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FELIPE MORAIS ZANON

From local processes to global patterns: how multiple stressors reshape freshwater phytoplankton community and ecosystem risk

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Tese apresentada ao Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais do Departamento de Biologia, Centro de Ciências Biológicas da Universidade Estadual de Maringá, como requisito parcial para obtenção do título de Doutor em Ecologia e Limnologia.

Área de concentração: Ecologia e Limnologia

Orientadora: Dr.ª Luzia Cleide Rodrigues
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“Em meio aos meus temores, eu confio em ti.
Em Deus, cuja palavra louvo, em Deus confio
e nada temerei.”

Salmos 56: 3-4

De processos locais a padrões globais: como múltiplos estressores remodelam a comunidade fitoplanctônica e o risco ecossistêmico em ambientes de água doce

RESUMO

Mudanças ambientais impulsionadas por atividades antropogênicas têm alterado a estrutura e a dinâmica de ecossistemas aquáticos em múltiplas escalas. Entre os principais fatores de impacto ambiental nesses sistemas, destacam-se o aquecimento climático, enriquecimento por nutrientes e alterações hidrológicas causadas por barramento, que frequentemente atuam de forma combinada sobre as comunidades biológicas. Nesse contexto, o fitoplâncton representa um modelo adequado para investigar essas respostas, devido à sua rápida resposta às variações ambientais e ao seu papel central em ecossistemas de água doce, principalmente para produtividade primária. Sendo assim, avaliou-se como múltiplos estressores ambientais afetam a diversidade e a dinâmica de comunidades fitoplanctônicas, integrando abordagens experimentais e preditivas. Realizou-se um experimento em mesocosmo para avaliar os efeitos do aquecimento, do enriquecimento de nutrientes e da perda de material alóctone sobre a diversidade beta temporal. Os resultados indicaram mudanças direcionais na composição das comunidades, com elevada rotatividade de espécies ao longo do tempo. Não foi observada homogeneização composicional consistente, porém análises baseadas em abundância evidenciaram episódios de homogeneização estrutural associados à dominância de poucos táxons, especialmente cianobactérias. Aplicou-se modelos preditivos em escala global para identificar bacias hidrográficas com maior risco de proliferação de cianobactérias potencialmente tóxicas. A integração de variáveis climáticas e antrópicas evidenciou *hotspots* de risco, principalmente em regiões do mundo com alta densidade populacional, destacando a importância dessa investigação devido seu impacto no uso de recursos hídricos pela população e serviços ecossistêmicos gerados por ecosistemas de agua doce. De forma geral, os resultados evidenciam que múltiplos estressores impulsionam a reorganização da comunidade fitoplanctônica, com mudanças direcionais, alterações na dominância de espécies e redução da singularidade local. Esses efeitos ocorrem de maneira consistente em diferentes escalas, desde respostas diretas em condições experimentais até padrões observados em escala global, indicando que a interação entre múltiplos estressores ambientais exerce papel determinante na reorganização das comunidades fitoplanctônicas, com destaque para o aumento da dominância de cianobactérias potencialmente formadoras de blooms tóxicos. Para socializar o conhecimento, entendendo a importancia da disseminação do conhecimento científico para a comunidade em uma linguagem acessível, elaborou-se um jogo de tabuleiro, no qual os jogadores se tornam líderes de institutos de pesquisa com o objetivo de praticar ações de preservação em ambientes aquáticos. Esse jogo foi desenvolvido com o intuito de ser aplicado a diferentes faixas etárias em contextos escolares ou recreacionais, sendo uma importante ferramenta de disseminação do conhecimento científico e conscientização de práticas ambientais para a população.

Palavras-chave: microalgas; diversidade beta; impactos antrópicos; múltiplos estressores; modelos preditivos; cianobactérias nocivas; ecossistemas aquáticos de agua doce; jogo de tabuleiro.

From local processes to global patterns: how multiple stressors reshape freshwater phytoplankton community and ecosystem risk

ABSTRACT

Environmental changes driven by human activities have altered the structure and dynamics of aquatic ecosystems across multiple scales. Among the main factors affecting these systems are global warming, nutrient enrichment, and hydrological alterations caused by damming, which often interact to impact biological communities. In this context, phytoplankton serves as a suitable model for investigating these responses due to its rapid response to environmental variations and its central role in freshwater ecosystems, particularly regarding primary productivity. Therefore, we assessed how multiple environmental stressors affect the diversity and dynamics of phytoplankton communities, integrating experimental and predictive approaches. A mesocosm experiment was conducted to evaluate the effects of warming, nutrient enrichment, and the litter loss on temporal beta diversity. The results indicated directional changes in community composition, with high species turnover over time. No consistent compositional homogenization was observed. However, abundance-based analyses revealed episodes of structural homogenization associated with the dominance of a few taxa, especially cyanobacteria. Global-scale predictive models were applied to identify river basins at higher risk of potentially toxic cyanobacterial blooms. The integration of climatic and anthropogenic variables revealed risk hotspots, particularly in densely populated regions, highlighting the importance of this investigation due to its impact on water resource use and freshwater ecosystem services. Overall, the findings demonstrate that multiple stressors drive the reorganization of the phytoplankton community, with shifts in composition, changes in species dominance, and a reduction in local uniqueness. These effects were consistently observed across different scales, ranging from direct experimental responses conditions to global predictive patterns, indicating that interactions among environmental stressors play a critical role in shaping phytoplankton communities. Particular attention should be given to the increased dominance of cyanobacteria, which may lead to the formation of potentially toxic blooms. Finally, to socialize knowledge, recognizing the importance of communicating scientific knowledge to society, A board game was created in which players act as leaders of research institutes responsible for implementing conservation actions in aquatic environments. This game was developed to be used with different age groups in school or recreational settings, serving as an important tool for science communication and raising public awareness of environmental practices.

***Keywords**:* microalgae; beta diversity; anthropic impacts; multiple stressors; predictive models; harmful cyanobacteria; freshwater ecosystems; board game.

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SUMMARY

1 GENERAL INTRODUCTION

In recent decades, the world has undergone intense environmental changes, driven primarily by human activities that have been rapidly altering natural systems (Steffen et al., 2011, 2015a; Waters et al., 2016). These processes have affected ecosystems at multiple levels and ecological scales, resulting in biodiversity loss and alterations in ecosystem functioning and services essential to human societies (Cardinale et al., 2012; Keck et al., 2025; Mooney et al., 2009; Pereira et al., 2024). Among the ecosystems most vulnerable to these changes are freshwater environments, which respond quickly to environmental variations due to their strong dependence on external factors and their intense connection with terrestrial ecosystems (Adrian et al., 2009; Allan, 2004; Dudgeon et al., 2006). In this context, multiple anthropogenic factors, such as climate change, dams, land-use changes, and eutrophication, act in combination on these systems, shaping the dynamics of freshwater biological communities (Cooper et al., 2013; Woodward; Perkins; Brown, 2010).

Increasing evidence suggests that these interactions among multiple stressors can generate nonlinear responses, often resulting in synergistic or antagonistic effects that cannot be predicted based on analyses of isolated factors (Crain; Kroeker; Halpern, 2008; Piggott; Townsend; Matthaei, 2015). In freshwater environments, this gap is particularly critical, as most stressors act in concert, mainly due to the high use of water resources by humans to carry out their activities (Jackson et al., 2015; Reid et al., 2019). As a result, understanding and predicting ecological responses in these systems becomes more complex, especially at the community level, where multiple stressors can drive changes in composition, biodiversity loss, and processes of biotic homogenization (Bussi et al., 2016; Moresco et al., 2024; Petsch, 2016). These changes in the structure of aquatic communities can, in turn, impact ecosystem stability and functionality (Birk et al., 2020; Piggott et al., 2015; Polazzo; Rico, 2021).

Phytoplankton stands out among these communities for its quick and efficient response to environmental variations, being highly sensitive to changes in nutrient availability, temperature, and hydrological regime (Padisák et al., 2010a; Reynolds, 2006). Therefore, this community tends to suffer the direct impacts of these stressors, often characterized by marked changes in composition and the dominance of a few opportunistic taxa (Rasconi; Winter; Kainz, 2017; Wang et al., 2025a). This results in a more homogeneous community that is potentially less stable over time (Pomati et al., 2011; Zanon et al., 2024). As a consequence, changes in phytoplankton structure can compromise the functioning of freshwater aquatic ecosystems,

affecting processes such as primary productivity, nutrient cycling, and energy transfer within food webs (Borics et al., 2021; Ma et al., 2024; Ptacnik et al., 2008).

Among the phytoplankton groups that benefit most from these changes, cyanobacteria stand out (Huisman et al., 2018; Paerl; Huisman, 2008). The growth of these organisms is favored by warming conditions, nutrient enrichment, and longer water residence times, which are often associated with human activities (O'Neil et al., 2012; Paerl; Paul, 2012). In addition, they exhibit high ecological plasticity, being capable of tolerating a wide range of environmental conditions (Huisman et al., 2018; Yadav et al., 2022; Zakhia et al., 2008). As a result, they can form extensive blooms, dominating phytoplankton biomass and reducing evenness and diversity at local and temporal scales (Moresco et al., 2024; Richardson et al., 2019a; Toporowska; Pawlik-skowrońska, 2014a). Moreover, many of these blooms are potentially toxic (cyanoHABs), directly impacting other aquatic communities and compromising essential ecosystem services, such as water supply (Codd; Morrison; Metcalf, 2005; He et al., 2016; Paerl; Otten, 2013).

Considering these effects on the structure of the phytoplankton community, diversity metrics have been widely used as fundamental tools for quantifying ecological patterns at different scales (Nabout et al., 2007; Wojciechowski et al., 2017; Zanon et al., 2024; Zhang et al., 2021). In particular, beta diversity allows for the assessment of variations in species composition and abundances across space and time, making it particularly useful for detecting processes of biotic homogenization and changes in community structure (Legendre, 2014, 2019; Pineda et al., 2020a). Furthermore, approaches that incorporate the temporal dynamics of these communities have contributed to a more integrated understanding of ecological responses to multiple stressors, allowing for the identification of species replacement patterns and directional changes in composition over time (Heino et al., 2024; Shimadzu; Dornelas; Magurran, 2015). In experimental studies, these patterns become even clearer, particularly when evaluating multiple stressors (Piggott et al., 2012). Mesocosms allow for the assessment of direct effects of environmental and anthropogenic variables on communities, making this approach valuable for evaluating human impact on aquatic communities (Kratina et al., 2015; Pacheco et al., 2022; Urrutia-Cordero et al., 2017).

Given the changes in the structure of phytoplankton communities and the increasing dominance of cyanobacteria, understanding and predicting the occurrence and spatial distribution of cyanoHABs has become essential. Despite advances in understanding the mechanisms that favor the formation of these blooms, their predictability remains limited. In this context, species distribution models have been widely used to assess current and future

occurrence patterns in response to environmental variables (Fuster-Alonso et al., 2025; Vasconcelos et al., 2024). Although studies using this approach on microorganisms are still scarce, recent evidence demonstrates its potential for describing the distribution of cyanobacteria under climate scenarios on continental scales (Guimarães; Silva; Silva, 2025; Zanon et al., 2025a). However, most of these studies consider environmental stress factors in isolation, neglecting interactions among multiple stressors that often determine nonlinear ecological responses (Elith; Leathwick, 2009; Frans; Liu, 2024). As a result, the ability to predict harmful algal bloom events in scenarios of global change remains limited, highlighting the need to incorporate multiple anthropogenic pressures into predictive models.

Another challenge for freshwater ecologists is the difficulty of translating scientific knowledge to society, especially when it comes to microorganisms (Brownell; Price; Steinman, 2013; Kokkinias et al., 2024). The anthropogenic impact on these communities is not immediately intuitive, making it difficult to understand outside academic circles and, consequently, to raise public awareness (Hayes, 1992; Plavén-Sigray et al., 2017). Therefore, it is important to seek more accessible tools that facilitate communication and understanding of these concepts without losing their meaning and importance. A promising alternative is the use of games, which allow for an interactive and playful exploration of how different factors interact and influence aquatic communities (Van Pelt et al., 2015; Wu; Lee, 2015). By simulating scenarios and their consequences, games can bring science closer to society, facilitating the understanding of environmental problems and encouraging a more critical and integrated view of natural systems.

In this regard, the studies conducted here are an excellent tool for achieving some of the Sustainable Development Goals (SDGs) proposed by the United Nations (UN). The 2030 Agenda for Sustainable Development encompasses the 17 proposed goals. These goals aim to protect the planet and improve the quality of life for everyone worldwide. The chapters of this thesis contribute directly to SDG 6 (related to water quality and sanitation), 13 (related to climate action), and 14 (related to the biota of aquatic ecosystems). Developing scientific foundations to support these goals is becoming increasingly important in the current global scenario, as achieving them can provide a better future for everyone.

Thus, the main objective of this thesis is to investigate how multiple environmental stressors resulting from anthropogenic activities shape the structure and dynamics of phytoplankton communities in freshwater ecosystems, integrating diversity metrics, experimental approaches, and predictive modeling to assess potential risks to ecosystem and human health under current and future scenarios. Specifically, the first manuscript aims to

assess the isolated and combined effects of warming, nutrient enrichment, and litter loss, through a mesocosm experiment, on the composition and diversity of the phytoplankton community, with an emphasis on biotic homogenization processes, temporal dynamics, and community structure. The second manuscript seeks to identify global river basins that represent hotspots for the formation of cyanoHABs, considering current and future scenarios. For this purpose, a composite index was calculated that integrates climate modeling of cyanobacteria, nutrient input (nitrogen and phosphorus), dams, and population density, allowing for the identification of areas at risk for water supply and public health. Finally, the third manuscript proposed the development of a board game as a strategy for science communication, to convey the effects of anthropogenic impacts on aquatic ecosystems in an accessible and integrated manner. By combining different approaches and scales, this thesis seeks to advance the understanding and prediction of the ecological responses of the phytoplankton community, particularly cyanobacteria, in freshwater environments, contributing both to scientific development and to bridging the gap between science and society.

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2 WARMING AND LAND-USE DRIVERS RESHAPE TEMPORAL BETA DIVERSITY IN PHYTOPLANKTON COMMUNITIES

Environmental stressors reshape Community

Abstract

Understanding how multiple environmental stressors shape biodiversity over time is critical for predicting ecological responses to global change. Here, we experimentally tested the effects of warming, nutrient enrichment, and litter input loss on freshwater phytoplankton communities over 160 days using a mesocosm approach. We hypothesized that environmental stressors would promote (i) divergence in community composition, (ii) compositional and structural biotic homogenization, and (iii) reduced community uniqueness. By integrating compositional and structural dimensions of temporal beta diversity, we show that only part of these expectations was supported. Communities exhibited strong directional compositional change driven by continuous species turnover, particularly under warming treatments, but did not show evidence of compositional homogenization. In contrast, abundance-based analyses revealed temporally dynamic responses, with warming, especially under variable regimes, and nutrient enrichment acting as the primary drivers of community reorganization, while litter input loss had comparatively weak effects. These stressors generated unstable trajectories characterized by shifts in species dominance, leading to episodic structural homogenization associated with the dominance of a few opportunistic taxa, particularly cyanobacteria, and reduced community uniqueness. Our results show that the compositional and structural dimensions of biodiversity may respond differently to environmental change, with high species turnover potentially masking structural homogenization driven by shifts in dominance. This highlights the importance of incorporating temporal dynamics and species dominance when predicting ecological responses in the context of global change.

Keywords: Structural homogenization; Beta diversity; Climate warming; Multiple stressors; Mesocosms.

2.1 Introduction

Anthropogenic impacts on ecosystems worldwide have intensified in recent decades (Steffen et al., 2015b; Vitousek et al., 1997; Watson et al., 2016), and understanding how these changes affect different levels of biological organization remains one of the main challenges of current ecology (Magnan et al., 2021; Marengo et al., 2012; Mckinney; Lockwood, 1999; Sax; Gaines, 2003). Global warming is one of the main drivers of the projected changes in the coming decades (Lee et al., 2023; Rossati, 2017), and may cause profound changes in the structure and functioning of biological communities (Bussi et al., 2016; Kravtsova et al., 2021; Viitasalo; Bonsdorff, 2022). These changes may be particularly pronounced in aquatic ecosystems, where the strong dependence on temperature and limited dispersal capacity make biological communities particularly sensitive to climate change (Reilly et al., 2015; Woodward; Perkins; Brown, 2010). Rising temperatures can induce direct physiological responses, such as increased metabolic demand (Rosenblatt; Schmitz, 2016), and may favor the growth of microorganisms, including phytoplankton (Antiqueira; Petchey; Romero, 2018; Moresco et al., 2024).

In addition to global warming, land-use changes constitute another major source of anthropogenic impact on freshwater ecosystems, particularly in regions undergoing agricultural and livestock expansion (Krienitz; Kasprzak; Koschel, 1996; Rizzo et al., 2020). These activities promote eutrophication processes by increasing the nutrient load (e.g., phosphorus and nitrogen) in these environments (Arbuckle; Downing, 2001; Bussi et al., 2016; Ferrareze, 2012). The removal of riparian zones intensifies this process by reducing the capacity to retain nutrients and particulate matter (Kreiling et al., 2021; Sabater et al., 2000). Furthermore, this removal decreases the input of allochthonous material into the water, affecting community interactions with available resources (Moore et al., 2004). Thus, global warming, together with impacts on land use, can generate synergistic effects on freshwater communities (Piggott; Townsend; Matthaei, 2015), potentially amplifying already projected impacts.

To evaluate the effects of these environmental stressors on freshwater communities, diversity indices are widely used, especially beta diversity (Jamoneau et al., 2017; Legendre, 2019; Whittaker, 1960). This metric can highlight regional and temporal changes in communities (Langenheder et al., 2012; Pineda et al., 2020b), as well as detect patterns of species loss and gain and shifts in community structure (Cochak et al., 2023; Guimarães Durán et al., 2024). Understanding how these dynamics unfold over time is essential to determine whether anthropogenic stressors promote compositional divergence, temporal instability, or processes of biotic homogenization (Hillebrand et al., 2018; Zanon et al., 2024) and whether

these patterns are driven by reductions in compositional variation or by shifts in species dominance.

Assessing the contribution of individual communities to beta diversity through the Local Contribution to Beta Diversity (LCBD) metric provides an additional perspective on biodiversity patterns (Legendre; De Cáceres, 2013). LCBD allows the identification of communities that are compositionally distinct from others and can reveal how community uniqueness changes under environmental stress (Heino; Alahuhta, 2019; Quirino et al., 2021). Because anthropogenic disturbances may alter species dominance and community structure, LCBD can help detect whether environmental stressors reduce the contribution of local communities to regional diversity through time. Furthermore, understanding whether site uniqueness is driven by such changes can help identify priority areas for preservation and restoration (Heino; Grönroos, 2017), particularly by clarifying how global warming and land-use change affect this uniqueness. The importance of these contributions may vary over time, especially under anthropogenic pressures (Souza et al., 2021), making the temporal analysis of this component of beta diversity an important and complementary approach at the regional scale.

Long-term mesocosm experiments provide a controlled framework to isolate key environmental drivers and assess their effects on freshwater communities (Kratina et al., 2015; Moresco et al., 2024; Polst et al., 2022). Although field studies are crucial for understanding human impact on biodiversity (Silva; Pelicice; Rodrigues, 2020; Zanon et al., 2025b), high stochasticity in such studies can weaken the detected response (Bell, 2001), making experimental approaches more robust in this context.

The phytoplankton community, that forms the base of aquatic food webs, is widely considered an excellent indicator of environmental change, especially in mesocosm experiments, due to its rapid and efficient response to environmental conditions (Reynolds, 1999; Sparks et al., 2017). Phytoplankton also play a fundamental role in freshwater ecosystems as primary producers and as components of carbon, nitrogen, and oxygen cycles (Padisák et al., 2010b). Under scenarios of rising temperatures and increased nutrient loads, cyanobacteria are often favored and may form large blooms (Yan et al., 2017a). These blooms may involve toxin-producing taxa, e.g., microcystins, saxitoxins (Chorus; Bartram, 1999; Paerl, 1988), which can negatively affect aquatic ecosystems through biodiversity loss, fish mortality, and reductions in ecosystem services such as water supply and recreation (O'Farrell; Bordet; Chaparro, 2012; Toporowska; Pawlik-skowrońska, 2014b). Cyanobacterial dominance may therefore play an

important role in reshaping biodiversity patterns in freshwater ecosystems (Amorim; Moura, 2021).

By incorporating temporal dynamics, this study moves beyond static assessments of phytoplankton beta diversity and examines how multiple anthropogenic stressors reshape community trajectories through time. We experimentally evaluate how warming, nutrient enrichment, and litter loss affect phytoplankton beta diversity in mesocosm.

We hypothesized that: (i) community composition would diverge through time between treatments exposed to environmental stressors and the control treatments; (ii) environmental stressors, particularly the combination of warming and nutrient enrichment, would promote structural and compositional biotic homogenization through time due to increased dominance of opportunistic taxa; and (iii) LCBD values would decrease in treatments exposed to environmental stressors, reflecting reduced community uniqueness relative to control mesocosms. The research questions, hypotheses, ecological mechanisms, and analytical approaches used to test these hypotheses are summarized in Table 1.

Table 1. Research questions, hypotheses, ecological mechanisms, and analytical approaches used to evaluate phytoplankton responses to environmental stressors.

Research question	Hypothesis	Ecological mechanism	Expected outcome	Analytical approach
Do environmental stressors alter phytoplankton community composition through time?	Community composition will diverge through time between treatments exposed to warming, nutrient enrichment, and litter loss and control treatments.	Environmental stress modifies species performance and resource availability, increasing species turnover.	Divergent trajectories of communities in response to environmental stress	Principal Response Curve - PRC analyses
Do environmental stressors promote biotic homogenization?	Warming and nutrient enrichment will promote compositional and structural homogenization through time.	Environmental filtering and competitive dominance favor a limited subset of opportunistic taxa.	Increased dominance and reduced structural differentiation among communities.	Temporal beta diversity - TBI analyses
Do environmental stressors reduce community uniqueness?	LCBD values will decrease in treatments exposed to environmental stressors.	Dominance by a few taxa reduces the contribution of local communities to total beta diversity.	Lower LCBD values in stressed treatments.	Local Contribution to Beta Diversity - LCBD analysis

2.2 Methodology

2.2.1 Experimental design and samplings

To investigate the effects of warming, increased nutrients, and litter loss in aquatic environments, a mesocosm experiment was developed, simulating natural lakes and their biotic interactions. The experiment lasted 160 days, beginning on September 12, 2022, and ending on March 3, 2023. The mesocosms were assembled in 310L polyethylene tanks at the Multidisciplinary Center for Chemical, Biological, and Agricultural Research (CPQBA) at the State University of Campinas (UNICAMP). Each mesocosm was developed to simulate natural lakes as closely as possible, i.e., most freshwater communities were introduced, reproducing the biotic interactions within these ecosystems, including bacterioplankton, phytoplankton, zooplankton, macroinvertebrates, and omnivorous fish.

Approximately 40 days before the start of the experiment, 60 experimental mesocosms were evenly distributed at equal distances. Each mesocosm was filled with 300 L of filtered, chlorine-free water supplied by the CPQBA's water distribution system. After filling, 300 mL of fine sediment collected from nearby natural lakes was added to promote microbiota colonization and to structure the sediment for benthic organisms.

From these same lakes, approximately 36.000L of water was collected and filtered through 60 µm and 20 µm mesh nets to obtain zooplankton and phytoplankton inocula, respectively. For each fraction, 15 L of water was concentrated, homogenized, and 200ml of each inoculum was added to every mesocosm. In addition, 200 mL of unfiltered lake water was added to include organisms smaller than 20 µm.

Thirty days before the start of the experiment, 6 g of dry *Inga* sp. leaves were added to each mesocosm to allow colonization by detritivorous macroinvertebrates through natural dispersion. At the start of the experiment, two males and three females of *Poecilia* sp., a top predatory omnivorous fish, were added into each mesocosm, completing the food web. All involving fish collection and experimentation were approved by the UNICAMP Ethics Committee on Animal Use (CEUA – number 5983-1/2022).

The experiment followed a randomized block design with five blocks (Figure 1) in a 3 × 2 × 2 factorial arrangement manipulating temperature, nutrient input, and litter manipulation, resulting in 12 treatment combinations with five replicates each (Table 2). The temperature treatment included three levels: (i) control (ambient temperature), (ii) constant warming of +4 °C above the control, and (iii) fluctuating warming ranging from +2 °C to +6 °C above the control temperature, representing thermal instability. Heating was automated using temperature

sensors in the control mesocosms and 500 W heaters in the warming treatments, all connected to a digital controller via underground cables. Control temperatures were recorded every 10 minutes, and warming treatments were adjusted in real time relative to these measurements. Constant warming was maintained at +4 °C above the control, whereas fluctuating warming ranged from +2 °C to +6 °C (+4 °C ± 2 °C). The +4 °C warming scenario was based on pessimistic carbon emission projections for 2100 (Lee et al., 2023). Temperature fluctuations followed four-day cycles, increasing by 1 °C per cycle.

Table 2. Factorial design of the experiment manipulating temperature, nutrient input, and litter input loss.

Factors	**Levels**
Temperature	Control (**C**)
	Constant warming +4 °C (**W_c**)
	Variable warming +2–6 °C (**W_v**)
Nutrients	Enrichment (**N**)
Litter	Input loss (**LL**)
Replicates	**Acronym**
5	C
5	N
5	LL
5	W_c
5	W_v
5	N x LL
5	W_c x N
5	W_v x N
5	W_c x LL
5	W_v x LL
5	W_c x N x LL
5	W_v x N x LL

Human influence on land use will be represented by two treatments: nutrient enrichment and litter loss. The increase in nutrients, phosphorus, and nitrogen, representing the impact of agricultural activities through surface runoff, had two levels: i) control, without nutritional enrichment, maintaining the natural abiotic conditions of the collected lake; ii) nutritional enrichment, addition of 1,546mg of nitrogen (urea) and 176mg of phosphorus (monoammonium phosphate – MAP), with a molar ratio of N:P of 19.41 (Ghiberto et al., 2009; Schiesari et al., 2023; Wang et al., 2019). The nutrients were added in three pulses, every 20 days, during the first 40 days of the experiment. The litter loss treatment, representing the deforestation of riparian vegetation, also had two levels: i) control, in which 12g of Inga sp.

leaf biomass was added every 40 days, simulating the natural entry of allochthonous material; ii) litter reduction, in which 80% less Inga sp. leaf biomass was added, 2.4 g every 40 days, simulating the loss of riparian vegetation and consequently less input of allochthonous material. These values were based on estimates of litterfall input in aquatic environments of the Atlantic Forest (Tonin et al., 2017). For full details regarding the experimental design and structure, see Rezende et al. (2026).

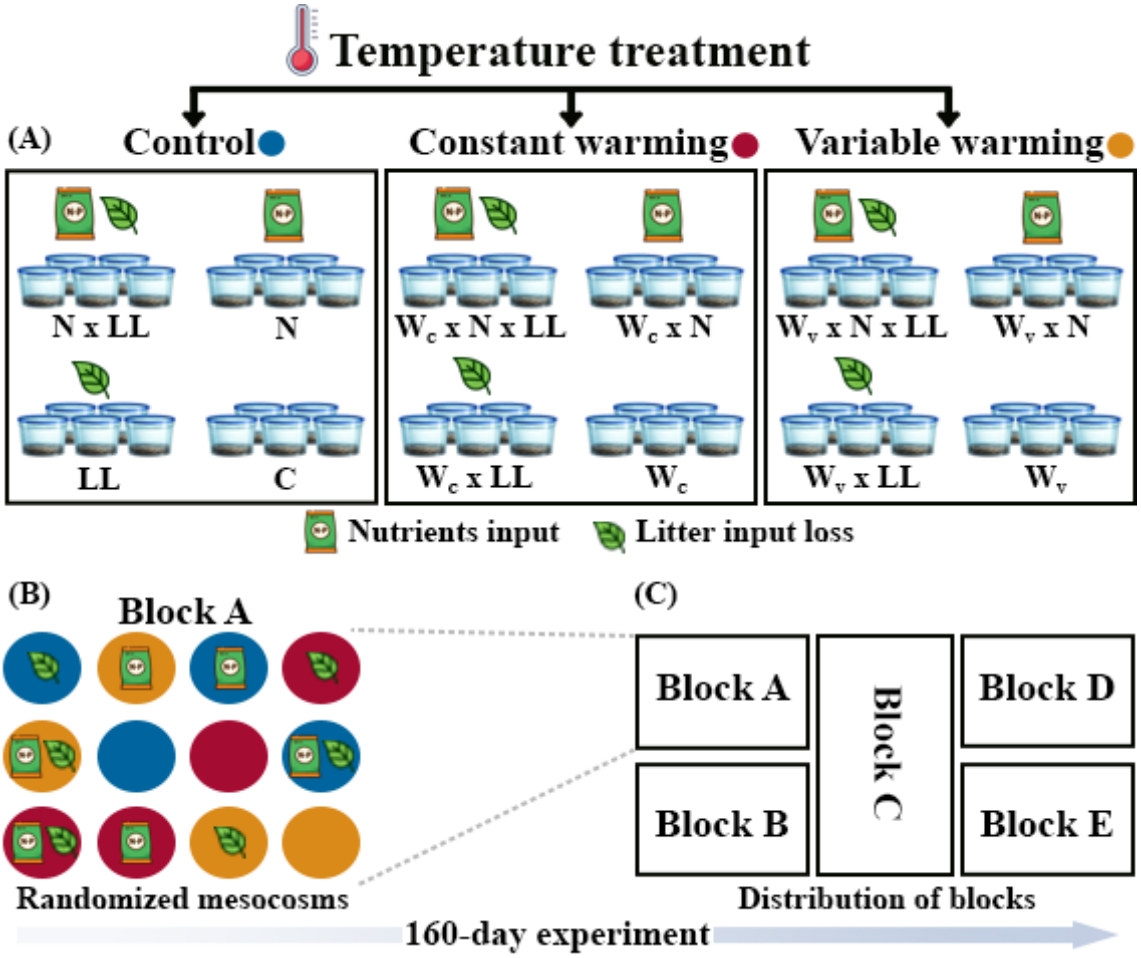

Figure 1: Schematic representation of experimental design. (A) Combination of three temperature treatments (control, constant warming, and variable warming) with nutrient enrichment and litter input loss, resulting in twelve treatment combinations. Each treatment was replicated five times. (B) The twelve treatment combinations were randomly assigned to mesocosms within each block. (C) Distribution of the five experimental blocks in the field. The experiment lasted 160 days.

The first four samplings occurred at time points 0, 3, 7, and 20, and the remaining samplings occurred every twenty days, resulting in 11 temporal samplings. Thus, with five replicates for each of the twelve treatment combinations, the sample size was 660. The phytoplankton community samples were collected at a depth of approximately 40 cm, in the subsurface of the mesocosms, using 100 ml glass bottles and fixed in situ with 1% acetic Lugol. Along with biotic sampling, physical and chemical variables were measured using a

multiparameter probe (Horiba U52). To quantify dissolved and total nutrients (phosphorus and nitrogen), water samples were collected for later measurement in the laboratory.

2.2.2 Laboratorial analysis

The identification of taxa was performed with the use of specialized bibliography (Bicudo; Menezes, 2006; Komárek; Anagnostidis, 1986, 1989, 2005). aPhytoplankton individuals were counted using an inverted microscope at 400× magnification (Lund; Kipling; Le Cren, 1958; Utermöhl, 1958). Richness was defined as the number of taxa recorded in each sample, and density was calculated according to the Lipps et al. (2023).

The water samples were used to determine the concentration of total phosphorus, orthophosphate, ammoniacal nitrogen, and nitrate. To determine total phosphorus, a saturated potassium persulfate solution was added to the samples, followed by digestion in an autoclave (120 °C and 1 atm) for 50 minutes. After reaching room temperature, a mixed reagent composed of antimony potassium tartrate, ammonium molybdate, diluted sulfuric acid, and ascorbic acid were added to the samples. For orthophosphate analysis, the samples did not undergo autoclave digestion, and only the mixed reagent was added. Quantification was performed by UV-Vis electronic absorption spectrophotometry at 882 nm (Mackereth; Heron; Talling, 1978). Nitrate concentrations were determined using a flow injection analysis (FIA) system, which involved a reaction with sulfanilamide and N-naphthyl (Giné et al., 1980). For the analysis of ammonia levels, sodium nitroprusside and phenol were used as reagents, which were determined by UV-Vis electronic absorption spectrophotometry at 630 nm (Koroleff, 1976).

2.2.3 Data analysis

Two data matrices were constructed to represent phytoplankton community composition (presence–absence data) and community structure (abundance data). Based on these matrices, *Jaccard* and *Bray–Curtis* dissimilarity indices were calculated, respectively. *Jaccard* dissimilarity was used to evaluate compositional differences among communities, whereas *Bray–Curtis* dissimilarity captured differences in community structure based on species abundances. These matrices were used in the analyses designed to test the study hypotheses. Community dynamics were evaluated using three complementary analytical approaches: Principal Response Curves (PRC) to assess treatment-specific community trajectories relative to the control, temporal beta diversity (TBI) to quantify compositional turnover through time, and Local Contribution to Beta Diversity (LCBD) to evaluate changes in community uniqueness among treatments.

To test the first hypothesis that community composition would diverge through time between treatments and the control, PRC analyses were performed (Ter Braak, 2023; Van den Brink; Braak, 1999). PRC is a multivariate method derived from Partial Redundancy Analysis (RDA) designed for temporal experimental studies. In this approach, time is included as a covariate, allowing the evaluation of treatment trajectories relative to the control, which was set as the reference level, following the standard PRC framework for experimental mesocosm studies. The first canonical axis represents the main pattern of temporal community change. Both presence–absence and abundance matrices were used to distinguish patterns related to species turnover and shifts in species dominance. PRC analyses were conducted using the *prc* function from the *prc* package, and diagrams were generated using the *plotprc* function (Van den Brink; Braak, 1999). Statistical significance was assessed using a permutation-based ANOVA, with the *anova* function from the *vegan* package (Oksanen et al., 2025).

To test the second hypothesis, which evaluated potential compositional and structural, biotic homogenization, Temporal Beta Diversity (TBI) was calculated (Legendre, 2019). This metric quantifies compositional changes between consecutive sampling dates within each mesocosm. *Jaccard* and *Bray–Curtis* dissimilarities were used to evaluate compositional and structural homogenization, respectively. Thus, eleven TBI values were obtained for each mesocosm in each distance matrix, and these were subsequently tested in regression models with time as the predictor variable. Temporal beta diversity was calculated using the *TBI* function from the *adespatial* package (Dray et al., 2012).

TBI values derived from presence/absence data showed linear trends and were therefore analyzed using beta regression, which is appropriate for proportional data ranging from 0 to 1 and accommodates heteroscedasticity and asymmetry (Ferrari; Cribari-Neto, 2004). In contrast, abundance-based TBI values exhibited nonlinear trends and were modeled using Generalized Additive Models (GAM) (Kosicki, 2020; Wood, 2026). GAMs were fitted assuming a beta distribution with a smoothed term for time and a restricted basis dimension ($k = 5$). Beta regressions were performed using the *betareg* function from the *betareg* package (Cribari-Neto; Zeileis, 2010), and GAM models were fitted using *gam* function from the *mgcv* package (Wood, 2026).

Finally, to test the third hypothesis, regarding community uniqueness among treatments, the contribution of each mesocosm to regional beta diversity (LCBD) was calculated (Legendre; De Cáceres, 2013). LCBD quantifies the contribution of each community to total beta diversity, allowing the identification of communities that are compositionally distinct from the others and the evaluation of how this contribution changes through time. LCBD values were calculated

using presence/absence and abundance data based on *Jaccard* and *Bray-Curtis* dissimilarities, respectively. To focus on treatment-level patterns, replicate mesocosms were averaged to obtain a single value per treatment. These values were plotted through time to evaluate temporal trends. LCBD was calculated using the *LCBD.comp* function from the *adespatial* package (Dray et al., 2012). All analyses were performed in R (R Development Core Team, 2025), and graphs were produced using the ggplot2 package (Wickham, 2016).

2.3 Results

A total of 196 taxa were identified, comprising approximately 50% green algae (mainly Chlorophyceae and Zygnematophyceae), 23% cyanobacteria, 21% phytoflagellates (primarily Dinophyceae and Chlamydophyceae), and 6% diatoms (mainly Bacillariophyceae). During the first 40 days of the experiment, the highest taxon richness was observed under nutrient input alone at the fourth sampling (day 20), whereas the lowest richness occurred in two samples with only two taxa: under variable warming with litter loss (day 3) and under nutrient input combined with litter loss (day 40). During the final 40 days, the highest number of taxa was again recorded under nutrient input alone at the last sampling (day 160), with 31 taxa, while the lowest richness was observed under variable warming with nutrient input at the same sampling time, with only four taxa.

Regarding phytoplankton abundance, during the first 40 days of the experiment, the highest value was recorded under nutrient input alone at the fourth sampling (day 20), reaching 9,333,187 ind. mL^{-1}, whereas the lowest value occurred under the same condition at the first sampling (day 0), with 4,590 ind. mL^{-1}. During the final 40 days, the highest abundance was again observed under nutrient input alone at the ninth sampling (day 120), with 968,835 ind. mL^{-1}, while the lowest value was recorded under constant warming combined with nutrient input and litter loss, with 4,256 ind. mL^{-1}. During the first 40 days, green algae accounted for approximately 99% of total abundance, with the remaining taxonomic groups contributing only 1%; in the final 40 days, green algae still dominated total abundance (~77%), however cyanobacteria increased their contribution to 21% and were the only group showing a significant increase in abundance over time ($p < 0.001$), whereas green algae declined significantly ($p < 0.001$).

The principal response curve captured pronounced differences in the temporal dynamics of phytoplankton community composition among treatments, both for presence/absence (Figure 2A) and abundance data (Figure 2B). The first axis explained 12% of the total variation in the presence/absence analysis and 14% in the abundance-based analysis and was statistically

significant based on permutation tests ($p < 0.05$). In both approaches, treatments exhibited distinct temporal trajectories relative to the control, with divergences becoming more pronounced over time, particularly from the middle of the experiment. While the overall temporal patterns were broadly consistent between presence/absence and abundance data, the abundance-based PRC showed stronger deviations, indicating that treatment effects were driven not only by changes in species occurrence but also by shifts in dominance structure within the phytoplankton community.

Several treatments exhibited the strongest deviations from the control in both presence/absence and abundance-based PRC analyses, particularly those involving nutrient input, either alone or in combination with warming (constant or variable) and/or litter loss. These deviations were primarily driven by a subset of species with high positive or negative scores along the first PRC axis. In both approaches, green algae and cyanobacteria were the main contributors with positive scores, particularly *Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerová & Cronberg, *Geitlerinema* sp., *Coelastrum proboscideum* Bohlin, and *Monoraphidium contortum* (Thuret) Komárková-Legnerová. In contrast, negative scores were mainly associated with phytoflagellate, such as *Parvodinium* sp3. and the desmid *Staurodesmus mucronatus* (Nägeli) Thomasson. Overall, the emergence and dominance of a few taxa drove the differences between the control and these treatments, while other species declined in occurrence and abundance.

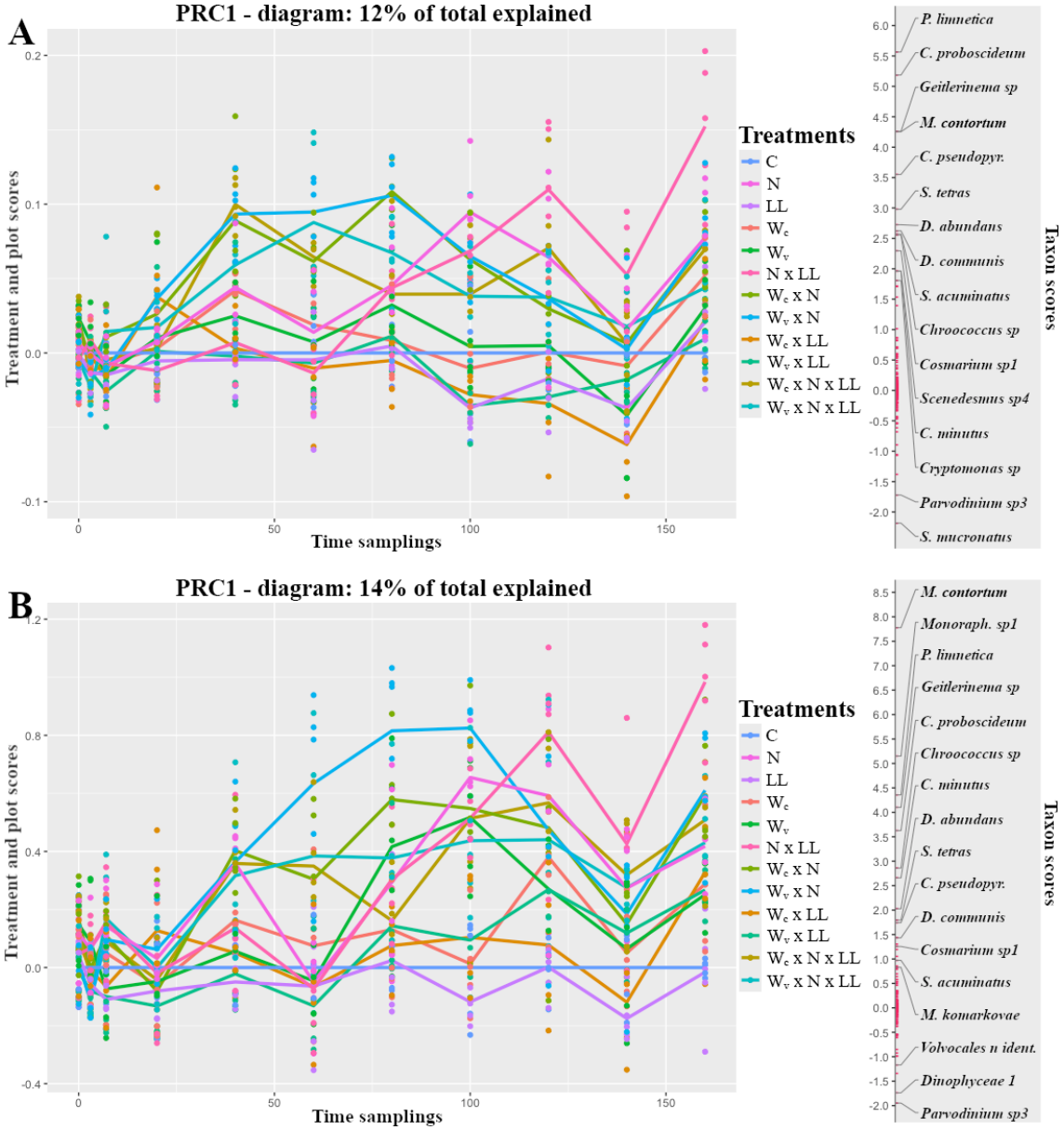

Figure 2: Principal response curves of treatments in relation to experimental control. A: Analysis and plot made with presence/absence data. B: Analysis and plot made with abundance data. The weights of the taxa are shown on the right side of the plot; these represent the affinity of each taxon with the pattern shown in the graph. *P. limnetica*: *Planktolyngbia limnetica*, *C. proboscideum*: *Coelastrum proboscideum*, *M. contortum*: *Monoraphidium contortum*, *C. pseudopyr.*: *Cosmarium pseudopyramidatum*, *S. tetras*: *Stauridium tetras*, *D. abundans*: *Desmodesmus abundans*, *D. communis*: *Desmodesmus communis*, *Scenedesmus acuminatus*, *C. minutus*: *Chroococcus minutus*, *S. mucronatus*: *Staurodesmus mucronatus*, *M. komarkovae*: *Monoraphidium komarkovae*.

Temporal beta diversity (TBI) revealed marked compositional dynamics across treatments throughout the experiment. Analyses based on presence/absence data showed predominantly positive temporal trends in TBI, with linear regressions indicating an increase in species turnover over time, particularly in treatments related to warming (Figure 3). This pattern indicates that phytoplankton communities did not converge toward similar compositions but instead became increasingly differentiated over time, suggesting directional changes from the initial to the final community. Abundance-based temporal beta diversity exhibited

pronounced non-linear dynamics, with generalized additive models identifying significant temporal patterns primarily in treatments involving nutrient input under variable warming, with or without litter loss, as well as in the control and in the treatment with nutrient input combined with litter loss (Figure 4). These trajectories reflect fluctuations in community structure associated with changes in species dominance rather than simple species replacement. In the treatment with variable warming and nutrient input, periods characterized by negative deviations of TBI from its temporal mean were associated with short-term structural homogenization, coinciding with the maximum deviations observed in the PRC. A similar correspondence between reduced abundance-based TBI and maximum PRC deviations was also observed under the combined effects of nutrient enrichment, variable warming, and reduced litter input and under nutrient enrichment with reduced litter input, although the timing of homogenization differed, occurring during the middle of the experiment and toward the end, respectively.

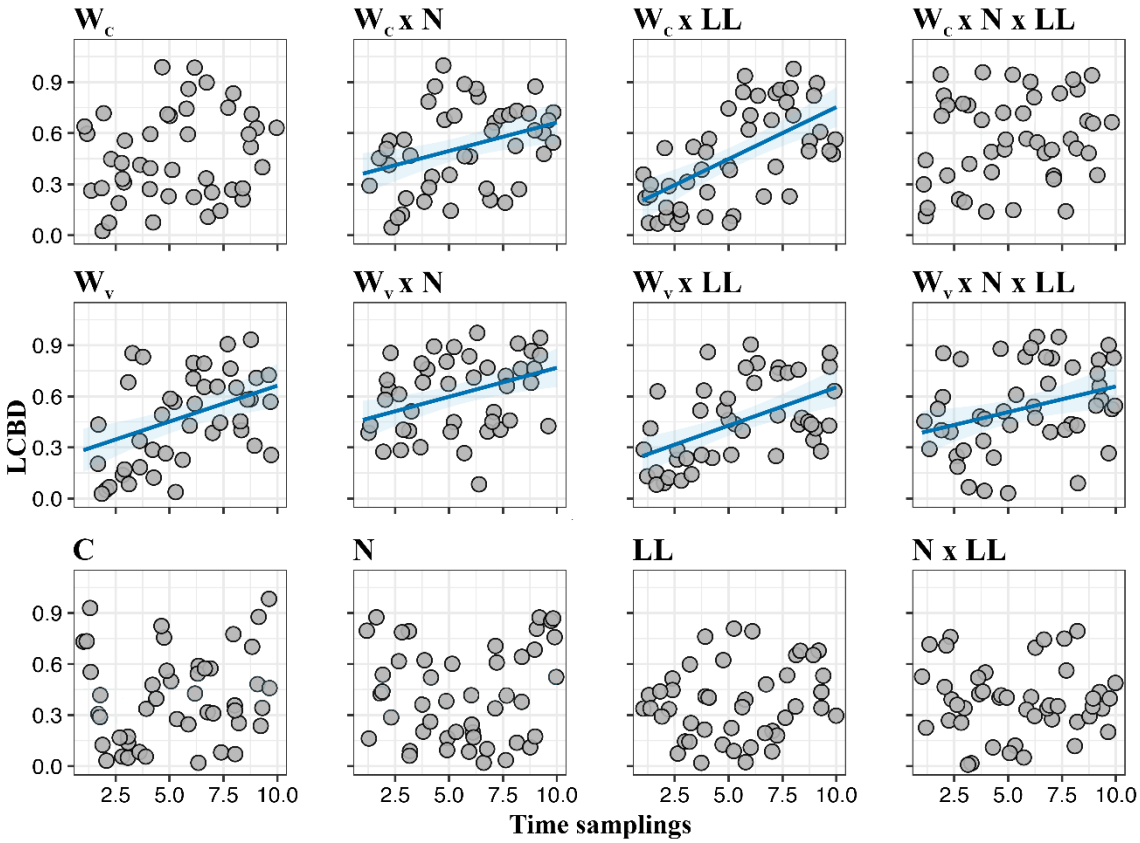

Figure 3: Beta regressions models relating TBI values calculated from presence/absence data between consecutive sampling dates for each experimental treatment. Shaded area around the regression line indicates standard error. Lines were added only in significant regressions.

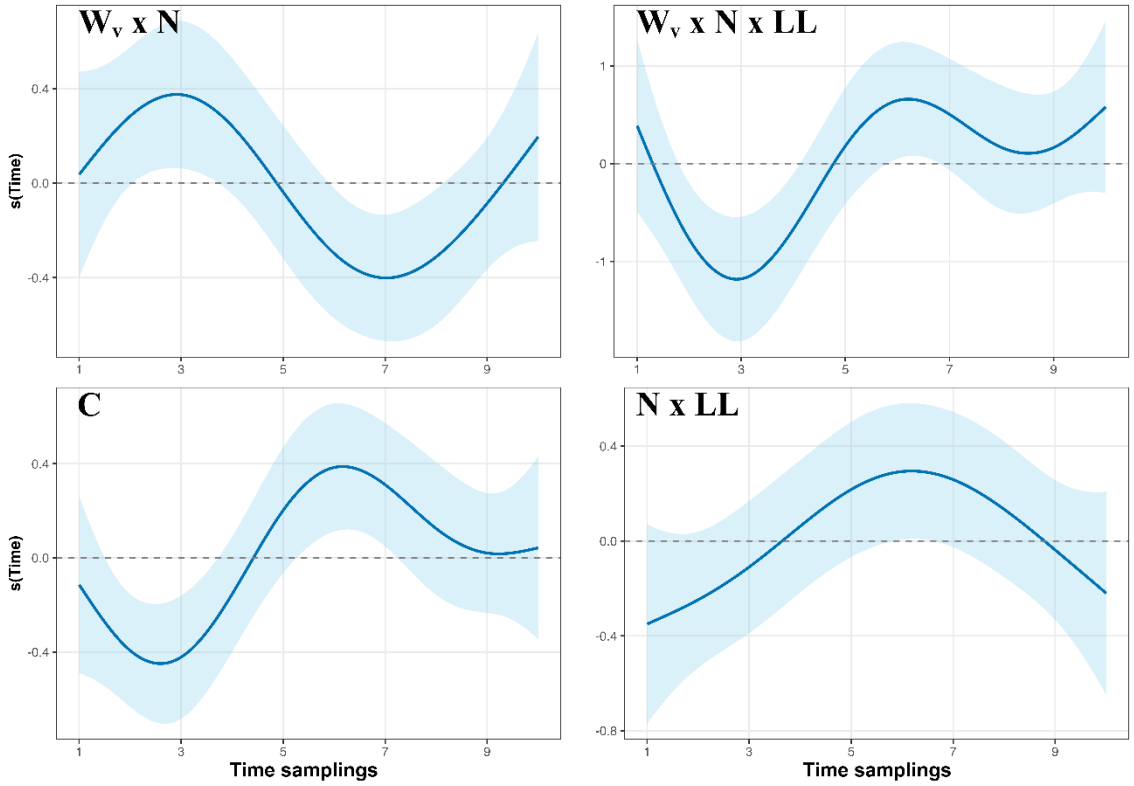

Figure 4: Temporal dynamics of TBI values with abundance data between treatments of generalized additive models (GAMs). The lines represent the estimated smooth function of time (s(Time)), representing the nonlinear effect of time. Positive and negative values indicate periods of increased or decreased temporal influence, respectively. The shaded areas show the standard error.

Local contributions to beta diversity exhibited contrasting temporal patterns depending on the type of data used (Figure 5). When calculated from presence/absence data, LCBD values showed few temporal changes over time, remaining consistently restricted between approximately 0.06 and 0.12 (Figure 5A). Distributions were narrow and exhibited only minor temporal shifts, indicating high compositional similarity among mesocosms. In contrast, abundance-based LCBD displayed wider variation and a progressive temporal shift toward higher values from intermediate to late sampling times (T60–T160) (Figure 5B). Distributions gradually moved to the right over time, indicating an increased contribution of individual mesocosms to total beta diversity based on abundance. Although LCBD values remained concentrated within comparable ranges at each sampling time, the overall increase in their magnitude suggests growing differentiation in community structure driven by changes in species dominance. Furthermore, lower LCBD values were observed under nutrient enrichment combined with warming, particularly during the middle of the experiment, indicating periods of structural homogenization. A similar pattern emerged when litter input was reduced, with lower local contributions occurring during phases of decreased structural differentiation.

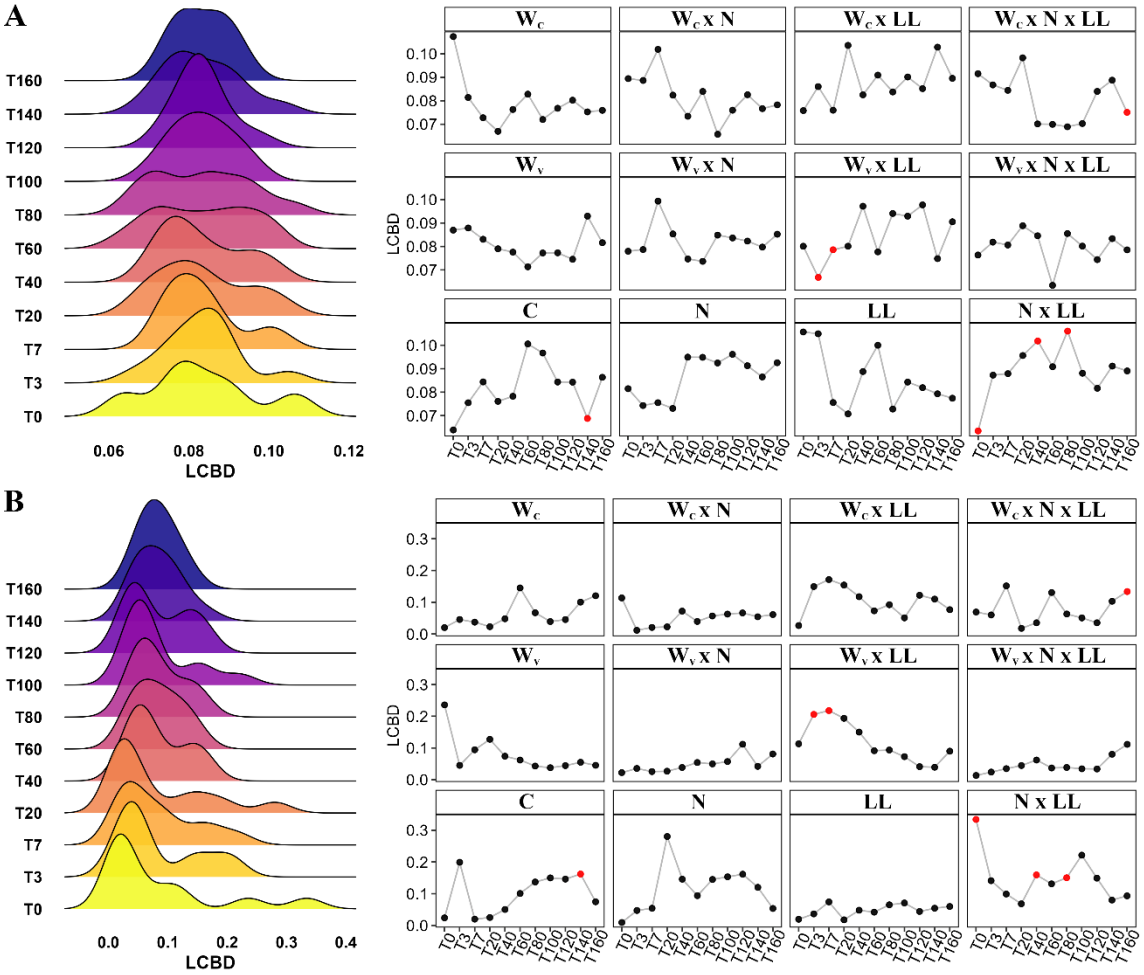

Figure 5: Temporal variation in local contributions to beta diversity (LCBD) for each experimental treatment. The graphs on the left show the distribution of LCBD values over sampling times, while the graphs on the right show the specific temporal trajectories for each treatment. Red points indicate significant LCBD values.

Generalized additive models revealed treatment-specific relationships between the abundance of phytoplankton taxonomic groups and environmental variables (Appendix A). Under nutrient enrichment with variable warming and under nutrient enrichment combined with reduced litter input, which also exhibited the strongest deviations in PRC and signs of community structural homogenization, cyanobacterial abundance was positively associated with nutrient concentrations, particularly phosphate, with an additional positive effect of turbidity in the latter condition. Under nutrient enrichment with variable warming, diatoms exhibited similar nutrient-related responses and a significant temporal trend in abundance, whereas under nutrient enrichment combined with reduced litter input, significant environmental relationships were detected exclusively for cyanobacteria. Other warming conditions, including variable warming alone, constant warming with reduced litter input, and constant warming with nutrient enrichment, showed significant temporal trends in cyanobacterial abundance, accompanied by positive associations with turbidity. Under the

combined effects of nutrient enrichment, variable warming, and reduced litter input, which was also characterized by community homogenization, cyanobacterial abundance was positively related to total phosphorus. Overall, cyanobacteria exhibited the highest number of significant associations with environmental variables across treatments.

2.4 Discussion

Our results show that warming and land-use-related stressors strongly altered the temporal dynamics of phytoplankton communities, generating divergent community trajectories and episodic structural homogenization. Community composition diverged progressively from the control over time, with continuous changes driven by species turnover and shifts in abundance, particularly under warming and nutrient enrichment. Rather than producing consistent compositional homogenization, these stressors promoted high temporal instability, with communities following distinct directional trajectories. Abundance-based analyses further revealed transient periods of structural homogenization, largely driven by the dominance of cyanobacteria and green algae under combined warming and nutrient enrichment. Consistently, LCBD values declined during these episodes of dominance, indicating reduced community uniqueness in stressed treatments, whereas control mesocosms maintained higher compositional distinctiveness. Together, these results suggest that multiple environmental stressors can generate complex temporal responses in phytoplankton communities, where homogenization and loss of biotic uniqueness occur episodically rather than as persistent trends. Our findings suggest that anthropogenic stressors may not necessarily drive gradual temporal homogenization in aquatic communities. Instead, warming and nutrient input drove community instability via high species turnover, while episodic dominance by opportunistic taxa led to transient phases of structural homogenization.

The differences in phytoplankton community composition between treatments became increasingly pronounced over time, with distinct temporal trajectories emerging mainly under warming, nutrient enrichment, and their interactions. These compositional changes were highly dynamic, reflecting continuous species turnover within each treatment. However, compositional divergence alone did not fully capture the magnitude of community reorganization observed under environmental stress, as evidenced by lower amplitudes of the compositional PRC. When species abundances were considered, treatment effects became more pronounced and structured, indicating that shifts in dominance played a central role in shaping community responses. Although community composition diverged among treatments through time, dominance by a small number of opportunistic taxa produced transient phases of structural

homogenization. This distinction between compositional change and structural reorganization has been increasingly recognized in aquatic systems, where variation in dominance often overlaps with species replacement in determining patterns at the community level (Hillebrand; Bennett; Cadotte, 2008; Magurran; Henderson, 2010).

In freshwater phytoplankton, environmental stressors such as warming and nutrient enrichment often promote strong asymmetries in abundance between taxa, leading to marked structural changes even in the absence of consistent compositional convergence (Richardson et al., 2019b; Verbeek et al., 2018; Yu et al., 2018). Together, these results indicate that abundance-based processes are more sensitive indicators of community reorganization under environmental stress, helping to explain how compositional instability can coexist with transient phases of structural homogenization driven by shifts in dominance.

The structural homogenization observed here driven by the dominance of a few taxa, has important ecological implications for freshwater ecosystems. When a small number of species disproportionately influence community structure, functional complementarity declines and ecosystem processes become concentrated in dominant taxa (Crawford et al., 2021; Hillebrand; Bennett; Cadotte, 2008; Olden; Rooney, 2006). Such simplification can reduce trophic complexity and functional redundancy, increasing ecosystem vulnerability to additional disturbances (Downing; Brown; Leibold, 2014; Sanders et al., 2018). In phytoplankton communities, these shifts may affect primary production, nutrient cycling, and increase the likelihood of harmful algal blooms, ultimately impacting water quality and ecosystem functioning (Amorim; Moura, 2021; Borics et al., 2021; Dokulil; Qian, 2021).

Warming and nutrient enrichment treatments had the strongest effect on phytoplankton community dynamics across the analyses performed, especially when acting in combination. Several studies have demonstrated that these environmental stressors strongly influence freshwater phytoplankton, reshaping community structure and favoring a limited subset of taxa (Peter; Sommer, 2015; Richardson et al., 2019b; Tadonléké, 2010). Notably, variable warming produced stronger community responses than constant warming, suggesting that thermal variability, rather than increases in mean temperature alone, may play a key role in shaping community dynamics. These findings highlight that thermal variability may be as important as mean warming in shaping phytoplankton community responses to global change.

This pattern highlights the potential importance of heatwave events under future climate scenarios. Previous studies have reported increased cyanobacterial biomass under such conditions, often associated with biodiversity loss and increased dominance (Jöhnk et al., 2008; Rasconi; Winter; Kainz, 2017). Our results are consistent with these findings and further show

that the interaction between variable warming and nutrient enrichment amplifies these effects, leading to pronounced structural reorganization. Thus, this suggests that nutrient inputs combined with thermal instability may intensify phytoplankton community reorganization and potentially affect ecosystem functioning. In contrast, litter loss had no detectable effect on community dynamics, likely because its influence on phytoplankton occurs indirectly through nutrient release, a process that is highly context-dependent across aquatic systems (Klug, 2002; Sherbo et al., 2023).

The compositional and structural changes observed in the phytoplankton community were mainly driven by cyanobacteria, although green algae (chlorophytes and zignematophytes) and diatoms (bacillariophytes) also contributed to the patterns observed. Cyanobacteria were strongly favored under high temperatures and greater nutrient availability, reflecting their competitive advantage over other phytoplankton groups, particularly in terms of growth rates and physiological tolerance (Paerl; Huisman, 2008; Reynolds, 2006). This dominance can promote recurrent episodes of proliferation, altering light availability and nutrient dynamics, restricting the development of less competitive taxa (Escalas et al., 2019). At the same time, some chlorophyte species were able to develop successfully and influence community structure, largely due to their rapid growth and high resource acquisition capacity, making treatments with nutrient inputs particularly favorable for this group (Reynolds et al., 2002; Reynolds, 2006).

In contrast, diatoms contributed more selectively to community dynamics and were mainly associated with treatments characterized by thermal variability, particularly under the combined effects of variable warming and nutrient enrichment (Margalef, 1978; Reynolds, 2006). Overall, the contrasting responses among phytoplankton groups reveal a community marked by temporal instability, in which changes in taxonomic composition are accompanied by phases of reduced structural differentiation, driven by reduced community evenness. This pattern highlights that environmental stressors generate dynamic and unstable community responses, rather than more consistent trajectories over time.

The dynamics of freshwater phytoplankton play a key role in ecosystem functioning and the provision of ecosystem services. Changes in dominance structure and temporal stability can directly affect regulatory, supporting, provisioning, and cultural services (Amorim; Moura, 2021; Naselli-Flores; Padisák, 2023; Petsch et al., 2022). In particular, primary production and nutrient cycling, which are linked to supporting services, are strongly influenced by phytoplankton dynamics, as observed in this study. Furthermore, episodes of extensive cyanobacterial proliferation can promote anoxia in aquatic environments, thereby increasing

methane production and greenhouse gas emissions, which impair climate regulation services and potentially transform these systems from greenhouse gas sinks into sources (Casper et al., 2000; Grasset et al., 2020). These proliferation events also compromise provisioning services, especially water and fish supplies, due to the production of toxins, rendering the water unfit for human consumption and causing fish mortality (Svirčev et al., 2019a). Cultural services are also affected, as recurrent blooms reduce the recreational use and aesthetic value of lakes and reservoirs (Naselli-Flores; Padisák, 2023). Overall, these findings highlight the vulnerability of freshwater ecosystems, as illustrated here by phytoplankton dynamics, to climate warming and nutrient enrichment, underscoring the need for management strategies and public policies to mitigate anthropogenic actions such as deforestation, agricultural activities, and high greenhouse gas emissions. In addition, these results reinforce the importance of studies that explicitly consider temporal and structural dynamics when assessing the responses of freshwater communities to environmental stress.

By integrating multiple environmental stressors with temporal and structural dimensions of beta diversity, our study demonstrates that phytoplankton communities respond to environmental change through complex and non-linear dynamics. Warming, particularly under variable regimes, and nutrient enrichment emerged as primary drivers of community reorganization, generating temporally unstable trajectories characterized by high species turnover and shifts in species dominance. Although compositional change followed a clear directional pattern over time, it did not result in homogenization. Instead, structural responses revealed transient phases of homogenization driven by the episodic dominance of a few opportunistic taxa, particularly cyanobacteria, leading to temporary reductions in community uniqueness. These findings show that compositional and structural dimensions of biodiversity may follow distinct pathways under environmental stress, with high species turnover masking structural homogenization driven by dominance shifts. Ultimately, our results highlight that warming and nutrient enrichment can reshape community dynamics over time, emphasizing the importance of accounting for temporal variability and species dominance when predicting ecological responses in the context of global change.

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3 CONVERGING CLIMATE AND HUMAN PRESSURES CREATE GLOBAL HOTSPOTS OF RISK TO FRESHWATER SECURITY FROM HARMFUL CYANOBACTERIAL BLOOMS

Abstract

Global environmental change is reshaping freshwater ecosystems, yet predictions of harmful cyanobacterial blooms (cyanoHABs) are still largely based on climate alone. Here, we show that the global risk of cyanoHABs is not only increasing, but also being redistributed by the combined effects of climatic and anthropogenic drivers. Using ecological niche models for three bloom-forming cyanobacteria, together with a susceptibility index that integrates climate suitability, nutrient inputs, human population, and river regulation, we mapped current and future risk across 225 river basins worldwide. Climate warming alone projected broad expansions of suitable conditions, especially in low-latitude regions. However, when human pressures were considered, these patterns shifted, with hotspots concentrated in densely populated and heavily modified basins. Some hotspots were shared among species, suggesting that bloom risk at global scales is driven more by common environmental conditions than by species-specific dynamics. While some regions remain consistently vulnerable, others are emerging as new hotspots, particularly in South America and Asia. Overall, our results show that climate alone captures only part of the problem, with human pressures playing a key role in determining where cyanoHABs are most likely to occur. This convergence of favorable conditions and human influence highlights river basins where risks to water quality and human exposure are likely to increase, placing a growing number of people at risk in regions that support some of the world's most intensively used freshwater resources.

Keywords: Cyanobacterial blooms; Human risk; Anthropogenic pressures; Water security; Global change

3.1 Introduction

Global environmental change is increasingly shaped by the interaction of multiple stressors, particularly global warming and increasing human pressures on landscapes, which together drive changes in species distribution, biological interactions, and invasion processes worldwide (Parmesan; Yohe; Andrus, 2003; Walther, 2010). These factors are widely associated with ecological responses across ecosystems, including shifts in species ranges, phenological changes, biotic homogenization, and reorganization of community structure (Isbell et al., 2023; Pecl et al., 2017; Scheffers et al., 2016).

Freshwater ecosystems are particularly sensitive to these changes, as biological communities respond strongly to environmental variations and directly influence water quality, ecosystem services, and ecosystem functioning (Dossena et al., 2012; Woolway; Sharma; Smol, 2022). In these systems, some biological responses to warming pose significant ecological and human health risks, with harmful cyanobacterial blooms (cyanoHABs) being a key example. Their proliferation compromises biodiversity and the structure of the food web (Paerl; Otten, 2013; Šulčius et al., 2017), as well as drinking water safety (Chorus; Welker, 2021). Rising temperatures are closely linked to cyanoHABs and have been associated with their expansion into regions where environmental conditions were previously unsuitable (Paerl; Huisman, 2008; Sukenik et al., 2012; Zanon et al., 2025a).

In addition to global warming, anthropogenic pressures have intensified over time in freshwater ecosystems, playing an important role in shaping aquatic communities across broad spatial and temporal scales (Dudgeon et al., 2006; Vörösmarty et al., 2010). The construction of dams and reservoirs, for example, alters water residence time, hydrological regimes, and thermal structure, conditions that are directly linked to the development of cyanoHABs (Grill et al., 2019; Paerl; Otten, 2013). Furthermore, nutrient enrichment driven by agriculture, urbanization, and the influx of wastewater has increased in river basins worldwide, reinforcing eutrophication processes and amplifying the frequency, persistence, and severity of these blooms (Carpenter et al., 1998; Wang et al., 2025b). Human population growth around hydrological systems further exacerbates these impacts, increasing nutrient loads through effluent discharge, pollution, and the loss of riparian vegetation that would buffer these inflows (Allan, 2004; Olokotum et al., 2020; Vörösmarty et al., 2004). Combined, these pressures interact with global warming to create new environmental conditions that may favor the spatial expansion of harmful cyanobacteria.

Because these drivers are unevenly distributed globally, their interaction is expected to produce spatially heterogeneous responses, with certain regions becoming more susceptible to bloom events than others (Vörösmarty et al., 2010). Susceptibility hotspots are likely to emerge where climatic suitability coincides with intense human pressures, creating conditions that favor the establishment and dominance of bloom-forming species (Huisman et al., 2018). In these regions, cyanobacterial blooms can lead to the release of cyanotoxins, particularly during cell lysis and bloom senescence (Svirčev et al., 2019b), posing risks to water quality and ecosystem integrity.

Therefore, identifying the river basins most susceptible to cyanoHABs amid ongoing environmental changes remains a crucial challenge. Current large-scale projections are typically based primarily on climatic variables, ignoring the combined influence of anthropogenic and environmental factors that strongly modulate freshwater ecosystems. As a result, the spatial distribution of areas favorable to the development of blooms may be underestimated or misrepresented worldwide. Here, we integrate climatic, anthropogenic, and environmental factors to map the current and future global distribution of the most problematic cyanobacterial species associated with large blooms and toxicity, *Raphidiopsis raciborskii* (Wołoszyńska) Aguilera & al., *Microcystis aeruginosa* (Kützing) Kützing, and *Planktothrix agardhii* (Gomont) Anagnostidis & Komárek, to identify river basins that represent hotspots of susceptibility to cyanobacterial HABs worldwide, thereby highlighting regions of elevated risk for ecosystem functioning and human health.

3.2 Methodology

3.2.1 Occurrence data

The occurrence records (geographic coordinate) for the three species were extracted from articles filtered from the *Web of Science* (WoS) and *Scopus* platforms, following the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) protocol to ensure standardization of the review process (Page et al., 2022). On the WoS platform, the search was performed by “topic”, using all databases, between the years 1975 to 2025, August. On the Scopus platform, the search was performed using “TITLE-ABS-KEY”, between the years 1960 to 2025, August. The searches were individual for each species, and the same search terms were used on both platforms: “*Microcystis aeruginosa*” AND “Freshwater” for the species *M. aeruginosa*, “*Planktothrix agardhii*” OR “*Oscillatoria agardhii*” for *P. agardhii and "Cylindrospermopsis raciborskii" OR "Anabaena raciborskii" OR "Raphidiopsis raciborskii"*

for *R. raciborskii*. In addition to the occurrence records obtained from scientific articles, data for all three species were compiled from the Global Biodiversity Information Facility (GBIF.org, 2025) and from research databases covering different regions of South America.

A total of 2428 articles were obtained for *M. aeruginosa* (WoS: 1278; Scopus: 1150), 1457 articles for *P. agardhii* (WoS: 805; Scopus: 652), and 2093 articles for *R. raciborskii* (WoS: 1192; Scopus: 901). The articles were then examined individually, and the geographic coordinates corresponding to the locations of occurrence were extracted. In cases where geographic coordinates were not provided but the sampling location was described accurately, the area was located on Google Earth and the coordinates were obtained manually. After this process, we obtained 1944 records of *R. raciborskii*, 1335 of *M. aeruginosa*, and 1775 of *P. agardhii*, including records from scientific articles, GBIF, and databases.

Using the *CoordinateCleaner* package in R v3.0.1 (Zizka et al., 2019), we performed data cleaning in which records corresponding to country centroids, research institutions, oceanic coordinates, duplicated latitude–longitude values, and invalid coordinates were removed. The resulting occurrence coordinates for each species were mapped onto the global river network provided by the HydroSHEDS database (Lehner; Grill, 2013), using a grid with 20-km resolution and 281.643 cells, built under the EPSG 6933 coordinate reference system. In total, 298 occurrences of *R. raciborskii*, 177 occurrences of *M. aeruginosa* and 453 occurrences of *P. agardhii* were mapped.

3.2.2 Environmental variables

Environmental variables from two categories were considered: bioclimatic and hydrological. Bioclimatic variables representing present and future conditions (2000, 2030, 2050 e 2090) were derived from the Coupled Model Intercomparison Project Phase 6-CMIP6 (Eyring et al., 2016), considering Shared Socioeconomic Pathways (SSPs) under pessimistic (SSP5-8.5) carbon emission scenarios. The SSP framework represents potential global development trajectories that integrate political, social, demographic, and socio-ecological components, providing a robust basis for assessing how different governance and resource-use contexts may influence climate change and its ecological impacts (Frame et al., 2018).

Climate predictors were sourced from the WorldClim v2.1 database at a spatial resolution of 10 arc-minutes (Fick; Hijmans, 2017). Variables presenting potential spatial discontinuities were excluded to avoid compromising model robustness (Booth, 2022). The final set of predictors included: annual mean temperature (BIO1); mean diurnal range (BIO2);

isothermality (BIO3); temperature seasonality (BIO4); maximum temperature of the warmest month (BIO5); minimum temperature of the coldest month (BIO6); annual temperature range (BIO7); annual precipitation (BIO12); precipitation of the wettest month (BIO13); precipitation of the driest month (BIO14); and precipitation seasonality (BIO15).

To represent climate uncertainty across future scenarios, we used the *chooseGCM* package version 1.0.2 (Esser et al., 2025) to select atmospheric–ocean general circulation models (AOGCMs). Models were selected using a K-means clustering procedure that identifies those best representing the overall climate variability space. Based on this approach, ACCESS-CM2 and FIO-ESM-2-0 were selected as representatives.

Hydrological variables were obtained from the HydroATLAS framework, derived from the HydroSHEDS database (Linke et al., 2019; Macedo et al., 2022). These variables describe both the topological structure of the river network and the hydrological characteristic of individual river reaches. Network topology was represented by the downstream segment ID (NEXT_DOWN) and the main river ID (MAIN_RIV), which together define longitudinal connectivity within each basin. Hydrological attributes included catchment area directly draining into each reach (CATCH_SKM, km²); long-term mean discharge (DIS_AV_CMS, $m^3 s^{-1}$); downstream distance to the terminal point of the network (DIST_DN_KM, km); upstream distance to headwaters (DIST_UP_KM, km); and natural annual mean (dis_m3_pyr, $m^3.s^{-1}$), minimum (dis_m3_pmn, $m^3.s^{-1}$), and maximum discharge (dis_m3_pmx, $m^3.s^{-1}$). Hydrological variables were treated as stationary and assumed to remain constant between present and future scenarios. This is due to the lack of data in the literature projecting these variables for future climate change scenarios.

To address multicollinearity among predictors, we calculated the variance inflation factor (VIF) using the *usdm* package v2.1.7 in R (Naimi; Araújo, 2016). Highly correlated variable pairs were identified, and variables with the highest VIF values were sequentially removed until not pairwise correlation exceeded 0.5. After filtering, the variables retained for analysis were BIO02, BIO03, BIO15, NEXT_DOWN, LENGTH_KM, DIST_DN_KM, DIST_UP_KM and dis_m3_pmn.

3.2.3 Generation of pseudo-absence data

Pseudo-absence data were generated to allow the use of ecological niche models based on machine learning algorithms. The inclusion of pseudo-absences informs algorithms regarding a negative class, and helps balance the datasets, reducing the biases inherent in

models that consider only presence and improving the ability of algorithms to distinguish between presences and absences (Sillero et al., 2021). For each species, ten sets of pseudo-absences were generated, with the number of pseudo-absences matching the number of occurrence records, thereby balancing the model. To retrieve realistic pseudo-absences distinguishable from actual occurrences, we used all predictor variables to obtain a presence-only distribution to each species using a corrected Mahalanobis distance with a inverted chi-squared transformation to obtain environmental suitability (Etherington, 2019). Pseudo-absences were randomly drawn outside the suitable area, thereby ensuring that they differ from occurrences both geographically and environmentally (Lobo; Jiménez-valverde; Real, 2008). The Mahalanobis distance is able to inform the distance between a recorded presence and the center of a multivariate space (i.e., the environmental optimum for that species) by describing the niche as an ellipsoidal envelope (Mahalanobis, 2018), making it more restrictive than the surface range envelope approach, which uses minimums and maximums to describe suitable area for the species. Finally, a binary matrix was built with occurrences (1) and pseudo-absences (0).

3.2.4 Ecological Niche Modeling (ENM)

Occurrence records, pseudo-absence data and environmental variables were used as inputs for ecological niche models (ENMs) to project the impacts of climate change on the global distribution of the three cyanobacterial species of public health concern analyzed in this study. Modeling procedures were conducted using the *caretSDM* package (https://github.com/luizesser/caretSDM) in software R. For each presence–pseudoabsence dataset, six machine-learning algorithms were employed, namely glmnet, k-Nearest Neighbors (KKNN), Mixture Discriminant Analysis (MDA), Naive Bayes, Neural Network (NNET) and Support Vector Machines with Radial Basis Function Kernel (SVMRadial). These models represent distinct methodological approaches and thus provide complementary projections of future distributions. To reduce biases and uncertainties associated with the individual models, we adopted an ensemble forecasting approach that integrates outputs from multiple ENMs to generate a final consensus prediction (Araújo; New, 2007).

Model construction employed a cross-validation method with K-fold subsampling, where K = 4. In this procedure, occurrence and pseudo-absence data were partitioned into K subsets of approximately equal size, ensuring that presences and pseudo-absences were equally represented within each subset. In each iteration, three subsets (75% of the data) were used for

model training and one subset (25%) for model testing. The procedure was repeated until each subset had been used as the test set once, and the entire K-fold cross-validation process was repeated 10 times, resulting in a total of 40 model projections. The same procedure was applied to each of the 10 pseudo-absence datasets, yielding a total of 400 projections per algorithm for each modeled species.

The climatic–environmental suitability (probability of occurrence) projected in each K-fold iteration was binarized into presence and absence based on the decision threshold that maximizes both sensitivity (the proportion of correctly predicted presences) and specificity (the proportion of correctly predicted absences). The binarized outputs from each model repetition were then summed and converted into an occurrence frequency for the species in the grid cells, allowing comparisons among models generated by different ENMs. This occurrence frequency reflects the climatic–environmental suitability of an area for the species and ranges from 0 to 1, where 0 indicates unsuitable conditions and 1 represents optimal conditions for species occurrence. Finally, climatic–environmental suitability was converted into presence and absence, where a threshold of 0.5 was applied to classify suitability values into presences ($\geq$ 0.5) and absences ($<$ 0.5).

The predictive performance of each ecological niche model (ENM) was assessed using the Receiver Operating Characteristic (ROC) method. This approach generates a curve in a bivariate space by plotting the true positive rate (sensitivity) against the false positive rate (1 − specificity) across multiple decision thresholds, from which confusion matrices were constructed to calculate performance metrics. Model performance was assessed using the Area Under the Curve (AUC) metric (Liu et al., 2005; Manel; Ceri Williams; Ormerod, 2001). Models with AUC values $\geq$ 0.9 were considered to exhibit good performance and were subsequently combined to generate the final consensus model. The climatic suitability of the resulting consensus model was obtained by averaging the suitability values of the well-performing models. To present the results, we divided the world into 225 river basins (Appendix B)

3.2.5 CyanoHABs susceptibility index

This index was developed to quantify the susceptibility of global river basins to potentially harmful cyanobacterial blooms. The main purpose was to combine anthropogenic pressure variables with ENMs outputs, moving beyond climate niche projections to better

assess the actual risk of bloom development, since the combined effects of warming, nutrients, and hydrology provide greater predictive power.

To represent anthropogenic pressure, we used projected values of population and nutrient-related variables within the Shared Socioeconomic Pathways (SSPs) framework from Beusen et al. 2022. These data correspond to model outputs generated by the IMAGE–Global Nutrient Model (IMAGE-GNM), which integrates socioeconomic drivers with biogeochemical and hydrological processes. We focused on the SSP5 (pessimistic) scenario and directly extracted values for the following time points: 2000, 2030, 2050, and 2070. The selected variables include population-related metrics and nutrient loading indicators (e.g., N and P inputs and transport to freshwater systems). These variables were incorporated into the index without additional modelling. Instead of recalculating nutrient fluxes, we relied on the original model outputs to avoid propagating additional uncertainty.

From the 137 variables available in the dataset, we selected 20 that are directly related to cyanobacterial bloom formation (Appendix C). All variables were normalized to a 0–1 scale, consistent with the ENMs climatic suitability values. After normalization, we applied a VIF collinearity test using the *usdm* package to remove highly correlated variables. This resulted in a final set of 10 variables representing anthropogenic pressure (Appendix C, Appendix D; Appendix E).

Data on reservoirs and dams, both existing and planned, were also included (Lehner et al., 2024). Because reservoir area was not available for planned dams, we used their location to assign presence (1) or absence (0) values to each grid cell. In total, the index combines 10 variables related to nutrient inputs and population, two variables representing dams, and one variable representing climatic suitability derived from ENMs (Table 1).

Table 1. Variables used to calculate susceptibility to cyanoHABs for river basins worldwide and the group to which they belong.

Description of variables used in the index	Group
Current Dams	Dams
Current Dams + for future	Dams
N delivery from aquaculture	Nitrogen
N delivery via runoff/erosion from agriculture	Nitrogen
Temporary storage in groundwater	Nitrogen
Total soil denitrification (agriculture + natural)	Nitrogen
P discharge from households to surface waters	Phosphorus

P removal in wastewater treatment plants	Phosphorus
P concentration at river mouth	Phosphorus
P delivery from point sources	Phosphorus
Area grassland	Population
Urban population with sewage connection / Total Population	Population
ENMs models	Warming

Weights (w_i) had to be assigned to each variable in the index calculations. These weights were determined based on the scientific literature on the associations among the variables used and the three species of focus in the study. Weights were assigned separately for each species-variable association. The strength of the association was categorized into three levels: strongly dependent (+++), dependent (++), and moderately dependent (+). These qualitative scores were then converted into numerical weights (18, 9, and 4.5, respectively), ensuring proportional differences in the variables' influence. This scale was designed to preserve relative importance, maintain interpretability, and avoid excessive weight disparities. The maximum value is arbitrary, since the calculations yielded whole numbers or values with few decimal places (Appendix F and G).

These weight values were divided by the number of variables within each group. For example, for the "phosphorus" group, which contained 4 variables, each variable was assigned a weight of 4.5 for strongly dependent relationships (+++), 3 for dependent relationships (++), and 1.5 for moderately dependent relationships (+) (Table S3). Thus, the index was calculated as:

$$Index = I(S \geq 0.5) \cdot \frac{\sum_{i=1}^{n} (X_i^{norm} \cdot w_i)}{\sum_{i=1}^{n} w_i}$$

Index: cyanoHABs susceptibility;

S: Climatic suitability derived from ENMs;

I(S ≥ 0.5): Indicator function restricting the index to suitable areas;

X_i^{norm}: Normalized (0 - 1) value of variable i;

w_i: Weight assigned to variable i, based on ecological evidence;

n: Total number of variables;

$\sum$: Summation across all variables included in the index

Table 2. Association between each environmental variable used in the index and each of the three species, showing strong dependence (+++), dependence (++), and moderate dependence (+).

Species	Infomation	Warming	Nutrient (nitrogen)	Nutrient (phosphorus)	Dams	Population	References
Microcystis aeruginosa	- Sensitive to high water column mixing; - Strongly dependent on nutrients (nitrogen and phosphorus); - Strongly related to high temperatures;	+++	+++	+++	+++	+++	Harke et al., 2016; Reynolds et al., 2002; Reynolds 1999
Planktothrix agardhii	- Can develop at lower temperatures; - Highly dependent on nutrients; - Can develop in turbid and highly mixed environments;	++	+++	+++	++	+++	Bonilla et al., 2012; Lenard & Poniewozik 2022; Reynolds 1999
Raphidiopsis raciborskii	- High phenotypic plasticity; - Can develop at lower temperatures; - Fixes nitrogen (does not depend on high concentrations in the environment); - High affinity for phosphorus (does not depend on high concentrations in the environment); - Can develop in environments with high water column mixing;	++	+	++	++	+++	Pagni et al., 2020; Bonilla et al., 2012; Padisak 1997; Reynolds 1999

To obtain an index value for each river basin, the average of the index values for each grid cell within a specific basin was calculated. Thus, each river basin was assigned a cyanoHABs susceptibility index value. Using these values, it was possible to identify the basins with the highest susceptibility to blooms by calculating the 90th percentile. Thus, the 10% of basins with the highest values were considered susceptibility hotspots. In addition, basins that were shared hotspots for more than one species were also identified. A schematic model summarizing the entire methodology is shown in Figure 1.

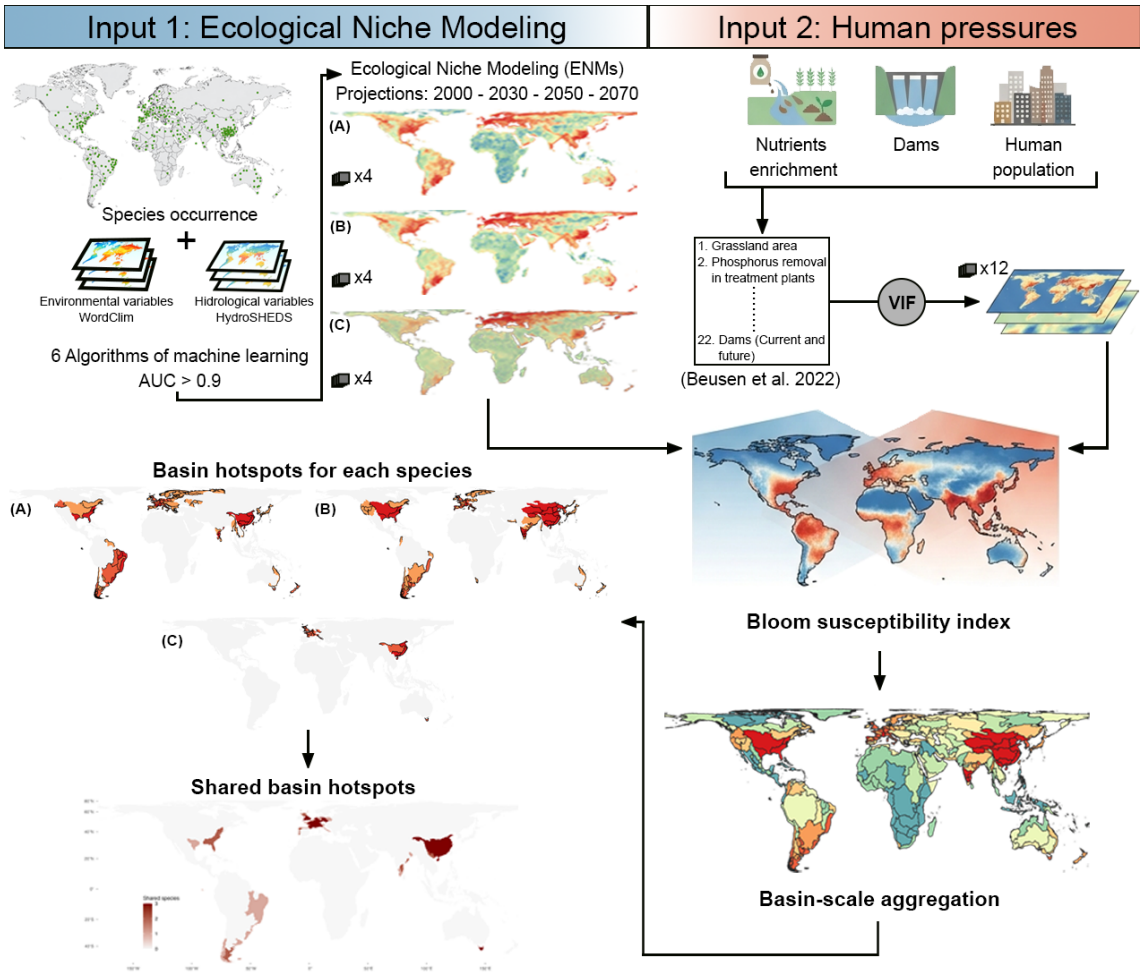

Fig. 1. Schematic model summarizing the ENM methodology and the index of susceptibility to harmful cyanobacterial blooms, as well as examples of output figures of the main study results.

3.3 Results

Climatic suitability for harmful cyanobacteria revealed a pronounced spatial redistribution of suitable conditions across global river basins between 2000 and 2070, with gains concentrated primarily in low-latitude regions (Fig. 2). The strongest and most spatially continuous increases were observed in the Amazon, Northeast South America, Orinoco,

Tocantins, and Arabian Peninsula basins. Several Asian basins also exhibited increased climatic suitability, although to a lesser extent, including the Ob, Yenisey, Lena, Inner Gobi, Syr Darya, Malay Peninsula, and Red Sea–East Coast basins.

Species-specific responses were evident. *Raphidiopsis raciborskii* and *Microcystis aeruginosa* showed stronger and more spatially extensive increases, particularly across Northeast South America basins and Asia. *Planktothrix agardhii* exhibited weaker and more spatially restricted increases, especially across Northern Hemisphere basins, including parts of the United States, Canada, and some African basins such as the Congo and Africa–North Interior. Overall, mean changes in suitability were slightly positive but small in magnitude among species, with increases and decreases unevenly distributed across basins.

In all European basins, all three species showed consistently high proportions of suitable areas for occurrence (≥ 0.5) across all projected years (Fig. 3A). In contrast, African basins showed consistently low suitability. Basins in North and South America showed an increasing suitable area over time, particularly for *R. raciborskii* and *M. aeruginosa*. *P. agardhii* showed limited suitability in these regions, not exceeding 25% of the basin area. A similar pattern was observed across Asian basins, although some showed localized increases.

Several basins exhibited marked increases in suitable areas (Fig. 3B). The Northeast South America–South Atlantic Coast basin (B16) showed the largest increase globally, exceeding 75% for *R. raciborskii*. The Tocantins basin ranked among the top increases for both *R. raciborskii* (reaching 100% suitable area) and *M. aeruginosa* (reaching 50%). For *M. aeruginosa*, two Asian basins, Brahamani (B143) and Vietnam Coast (B209), reached exceptionally high values (100% and 97%, respectively). The basins with the largest increases for *P. agardhii* were restricted to the Northern Hemisphere, with the Hong–Red River basin (B162) reaching 89%.

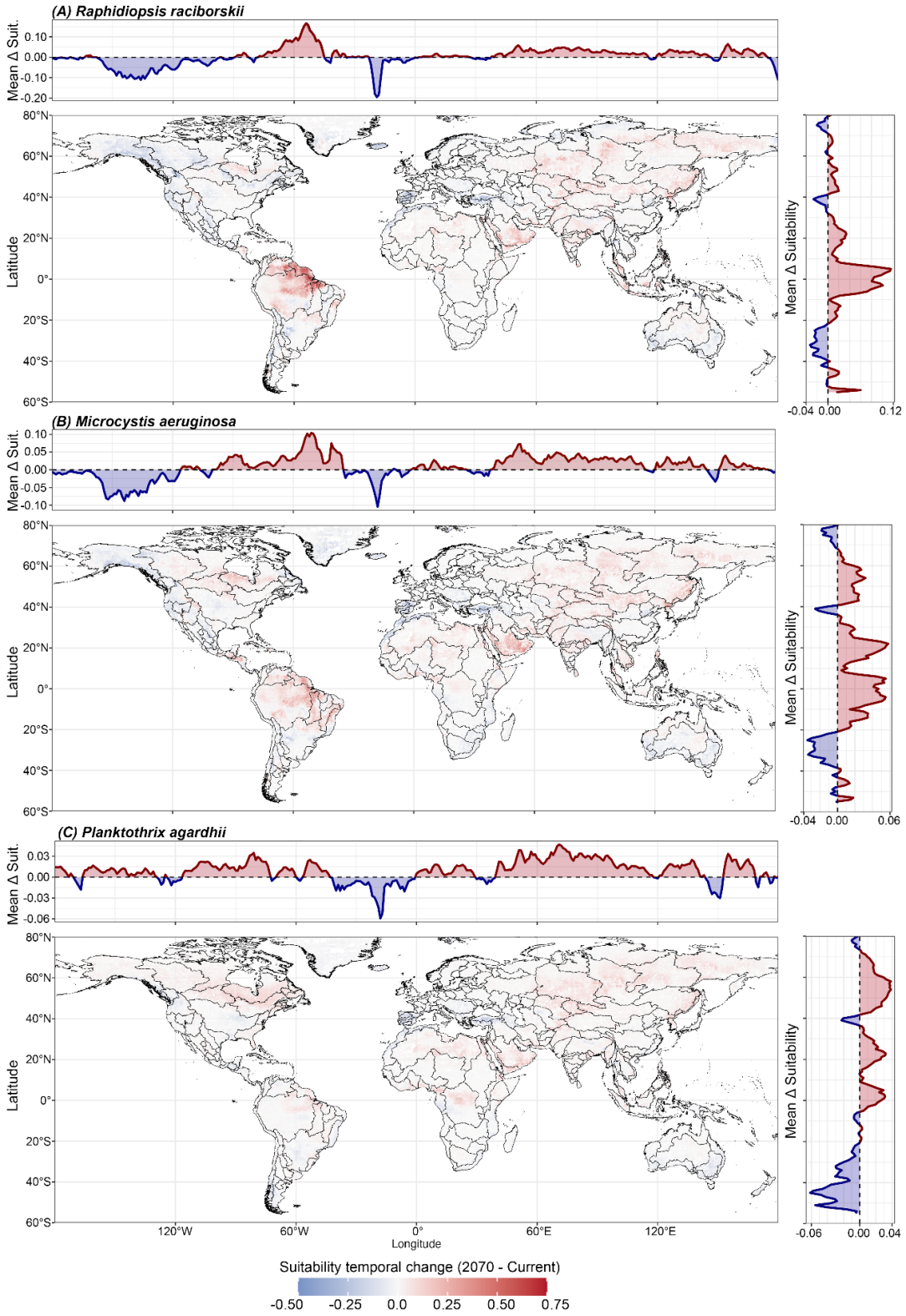

Fig. 2. Temporal change in bloom susceptibility (Δ index) between 2000 and 2070 across global river basins. Maps show basin-scale changes in susceptibility for three cyanobacterial species: (A) *Raphidiopsis raciborskii*, (B) *Microcystis aeruginosa*, and (C) *Planktothrix agardhii*. The susceptibility index integrates climatic suitability and anthropogenic pressure. Positive values (red) indicate increased susceptibility, whereas negative values (blue) indicate decreased susceptibility over time, revealing spatially heterogeneous shifts in bloom risk across freshwater systems. Density plots summarize mean changes in suitability along longitudinal (top) and latitudinal (side) gradients.

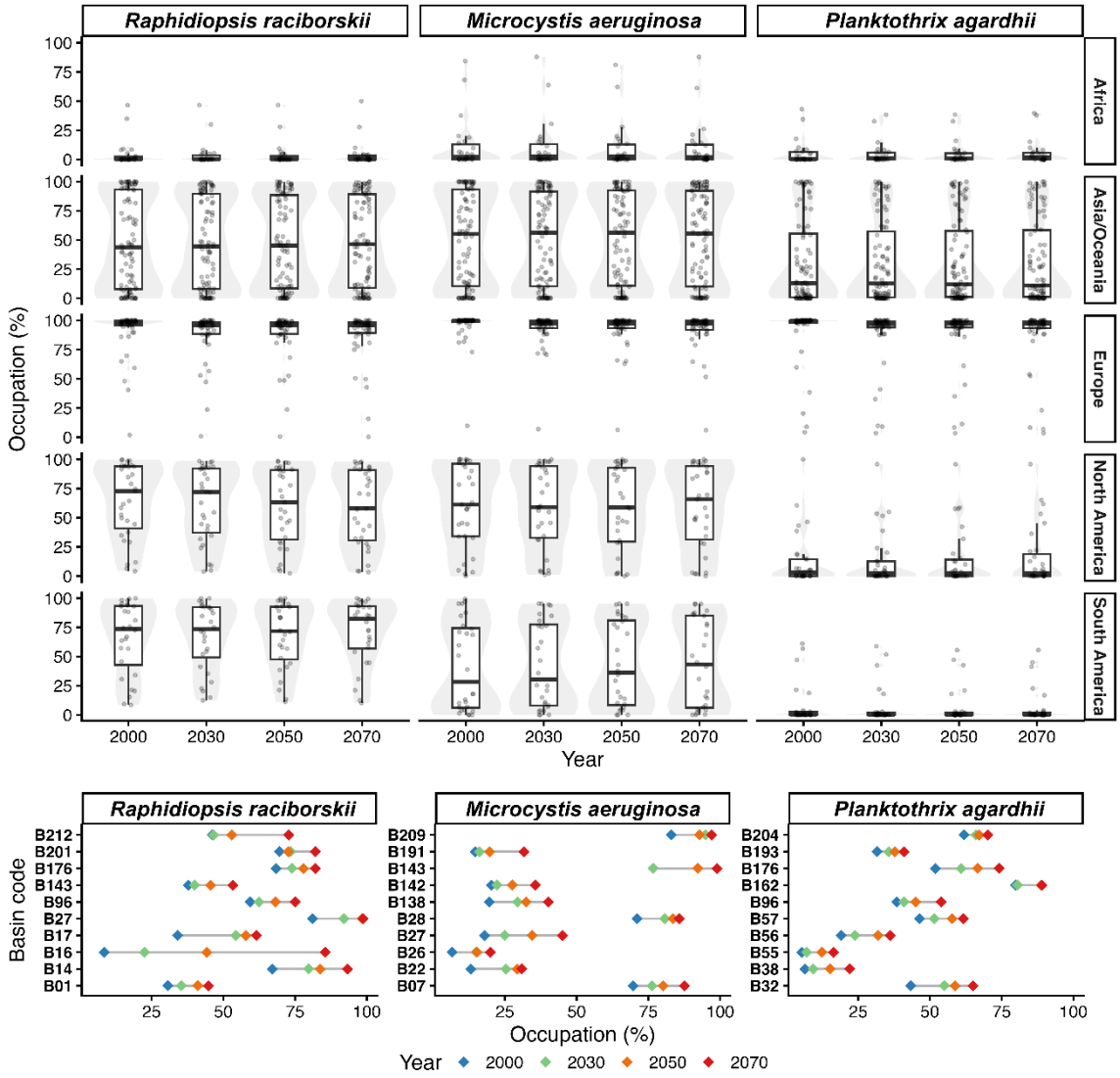

Fig. 3. Temporal variation in the proportion of basin area classified as suitable (suitability ≥ 0.5) for each species. (A) Distribution of suitable areas across basins by continent for each species in 2000, 2030, 2050, and 2070. Boxplots represent the median, interquartile range, and variability among basins, with individual points indicating basin-level values. (B) Top 10 basins with the greatest increase in suitable areas between 2000 and 2070 for each species. Points represent the proportion of basin area classified as suitable in each projected year. Basin codes: South America (B01: Amazon; B07: Grijalva–Usumacinta; B14: North Brazil, South Atlantic Coast; B16: Northeast South America, South Atlantic Coast; B17: Orinoco; B22: São Francisco; B26: Southern Central America; B27: Tocantins; B28: Uruguay - Brazil, South Atlantic Coast), North America (B38: Hudson Bay Coast; B55: Saskatchewan - Nelson; B56: St. John; B57: St. Lawrence), Europe (B96: Russia, Southeast Coast) and Asia (B142: Bohai - Korean Bay, North Coast; B143: Brahamani; B162: Hong (Red River); B176: Lake Balkash; B191: Philippines; B193: Red Sea, East Coast; B201: Sri Lanka; B204: Syr Darya; B209: Vietnam, Coast; B212: Yasai).

When anthropogenic pressures were incorporated, the spatial pattern of susceptibility differed from that observed for climatic suitability alone (Fig. 4). Positive changes in the index were observed across most basins, with the strongest increases concentrated in Northeast South America basins, particularly for *R. raciborskii*, and across parts of South and Southeast Asia, where several basins exhibited consistently higher values. Additional increases were observed

across North America and Eurasia, although with generally lower magnitudes. Notable increases were observed in several basins, including Northeast South America, North Brazil, La Plata, Orinoco, and Tocantins in South America, as well as Yasai, India North East Coast, Krishna, Pennar, India East Coast, and Cauvery in Asia.

Consistent with the climatic suitability models, all three species showed overall increases in the index. However, the magnitude of change differed among species. *R. raciborskii* exhibited the greatest increases, whereas *P. agardhii* showed comparatively weaker responses. Decreases in susceptibility were limited and spatially dispersed across basins for all species.

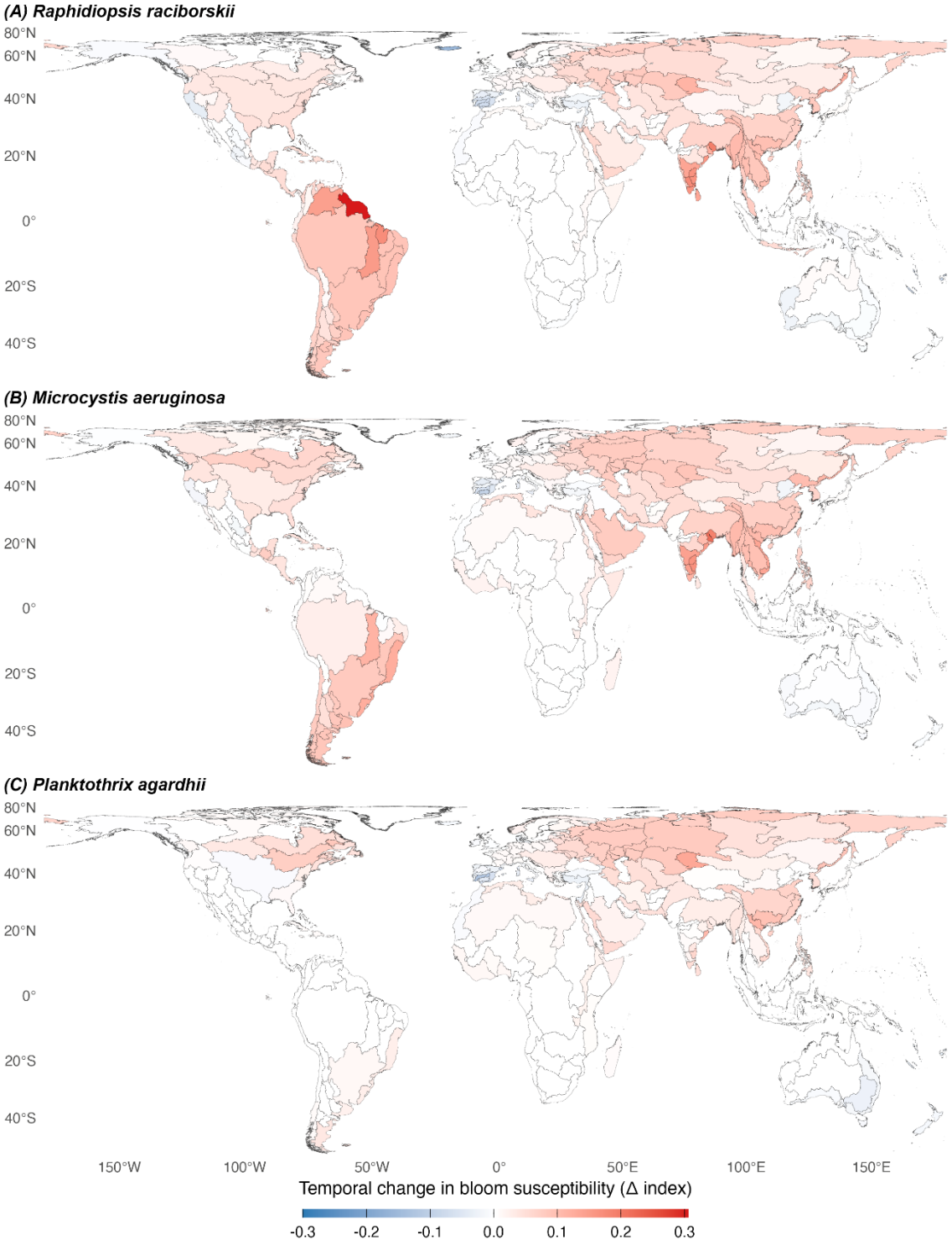

Fig 4. Temporal variation in susceptibility to cyanoHABs between 2000 and 2070. The map plot shows the river basins that experienced increases or decreases in susceptibility over the prediction years for the three cyanobacterial species: (A) *R. raciborskii*, (B) *M. aeruginosa*, and (C) *P. agardhii*. Blue shades indicate decreased susceptibility, while red shades indicate increased susceptibility.

Susceptibility hotspots included both persistent and emerging basins across global river networks (Fig. 5). Persistent hotspots were identified mainly in the eastern United States,

Europe, and parts of Asia, remaining as hotspots in all projections (2000, 2030, 2050, 2070). Emerging hotspots were mainly observed in basins in South America and Asia.

Only a few river basins ceased to be hotspots across future predictions, all of which were in Europe. The species that experienced the greatest loss of hotspots was *P. agardhii*, with six losses, while *R. raciborskii* and *M. aeruginosa* had only two losses. The latter two species exhibited a greater number of persistent and emerging critical hotspots in both the Northern and Southern Hemispheres, while *P. agardhii* exhibited fewer emerging areas, restricted the Northern Hemisphere, and a more stable spatial pattern over time.

Hotspots identified by the susceptibility index were used to assess the overlap among species (Fig. 6). Most basins were shared by two or three species, with the largest number classified as hotspots for all, indicating that the formation of these hotspots is driven primarily by common environmental conditions (Fig. 6A, B). Although single-species hotspots were less common, *R. raciborskii* exhibited eight unique hotspots (Fig. 6B). Network analysis corroborates this pattern, revealing a highly interconnected structure in which many basins are linked to multiple species, rather than forming isolated, species-specific hotspots (Fig. 6C). These shared basins are concentrated primarily in North America, Europe, and East Asia. Furthermore, emerging hotspots, particularly in South American basins, were limited to only one or two species. Despite the high overlap in hotspots among the species, *R. raciborskii* and *P. agardhii* did not share any basins.

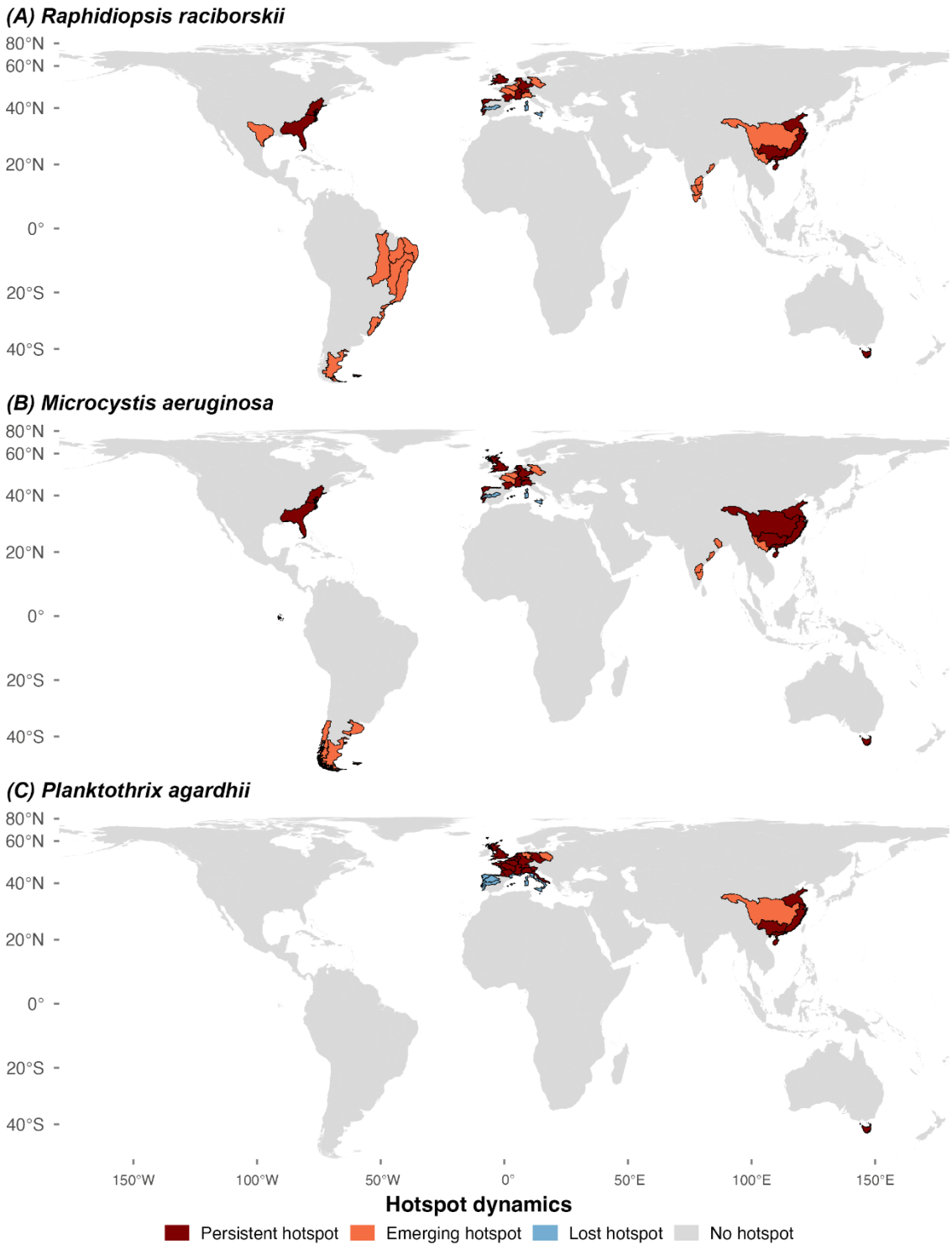

Fig 5. Spatiotemporal changes in cyanoHABs susceptibility hotspots across global river basins. Maps show river basins classified according to changes in hotspot status for three cyanobacterial species: (A) *Raphidiopsis raciborskii*, (B) *Microcystis aeruginosa*, and (C) *Planktothrix agardhii*. Hotspots were identified in this study as the top 10% of basins with the highest susceptibility values (≥ 90th percentile). Persistent hotspots (brown) remained hotspots across all years (2000, 2030, 2050, and 2070), whereas emerging hotspots (orange) appeared after 2000. Lost hotspots (blue) correspond to basins classified as hotspots in 2000 but not in subsequent years. Grey indicates basins that were not classified as hotspots.

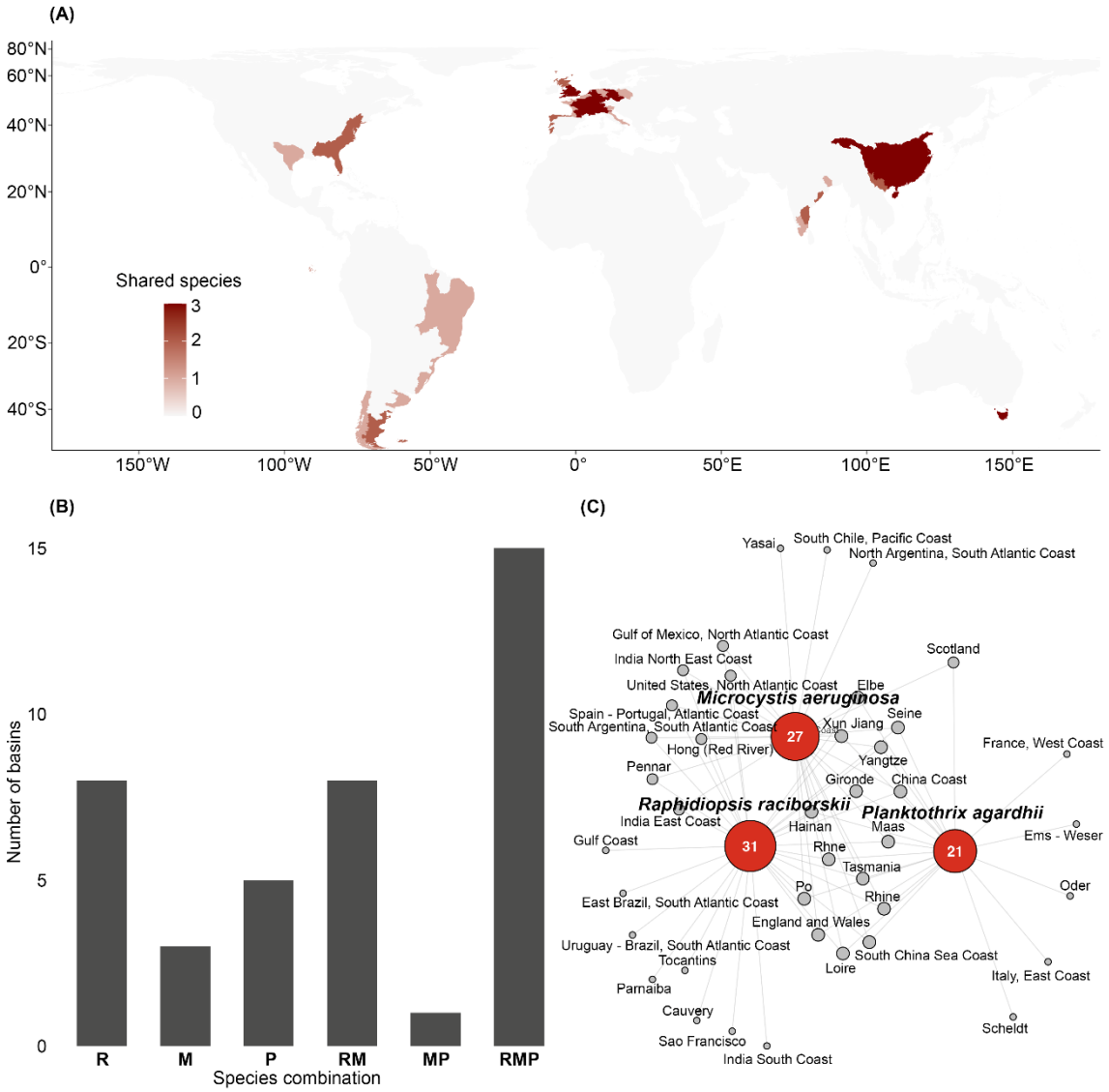

Fig 6. Overlap of susceptibility hotspots among cyanobacterial species across global river basins. (A) River basins identified in this study as susceptibility hotspots (top 10% of basins based on the susceptibility index) shared among species. Color intensity indicates the number of species for which each basin was classified as a hotspot (1–3). (B) Number of shared hotspot basins among species. R: *Raphidiopsis raciborskii*; M: *Microcystis aeruginosa*; P: *Planktothrix agardhii*. (C) Network representation of shared hotspots among species. Nodes represent species, and links indicate basins classified as hotspots for one or more species. Node size is proportional to the number of hotspot basins associated with each species, with values shown within nodes.

3.4 Discussion

Results indicate that susceptibility to harmful cyanobacterial blooms is not increasing uniformly across global river basins, but is instead being spatially redistributed under the combined influence of climatic and anthropogenic factors. By integrating climate suitability with human pressures, we reveal patterns that differ substantially from those based on climate

alone. These results show that, while some basins remain prone to bloom events, new basins will emerge as hotspots of susceptibility, highlighting the growing risk to freshwater ecosystems and human health.

Notably, global warming alone explains only part of the observed patterns. Although rising temperatures identify potential basins for the expansion of favorable conditions, the combined influence of anthropogenic factors determines the actual susceptibility to blooms. The developed index highlights the critical role of nutrient dynamics, human population density, and river regulation in shaping bloom risk across global river basins.

Most hotspot basins are concentrated in densely populated regions, revealing a direct overlap between areas highly susceptible to cyanobacterial blooms and regions of intensive human use of freshwater resources (Huang et al., 2018; Laziou; Lemoy, 2025). This pattern is associated with the combined effects of anthropogenic pressures, including high densities of wastewater treatment infrastructure and extensive river regulation through dams, particularly in regions such as Central Europe, Southeast Asia, and the eastern United States (Lehner et al., 2024; Macedo et al., 2022). These pressures alter nutrient dynamics and hydrological regimes, creating favorable conditions for cyanobacterial proliferation (Padisák; Crossetti; Naselli-Flores, 2009; Paerl; Otten, 2013; Reynolds et al., 2002). As a result, many hotspot basins here represent systems where ecological vulnerability coincides with strong human dependence on freshwater resources, increasing risks to water supply, food production, and economic activities (He et al., 2016; Paerl; Paul, 2012; Weir; Kourantidou; Jin, 2022).

This overlap between river basins that are both susceptibility hotspots and densely populated raises serious concerns. CyanoHABs are linked to losses of ecosystem services provided by freshwater environments (Huisman et al., 2018), including resources such as drinking water and food sources derived from fish and crustaceans (Golden et al., 2021; McIntyre; Liermann; Revenga, 2016). Some of the basins identified as hotspots in this study already exhibit these conditions, such as the United States – North Atlantic Coast basin, where persistent cyanobacterial blooms have been reported (Clark et al., 2017). This indicates that the problem is not limited to the future, highlighting the immediate need for monitoring, management, and restoration programs in freshwater systems. Many regions worldwide are already experiencing pressures on water availability and fisheries resources, which may be further exacerbated by recurrent and persistent potentially toxic blooms.

Clearly, although certain river basins remain persistent hotspots of vulnerability, some basins have emerged over time, particularly on the South American continent. Basins located in northeastern Brazil, such as the Tocantins, Parnaíba, São Francisco, East Brazil–South Atlantic Coast, and Uruguay Brazil–South Atlantic Coast already face serious problems with these blooms (Soares et al., 2013). This indicates that in the future these basins may face even more serious problems, particularly because it is a region where water scarcity affects a large portion of the population (Sena et al., 2018).

The spatial patterns identified in this study are consistent with regions where cyanobacterial blooms have already been extensively documented, particularly in Europe and Asia. Basins in southern Asia, especially those associated with large shallow lakes and reservoirs (e.g., Lake Taihu and the Three Gorges Reservoir), have experienced recurrent and severe bloom events linked to high nutrient loads and rapid urbanization (Li et al., 2025; Zheng et al., 2011). Similarly, across Europe, numerous temperate lakes and river basins report increasing cyanobacterial dominance in regions influenced by intensive agriculture and climate warming (Carvalho et al., 2013; Svirčev et al., 2019b). In both regions, blooms are no longer sporadic but have become recurrent and, in some cases, persistent features in freshwater systems. The overlap between the hotspots identified here and these regions reinforces the index's predictive capacity, indicating that many highly susceptible basins are already experiencing cyanoHABs (Dziga et al., 2017; Wilk-Woźniak et al., 2024), further increasing concerns about the future in both these regions and emerging hotspots.

Species-specific responses at the identified hotspots reveal important spatial patterns in future cyanobacterial blooms. *R. raciborskii* showed the highest number of emerging basins, reflecting its expansion potential linked to phenotypic plasticity, which allows it to establish under a wide range of environmental conditions (Bonilla et al., 2012; Dokulil, 2016; Zheng et al., 2023). Its invasive potential is evident in emerging hotspots in Europe and southern South America. In contrast, *M. aeruginosa* and *P. agardhii* showed more stable distributions, with most hotspots remaining consistent over time. These differences suggest that species with greater ecological flexibility may increasingly drive future bloom dynamics, while others persist in historically suitable regions. Despite this, consistent hotspot patterns across species indicate broader community-level responses, suggesting that ongoing environmental changes may increase susceptibility to blooms beyond these three species.

A major consequence of cyanobacterial blooms is the release of cyanotoxins into freshwater systems, posing risks to aquatic ecosystems and human populations (Song et al., 2026; Van Apeldoorn et al., 2007). Many bloom-forming cyanobacteria, including those investigated here, produce toxins such as microcystins, saxitoxins, and cylindrospermopsins, which can contaminate drinking water and disrupt aquatic food webs (Huisman et al., 2018; Paerl; Otten, 2013). Exposure may occur directly or through bioaccumulation in fish and crustaceans, particularly in regions where freshwater resources support food production (Falfushynska et al., 2023; Magalhães et al., 2003), and has been linked to serious health concerns, including hepatic and neurological damage and contamination incidents worldwide (Azevedo et al., 2002; Carmichael, 2001; Giannuzzi et al., 2011; Svirčev et al., 2019b).

Beyond toxicity, blooms can induce hypoxia, alter trophic interactions, reduce biodiversity, and contribute to greenhouse gas emissions, compromising ecosystem functioning and stability (Huisman et al., 2018; Igwaran et al., 2024; Loreau et al., 2001; Yan et al., 2017b). These effects extend to economic sectors by increasing water treatment costs, reducing fish stocks, and limiting recreational and tourism use of water bodies (Dodds et al., 2009; Wolf; Georgic; Klaiber, 2017). Together, these impacts indicate that expanding conditions favorable to blooms represent a growing threat to human health and water security, particularly in basins identified as susceptibility hotspots.

The spatial reorganization of proliferation risk identified in this study underscores the need for integrated management strategies addressing both persistent and emerging hotspots and the interacting drivers of cyanoHABs at the river basin scale. Most countries regulate cyanobacterial biomass and, particularly, microcystins in drinking water. However, other cyanotoxins remain largely overlooked (Cobo et al., 2023). Some U.S. states within identified hotspot basins lack cyanotoxin regulations, and a similar situation occurs in China, which encompasses a large portion of the hotspots in Southeast Asia. Brazil is the only country encompassing hotspot basins with current legislation covering microcystins, cylindrospermopsins, and saxitoxins (Aguilera et al., 2023; Cobo et al., 2023). Regulation of recreational waters is even more limited worldwide (Cobo et al., 2023). These gaps highlight the need to update and strengthen public policies, especially in countries that include these hotspot basins.

Coordinated actions to mitigate nutrient inputs, land use, and hydrological changes are essential, as their interaction with climate change exacerbates algal blooms. The global

distribution of the vulnerable basins identified here indicates that this is a widespread challenge requiring international cooperation, information sharing, and region-specific solutions. Without proactive and coordinated interventions, the continued expansion and intensification of harmful cyanobacterial blooms may compromise freshwater security, ecosystem resilience, and human well-being in some of the world's most heavily used river basins.

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4 DEVELOPMENT OF A PROTOTYPE BOARD GAME FOR SCIENCE DISSEMINATION IN AQUATIC ECOSYSTEMS: *ECOLOGIST, PRESERVATION WORK*

4.1 Introduction

Transforming scientific knowledge generated within universities into information accessible to society is a major challenge, primarily due to the difficulty of translating scientific language into clear and engaging terms (Bueno, 2010; Burns; O'Connor; Stocklmayer, 2003). Currently, humanity's intense exploitation of nature is generating unprecedented impacts, making the dissemination of scientific knowledge across all sectors of society essential. (Steffen et al., 2015b). This is one of the primary ways to promote greater public awareness and strengthen environmental education among children, youth, and adults (Jacobi, 2003).

Among the environments most affected by human activity, aquatic environments stand out, as they are directly linked to people's daily lives (Dudgeon et al., 2006). From bathing, drinking water, and cooking to participating in recreational activities such as water sports, these are ways in which the general population interacts with the water resources generated by streams, rivers, and lakes. Because these environments are strongly affected by human activities, society also experiences the consequences of such impacts.

In this perspective, developing tools that facilitate the dissemination of scientific knowledge to society is essential (National Academies of Sciences, 2017). Board games stand out among these tools because they provide a playful and engaging approach to learning, in addition to stimulating cognitive, social, and problem-solving skills across different age groups (Carvalho; Oliveira, 2024; Xavier et al., 2024).

Therefore, the objective of this chapter was to design and propose a board game in which players take on the role of research institute directors and must implement conservation practices in freshwater aquatic environments. This game aims to disseminate scientific knowledge through a playful, competitive, and accessible approach suitable for different age groups. The goal is to highlight how human impact on these systems is harmful and that mitigating these effects requires extensive research, collaboration, funding, and technology.

4.2 Methodology

The game was designed and developed with various anthropogenic impacts on freshwater environments being considered, some of which are investigated in this thesis and others that were not tested here, but several studies have demonstrated the influence of these stressors on these environments. This game is recommended for 2 to 4 players, and lasts

between 60 and 90 minutes, depending on the number of players. The game is expected to be rated as light to moderate in complexity. However, direct difficulty ratings from specialized sites such as BoardGameGeek – BGG (https://boardgamegeek.com/) require several full games to be played and rated by different players, who assign a score from 1 to 5, with games closer to 5 being rated as more difficult.

The game mechanics were inspired by well-established modern board games such as *Apiary*, *Stone Age*, *Agricola*, *Everdell*, and *Era of Innovation*, in which worker placement and turn-based rules within each round serve as the primary framework for gameplay, just as in the game proposed here. For more information about these board games, visit the Ludopedia website (https://ludopedia.com.br/).

Digital illustration was used to design the main game board, with the help of Adobe Photoshop. The colors were chosen to match each environment, making it easier to distinguish between them, as were the illustrative elements for each, which were created to best represent each location. The aquatic environments shown on the board were included independently for gameplay purposes and do not represent connected ecosystems. Textured brushes with varying opacity were used to compose the drawings, creating overlays and depth in the illustration. All freshwater environments on the board are real, and the drawings were created to best represent these environments. The player boards and all game cards were created with the help of artificial intelligence (ChatGPT – OpenAI).

4.3 Results

4.3.1 Board game title

Ecologist, preservation work

4.3.2 Game rules manual

This board game is recommended for players ages 10 and up and is best played by 3 or 4 players. All components are necessary for a full gaming experience, if any component is missing, players may use an alternative marker in its place.

Freshwater environments are under threat worldwide. Lakes, streams, and rivers that sustain life on Earth suffers from the impacts of human activity. Pollution, uncontrolled exploitation, and environmental negligence have made these habitats a focus of conservation research. In *Ecologist: Preservation Work*, each player will lead an Ecological Research Institute, taking on the role of experts dedicated to protecting aquatic environments. Your mission will be to mobilize teams of ecologists, invest in technology, expand scientific research, and manage financial resources to mitigate environmental impacts before it’s too late.

With each round, new challenges will arise. Environmental impacts will threaten different ecosystems. Strategic decisions will be essential. Only the most efficient and strategically prepared institute will be recognized as a leading center for environmental preservation. Here, being environmentally conscious is not enough, only strategic decisions will earn your institute worldwide recognition.

4.3.3 Overview

Ecologist: preservation work is a competitive worker-placement game for up to 4 players, in which each player controls an ecological research institute trying to preserve freshwater aquatic environments while competing with other institutes for scientific prestige and environmental recognition.

4.3.4 Game Objective

Earn as many victory points as possible, which will be awarded to players as follows:

- Preservation of aquatic environments;
- Achievement of individual objectives;
- Greater preservation efforts in the environment;

4.3.5 Components

- 1 Main board;
- 5 Research Institute Player Boards (Appendix K);
- 10 Ecologists (meeples) from each research institute (the institutes are distinguished by color);
- 5 six-sided green dice;
- 12 Impact Event Cards (Appendix H);
- 12 Joker cards (Appendix I);
- 1 Scoring Marker for each research institute;
- 20 Preservation Markers for each research institute (colors distinguish the institutes);
- 10 Environmental Impact Markers (1 for each environment);
- End-of-game individual objective cards (Fig. 1 and (Appendix J);

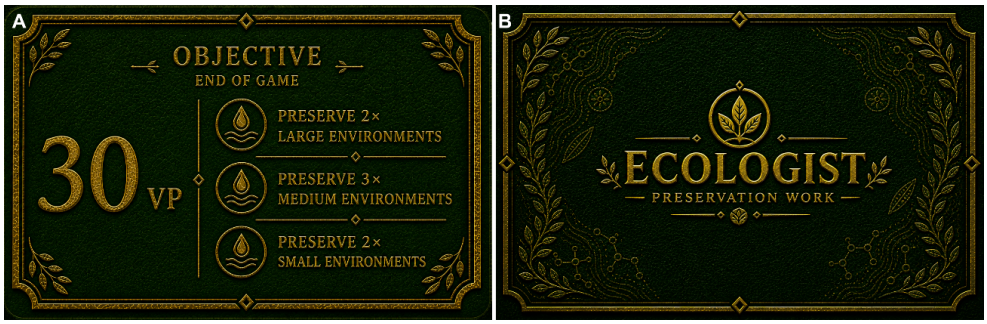

Fig. 1: Example of an end-game objective card. Each card reveals specific objectives that players must complete to earn the corresponding victory points. A) Front of the card. B) Back of the card.

4.3.6 Game Preparation

1. Place the main board in the center of the table (Fig. 2);
2. Shuffle the Institute Boards and deal 1 to each player (Fig. 3);
3. Each player then takes all the components in the color of their respective research institute;
4. Shuffle the Impact Event Cards and form a deck with the cards face down;
5. Shuffle the Joker cards and form a deck face down;
6. Shuffle the Individual Objective Cards and deal 1 to each player;
7. Place the dice next to the board;
8. Place the impact markers in each aquatic environment on the board at the start of the trail (value 1);
9. Each player starts with 4 Ecologists (meeples) available;

Fig. 2: The main game board. It shows all the freshwater environments that need to be preserved, as well as the locations where resources can be collected. The environments represented are independent and not hydrologically connected.

Fig. 3: Example of a player board, in this case from the Latin American Research Institute.

4.3.7 Set First Player

Choose the first player in one of the following ways:

- The player who most recently visited a natural aquatic environment;

or

- Everyone rolls 1 die, and the person with the highest roll goes first;

The turn order proceeds clockwise. At the end of each round, the starting player should be passed to the player on the left, also proceeding clockwise.

4.3.8 Ecologists (Meeples)

Each Ecologist represents a field specialist affiliated with the player's research institute. Ecologists are responsible for:

- Raise funds;
- Carry out conservation actions;
- Expand the institute's scope of operations;

"Each ecologist sent into the field is an expert mobilized by their institute to conduct research, invest in and work directly on environmental preservation.*"*

4.3.9 Player Boards - Research institutes

Each player has a unique Institute Board, with its own visual identity (such as Latin American, American, Asian institutes, among others), as well as a worker placement area that grants a specialty to each player, creating competition and asymmetry among the players. This exclusive space can be used as follows:

During Phase 1 - Fundraising, the player may place 1 Ecologist in this space. By doing so, they receive:

- An immediate resource (defined by the player board);
- A special ability that can be used during Phase 2 — Conservation efforts;

4.3.10 Rules for using this site

- Only 1 Ecologist may be assigned to this space per round;
- The payment is received immediately;
- The ability can be used in Phase 2;
- The Ecologist remains assigned until Phase 3;
- It cannot be used in Phase 2;

"The stages of the game will be explained below"

"Each board specifies which resource and which ability are granted"

4.3.11 Game Structure

The game lasts for 6 rounds or until an aquatic environment reaches its maximum impact level. Each round consists of 3 phases:

1. Fundraising
2. Preservation
3. Final resolution

Phase 1 - Fundraising

Players take turns placing Ecologists at fundraising sites, following the turn order. These sites are exclusively used to collect resources, which will be used in Phase 2 to preserve freshwater environments. For all resource collection, dice combinations will be used, these combinations are specific to each site and will be explained below. The fundraising sites are as follows:

I. University center – Research tokens / Ecologists

In this place, players can choose to earn research tokens or recruit more ecologists for their research institute. If the player chooses to receive the tokens, the dice combinations will be as follows:

- 1–2: 1 Research
- 3–4: 2 Research
- 5–6: 3 Research

If the player chooses to recruit more ecologists for their research institute, the dice combinations are as follows:

- 1: Failure
- 2–5: +1 Ecologist
- 6: +2 Ecologists

II. Technology Center – Technology tokens

At this place, players will earn technology tokens for their research institute. The dice combinations required to earn these tokens are as follows:

- 1–2: 1 Technology
- 3–4: 2 Technologies
- 5–6: 3 Technologies

III. Investment Center – Money

In this place, players can choose to earn money for their research institute. This is the main source of funding for research institutes, and these funds are essential for preserving freshwater environments. The combinations of dice needed to earn money are as follows:

- Win money equal to the number on the dice (e.g., dice roll = 5 / money won = 5);

Exclusivity Bonus

If, after all players have assigned their ecologists, only one player has ecologists at the resource site described above, that player may choose to gain +1 resource from that site.

"At the University center, the bonus can only be +1 Research"

Dice Resolution

For each ecologist assigned to a resource area, a dice will be rolled, the number rolled determines the number of resources the player will receive. The dice are rolled after all players have assigned their ecologists. In the case of the University location, the player must state which resource they want (research tokens or to recruit ecologists) before rolling the dice. Phase 1 ends when all players have collected their resources via the dice roll and returned their ecologists to their research institute.

"If you have placed your ecologist on your player board, they will return to your institute and will only be available again in Phase 3"

Phase 2 — Preservation

During this phase, players will assign their available ecologists at their Research Institute to freshwater environments to preserve them. This phase of the game begins by revealing two types of cards: *Environmental Impact Events* and *Jokers*.

Environmental impact events

These cards will introduce environmental impacts caused by human activities into the game, thereby affecting the aquatic environments on the board. These cards will show the level of impact for each type of environment (Fig. 4a), the cost of preservation (Fig. 4b), victory points (Fig. 4c), and specific details about that impact (Fig. 4d). The types of environments are categorized as follows:

- Large spaces – impact scale of 1 – 10;
- Medium spaces – impact scale of 1 – 7;
- Small spaces – impact scale of 1 – 5;

Each type of environment will have a specific cost, impact level, and victory points. These values will vary among the environmental impact cards.

Fig. 4: Example of an impact event card, specifically regarding microplastics. a) Impact level. b) Cost of preservation. c) Victory points earned per preservation action. d) Card specifics. A) Front of the card. B) Back of the card.

Joker Cards

These cards will add more dynamism to the game, bringing benefits or drawbacks to all players, who will have to face them during that round of environmental preservation (Fig. 5). They are linked to gains or losses of resources. If the card revealed during the round results in a loss of resources and a player does not have enough resources to lose, they must move back one space on the victory point track due to insufficient resources.

Fig. 5: Example of a Joker card, which in this case gives players 2 additional research tokens. A) Front of the card. B) Back of the card.

Placement of Ecologists

It's time to take action! Players will assign their available ecologists from their Research Institute to the impacted aquatic environments. Players take turns assigning ecologists and may assign only one ecologist at a time. This phase ends when the last player with an available ecologist places it on the board or simply passes their turn. When assigning an ecologist to an aquatic environment, follow these steps:

1. Pay the fees specified in the impact event card;
2. Return one level on the impact trail for that environment;
3. Earn the total number of victory points indicated on the impact event card for performing a conservation action;
4. Place your institute's marker in that area to indicate that you have preserved it;

"Keep in mind that each type of environment comes with a cost and yields different victory points"

Presence Bonus

When a player places their 4th Institute token in the same aquatic environment, indicating that they have preserved that environment 4 times, they may purchase one more end-game individual objective card.

Blocks

Allocation spaces, indicated by a leaf icon, can only be occupied by one Ecologist at a time, except for fundraising sites, which can be shared by more than one Ecologist.

Late Fundraising

Ecologists may be placed at resource fundraising sites during Phase 2; however, the acquisition of resources will not be resolved until Phase 3. In other words, this fundraising cannot be used to acquire resources for that round, only for future rounds.

4. Final resolution

This is the stage at which research institutes send their ecologists back after successfully preserving the environment. Follow the steps below:

1. Resolve late fundraising (follow the same instructions as in Phase 1);
2. Return Ecologists;
3. Discard the impact card and joker revealed during the round;
4. Start a new round if it is not the 6th round. If it is, proceed directly to the end of the game and final scoring;

4.3.12 End of the game and final score

The game ends at the end of the 6th round or if any aquatic habitat reaches its maximum level on the impact track. When the end of the game is activated, players will calculate their final scores. To simplify the process, all VP earned during the game for preserving habitats should be placed on the scoring track immediately. Other scores:

- Individual end-of-game objectives
- More Institute markers in different types of environments:
    a. Large environments - 1º = 15 PV; 2º = 10; PV; 3º = 7 PV;
    b. Medium environments - 1º = 10 PV; 2º = 7; PV; 3º = 4 PV;
    c. Small environments - 1º = 7 PV; 2º = 5; PV; 3º = 2 PV;

The player whose Research Institute has earned the most victory points at the end of the game wins. In the event of a tie, the player with the most Institute markers in the environments wins. If the tie persists, the player who received the most bonus victory points from Institute markers wins.

"Every great change begins with those who choose to protect what matters."

4.4 Considerations

The next step for this game is to test its effectiveness and feasibility in player learning. Here, we have only developed and proposed the game; however, we understand that its application to different age groups and in different contexts is extremely important, given that the main objective in creating this game is to popularize science and establish environmental education practices for players.

The board game can be tested in the classroom, in assessment or introductory contexts for specific content, for elementary and high school students, and even in specific higher education situations. This game can make a significant contribution to various aspects of student learning, developing not only their scientific understanding but also their critical thinking skills regarding environmental responsibility. In addition to school contexts, this game can easily be played during recreational activities across a wide range of age groups, from older children to adults, serving as a powerful tool for raising environmental awareness.

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5 FINAL CONSIDERATIONS

This thesis examines the effects of multiple anthropogenic stressors on phytoplankton communities in freshwater environments across different scales. The integration of experimental and predictive approaches has made it possible to identify important and consistent patterns of community reorganization, even across different contexts and methodologies.

At the local scale, the mesocosm experiment indicates that warming and nutrient enrichment are the main factors driving the reorganization of the phytoplankton community over time. Although no consistent compositional homogenization was observed, there were clear changes in community structure associated with the dominance of a few taxa, especially cyanobacteria. These patterns indicate dynamics marked by temporal instability and variations in dominance, rather than compositional convergence. On a global scale, the results indicate that the risk of potentially toxic cyanobacterial blooms (cyanoHABs) is associated with a combination of climatic and anthropogenic factors, rather than with isolated variables such as climate models alone. Regions with higher human pressure have the most favorable conditions for these events, both currently and in the future, highlighting the role of multiple stressors in identifying the most vulnerable areas in freshwater ecosystems.

Integrated results indicate that the dominance patterns observed at the local scale, particularly for cyanobacteria, are associated with environmental conditions influenced by anthropogenic factors. These conditions were also evident at the global scale, based on the identification of river basins at higher risk of bloom events. While the experiment showed how multiple stressors favor the dominance of these organisms over time, the models indicated where these conditions tend to occur, favoring the occurrence of cyanoHABs. This suggests that changes in community dominance are one of the main mechanisms linking local responses to global risk patterns. In addition to these findings, this thesis also highlights the importance of making this knowledge more accessible. The board game was developed as a way to translate the effects of human impacts on aquatic ecosystems into a more understandable format, especially considering that many of these processes are not directly observable. This type of approach can help bring ecological concepts closer to society and increase awareness of anthropogenic impacts on freshwater ecosystems. Overall, this thesis underscores the importance of considering multiple anthropogenic stressors and different scales to better understand and predict the ecological responses of phytoplankton and other biological groups in freshwater ecosystems.

APPENDIX A - Table: Generalized additive models (GAMs) of the abundance of each phytoplankton group and environmental variables with a smoothed term for time (s(Time)). Interactions between environmental variables and time were also included. Gray dashed lines indicate significant relationships. Treat: Treatment codes, for more information see Table 2 in methodology. Environmental variables: DO = dissolved oxygen; Cond. = electrical conductivity; Turb. = turbidity; DOsat = dissolved oxygen saturation; TDS = total dissolved solids; TP = total phosphorus; NH4 = ammonium; NO3 = nitrate; PO4 = orthophosphate; ORP = oxidation-reduction potential; Temp = water temperature.

Greens				Cyanobacteria				Diatoms				Phytoflagellates			
Variable	Estimate	p_value	Treat	Variable	Estimate	p_value	Treat	Variable	Estimate	p_value	Treat	Variable	Estimate	p_value	Treat
DO	-1.7530	0.7113	Wc	DO	-27.8515	0.0211	Wc	DO	-7.1532	0.2645	Wc	DO	2.1175	0.6261	Wc
Cond.	42.3121	0.7759	Wc	Cond.	-101.3544	0.6727	Wc	Cond.	103.0170	0.6149	Wc	Cond.	-269.8057	0.0304	Wc
Turb.	0.1419	0.0465	Wc	Turb.	0.1199	0.3794	Wc	Turb.	-0.0820	0.3877	Wc	Turb.	-0.0210	0.7393	Wc
DOsat	0.1516	0.6879	Wc	DOsat	2.1139	0.0265	Wc	DOsat	0.5291	0.2999	Wc	DOsat	-0.1835	0.5956	Wc
TDS	-77.6730	0.7425	Wc	TDS	190.5214	0.6200	Wc	TDS	-134.4024	0.6776	Wc	TDS	432.7837	0.0284	Wc
Temp:Time	-0.0035	0.5018	Wc	Temp:Time	0.0111	0.2140	Wc	Temp:Time	0.0208	0.0158	Wc	Temp:Time	0.0044	0.2924	Wc
DO:Time	-0.0053	0.9163	Wc	DO:Time	0.1647	0.1076	Wc	DO:Time	0.1943	0.0142	Wc	DO:Time	0.0267	0.5222	Wc
DOsat:Time	0.0003	0.9328	Wc	DOsat:Time	-0.0124	0.1263	Wc	DOsat:Time	-0.0149	0.0162	Wc	DOsat:Time	-0.0020	0.5523	Wc
TDS:Time	0.6024	0.8440	Wc	TDS:Time	0.5272	0.9119	Wc	TDS:Time	4.7712	0.2675	Wc	TDS:Time	-4.9079	0.0485	Wc
s(Time)	1.0003	0.4834	Wc	s(Time)	2.4149	0.1964	Wc	s(Time)	1.0003	0.0171	Wc	s(Time)	1.0037	0.2469	Wc
(Intercept)	5.8910	0.3248	Wc x LL	(Intercept)	25.4886	0.0645	Wc x LL	(Intercept)	6.9572	0.7220	Wc x LL	(Intercept)	28.7877	0.0122	Wc x LL
Temp	0.5150	0.0815	Wc x LL	Temp	-0.8582	0.2514	Wc x LL	Temp	1.0109	0.3042	Wc x LL	Temp	-0.5683	0.3268	Wc x LL
pH	0.0860	0.8243	Wc x LL	pH	2.8394	0.0249	Wc x LL	pH	0.8557	0.4889	Wc x LL	pH	-0.2544	0.7565	Wc x LL
DO	4.2054	0.0671	Wc x LL	DO	-7.7898	0.2199	Wc x LL	DO	-2.5554	0.7238	Wc x LL	DO	-1.4901	0.7420	Wc x LL
Turb.	0.1094	0.0230	Wc x LL	Turb.	0.0922	0.4554	Wc x LL	Turb.	0.1170	0.4410	Wc x LL	Turb.	-0.0932	0.3586	Wc x LL
DOsat	-0.3539	0.0614	Wc x LL	DOsat	0.5579	0.2668	Wc x LL	DOsat	0.2753	0.6428	Wc x LL	DOsat	0.1011	0.7843	Wc x LL
TP	0.0055	0.6393	Wc x LL	TP	-0.0300	0.3311	Wc x LL	TP	0.0892	0.0133	Wc x LL	TP	-0.0203	0.4063	Wc x LL
Temp:Time	-0.0060	0.0774	Wc x LL	Temp:Time	0.0047	0.5063	Wc x LL	Temp:Time	-0.0278	0.0153	Wc x LL	Temp:Time	0.0001	0.9849	Wc x LL
pH:Time	0.0053	0.3396	Wc x LL	pH:Time	-0.0321	0.0303	Wc x LL	pH:Time	-0.0011	0.9483	Wc x LL	pH:Time	0.0042	0.6761	Wc x LL
DO:Time	-0.0430	0.1046	Wc x LL	DO:Time	0.0307	0.5945	Wc x LL	DO:Time	-0.1515	0.0920	Wc x LL	DO:Time	-0.0381	0.3786	Wc x LL
Cond.:Time	3.0687	0.0231	Wc x LL	Cond.:Time	2.4732	0.3777	Wc x LL	Cond.:Time	3.3154	0.4457	Wc x LL	Cond.:Time	0.1627	0.9408	Wc x LL
DOsat:Time	0.0034	0.0990	Wc x LL	DOsat:Time	-0.0019	0.6656	Wc x LL	DOsat:Time	0.0109	0.1189	Wc x LL	DOsat:Time	0.0029	0.3891	Wc x LL

Greens				Cyanobacteria				Diatoms				Phytoflagellates			
TDS:Time	-4.9298	0.0200	Wc x LL	TDS:Time	-3.4746	0.4406	Wc x LL	TDS:Time	-5.8024	0.3944	Wc x LL	TDS:Time	-0.0690	0.9839	Wc x LL
s(Time)	1.0002	0.1072	Wc x LL	s(Time)	3.5349	0.0359	Wc x LL	s(Time)	1.0005	0.0058	Wc x LL	s(Time)	1.0008	0.5600	Wc x LL
pH	-0.6069	0.3970	Wc x N x LL	pH	0.4343	0.6040	Wc x N x LL	pH	-3.1027	0.0619	Wc x N x LL	pH	-2.7599	0.0039	Wc x N x LL
Cond.	-188.3624	0.3077	Wc x N x LL	Cond.	-72.5211	0.7279	Wc x N x LL	Cond.	-223.0615	0.6051	Wc x N x LL	Cond.	-935.7024	0.0032	Wc x N x LL
Turb.	0.0538	0.0892	Wc x N x LL	Turb.	-0.1061	0.0223	Wc x N x LL	Turb.	0.1365	0.0394	Wc x N x LL	Turb.	-0.0814	0.0884	Wc x N x LL
TDS	305.2341	0.2967	Wc x N x LL	TDS	122.3436	0.7111	Wc x N x LL	TDS	432.8857	0.5237	Wc x N x LL	TDS	1507.7483	0.0025	Wc x N x LL
NH4	-0.0018	0.1245	Wc x N x LL	NH4	0.0002	0.9076	Wc x N x LL	NH4	-0.0060	0.0099	Wc x N x LL	NH4	-0.0006	0.6644	Wc x N x LL
TP	-0.0016	0.9006	Wc x N x LL	TP	0.0254	0.1504	Wc x N x LL	TP	-0.0892	0.0033	Wc x N x LL	TP	-0.0132	0.4565	Wc x N x LL
pH:Time	0.0042	0.6504	Wc x N x LL	pH:Time	0.0046	0.6555	Wc x N x LL	pH:Time	-0.0028	0.8960	Wc x N x LL	pH:Time	0.0268	0.0155	Wc x N x LL
Cond.:Time	2.0016	0.4313	Wc x N x LL	Cond.:Time	1.7659	0.5201	Wc x N x LL	Cond.:Time	1.4705	0.8012	Wc x N x LL	Cond.:Time	7.9358	0.0293	Wc x N x LL
Turb.:Time	0.0001	0.8283	Wc x N x LL	Turb.:Time	0.0016	0.0109	Wc x N x LL	Turb.:Time	-0.0032	0.0167	Wc x N x LL	Turb.:Time	0.0007	0.2715	Wc x N x LL
TDS:Time	-3.1449	0.4307	Wc x N x LL	TDS:Time	-2.8265	0.5114	Wc x N x LL	TDS:Time	-2.7043	0.7665	Wc x N x LL	TDS:Time	-12.8235	0.0243	Wc x N x LL
TP:Time	0.0000	0.8710	Wc x N x LL	TP:Time	-0.0002	0.6098	Wc x N x LL	TP:Time	0.0022	0.0021	Wc x N x LL	TP:Time	0.0003	0.3596	Wc x N x LL
pH	0.2123	0.7407	Wc x N	pH	2.9409	0.0013	Wc x N	pH	-0.1367	0.9096	Wc x N	pH	-0.2394	0.7021	Wc x N
Cond.	-135.2583	0.5233	Wc x N	Cond.	413.2374	0.0683	Wc x N	Cond.	-466.5001	0.2669	Wc x N	Cond.	462.0890	0.0088	Wc x N
Turb.	0.0651	0.0100	Wc x N	Turb.	-0.0664	0.0819	Wc x N	Turb.	-0.0494	0.2643	Wc x N	Turb.	-0.0030	0.9039	Wc x N
TDS	219.6747	0.5182	Wc x N	TDS	-695.3331	0.0563	Wc x N	TDS	778.9882	0.2490	Wc x N	TDS	-730.9979	0.0099	Wc x N
NH4	-0.0006	0.6661	Wc x N	NH4	0.0018	0.1752	Wc x N	NH4	-0.0002	0.9126	Wc x N	NH4	0.0036	0.0059	Wc x N
NO3	0.3851	0.9551	Wc x N	NO3	20.5373	0.0311	Wc x N	NO3	3.9476	0.7343	Wc x N	NO3	-7.9014	0.2752	Wc x N
PO4	-0.0799	0.2233	Wc x N	PO4	-0.2835	0.0054	Wc x N	PO4	0.0327	0.7417	Wc x N	PO4	-0.0260	0.7235	Wc x N
pH:Time	-0.0039	0.5912	Wc x N	pH:Time	-0.0317	0.0001	Wc x N	pH:Time	0.0015	0.8989	Wc x N	pH:Time	0.0075	0.2529	Wc x N
Turb.:Time	-0.0003	0.5272	Wc x N	Turb.:Time	0.0013	0.0384	Wc x N	Turb.:Time	-0.0002	0.8078	Wc x N	Turb.:Time	0.0010	0.0615	Wc x N
TP:Time	0.0000	0.9110	Wc x N	TP:Time	-0.0001	0.7511	Wc x N	TP:Time	0.0001	0.9039	Wc x N	TP:Time	-0.0010	0.0011	Wc x N
PO4:Time	0.0009	0.4152	Wc x N	PO4:Time	0.0047	0.0051	Wc x N	PO4:Time	-0.0006	0.7002	Wc x N	PO4:Time	0.0005	0.6825	Wc x N
s(Time)	1.0000	0.3096	Wc x N	s(Time)	1.0004	0.0313	Wc x N	s(Time)	2.2940	0.2196	Wc x N	s(Time)	1.1757	0.2733	Wc x N
Temp	0.0881	0.7968	Wv	Temp	1.0596	0.1288	Wv	Temp	-1.3083	0.0340	Wv	Temp	0.2575	0.4893	Wv
pH	-0.6393	0.2629	Wv	pH	-0.8507	0.4262	Wv	pH	2.7538	0.0027	Wv	pH	0.1500	0.8166	Wv
Turb.	0.0876	0.2182	Wv	Turb.	-0.6422	0.0006	Wv	Turb.	-0.0615	0.5426	Wv	Turb.	-0.0477	0.5157	Wv
NH4	0.0039	0.1592	Wv	NH4	0.0021	0.6936	Wv	NH4	0.0077	0.0879	Wv	NH4	0.0090	0.0045	Wv

Greens				Cyanobacteria				Diatoms				Phytoflagellates			
NO3	9.1149	0.0887	Wv	NO3	-15.1209	0.1275	Wv	NO3	20.1145	0.0586	Wv	NO3	10.5946	0.0879	Wv
TP	0.1979	0.0140	Wv	TP	0.2603	0.0151	Wv	TP	-0.0069	0.9492	Wv	TP	0.0978	0.2210	Wv
PO4	0.1342	0.0377	Wv	PO4	0.1492	0.1885	Wv	PO4	0.1078	0.1927	Wv	PO4	0.0653	0.4449	Wv
Temp:Time	-0.0081	0.1256	Wv	Temp:Time	-0.0159	0.0245	Wv	Temp:Time	0.0238	0.0938	Wv	Temp:Time	-0.0192	0.0016	Wv
pH:Time	0.0125	0.1490	Wv	pH:Time	0.0183	0.1689	Wv	pH:Time	-0.0331	0.0265	Wv	pH:Time	0.0103	0.2510	Wv
DO:Time	-0.0540	0.1754	Wv	DO:Time	-0.0579	0.3276	Wv	DO:Time	0.1786	0.0691	Wv	DO:Time	-0.1146	0.0076	Wv
Turb.:Time	0.0006	0.4638	Wv	Turb.:Time	0.0060	0.0002	Wv	Turb.:Time	-0.0006	0.7407	Wv	Turb.:Time	0.0017	0.0619	Wv
DOsat:Time	0.0041	0.1917	Wv	DOsat:Time	0.0045	0.3342	Wv	DOsat:Time	-0.0142	0.0671	Wv	DOsat:Time	0.0091	0.0070	Wv
NO3:Time	-0.0593	0.2238	Wv	NO3:Time	0.1462	0.0485	Wv	NO3:Time	-0.0166	0.8748	Wv	NO3:Time	-0.0710	0.1776	Wv
TP:Time	-0.0018	0.0284	Wv	TP:Time	-0.0029	0.0098	Wv	TP:Time	0.0009	0.5393	Wv	TP:Time	-0.0016	0.0618	Wv
PO4:Time	-0.0064	0.0433	Wv	PO4:Time	-0.0062	0.1278	Wv	PO4:Time	-0.0008	0.8715	Wv	PO4:Time	-0.0096	0.0072	Wv
s(Time)	1.0000	0.3671	Wv	s(Time)	1.0004	0.0121	Wv	s(Time)	3.2908	0.0218	Wv	s(Time)	1.3522	0.0071	Wv
Temp	0.7807	0.0432	Wv x LL	Temp	1.0407	0.1988	Wv x LL	Temp	0.4868	0.4865	Wv x LL	Temp	0.6895	0.1930	Wv x LL
NH4	-0.0042	0.0096	Wv x LL	NH4	-0.0097	0.0054	Wv x LL	NH4	-0.0010	0.7521	Wv x LL	NH4	-0.0001	0.9452	Wv x LL
NH4:Time	0.0000	0.2634	Wv x LL	NH4:Time	0.0001	0.0455	Wv x LL	NH4:Time	0.0001	0.4652	Wv x LL	NH4:Time	0.0000	0.1684	Wv x LL
NO3:Time	0.0998	0.0445	Wv x LL	NO3:Time	0.0071	0.9381	Wv x LL	NO3:Time	-0.3154	0.2299	Wv x LL	NO3:Time	0.0346	0.5579	Wv x LL
TP:Time	-0.0003	0.3250	Wv x LL	TP:Time	-0.0012	0.0319	Wv x LL	TP:Time	0.0010	0.3694	Wv x LL	TP:Time	0.0000	0.9210	Wv x LL
pH	-0.0032	0.9960	Wv x N x LL	pH	3.3500	0.0026	Wv x N x LL	pH	3.6077	0.0126	Wv x N x LL	pH	0.8204	0.2637	Wv x N x LL
Cond.	-71.6205	0.8425	Wv x N x LL	Cond.	1477.0803	0.0093	Wv x N x LL	Cond.	1379.1686	0.0964	Wv x N x LL	Cond.	154.3501	0.7133	Wv x N x LL
TDS	96.5382	0.8650	Wv x N x LL	TDS	-2262.6973	0.0105	Wv x N x LL	TDS	-2117.4847	0.1039	Wv x N x LL	TDS	-257.7170	0.6956	Wv x N x LL
NO3	3.1901	0.5668	Wv x N x LL	NO3	-25.7313	0.0385	Wv x N x LL	NO3	-8.4419	0.4937	Wv x N x LL	NO3	13.5409	0.1074	Wv x N x LL
TP	-0.0029	0.7130	Wv x N x LL	TP	-0.0482	0.0280	Wv x N x LL	TP	-0.0242	0.1587	Wv x N x LL	TP	0.0000	0.9997	Wv x N x LL
pH:Time	-0.0035	0.5520	Wv x N x LL	pH:Time	-0.0360	0.0006	Wv x N x LL	pH:Time	-0.0146	0.2927	Wv x N x LL	pH:Time	-0.0008	0.8990	Wv x N x LL
ORP:Time	0.0001	0.7487	Wv x N x LL	ORP:Time	-0.0013	0.0022	Wv x N x LL	ORP:Time	0.0003	0.5043	Wv x N x LL	ORP:Time	0.0004	0.0952	Wv x N x LL
Cond.:Time	-0.3024	0.9398	Wv x N x LL	Cond.:Time	-24.4866	0.0010	Wv x N x LL	Cond.:Time	-11.6925	0.2059	Wv x N x LL	Cond.:Time	0.9663	0.8361	Wv x N x LL
TDS:Time	0.7274	0.9079	Wv x N x LL	TDS:Time	37.7824	0.0010	Wv x N x LL	TDS:Time	17.5025	0.2288	Wv x N x LL	TDS:Time	-1.3957	0.8476	Wv x N x LL
NH4:Time	0.0000	0.1243	Wv x N x LL	NH4:Time	0.0000	0.2388	Wv x N x LL	NH4:Time	0.0001	0.0315	Wv x N x LL	NH4:Time	0.0000	0.3889	Wv x N x LL
TP:Time	0.0002	0.5054	Wv x N x LL	TP:Time	0.0009	0.0453	Wv x N x LL	TP:Time	-0.0001	0.8558	Wv x N x LL	TP:Time	-0.0004	0.1834	Wv x N x LL
pH	0.9579	0.0488	Wv x N	pH	0.3909	0.6692	Wv x N	pH	3.1124	0.0259	Wv x N	pH	-0.3071	0.6544	Wv x N

Greens				Cyanobacteria				Diatoms				Phytoflagellates			
TP	0.0161	0.0553	Wv x N	TP	-0.0415	0.0116	Wv x N	TP	0.0184	0.3739	Wv x N	TP	0.0166	0.1414	Wv x N
PO4	-0.0350	0.2722	Wv x N	PO4	-0.1348	0.0508	Wv x N	PO4	0.0807	0.3397	Wv x N	PO4	-0.1390	0.0335	Wv x N
Temp:Time	0.0044	0.2013	Wv x N	Temp:Time	-0.0053	0.2819	Wv x N	Temp:Time	0.0258	0.0119	Wv x N	Temp:Time	-0.0104	0.0773	Wv x N
DO:Time	0.0349	0.2159	Wv x N	DO:Time	0.0044	0.9110	Wv x N	DO:Time	0.2203	0.0078	Wv x N	DO:Time	-0.0563	0.2380	Wv x N
Cond.:Time	-2.9380	0.1952	Wv x N	Cond.:Time	-3.5440	0.2558	Wv x N	Cond.:Time	-13.5274	0.0400	Wv x N	Cond.:Time	-4.8639	0.1759	Wv x N
DOsat:Time	-0.0026	0.2518	Wv x N	DOsat:Time	0.0000	0.9899	Wv x N	DOsat:Time	-0.0178	0.0075	Wv x N	DOsat:Time	0.0047	0.2235	Wv x N
TDS:Time	4.7066	0.1892	Wv x N	TDS:Time	5.5643	0.2583	Wv x N	TDS:Time	22.4087	0.0316	Wv x N	TDS:Time	7.3650	0.1900	Wv x N
NH4:Time	0.0000	0.6663	Wv x N	NH4:Time	0.0000	0.8086	Wv x N	NH4:Time	-0.0002	0.0202	Wv x N	NH4:Time	0.0001	0.0861	Wv x N
NO3:Time	0.1355	0.1159	Wv x N	NO3:Time	-0.0231	0.8461	Wv x N	NO3:Time	0.5129	0.0356	Wv x N	NO3:Time	-0.1880	0.1495	Wv x N
TP:Time	-0.0002	0.1818	Wv x N	TP:Time	0.0006	0.0018	Wv x N	TP:Time	0.0000	0.9256	Wv x N	TP:Time	-0.0002	0.1337	Wv x N
PO4:Time	0.0006	0.5899	Wv x N	PO4:Time	0.0041	0.0204	Wv x N	PO4:Time	-0.0156	0.0011	Wv x N	PO4:Time	-0.0003	0.8804	Wv x N
s(Time)	2.1633	0.2260	Wv x N	s(Time)	2.6479	0.0968	Wv x N	s(Time)	2.9133	0.0168	Wv x N	s(Time)	1.2697	0.2565	Wv x N
(Intercept)	19.4942	0.0011	C	(Intercept)	-21.4084	0.4514	C	(Intercept)	29.0644	0.0455	C	(Intercept)	17.8412	0.0200	C
Temp	0.1262	0.7204	C	Temp	0.1614	0.9443	C	Temp	-1.8408	0.0494	C	Temp	-0.6329	0.2500	C
pH	0.2632	0.6604	C	pH	-1.8148	0.5921	C	pH	2.8252	0.0389	C	pH	1.4900	0.1111	C
DO	4.0002	0.1738	C	DO	-3.9907	0.8189	C	DO	-18.1479	0.0177	C	DO	-8.5128	0.0580	C
Cond.	-8.7725	0.9585	C	Cond.	1648.8821	0.1947	C	Cond.	764.9794	0.1212	C	Cond.	564.5759	0.0111	C
DOsat	-0.3180	0.1851	C	DOsat	0.1791	0.9004	C	DOsat	1.5077	0.0169	C	DOsat	0.6877	0.0597	C
TDS	-9.5885	0.9714	C	TDS	-2525.6633	0.2166	C	TDS	-1189.7792	0.1317	C	TDS	-895.2304	0.0115	C
NO3	1.5535	0.7224	C	NO3	75.1205	0.0160	C	NO3	7.4455	0.4925	C	NO3	3.3576	0.5890	C
TP	0.0375	0.0712	C	TP	-0.2355	0.0384	C	TP	-0.0182	0.6603	C	TP	0.0140	0.6146	C
PO4	-0.0088	0.8498	C	PO4	-0.8993	0.0225	C	PO4	-0.1000	0.1850	C	PO4	-0.0126	0.8485	C
Temp:Time	-0.0045	0.1869	C	Temp:Time	0.0115	0.5893	C	Temp:Time	0.0135	0.1735	C	Temp:Time	-0.0004	0.9302	C
pH:Time	-0.0086	0.2459	C	pH:Time	0.0186	0.5933	C	pH:Time	-0.0456	0.0187	C	pH:Time	-0.0078	0.4099	C
DO:Time	-0.0693	0.0300	C	DO:Time	0.1245	0.4709	C	DO:Time	-0.0016	0.9847	C	DO:Time	0.0275	0.5136	C
Cond.:Time	0.9099	0.7587	C	Cond.:Time	-13.5000	0.2859	C	Cond.:Time	-8.6187	0.2573	C	Cond.:Time	-9.4231	0.0113	C
DOsat:Time	0.0056	0.0287	C	DOsat:Time	-0.0088	0.5273	C	DOsat:Time	-0.0005	0.9359	C	DOsat:Time	-0.0022	0.5071	C
TDS:Time	-1.1834	0.7980	C	TDS:Time	20.3064	0.3118	C	TDS:Time	13.0137	0.2714	C	TDS:Time	14.7138	0.0113	C
NH4:Time	0.0000	0.5170	C	NH4:Time	0.0001	0.5648	C	NH4:Time	0.0001	0.3385	C	NH4:Time	0.0001	0.0081	C

Greens				Cyanobacteria				Diatoms				Phytoflagellates			
NO3:Time	0.0032	0.9534	C	NO3:Time	-0.5173	0.0485	C	NO3:Time	-0.0592	0.6582	C	NO3:Time	-0.1321	0.0381	C
TP:Time	-0.0008	0.0230	C	TP:Time	0.0020	0.1269	C	TP:Time	0.0001	0.9241	C	TP:Time	0.0000	0.9307	C
s(Time)	1.0010	0.2497	C	s(Time)	3.2602	0.1433	C	s(Time)	3.4976	0.0430	C	s(Time)	1.0002	0.5815	C
pH	0.6182	0.2294	LL	pH	7.4910	0.0024	LL	pH	0.7949	0.3856	LL	pH	-0.5348	0.5297	LL
Turb.	0.1010	0.1153	LL	Turb.	0.1288	0.4903	LL	Turb.	-0.2997	0.0157	LL	Turb.	-0.0721	0.4445	LL
NH4	-0.0006	0.7565	LL	NH4	0.0003	0.9670	LL	NH4	0.0075	0.0356	LL	NH4	0.0011	0.7521	LL
NO3	5.1189	0.3476	LL	NO3	50.2456	0.0155	LL	NO3	-3.5630	0.7091	LL	NO3	-17.5064	0.0153	LL
pH:Time	-0.0013	0.8353	LL	pH:Time	-0.0763	0.0008	LL	pH:Time	-0.0053	0.6221	LL	pH:Time	-0.0066	0.5102	LL
Turb.:Time	-0.0004	0.6122	LL	Turb.:Time	-0.0002	0.9041	LL	Turb.:Time	0.0045	0.0084	LL	Turb.:Time	0.0000	0.9844	LL
NO3:Time	-0.0121	0.7926	LL	NO3:Time	-0.3572	0.0173	LL	NO3:Time	0.1569	0.0945	LL	NO3:Time	0.1768	0.0040	LL
PO4:Time	0.0012	0.4928	LL	PO4:Time	-0.0002	0.9455	LL	PO4:Time	0.0010	0.7326	LL	PO4:Time	0.0074	0.0005	LL
s(Time)	1.0000	0.8602	LL	s(Time)	3.1724	0.0314	LL	s(Time)	1.0004	0.5138	LL	s(Time)	3.0313	0.0587	LL
(Intercept)	17.3563	0.0004	N	(Intercept)	13.5555	0.3129	N	(Intercept)	15.4716	0.3040	N	(Intercept)	-5.9180	0.5592	N
Temp	0.3171	0.2702	N	Temp	0.4714	0.5753	N	Temp	-1.0107	0.3266	N	Temp	1.3653	0.0268	N
pH	1.1021	0.0021	N	pH	-2.1180	0.0304	N	pH	1.9495	0.0526	N	pH	-1.2016	0.1223	N
Cond.	-152.3964	0.4981	N	Cond.	110.9941	0.8698	N	Cond.	2121.6181	0.0022	N	Cond.	249.0639	0.6127	N
TDS	237.9905	0.5067	N	TDS	-142.0513	0.8955	N	TDS	-3431.1466	0.0021	N	TDS	-371.0535	0.6347	N
NO3	0.5278	0.8453	N	NO3	4.5811	0.4853	N	NO3	19.9014	0.0342	N	NO3	14.8918	0.0270	N
Temp:Time	-0.0079	0.0369	N	Temp:Time	-0.0059	0.5476	N	Temp:Time	0.0220	0.0394	N	Temp:Time	-0.0157	0.0983	N
pH:Time	-0.0263	0.0001	N	pH:Time	0.0261	0.0414	N	pH:Time	-0.0372	0.0122	N	pH:Time	0.0203	0.0507	N
DO:Time	-0.0724	0.0154	N	DO:Time	-0.0201	0.7523	N	DO:Time	0.0245	0.7134	N	DO:Time	-0.0292	0.6175	N
DOsat:Time	0.0062	0.0120	N	DOsat:Time	0.0018	0.7312	N	DOsat:Time	-0.0013	0.8136	N	DOsat:Time	0.0025	0.6067	N
NH4:Time	0.0000	0.2411	N	NH4:Time	0.0001	0.0339	N	NH4:Time	0.0001	0.0807	N	NH4:Time	0.0000	0.3375	N
NO3:Time	0.0808	0.0256	N	NO3:Time	-0.1557	0.0364	N	NO3:Time	-0.0938	0.2362	N	NO3:Time	-0.1312	0.0323	N
s(Time)	1.0003	0.0074	N	s(Time)	1.8371	0.8382	N	s(Time)	1.0002	0.0618	N	s(Time)	3.4047	0.0368	N
Turb.	-0.0040	0.6261	N x LL	Turb.	0.0836	0.0479	N x LL	Turb.	0.0168	0.5379	N x LL	Turb.	0.0458	0.0016	N x LL
TDS	652.4315	0.0789	N x LL	TDS	-4008.0741	0.0476	N x LL	TDS	-1165.9585	0.2496	N x LL	TDS	-391.3590	0.5184	N x LL
PO4	0.0006	0.9483	N x LL	PO4	0.2452	0.0008	N x LL	PO4	0.0345	0.2942	N x LL	PO4	0.0064	0.6973	N x LL
pH:Time	-0.0034	0.4348	N x LL	pH:Time	-0.0014	0.9168	N x LL	pH:Time	0.0217	0.0378	N x LL	pH:Time	0.0097	0.1629	N x LL

Greens				Cyanobacteria				Diatoms				Phytoflagellates			
Turb.:Time	0.0001	0.5647	N x LL	Turb.:Time	-0.0010	0.0808	N x LL	Turb.:Time	-0.0003	0.5002	N x LL	Turb.:Time	-0.0007	0.0021	N x LL
PO4:Time	0.0001	0.7070	N x LL	PO4:Time	-0.0027	0.0008	N x LL	PO4:Time	0.0005	0.5089	N x LL	PO4:Time	-0.0004	0.2285	N x LL

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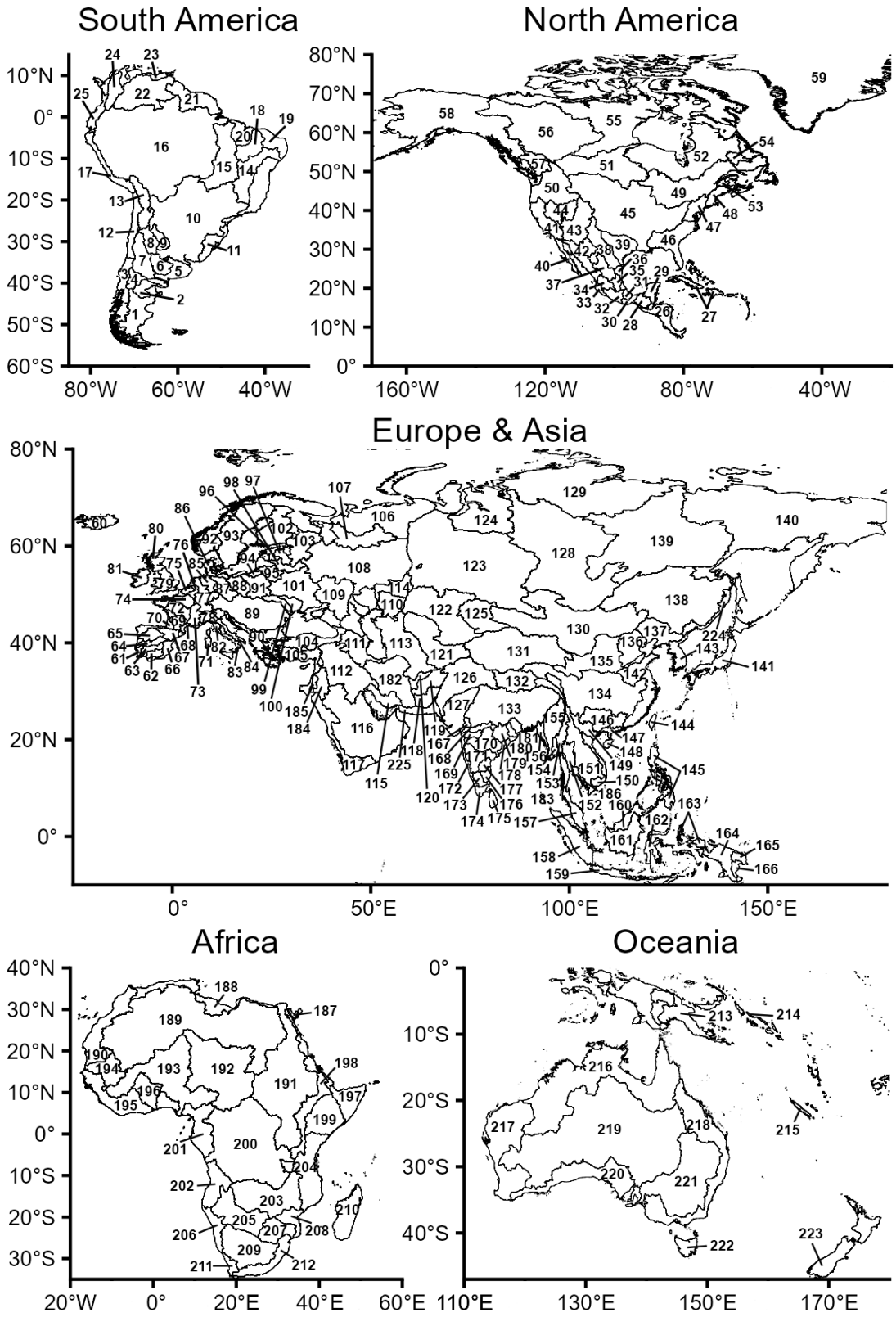
APPENDIX B - Figure: 225 river basins worldwide, divided by continent. 1: South Argentina-South Atlantic Coast, 2: Central Patagonia Highlands, 3: South Chile-Pacific Coast, 4: Negro, 5: North Argentina-South Atlantic Coast, 6: Pampas Region, 7: South America-Colorado, 8: Salinas Grandes, 9: Mar Chiquita, 10: La Plata, 11: Uruguay - Brazil-South Atlantic Coast, 12: North Chile-Pacific Coast, 13: La Puna Region, 14: Sao Francisco, 15: Tocantins, 16: Amazon, 17: Peru-Pacific Coast, 18: Parnaiba, 19: East Brazil-South Atlantic Coast, 20: North Brazil-South Atlantic Coast, 21: Northeast South America-South Atlantic Coast, 22: Orinoco, 23: Caribbean Coast, 24: Magdalena, 25: Colombia - Ecuador-Pacific Coast, 26: Southern Central America, 27: Caribbean, 28: Grijalva - Usumacinta, 29: Yucatn Peninsula, 30: Isthmus of Tehuantepec, 31: Papaloapan, 32: Ro Balsas, 33: Pacific Central Coast, 34: Ro Lerma, 35: Ro Verde, 36: North Gulf, 37: Mexico-Interior, 38: Ro Grande - Bravo, 39: Gulf Coast, 40: Baja California, 41: California, 42: Mexico-Northwest Coast, 43: North America-Colorado, 44: Great Basin, 45: Mississippi - Missouri, 46: Gulf of Mexico-North Atlantic Coast, 47: United States-North Atlantic Coast, 48: Atlantic Ocean Seaboard, 49: St Lawrence, 50: Columbia and Northwestern United States, 51: Saskatchewan - Nelson, 52: Hudson Bay Coast, 53: St John, 54: Churchill, 55: Northwest Territories, 56: Mackenzie, 57: Fraser, 58: Pacific and Arctic Coast, 59: Arctic Ocean Islands, 60: Iceland, 61: Spain - Portugal-Atlantic Coast, 62: Guadalquivir, 63: Guadiana, 64: Tagus, 65: Douro, 66: Spain-South and East Coast, 67: Ebro, 68: France-South Coast, 69: Gironde, 70: France-West Coast, 71: Mediterranean Sea Islands, 72: Loire, 73: Rhne, 74: Seine, 75: Scheldt, 76: Maas, 77: Rhine, 78: Po, 79: England and Wales, 80: Scotland, 81: Ireland, 82: Tiber, 83: Italy-West Coast, 84: Italy-East Coast, 85: Ems - Weser, 86: Denmark - Germany Coast, 87: Elbe, 88: Oder, 89: Danube, 90: Adriatic Sea - Greece - Black Sea Coast, 91: Wisla, 92: Scandinavia-North Coast, 93: Sweden, 94: Poland Coast, 95: Neman, 96: Baltic Sea Coast, 97: Narva, 98: Daugava, 99: Dniester, 100: Black Sea-North Coast, 101: Dnieper, 102: Finland, 103: Neva, 104: Black Sea-South Coast, 105: Mediterranean Sea-East Coast, 106: Russia-Barents Sea Coast, 107: Northern Dvina, 108: Volga, 109: Don, 110: Caspian Sea Coast, 111: Caspian Sea-South West Coast, 112: Tigris - Euphrates, 113: Caspian Sea-East Coast, 114: Ural, 115: Persian Gulf Coast, 116: Arabian Peninsula, 117: Red Sea-East Coast, 118: Hamun-i-Mashkel, 119: Helmand, 120: Farahrud, 121: Amu Darya, 122: Syr Darya, 123: Ob, 124: Kara Sea Coast, 125: Lake Balkash, 126: Indus, 127: Sabarmati, 128: Yenisey, 129: Siberia-North Coast, 130: Gobi Interior, 131: Tarim Interior, 132: Plateau of Tibet Interior, 133: Ganges - Bramaputra, 134: Yangtze, 135: Huang He, 136: Ziya He-Interior, 137: Bo Hai - Korean Bay-North Coast, 138: Amur, 139: Lena, 140: Siberia-West Coast, 141: Japan, 142: China Coast, 143: North and South Korea, 144: Taiwan, 145: Philippines, 146: Xun Jiang, 147: South China Sea Coast, 148: Hainan, 149: Hong (Red River), 150: Viet Nam-Coast, 151: Mekong, 152: Chao Phraya, 153: Salween, 154: Sittang, 155: Irrawaddy, 156: Bay of Bengal-North East Coast, 157: Peninsula Malaysia, 158: Sumatra, 159: Java - Timor, 160: North Borneo Coast, 161: Kalimantan, 162: Sulawesi, 163: Palau and East Indonesia, 164: Irian Jaya Coast, 165: Sepik, 166: Fly, 167: Mahi, 168: Narmada, 169: Tapti, 170: Godavari, 171: Krishna, 172: India West Coast, 173: Cauvery, 174: India South Coast, 175: Sri Lanka, 176: India East Coast, 177: Pennar, 178: India North East Coast, 179: Mahandi, 180: Brahamani, 181: Yasai, 182: Central Iran, 183: Andaman - Nicobar Islands, 184: Eastern Jordan - Syria, 185: Dead Sea, 186: Gulf of Thailand Coast, 187: Sinai Peninsula, 188: Mediterranean South Coast, 189: Africa-North Interior, 190: Africa-North West Coast, 191: Nile, 192: Lake Chad, 193: Niger, 194: Senegal, 195: Africa-West Coast, 196: Volta, 197:

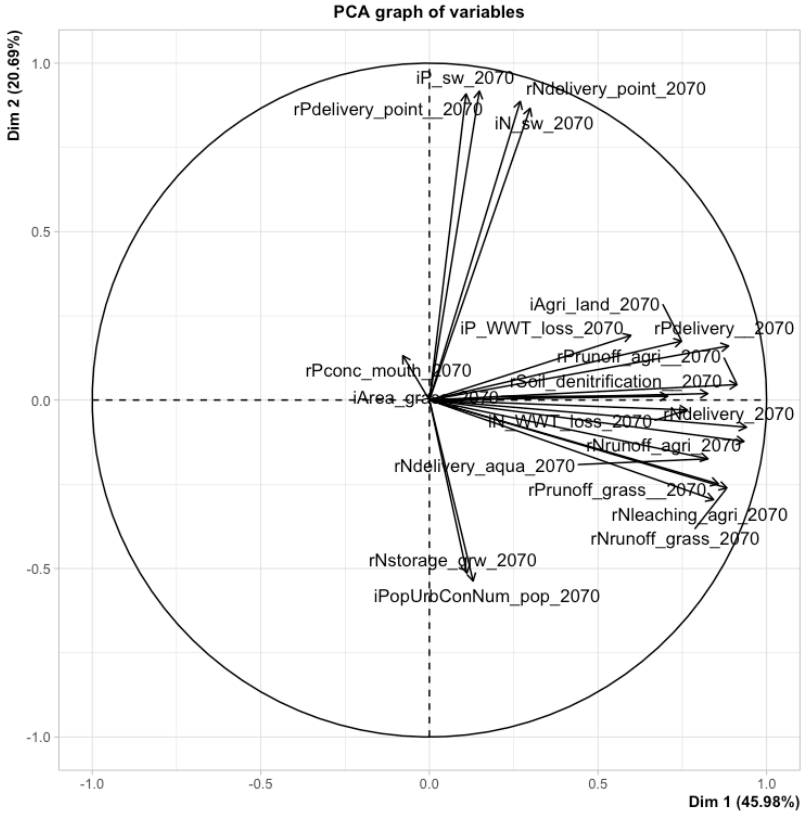
Africa Red Sea-Gulf of Aden Coast, 198: Rift Valley, 199: Shebelli - Juba, 200: Congo, 201: Gulf of Guinea, 202: Angola-Coast, 203: Zambezi, 204: Africa-East Central Coast, 205: Africa-South Interior, 206: Namibia-Coast, 207: Limpopo, 208: Africa-Indian Ocean Coast, 209: Orange, 210: Madasgacar, 211: South Africa-West Coast, 212: South Africa-South Coast, 213: Papua New Guinea Coast, 214: Solomon Islands, 215: South Pacific Islands, 216: Australia-North Coast, 217: Australia-West Coast, 218: Australia-East Coast, 219: Australia-Interior, 220: Australia-South Coast, 221: Murray - Darling, 222: Tasmania, 223: New Zealand, 224: Russia-South East Coast, 225: Arabian Sea Coast.


South America
North America
Europe & Asia
Africa
Oceania

APPENDIX C - Table: 20 anthropogenic pressure variables selected from Beussen et al. (2022) that are most closely associated with cyanobacterial blooms, and their collinearity values. The variables projected for 2070 were used.

All variables	**VIF**
Area agriculture	2849.76
Area grassland	1806.62
N discharge from households to surface waters	72728.62
N removal in wastewater treatment plants	328.53
P discharge from households to surface waters	72152.38
P removal in wastewater treatment plants	1224.01
Urban population with sewage connection / Total Population	14.94
N delivery total	524.53
N delivery from aquaculture	610.03
N delivery from point sources	54008.42
N leaching agricultural land	3399.77
N delivery via runoff/erosion from agriculture	1597.16
N delivery via runoff/erosion from grassland	2166.98
Temporary N storage in groundwater	100.93
P concentration at river mouth	41.98
P delivery total	483.80
P delivery from point sources	57115.36
P delivery via runoff/erosion from agriculture	2508.88
P delivery via runoff/erosion from grassland	894.84
Total soil denitrification (agriculture + natural)	2079.64

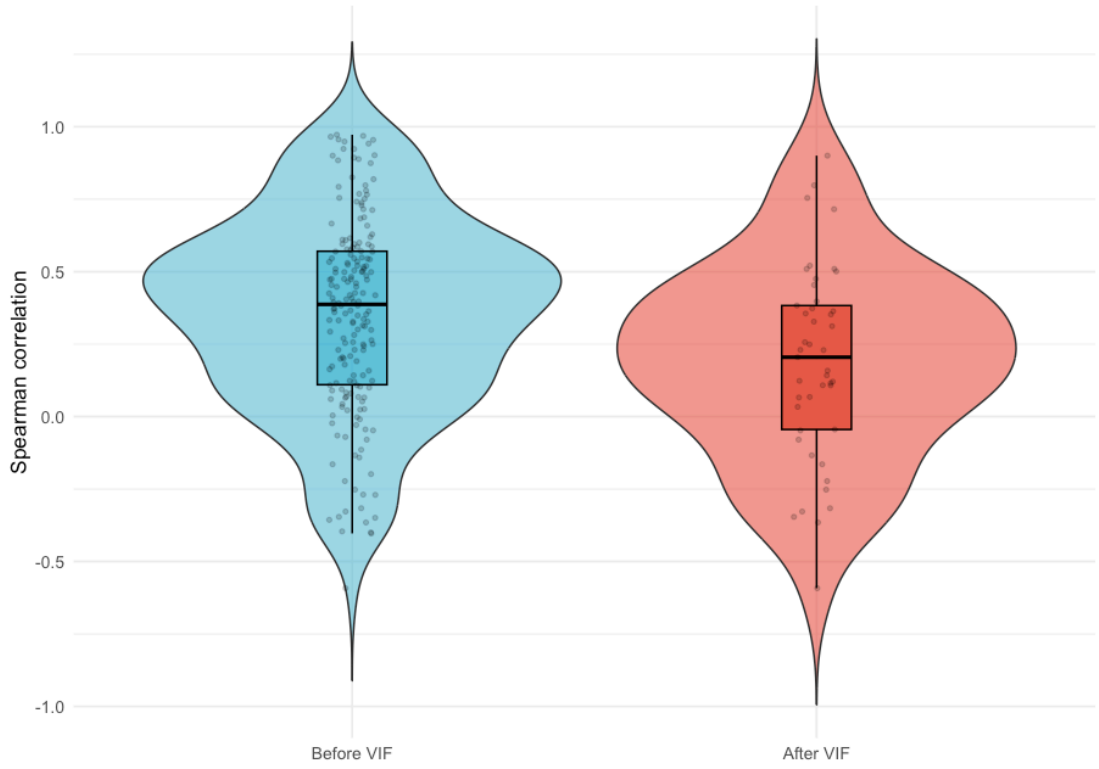
APPENDIX D - Figure: Principal Component Analysis (PCA) of the 20 variables selected from Beussen et al. (2022). The variables projected for 2070 were used.



APPENDIX E - Table: Anthropogenic pressure variables used in the cyanoHAB index and their collinearity values. These variables were selected based on their VIF values using the *usdm* package in R.

Selected variables	**VIF**
Area grassland	2.71
P removal in wastewater treatment plants	4.34
P discharge from households to surface waters	2.36
Urban population with sewage connection / Total Population	1.87
N delivery from aquaculture	3.45
N delivery via runoff/erosion from agriculture	5.20
Temporary N storage in groundwater	1.93
P concentration at river mouth	1.92
P delivery from point sources	3.72
Total soil denitrification (agriculture + natural)	5.49

APPENDIX F - Figure: Spearman's correlation coefficients between anthropogenic pressure variables before and after removing those with a variance inflation factor > 5.



APPENDIX G - Table: Anthropogenic pressure variables used in the cyanoHAB index and their collinearity values. These variables were selected based on their VIF values using the *usdm* package in R.

Variable	Group	*M. aeruginosa*	*P. agardhii*	*R. raciborskii*	w_*M. aeruginosa*	w_*P. agardhii*	w_*R. raciborskii*	%_*M. aeruginosa*	%_*P. agardhii*	%_*R. raciborskii*
P discharge from households to surface waters	Phosphorus	+++	+++	++	4.5	4.5	3	5	5.7692	5
P removal in wastewater treatment plants	Phosphorus	+++	+++	++	4.5	4.5	3	5	5.7692	5
P concentration at river mouth	Phosphorus	+++	+++	++	4.5	4.5	3	5	5.7692	5
P delivery from point sources	Phosphorus	+++	+++	++	4.5	4.5	3	5	5.7692	5
N delivery from aquaculture	Nitrogen	+++	+++	+	4.5	4.5	1.5	5	5.7692	3
N delivery via runoff/erosion from agriculture	Nitrogen	+++	+++	+	4.5	4.5	1.5	5	5.7692	3
Temporary storage in groundwater	Nitrogen	+++	+++	+	4.5	4.5	1.5	5	5.7692	3
Total soil denitrification (agriculture + natural)	Nitrogen	+++	+++	+	4.5	4.5	1.5	5	5.7692	3
Area grassland	Population	+++	+++	+++	9	9	9	10	11.5385	15
Urban population with sewage connection / Total Population	Population	+++	+++	+++	9	9	9	10	11.5385	15
Current Dams	Dams	+++	++	++	9	6	6	10	7.6923	10
Current Dams + for future	Dams	+++	++	++	9	6	6	10	7.6923	10
ENMs	Warming	+++	++	++	18	12	12	20	15.3846	20
	Sum weight				**90**	**78**	**60**	**100**	**100**	**100**

APPENDIX H - The impacts depicted on the game cards represent some of the main threats to freshwater ecosystems around the world. Although they appear as game mechanics, they are all based on real environmental issues that affect biodiversity, water quality, and the balance of these environments. Below are all the impact cards from the board game *Ecologist: preservation work*:

Climate change

Rising global temperatures directly affect water temperatures, influence rainfall patterns, and intensify droughts and floods, profoundly altering aquatic ecosystems and affecting species and ecological processes.

Damming

The construction of dams disrupts the natural flow of rivers, alters habitats, makes it difficult for species to migrate, and changes the physical and chemical properties of the water.

Microplastic

Tiny plastic fragments pollute rivers, lakes, and oceans, where they are ingested by various aquatic organisms and accumulate in the food web. These particles are the result of society's growing consumption of plastic.

Eutrophication

Excess nutrients in the water, usually caused by human activities. This process affects the entire food web in these environments and is extremely harmful.

Biological invasion

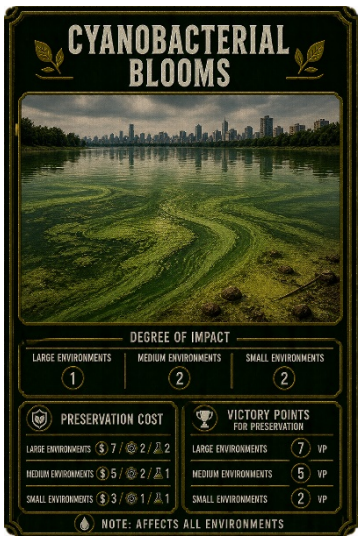
Species that are introduced, usually by human activity, outside their natural range. This can lead to competition with native species, disrupt food webs, and cause severe ecological imbalances.

Riparian vegetation loss

The removal of vegetation from riversides, leading to increased erosion and sedimentation in aquatic environments, thereby reducing the natural protection of these systems.

Wildfires

Fires release large amounts of ash and sediment into water bodies, degrading habitats and compromising environmental quality.

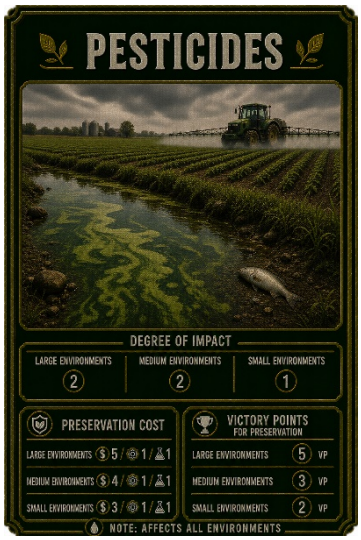


Cyanobacterial blooms

Excessive growth of cyanobacteria, which may release toxins harmful to wildlife, drinking water, and human health.

Sewage discharge

Improper sewage discharge contaminates aquatic environments, reduces water quality, and promotes the proliferation of harmful organisms.



Pesticides

Chemicals used in agriculture, which can end up in rivers and lakes, affecting the health of aquatic organisms.

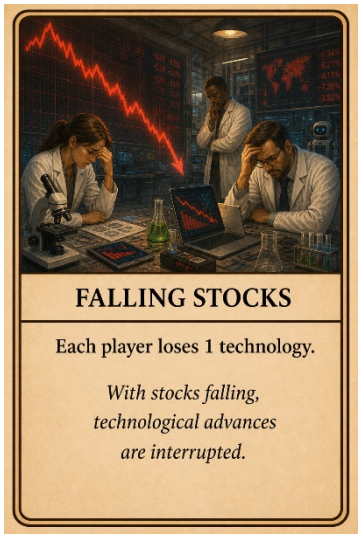
Toxic metals

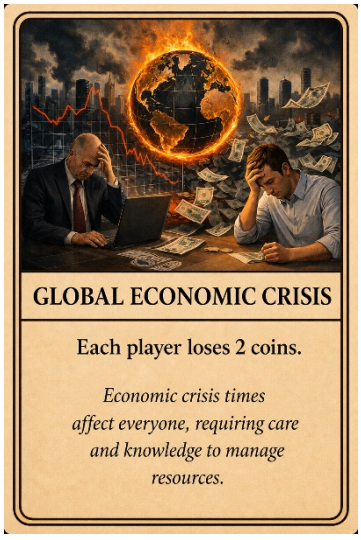
Heavy metals from industrial and mining activities can accumulate in the environment and in living organisms, causing long-term toxic effects.

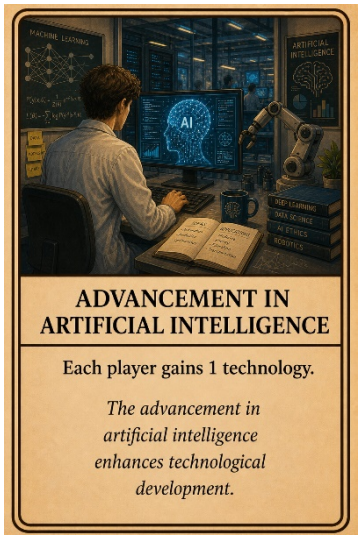
Overfishing

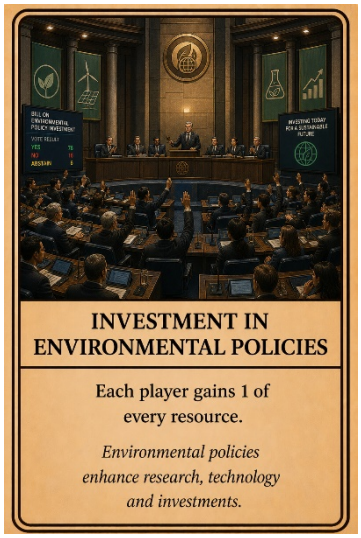
The overexploitation of fishery resources, which reduces natural populations and disrupts the balance of aquatic food chains.

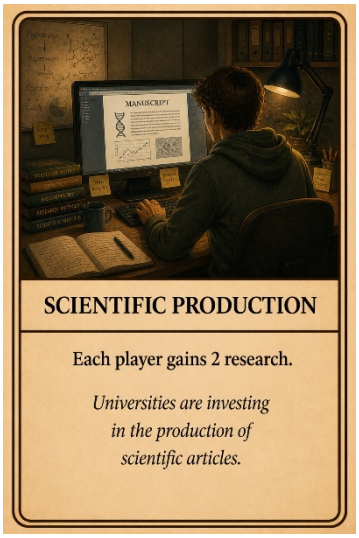
APPENDIX I - The Joker cards add an important dynamic to the game, particularly in balancing resources among the institutes. Below are all the Joker cards in the game:











APPENDIX J - Objective cards are essential for Institutes that want to win this game. They help players earn victory points and may be the key factor in determining which Institute ends up with the most preserved resources. Below are all the individual end-game objective cards:

APPENDIX K - Research institutes introduce an asymmetrical game by offering different types of resources in their worker placement area. These institutes were inspired by different regions of the world. Below are the 5 players boards:


EUROPEAN INSTITUTE
+ 2 reserach
+ 1 technology
You can re-roll
the dice twice at the
technology center
MONEY
TECHNOLOGY
RESEARCH


AFRICAN INSTITUTE
+ 1 ecologist
+ 1 research
At the university center,
+1 to the dice value
MONEY
TECHNOLOGY
RESEARCH


ASIAN INSTITUTE
+ 3 technology
At the investment center,
+2 to the dice value
MONEY
TECHNOLOGY
RESEARCH

ACADEMIC TRAJECTORY

Professional experience

- Science teacher for 6th to 9th grade students at Piemont School throughout the 2022 academic year;

- Environmental consulting services for fish rescue at hydroelectric power plants from 2024 to 2026;

Participation in research and/or extension projects

- Participation as a fellow in the extension project titled “Patrulheiros da sustentabilidade”, coordinated by Dr. Altair Bertonha, a professor at the State University of Maringá. This project is a partnership between the State University of Maringá and the government of the state of Paraná. 2025 – 2026;

- Participation in Programa de Pesquisas Ecológicas de Longa Duração (PELD) – A Planície de Inundação do Alto Rio Paraná / CNPq (Processo n. 441356/2020-6). 2022 – 2026;

- Participation in the project titled “Predizendo os efeitos de mudanças globais na estructura, funcionamento e estabilidade de redes tróficas de agua doce: uma abordagem experimental em mesocosmos”, coordinated by Dr. Gustavo Quevedo Romero, full professor at the University of Campinas (UNICAMP). This project was a partnership between the University of Campinas and the State University of Maringá. 2021–2026;

- Participation in the project titled “Biodiversity and freshwater ecosystem functioning in the Anthropocene”, coordinated by Dr. Roger Paulo Mormul, a professor at the State University of Maringá. 2023–2026;

- Participation in the program “NAPI Biodiversidade: Serviços Ecossistêmicos”, coordinated by Dr. Claudia Costa Bonecker, a researcher at the State University of Maringá. 2023–2026;

- Participation as a fellow in the project titled “BIOCAR – Avaliação e mapeamento dos estoques de carbono e fluxos de gases de efeito estufa da biota aquática no reservatorio de Itaipu”, coordinated by Dr. Roger Paulo Mormul, a professor at the State University of Maringá. This project is a partnership between Itaipu Parquetec and several Brazilian universities, including the State University of Maringá. 2023–2026;

Journal reviewer

- Acta Limnologica Brasiliensia. 2024 – present;

- Aquatic Sciences. 2024 – present;

- Hydrobiologia. 2025 – present;
- Harmful Algae. 2026 – present;
- Scientific Reports. 2026 – present;
- Environmental Monitoring and Assessment. 2026 – present;

Participation in scientific and/or extension events

- 5° edição da semana Estadual de Ciência, Tecnologia e Ensino Superior – Paraná Faz Ciência 2025: A Planície de Inundação do Alto Rio Paraná;
- 1° Encontro Brasileiro de Diatomologia 2024;
- 21° Semana Nacional de Ciência e Tecnologia - SNCT 2024. Conversa com o cientista sobre a biodiversidade no Bioma Mata Atlântica;
- 37th SIL International Congress on Limnology 2024;
- Exposição Ciência, Arte E Tecnologias Na Maringá Do Passado E Do Presente 2023;
- Exposição de divulgação científica "Nupélia 40 anos comprometidos com o meio ambiente" 2023;
- Métodos em internacionalização e construção de perfis internacionais 2023;
- VIII Mostra Científica - PELD/CNPq, UEM, Nupélia, PEA - PGB. Ecologia do Fitoplâncton e Perifíton na Planície de inundação do Alto Rio Paraná 2022;
- XVIII Congresso Brasileiro de Limnologia 2022;

Event organisation

- XXXV Ciclo De Debates Em Ecologia De Água Doce 2025;
- Pint of Science. 2024;

Student advising

- Gabriele Corrêa Machado Xavier. Impacto do barramento sobre a singularidade biótica funcional fitoplanctônica em um grande rio Amazônico. Início: 2025. Iniciação

científica (Graduando em Ciências Biológicas) – State University of Maringa. (co-advisor).

- Jeniffer Amanda Marciano. Influência de barramento sobre a composição e riqueza da comunidade epifítica em lagos da planície de inundação do alto rio Paraná. 2024. Iniciação Científica. (Graduando em Ciências Biológicas) - State University of Maringa, Conselho Nacional de Desenvolvimento Científico e Tecnológico. (co-advisor).

- Jeniffer Amanda Marciano. Impacto do barramento sobre a comunidade perifítica em lagos de inundação subtropicais. 2024. Iniciação Científica. (Graduando em Ciências Biológicas) - State University of Maringa, Conselho Nacional de Desenvolvimento Científico e Tecnológico. (co-advisor).

Examination Committees

- Participation in the evaluation committee of Tallys Henrique de Lima. Influência dos eventos climáticos na composição e diversidade beta da comunidade zooplanctônica em uma planície de inundação neotropical (Brasil). 2024. Final Project (Bachelor's Degree in Biological Sciences) - State University of Maringá;

- Participation in the evaluation committee of Ana Laura Reinaldo Constantino. Teia trófica aquático-terrestre: o papel dos morcegos no acoplamento de hábitats em uma planície de inundação neotropical. 2025. Evaluation of the master's project - State University of Maringá;

- Participation in the evaluation committee of Matheus Henrique de Oliveira de Matos. Efeito do aquecimento, adição de nutrientes e aporte de detritos sobre a estrutura da comunidade de amebas testáceas. 2025. Evaluation of the master's project - State University of Maringá;

Abstract presentations

- **Zanon, F. M.**; Comparsi, D. M.; Oliveira, F. R. F.; Romero, G. Q.; Rodrigues, L. C. Warming and land use affect phytoplankton beta diversity: a mesocosm experiment approach. 2024.

- Jesus, G. A. S.; **Zanon, F. M.**; Corredor, L. A. O.; Pineda, A.; Jati, S.; Rodrigues, L. C. Twenty-three years of observations unveil altered biomass variation of phytoplankton due to damming in subtropical regions. 2024.

- Jesus, G. A. S.; Batista, D. C.; Souza, Y. R.; **Zanon, F. M.**; Corredor, L. A. O.; Marciano, J. A.; Correa, G.; Viana, A. L. C.; Shimokawa, M.; Paini, G. F.; Fedrigo, E.; Silva, V.; Pineda, A.; Jati, S.; Rodrigues, L. C. O mundo da ficoflórula em 3D: o uso de modelos realistas na divulgação científica. 2024.

- Jesus, G. A. S.; Batista, D. C.; Souza, Y. R.; **Zanon, F. M.**; Corredor, L. A. O.; Marciano, J. A.; Correa, G.; Viana, A. L. C.; Shimokawa, M.; Paini, G. F.; Fedrigo, E.;

Pineda, A.; Jati, S.; Rodrigues, L. C. Desvendando o mundo das algas e cianobactérias com metodologias participativas. 2024.

- Hein, G.; Pinha, L. S.; Silva, J. D.; **Zanon, F. M.**; Rodrigues, L. C. Effects of global changes: The interaction between CO2 enhancement and eutrophication shape *Corbicula flumineas* impact on phytoplankton community. 2024.

Scientific articles published in international journals

- Iatskiu, P., **F. M. Zanon**, M. J. Silveira, L. M. Nogueira, S. Jati, & L. C. Rodrigues, 2026. Dormant phytoplankton in shallow lake sediments: cyanobacteria, green algae, diatoms and phytoflagellates are recruited. Springer Science and Business Media Deutschland GmbH. Hydrobiologia. https://doi.org/10.1007/s10750-026-06159-2.

- Lima, E. O., A. C. Souza-Silva, G. A. S. Jesus, **F. M. Zanon**, J. V. F. Silva, L. C. Rodrigues, & C. C. Bonecker, 2025. First record of the non-native rotifer Kellicottia bostoniensis (Rousselet, 1908) in Bromeliaceae phytotelma. Brazilian Journal of Biology 85. https://doi.org/10.1590/1519-6984.289526.

- **Zanon, F. M.**, B. H. M. Stabile, B. M. Campos, É. O. de Lima, M. J. A. Sampaio, Y. R. de Souza, L. R. Tolardo, M. K. Gomes, L. S. C. de Moraes, G. S. Hein, J. D. da Silva, L. da S. Pinha, L. O. Santana, M. Albuquerque, V. da Silva, J. V. Bredariol, G. A. L. da Silva, G. D. da Silva, A. A. A. Ferreira, L. F. Esser, V. F. B. da Silva, M. R. Lima, R. Ré, D. Bailly, & L. C. Rodrigues, 2025b. Climate change will boost the invasion of the harmful cyanobacterium Raphidiopsis raciborskii in South America. Elsevier B.V. Harmful Algae 149. https://doi.org/10.1016/j.hal.2025.102957. **(EXAME GERAL DE QUALIFICAÇÃO DO DOUTORADO)**

- Matos, M. H. de O., J. V. Bredariol, Y. R. de Souza, J. V. F. da Silva, V. M. S. Castro, **F. M. Zanon**, L. O. Santana, G. A. L. da Silva, J. R. Kloss, T. A. Pagioro, & L. F. M. Velho, 2025. Microplastics and warming: dual threats to planktonic protist communities in freshwater ecosystems. Springer Science and Business Media Deutschland GmbH. Hydrobiologia. https://doi.org/10.1007/s10750-025-05994-z.

- **Zanon, F. M.**, P. Iatskiu, M. J. Lemke, L. F. M. Velho, & L. C. Rodrigues, 2025a. Phytoplankton functional groups evidence environmental changes between two floodplain lakes in the early and late stages of restoration. Hydrobiologia. https://doi.org/10.1007/s10750-025-06043-5.

- **Zanon, F. M.**, A. Pineda, F. M. Lansac-Tôha, & L. C. Rodrigues, 2024. Impact of a run-of-river dam in an Amazonian large river on the spatial and temporal patterns of phytoplankton beta diversity. Biological Conservation 295: 1–12. https://doi.org/10.1016/j.biocon.2024.110656.

- Pineda, A., B. M. Campos, **F. Zanon**, R. Felicio, & L. C. Rodrigues, 2024. Impact of run-of-river damming on increasing phytoplankton biomass and species shift in a large Amazonian river. Elsevier. Science of The Total Environment: 176154. https://doi.org/10.1016/j.scitotenv.2024.176154.

- Cochak, C., **F. M. Zanon**, A. Pineda, F. M. Lansac-tôha, S. Jati, & L. F. M. Velho, 2023. Beta diversity of freshwater algal communities: Influence of different dispersal mechanisms. Aquatic Sciences 86: 1–13. https://doi.org/10.1007/s00027-023-01040-z.

Scientific articles submitted to international journals

- Zhang, R., Huang, Q., Yang, J., Zhou, Q., Chi, S., **Zanon, F. M.**, Huang, M., Wang, J. Environmental drivers shape spatial patterns of ecological uniqueness in lake macroinvertebrates across China. Submitted to: Water Biology and Security.

- Rezende, F., Montoia-Comparsi, D., Valente-Neto, F., Rosa, P., Zorzetti, L., Donohue, I., Antiqueira, P. A., Gonzalez, A., Santana, L., Ortega-Corredor, L., Matos, M., **Zanon, F. M.**, Velho, F. M., Rodrigues, L. C., Romero, G. Ecosystem multifunctionality shows unique stability responses to global change drivers. Submitted to: Nature Ecology and Evolution. In Majorrevisions.