in which the Jaccard index was evaluated at 0.74. The other algorithms and the ensemble were evaluated above 0.9. Overall, the Brazilian territory has shown suitability for the occurrence of cyanoHABs. On the other hand, the northern and southern regions presented low suitability, which expanded following the projections for future climate scenarios. The core Brazilian regions exhibited high suitability values, indicating potential areas for cyanobacteria growth. We observed an expansion of the low-suitability regions in future scenarios, increasing further for projections with longer future times (Figure 1). We discovered that few water reservoirs exhibit a disparity between their present and future suitability, with only a few locations showing a decrease or increase in their values. Overall, most units showed no difference, indicating similar concerns for both the present and the future (Figure 2). Each projection has a variation in the number of water reservoirs that intensifies their growth potential for cyanoHABs, such as seven units increasing suitability in 2040 compared to four units in 2100. On the other hand, two units decreased suitability in 2040, whereas eight units decreased in 2100, thereby reducing the growth potential in the distant future.

Although the data indicate a reduction in CyanoHABs' growth potential, the picture changes when we examine actual suitability values. Most units have high suitability values in the three initial projections (for example, 2040, 2060, and 2080) (Figure 3). However, there was greater variation in suitability values in 2100 than in the other scenarios.

The Correlation (R) values were consistently high in all years analyzed, ranging from 0.94 to 0.97, with extremely low significance values (p < 0.001). This result indicates a strong relationship between current and future suitability, suggesting that current conditions are good indicators of future ones, albeit with significant variations over time. For 2040, most points are close to the reference line (1:1), suggesting that future suitability does not diverge significantly from current suitability. A few blue dots above the line indicate a slight upward trend in suitability. In 2060, there will be a strong correlation, similar to that of 2040. However, a slight increase in the dispersion of the points is observed. Some locations show increased future suitability (blue dots), while others indicate a decrease (red dots). By 2080, the dispersion of points increases significantly, indicating more pronounced changes in future suitability. A more balanced mix of blue and red dots suggests that both increases and decreases in fitness are more common. And finally, in 2100, the dispersion is even greater, with a slightly lower correlation, although still high. This increase in variability suggests that climate change will have a more complex and heterogeneous impact on the suitability of cyanoHAB habitats. Red dots become more prevalent, indicating a greater trend of decreasing future suitability in several regions. Overall, the results suggest that although current suitability is a good predictor of future suitability, climate change introduces significant variability. Over time, some areas are expected to

Evaluating the growth potential...



**Figure 1.** Suitability maps for Brazil based on current and projected global climate models for the years 2040, 2060, 2080, and 2100. The colors range from white to red; the most suitable cells are red.

become more suitable for certain species (indicated by blue dots), while others will become less suitable (indicated by red dots)

#### 4. Discussion

We observed a high correlation between the current and future suitability of cyanobacteria in different decades, as evidenced by correlation coefficients (R) greater than 0.94 in all cases, with statistical significance (p < 0.001). However, we observed important variations in suitability over time, suggesting a significant impact of climate change. The future suitability of cyanobacteria

decreased significantly compared to the current suitability in 2100, as illustrated by the spread of points below the red line of equality. This declining trend is consistent with the hypothesis that excessively high temperatures predicted for the end of the 21<sup>st</sup> century will cause significant damage to cyanobacterial photosynthetic systems, particularly photosystem II, resulting in reduced photosynthetic efficiency. For 2040 and 2060, most points are close to the line of equality, indicating that future suitability does not differ drastically from current suitability in these periods. This result may suggest that, until these decades, cyanobacteria can still



**Figure 2.** A forest plot illustrates the disparity in suitability between future and present conditions. In the depiction, blue points represent water reservoirs where future suitability is projected to decline. In contrast, white points indicate no discernible difference, and red points signify an increase in suitability.

maintain the photosynthetic efficiency necessary to survive and proliferate. In 2080 and 2100, increased dispersion of points indicates an increasing variability in the response of cyanobacteria to future conditions, with several localities showing a notable decrease in suitability. The points representing an increase in suitability (in red) are limited and rare, suggesting that cyanobacteria can benefit only from predicted environmental changes under specific conditions. The predominance of points indicating a decrease in suitability (in blue) reinforces the concern that climate change, particularly rising temperatures, is unfavorable for most cyanobacteria.

The observed variations indicate that the impacts are not uniform in all regions studied. Our geographical assessment of the growth potential of harmful cyanobacteria revealed that northern and southern Brazilian regions are not particularly susceptible to this potential for growth, with the highest susceptibility found in the Southeast, Central–West, and Northeast regions. The lack

Acta Limnologica Brasiliensia, 2025, vol. 37, e5

of suitability observed in the southern region may reflect incomplete data on regional distribution or concentration in centers of high human density (Whittaker et al., 2005). Another explanation for the low occurrence in the north is that lotic environments are less conducive to flowering than lentic environments (Komárek et al., 2014). On the other hand, the core Brazilian areas showed high suitability values, indicating areas susceptible to the growth of cyanobacteria and potential bloom events. Overall, both the current and future niches of cyanoHAB may suggest that these species already have the potential to occur in a large part of the country, with an emphasis on the central region of Brazil, which increases the possibilities of flowering in these areas. Despite the data limitations in describing the niche for each species, the higher taxon approach provides an overview of their potential distribution, assisting decision-makers in elaborating a warning map for cyanobacteria blooms as a proposal for monitoring lentic environments.



**Figure 3.** The charts display the relationship between the current and future suitability of environmental variables for 2040, 2060, 2080, and 2100. Each point represents a suitability value for an environmental variable at a given location. The diagonal red line indicates the reference line where future suitability equals current suitability. The color of the dots indicates predicted changes in future suitability: blue represents increases, red represents decreases, and white represents constancy.

Most water reservoirs showed no difference, evidencing similar concerns for present and future scenarios. Each projection showed a variation in the number of water reservoirs that intensify the growth potential of cyanoHABs, with seven units increasing suitability in 2040, compared to four units in 2100. On the other hand, two units decreased their suitability in 2040, while eight units declined by 2100, indicating a reduction in the growth potential of harmful cyanobacteria in the more distant future (by 2100). However, the scenario changed when we looked at actual adequacy values. Most units had high suitability values in the three initial projections (2040, 2060, and 2080), and by 2100, there was greater variation in suitability values.

Knowing that the concentration of  $CO_2$  in the atmosphere will reach 794–1150 ppm by 2100 (Intergovernmental Panel on Climate Change, 2022) and that in environments where there

may have a significant competitive advantage over other aquatic organisms and form blooms, an explanation for the decline in suitability in 2040 and of eight units in 2100, it could be excessively high temperatures. Excessively high temperatures have been widely recognized as causing significant damage to the photosynthetic systems of cyanobacteria. Considering that photosystem II is crucial for photosynthesis and is particularly sensitive to thermal stress combined with the denaturation of proteins in PSII, we would have a reduction in the photosynthetic efficiency of cyanobacteria (Walter Helbling et al., 2015). Another point is that if the number of susceptible areas for cyanoHABs decreases, we could expect two extremes in the climate change scenario: a more significant frequency of storms and prolonged

are few available nutrients, such as nitrogen and

phosphorus, and high levels of CO<sub>2</sub>, cyanobacteria

droughts. The frequency of extreme rain events will change precipitation limits, and heavy rains will occur more frequently (Trenberth et al., 2003).

Consequently, changes in rainfall patterns will lead to favorable conditions for the growth of cyanobacteria due to a more significant entry of nutrients into bodies of water during heavy rains (Budai & Clement, 2007). Such conditions can contribute to intensifying eutrophication and prolonged heating periods without mixing the water column (Charlton et al., 2018). Primarily, precipitation episodes produce changes in physicochemical conditions (e.g., temperature, nutrients, light, and conductivity). These changes, in turn, depend on the particularities of the precipitation event, the basin's hydrology, the use of the soil in the catchment area, and the trophic state of the aquatic system (Nóges et al., 2011). On the other hand, the frequent occurrence of heavy rain events can also lead to a temporary halt in the proliferation of cyanobacteria due to discharge and destratification, and significant storm events have a long-term adverse effect on cyanobacteria proliferation (Xiao et al., 2017).

Cyanobacteria have become a global concern because they possess the potential to produce a range of metabolites with biological activity. Knowledge about the distribution patterns of Neotropical cyanobacteria is essential, but it remains inconsistent and fragmented. Some species of cyanobacteria are widely distributed, but most of the group occurs in restricted environments. Therefore, while niche models indicate a wide distribution, the presence of cyanoHAB representative species will also depend on local conditions, which climate change can facilitate, thereby increasing bloom events. Usually, information about cyanobacteria occurrences is not randomly distributed in the geographic space. In general, the geographic distributions of these species present numerous information gaps (Wallacean deficit), often related to the need for more collection efforts. Although knowledge of the spatial and temporal distributions of cyanobacteria species in the environment at local, regional, and continental scales is limited (Naselli-Flores & Padisák, 2016), it is possible to make estimates to overcome the lack of information on the distribution of these species based on their ecological niche.

Our findings indicate that areas of suitability for the current scenario have high human density, and the supply reservoirs have persistent blooming histories. Regarding the future scenario, our projection results indicate an increase in the areas

with the potential distribution of the two species. Therefore, monitoring toxic cyanobacteria and cyanotoxins is essential to identifying potential risk sites. Usually, monitoring programs collect samples in the field and analyze them in the laboratory, requiring time, sophisticated equipment, and specialized staff, limiting the collection points and frequency. Consequently, conventional monitoring programs are limited to providing a generic assessment of the ecological quality of the studied sites and are insufficient for providing monitored bloom development warning systems throughout the monitored water body (Hunter et al., 2010). It is well known that the rapid detection capability of potentially toxic cyanobacteria can be accomplished through the ability to detect both remote images and packages and arrays that can detect and provide realtime information (Stumpf et al., 2016). In countries such as the United States, rapid advances are being made in detecting events and, in some cases, predicting their occurrence, which may potentially reduce their impacts (Sellner et al., 2003). Such advances and techniques are still far from widespread in Brazil, which may underestimate the current occurrence rates of bloom events in the country, affecting the availability of event data.

Finally, we can consider that temperature is the primary barrier to expanding into latitudes for most species with distributions in low latitudes (temperate climates). Considering the occurrence data of R. raciborskii at low temperatures, its presence is possible at temperatures below 12°C (Pagni et al., 2020). To ensure the successful dispersal of cyanobacteria, traveling along river courses is the most evident form of dispersal, as the desiccation risk can be controlled (Padisák et al., 2016). The successful dispersal of R. raciborskii is primarily attributed to its ability to tolerate travel in river courses. (Padisák, 1997). For M. aeruginosa, which forms colonies surrounded by mucilage, the environmental variables play a role in the early formation of the colonies and influence the size and morphology of the resulting colonies (Xiao et al., 2017). The species P. agardhii is a widespread cyanobacterium that changes in time scale from days to weeks due to cloudiness or wind-induced sediment resuspension in shallow and turbid lakes. Changes in light conditions affect microcystin production. Thus, P. agardhii is more toxic during periods of sunny weather when recreational activities in lakes are more attractive (Tonk et al., 2005).

# 5. Conclusion

The variations we observed indicate that the effects of climate change are not uniform across the different regions analyzed. Regions that are currently favorable may become less suitable, and vice versa. This result suggests that regional factors and environmental conditions play a crucial role in the future viability of cyanobacteria. Therefore, the results indicate that although cyanobacteria can maintain relatively stable fitness in the short term (until 2040) and long term (until 2100), a significant decrease in their fitness is expected due to the adverse impact of excessively high temperatures in their photosynthetic functions. These findings highlight the urgent need to implement climate change mitigation actions to protect aquatic ecosystems and the biodiversity they support.

# Acknowledgements

AG thanks FAPEG-CAPES (Fundação de Amparo à Pesquisa do Estado de Goiás – Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) Process N.º: 88887.162778/2018-00) for her Ph.D. scholarship. DPS was supported by a productivity grant from CNPq (Process N.º: 307514/2023-4) and research resources from FAPEG (Process N.º: 202310267001380).

# Data availability

All datasets and codes used in this study are publicly available at Zenodo (https://zenodo. org/records/14889278). This repository provides access to the raw and processed data and the scripts used for analysis, ensuring transparency and reproducibility. Researchers and interested readers are encouraged to explore and utilize these resources for further studies and validations.

#### References

- Andrade, A.F.A., Velazco, S.J.E., & De Marco Júnior, P., 2020. ENMTML: an R package for a straightforward construction of complex ecological niche models. Environ. Model. Softw. 125, 104615. http://doi. org/10.1016/j.envsoft.2019.104615.
- Araújo, M.B., & New, M., 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22(1), 42-47. PMid:17011070. http://doi.org/10.1016/j. tree.2006.09.010.
- Booth, T.H., Nix, H.A., Busby, J.R., & Hutchinson, M.F., 2014. Bioclim: the first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. Divers. Distrib. 20(1), 1-9. http://doi.org/10.1111/ddi.12144.

- Budai, P., & Clement, A., 2007. Estimation of nutrient load from urban diffuse sources: experiments with runoff sampling at pilot catchments of Lake Balaton, Hungary. Water Sci. Technol. 56(1), 295-302. PMid:17711027. http://doi.org/10.2166/ wst.2007.464.
- Cameron, E.S., Krishna, A., Emelko, M.B., & Müller, K.M., 2024. Sporadic diurnal fluctuations of cyanobacterial populations in oligotrophic temperate systems can prevent accurate characterization of change and risk in aquatic systems. Water Res. 252, 121199. PMid:38330712. http://doi.org/10.1016/j. watres.2024.121199.
- Chapra, S.C., Boehlert, B., Fant, C., Bierman Junior, V.J., Henderson, J., Mills, D., Mas, D.M.L., Rennels, L., Jantarasami, L., Martinich, J., Strzepek, K.M., & Paerl, H.W., 2017. Climate change impacts on harmful algal blooms in u.s. freshwaters: a screening-level assessment. Environ. Sci. Technol. 51(16), 8933-8943. PMid:28650153. http://doi. org/10.1021/acs.est.7b01498.
- Charlton, M.B., Bowes, M.J., Hutchins, M.G., Orr, H.G., Soley, R., & Davison, P., 2018. Mapping eutrophication risk from climate change: future phosphorus concentrations in English rivers. Sci. Total Environ. 613–614, 1510-1526. PMid:28886914. http://doi.org/10.1016/j.scitotenv.2017.07.218.
- De Marco, P., & Nóbrega, C.C., 2018. Evaluating collinearity effects on species distribution models: an approach based on virtual species simulation. PLoS One 13(9), e0202403. PMid:30204749. http://doi. org/10.1371/journal.pone.0202403.
- Diniz Filho, J.A.F., Ferro, V.G., Santos, T., Nabout, J.C., Dobrovolski, R., & De Marco Jr, P., 2010. The three phases of the ensemble forecasting of niche models: geographic range and shifts in climatically suitable areas of *Utetheisa ornatrix* (Lepidoptera, Arctiidae). Rev. Bras. Entomol. 54(3), 339-349. http://doi. org/10.1590/S0085-56262010000300001.
- Domisch, S., Amatulli, G., & Jetz, W., 2015. Nearglobal freshwater-specific environmental variables for biodiversity analyses in 1 km resolution. Sci. Data 2(1), 150073. PMid:26647296. http://doi. org/10.1038/sdata.2015.73.
- Fick, S.E., & Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37(12), 4302-4315. https://doi.org/10.1002/joc.5086.
- Global Biological Information Facility GBIF, 2023. Global biodiversity information facility [online]. Retrieved in 2023, May 15, from http://www.gbif.org.
- Goncharenko, I., Krakhmalnyi, M., Velikova, V., Ascencio, E., & Krakhmalnyi, A., 2021. Ecological niche modeling of toxic dinoflagellate *Prorocentrum cordatum* in the Black Sea. Ecohydrol. Hydrobiol. 21(4), 747-759. http://doi.org/10.1016/j. ecohyd.2021.05.002.

- Guimaráes, A., da Silva, P.H., Carneiro, F.M., & Silva, D.P., 2020. Using distribution models to estimate blooms of phytosanitary cyanobacteria in Brazil. Biota Neotrop. 20(2), e20190756. https://doi. org/10.1590/1676-0611-bn-2019-0756.
- Guisan, A., Edwards, T.C., & Hastie, T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol. Model. 157(2-3), 89-100. http://doi. org/10.1016/S0304-3800(02)00204-1.
- Hamilton, C., 2018. Climate change. In: Juergensmeyer, M., Sassen, S., Steger, M.B., & Faessel, V., eds, The Oxford Handbook of Global Studies. Oxônia: Oxford University Press, 631-646. http://doi. org/10.1093/oxfordhb/9780190630577.013.23.
- Hong, Y., Steinman, A., Biddanda, B., Rediske, R., & Fahnenstiel, G., 2006. Occurrence of the toxin-producing cyanobacterium *Cylindrospermopsis raciborskii* in Mona and Muskegon Lakes, Michigan.
  J. Great Lakes Res. 32(3), 645-652. https://doi.org/10.3394/0380-1330(2006)32[645:OOTTCC]2.0.CO;2.
- Huisman, J., Codd, G.A., Paerl, H.W., Ibelings,
  B.W., Verspagen, J.M.H., & Visser, P.M., 2018.
  Cyanobacterial blooms. Nat. Rev. Microbiol. 16(8),
  471-483. PMid:29946124. http://doi.org/10.1038/
  s41579-018-0040-1.
- Hunter, P.D., Tyler, A.N., Carvalho, L., Codd, G.A., & Maberly, S.C., 2010. Hyperspectral remote sensing of cyanobacterial pigments as indicators for cell populations and toxins in eutrophic lakes. Remote Sens. Environ. 114(11), 2705-2718. http://doi. org/10.1016/j.rse.2010.06.006.
- Igwaran, A., Kayode, A.J., Moloantoa, K.M., Khetsha, Z.P., & Unuofin, J.O., 2024. Cyanobacteria Harmful Algae Blooms: Causes, Impacts, and Risk Management. Water Air Soil Pollut. 235(1), 1-26. http://doi.org/10.1007/s11270-023-06782-y.
- Intergovernamental Panel on Climate Change, 2022. Climate Change 2022 - Impacts, Adaptation and Vulnerability. Working Group II contribution to the Sixth Assessment Report of the Intergovernamental Panel on Climate Change. Cambridge: Cambridge University Press. https://doi. org/10.1017/9781009325844.
- Kimambo, O.N., Gumbo, J.R., & Chikoore, H., 2019. The occurrence of cyanobacteria blooms in freshwater ecosystems and their link with hydrometeorological and environmental variations in Tanzania. Heliyon 5(3), e01312. PMid:30899834. http://doi.org/10.1016/j.heliyon.2019.e01312.
- Kimambo, O.N., Gumbo, J.R., Msagati, T.A.M., & Chikoore, H., 2022. Harmful algae in aquaculture systems in Ngerengere Catchment, Morogoro, Tanzania: descriptive community structure and environmental concerns. Phys. Chem. Earth Parts

ABC 125, 103103. http://doi.org/10.1016/j. pce.2021.103103.

- Komárek, J., Kaštovský, J., Mareš, J., & Johansen, J.R., 2014. Taxonomic classification of cyanoprokaryotes (cyanobacterial genera) 2014, using a polyphasic approach. Preslia 86, 295-335.
- Leroy, B., Delsol, R., Hugueny, B., Meynard, C.N., Barhoumi, C., Barbet-Massin, M., & Bellard, C., 2018. Without quality presence–absence data, discrimination metrics such as TSS can be misleading measures of model performance. J. Biogeogr. 45(9), 1994-2002. http://doi.org/10.1111/jbi.13402.
- Lobo, J.M., & Tognelli, M.F., 2011. Exploring the effects of quantity and location of pseudo-absences and sampling biases on the performance of distribution models with limited point occurrence data. J. Nat. Conserv. 19(1), 1-7. http://doi.org/10.1016/j. jnc.2010.03.002.
- Ma, J., & Wang, P., 2021. Effects of rising atmospheric CO2 levels on physiological response of cyanobacteria and cyanobacterial bloom development: a review. Sci. Total Environ. 754, 141889. PMid:32920383. http://doi.org/10.1016/j.scitotenv.2020.141889.
- Mantzouki, E., Lürling, M., Fastner, J., de Senerpont Domis, L., Wilk-Woźniak, E., Koreivienė, J., Seelen, L., Teurlincx, S., Verstijnen, Y., Krztoń, W., Walusiak, E., Karosienė, J., Kasperovičienė, J., Savadova, K., Vitonytė, I., Cillero-Castro, C., Budzyńska, A., Goldyn, R., Kozak, A., Rosińska, J., Szelag-Wasielewska, E., Domek, P., Jakubowska-Krepska, N., Kwasizur, K., Messyasz, B., Pełechaty, A., Pełechaty, M., Kokocinski, M., García-Murcia, A., Real, M., Romans, E., Noguero-Ribes, J., Duque, D.P., Fernández-Morán, E., Karakaya, N., Häggqvist, K., Demir, N., Beklioğlu, M., Filiz, N., Levi, E.E., Iskin, U., Bezirci, G., Tavşanoğlu, Ü.N., Özhan, K., Gkelis, S., Panou, M., Fakioglu, Ö., Avagianos, C., Kaloudis, T., Çelik, K., Yilmaz, M., Marcé, R., Catalán, N., Bravo, A.G., Buck, M., Colom-Montero, W., Mustonen, K., Pierson, D., Yang, Y., Raposeiro, P.M., Gonçalves, V., Antoniou, M.G., Tsiarta, N., McCarthy, V., Perello, V.C., Feldmann, T., Laas, A., Panksep, K., Tuvikene, L., Gagala, I., Mankiewicz-Boczek, J., Yağcı, M.A., Çınar, Ş., Çapkın, K., Yağcı, A., Cesur, M., Bilgin, F., Bulut, C., Uysal, R., Obertegger, U., Boscaini, A., Flaim, G., Salmaso, N., Cerasino, L., Richardson, J., Visser, P.M., Verspagen, J.M.H., Karan, T., Soylu, E.N., Maraşlıoğlu, F., Napiórkowska-Krzebietke, A., Ochocka, A., Pasztaleniec, A., Antão-Geraldes, A.M., Vasconcelos, V., Morais, J., Vale, M., Köker, L., Akçaalan, R., Albay, M., Špoljarić Maronić, D., Stević, F., Žuna Pfeiffer, T., Fonvielle, J., Straile, D., Rothhaupt, K.O., Hansson, L.A., Urrutia-Cordero, P., Bláha, L., Geriš, R., Fránková, M., Koçer, M.A.T., Alp, M.T., Remec-Rekar, S., Elersek, T., Triantis, T., Zervou, S.K., Hiskia, A., Haande, S., Skjelbred, B., Madrecka, B., Nemova, H., Drastichova,

I., Chomova, L., Edwards, C., Sevindik, T.O., Tunca, H., Önem, B., Aleksovski, B., Krstić, S., Vucelić, I.B., Nawrocka, L., Salmi, P., Machado-Vieira, D., de Oliveira, A.G., Delgado-Martín, J., García, D., Cereijo, J.L., Gomà, J., Trapote, M.C., Vegas-Vilarrúbia, T., Obrador, B., Grabowska, M., Karpowicz, M., Chmura, D., Úbeda, B., Gálvez, J.Á., Özen, A., Christoffersen, K.S., Warming, T.P., Kobos, J., Mazur-Marzec, H., Pérez-Martínez, C., Ramos-Rodríguez, E., Arvola, L., Alcaraz-Párraga, P., Toporowska, M., Pawlik-Skowronska, B., Niedźwiecki, M., Pęczuła, W., Leira, M., Hernández, A., Moreno-Ostos, E., Blanco, J.M., Rodríguez, V., Montes-Pérez, J.J., Palomino, R.L., Rodríguez-Pérez, E., Carballeira, R., Camacho, A., Picazo, A., Rochera, C., Santamans, A.C., Ferriol, C., Romo, S., Soria, J.M., Dunalska, J., Sieńska, J., Szymański, D., Kruk, M., Kostrzewska-Szlakowska, I., Jasser, I., Žutinić, P., Gligora Udovič, M., Plenković-Moraj, A., Frąk, M., Bańkowska-Sobczak, A., Wasilewicz, M., Özkan, K., Maliaka, V., Kangro, K., Grossart, H.P., Paerl, H.W., Carey, C.C., & Ibelings, B.W., 2018. Temperature Effects explain continental scale distribution of cyanobacterial toxins. Toxins (Basel) 10(4), 156. PMid:29652856. http://doi. org/10.3390/toxins10040156.

- Marrone, B.L., Banerjee, S., Talapatra, A., Gonzalez-Esquer, C.R., & Pilania, G., 2024. Toward a Predictive Understanding of Cyanobacterial Harmful Algal Blooms through AI Integration of Physical, Chemical, and Biological Data. ACS ES T Water 4(3), 844-858. PMid:38482341. http://doi.org/10.1021/ acsestwater.3c00369.
- Meriggi, C., Drakare, S., Polaina Lacambra, E., Johnson, R.K., & Laugen, A.T., 2022. Species distribution models as a tool for early detection of the invasive *Raphidiopsis raciborskii* in European lakes. Harmful Algae 113, 102202. PMid:35287933. http://doi. org/10.1016/j.hal.2022.102202.
- Naselli-Flores, L., & Padisák, J., 2016. Blowing in the wind: how many roads can a phytoplanktont walk down? A synthesis on phytoplankton biogeography and spatial processes. Hydrobiologia. 764, 303-313. http://doi.org/10.1007/s10750-015-2519-3.
- Nóges, P., Nóges, T., Ghiani, M., Sena, F., Fresner, R., Friedl, M., & Mildner, J., 2011. Increased nutrient loading and rapid changes in phytoplankton expected with climate change in stratified South European lakes: sensitivity of lakes with different trophic state and catchment properties. Hydrobiologia 667(1), 255-270. http://doi.org/10.1007/s10750-011-0649-9.
- Padisák, J., & Naselli-Flores, L., 2021. Phytoplankton in extreme environments: importance and consequences of habitat permanency. Hydrobiologia 848(1), 157-176. http://doi.org/10.1007/s10750-020-04353-4.

- Padisák, J., 1997. Cylindrospermopsis raciborskii (Woloszynska) Seenayya et Subba Raju, an expanding, highly adaptive cyanobacterium: worldwide distribution and review of its ecology. Arch. Hydrobiol. Suppl. Monogr. Beitr. 107(4), 563-593.
- Padisák, J., Vasas, G., & Borics, G., 2016. Phycogeography of freshwater phytoplankton: traditional knowledge and new molecular tools. Hydrobiologia 764(1), 3-27. http://doi.org/10.1007/s10750-015-2259-4.
- Paerl, H.W., & Huisman, J., 2009. Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. Environ. Microbiol. Rep. 1(1), 27-37. http://doi.org/10.1111/j.1758-2229.2008.00004.x.
- Paerl, H.W., & Paul, V.J., 2012. Climate change: links to global expansion of harmful cyanobacteria. Water Res. 46(5), 1349-1363. PMid:21893330. http://doi. org/10.1016/j.watres.2011.08.002.
- Pagni, R.L., de Falco, P.B., & Dos Santos, A.C.A., 2020. Autecology of *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba Raju. Acta Limnol. Bras. 32, e24. https://doi.org/10.1590/S2179-975X10317.
- Peterson, A.T., 2011. Ecological niche conservatism: a time-structured review of evidence. J. Biogeogr. 38(5), 817-827. http://doi.org/10.1111/j.1365-2699.2010.02456.x.
- Phillips, S.J., & Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31(2), 161-175. http://doi.org/10.1111/j.0906-7590.2008.5203.x.
- Phillips, S.J., Anderson, R.P., & Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Modell. 190(3-4), 231-259. http://doi.org/10.1016/j.ecolmodel.2005.03.026.
- Poniedziałek, B., Rzymski, P., & Kokociński, M., 2012. Cylindrospermopsin: water-linked potential threat to human health in Europe. Environ. Toxicol. Pharmacol. 34(3), 651-660. http://doi. org/10.1016/j.etap.2012.08.005.
- Prakash, R., Lee, J., Kim, S.H., Lee, H.Y., & Lee, J., 2024. Insight into the interaction between ionic nanobubbles and cyanobacteria: elucidating the role of surfactant and zeta potential in the inactivation of harmful cyanobacteria. Chem. Eng. Sci. 287, 119699. http://doi.org/10.1016/j.ces.2023.119699.
- Sellner, K.G., Doucette, G.J., & Kirkpatrick, G.J., 2003. Harmful algal blooms: Causes, impacts and detection. J. Ind. Microbiol. Biotechnol. 30(7), 383-406. PMid:12898390. http://doi.org/10.1007/ s10295-003-0074-9.
- Simić, S.B., Dordević, N.B., & Milošević, D., 2017. The relationship between the dominance of Cyanobacteria species and environmental variables in different seasons and after extreme precipitation.

Fundam. Appl. Limnol. 190(1), 1-11. http://doi. org/10.1127/fal/2017/0975.

- Sistema de Acompanhamento de Reservatórios SAR, 2023. Dados [online]. Retrieved in 2025, March 31, from https://dados.gov.br/dados/conjuntos-dados/ sistema-de-acompanhamento-de-reservatoriossistema-interligado-nacional1.
- Soberón, J., 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecol. Lett. 10(12), 1115-1123. PMid:17850335. http://doi. org/10.1111/j.1461-0248.2007.01107.x.
- Stockwell, J.D., Doubek, J.P., Adrian, R., Anneville, O., Carey, C.C., Carvalho, L., De Senerpont Domis, L.N., Dur, G., Frassl, M.A., Grossart, H.P., Ibelings, B.W., Lajeunesse, M.J., Lewandowska, A.M., Llames, M.E., Matsuzaki, S.I.S., Nodine, E.R., Nóges, P., Patil, V.P., Pomati, F., Rinke, K., Rudstam, L.G., Rusak, J.A., Salmaso, N., Seltmann, C.T., Straile, D., Thackeray, S.J., Thiery, W., Urrutia-Cordero, P., Venail, P., Verburg, P., Woolway, R.I., Zohary, T., Andersen, M.R., Bhattacharya, R., Hejzlar, J., Janatian, N., Kpodonu, A.T.N.K., Williamson, T.J., & Wilson, H.L., 2020. Storm impacts on phytoplankton community dynamics in lakes. Glob. Change Biol. 26(5), 2756-2784. PMid:32133744. http://doi.org/10.1111/gcb.15033.
- Stumpf, R.P., Davis, T.W., Wynne, T.T., Graham, J.L., Loftin, K.A., Johengen, T.H., Gossiaux, D., Palladino, D., & Burtner, A., 2016. Challenges for mapping cyanotoxin patterns from remote sensing of cyanobacteria. Harmful Algae 54, 160-173. http:// doi.org/10.1016/j.hal.2016.01.005.
- Tonk, L., Visser, P.M., Christiansen, G., Dittmann, E., Snelder, E.O.F.M., Wiedner, C., Mur, L.R., & Huisman, J., 2005. The microcystin composition of the cyanobacterium *Planktothrix agardhii* changes toward a more toxic variant with increasing light intensity. Appl. Environ. Microbiol. 71(9), 5177-5181. PMid:16151102. http://doi.org/10.1128/ AEM.71.9.5177-5181.2005.
- Trenberth, K.E., Dai, A., Rasmussen, R.M., & Parsons, D.B., 2003. The changing character of precipitation. Forum 1205-1217. http://doi.org/10.1175/BAMS-84-9-1205.
- Tuchyňa, J., & Haas, M., 2025. Impact of Climate Change-Driven Droughts on the Concentration of Heavy Metals and Other Elements in Freshwater Cyanobacteria of the Genus Oscillatoriales in the Tatra Mountains. Sustainability (Basel) 17(3), 1119. http://doi.org/10.3390/su17031119.

- VanDerWal, J., Shoo, L.P., Graham, C., & Williams, S.E., 2009. Selecting pseudo-absence data for presenceonly distribution modeling: how far should you stray from what you know? Ecol. Modell. 220(4), 589-594. http://doi.org/10.1016/j.ecolmodel.2008.11.010.
- Vanhatalo, J., Veneranta, L., & Hudd, R., 2012. Species distribution modeling with Gaussian processes: a case study with the youngest stages of sea spawning whitefish (*Coregonus lavaretus* L. s.l.) larvae. Ecol. Model. 228, 49-58. http://doi.org/10.1016/j. ecolmodel.2011.12.025.
- Vieira, T.B., Pavanelli, C.S., Casatti, L., Smith, W.S., Benedito, E., Mazzoni, R., Sánchez-Botero, J.I., Garcez, D.S., Lima, S.M.Q., Pompeu, P.S., Agostinho, C.S., Montag, L.F.A., Zuanon, J., Aquino, P.P.U., Cetra, M., Tejerina-Garro, F.L., Duboc, L.F., Corrêa, R.C., Pérez-Mayorga, M.A., Brejão, G.L., Mateussi, N.T.B., Castro, M.A., Leitão, R.P., Mendonça, F.P., Silva, L.R.P.D., Frederico, R., & De Marco, P., 2018. A multiple hypothesis approach to explain species richness patterns in neotropical stream-dweller fish communities. PLoS One 13(9), e0204114. PMid:30231064. http://doi.org/10.1371/ journal.pone.0204114.
- Walter Helbling, E., Banaszak, A.T., & Villafañe, V.E., 2015. Global change feed-back inhibits cyanobacterial photosynthesis. Sci. Rep. 5, 14514. PMid:26415603. http://doi.org/10.1038/srep14514.
- Whittaker, R.J., Araujo, M.B., Paul, J., Ladle, R.J., Watson, J.E.M., & Willis, K.J., 2005. Conservation biogeography: assessment and prospect. Diversity Distrib., 11(1), 3-23. http://doi.org/10.1111/j.1366-9516.2005.00143.x.
- Xiao, M., Willis, A., Burford, M.A., & Li, M., 2017. Review: a meta-analysis comparing cell-division and cell-adhesion in Microcystis colony formation. Harmful Algae. 67, 85-91. http://doi.org/10.1016/j. hal.2017.06.007.
- Yang, Y., Chen, Y., Cai, F., Liu, X., Wang, Y., & Li, R., 2018. Toxicity-associated changes in the invasive cyanobacterium *Cylindrospermopsis raciborskii* in response to nitrogen fluctuations. Environ. Pollut. 237, 1041-1049. PMid:29153475. http://doi. org/10.1016/j.envpol.2017.11.024.

Received: 16 January 2024 Accepted: 12 March 2025

Associate Editor: Bárbara Dunck.