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The future of algal blooms in lakes globally is in our hands

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ABSTRACT

Lakes are fundamental to society and nature, yet they are currently exposed to excessive nutrients and climate change, resulting in algal blooms. In the future, this may change, but how and where still needs more scientific attention. Here, we explore future trends in algal blooms in lakes globally for >3500 'representative lakes' for the year 2050, considering the attribution of both nutrient and climate factors. We soft-coupled a process-based lake ecosystem model (PCLake+) with a watershed nutrient model (MARINA-Multi) to assess trends in algal blooms in terms of the Trophic State Index for chlorophyll-*a* (TSI-Chl*a*). Globally between 2010 and 2050, we show a rising trend in algal blooms under fossil-fuelled development (TSI-Chl*a* increase in 91 % of lakes) and a declining trend under sustainable development (TSI-Chl*a* decrease in 63 % of lakes). These changes are significantly attributed to nutrients. While not always significant, climate change attributions point to being unfavourable for lakes in 2050, exacerbating lake water quality. Our study stresses prioritising responsible nutrient and climate management on policy agendas. This implies that the future of algal blooms in lakes is in our hands.

1. Introduction

Lakes provide various ecosystem services such as food production, water use, climate regulation, recreational activities, and nutrient retention (Rinke et al., 2019). The provision of these ecosystem services depends on the lake ecosystem's health (Janssen et al., 2021). Eutrophic lakes are more likely to be dominated by algal blooms, which can deteriorate the habitat of macrophytes and benthic communities, resulting in increased water turbidity (Paerl and Paul, 2012). As non-eutrophic lakes are less likely to be dominated by algal blooms, they are more likely to provide ecosystem services, while algal bloom-dominated lakes have a lower potential to provide these services (Janssen et al., 2021). Many definitions of algal blooms exist (Carstensen et al., 2007; Carvalho et al., 2013; Janssen et al., 2019a; Watson et al., 2015). In our study, we based the definition of algal bloom-dominated lakes on Janssen et al. (2019a) *'locations with a high phytoplankton biomass, including algal scums, reaching a critical level* (e.g., *chlorophyll-a, dry weight*) *at which they are expected to threaten ecosystem services'*. As quantitative analysis of phytoplankton biomass via cell counting is very time-consuming (Kasprzak et al., 2008), chlorophyll-a is commonly used as a proxy (Søndergaard et al., 2011).

Global studies have highlighted fluctuations in chlorophyll-*a* (Chl-*a*) concentrations in the past decades (Fang et al., 2022; Ho et al., 2019; Hou et al., 2022; Kraemer et al., 2022). Ample research shows that this can be attributed to two main factors: the change in nutrient loadings (nitrogen and phosphorus) and the effects of climate change (Moss et al., 2011; Paerl et al., 2011; Paerl and Huisman, 2008; Quinlan et al., 2021; Woolway et al., 2021a). Although eutrophication is a global issue, it is often addressed locally (Suresh et al., 2023). Consequently, little is known about future trends in algal blooms in lakes *globally* and the relative role played by each factor (Janssen et al., 2019a). To date, only statistical approaches have been applied to model future algal blooms globally (Janse et al., 2015). However, statistical approaches do not consider the underlying biological processes in a lake and are limited to system conditions of the past (Cuddington et al., 2013). Hence, process-based models have been recommended for analysing future trends in algal blooms globally (Janssen et al., 2019a; Ralston and Moore, 2020).

Here, we explore future trends in algal blooms in lakes globally for >3500 'representative lakes' for the year 2050, considering the attribution of both nutrient and climate factors using a new model system that soft-couples the process-based lake ecosystem model PCLake+ (Janssen et al., 2019b) with the watershed model MARINA-Multi . We use the year 2010 as the baseline and two opposite future climate and

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socio-economic development scenarios for 2050: “fossil-fuelled development” (RCP8.5-SSP5) and “sustainable development” (RCP2.6-SSP1). Firstly, we simulate the Chl-*a* concentration in the representative lakes using the new model system. Then, we use Chl-*a* concentrations to calculate the Trophic State Index (TSI-Chl*a*) (Carlson, 1977) and assess future trends in algal blooms. Finally, we investigate the attribution of the nutrient and climate factors by performing an attribution analysis for each development scenario. The results of our study help to better understand algal bloom dynamics at a global scale, and thus, aid in developing effective policies for global lake water quality management, contributing to the achievement of clean water for nature and society.

2. Methods

2.1. A new soft-coupled model system

In this study, we developed a new model system by soft-coupling the PCLake+ and the MARINA-Multi model. PCLake+ is a process-based lake ecosystem model (Janssen et al., 2019b). MARINA-Multi is short for Model to Assess River Inputs of pollutaNts to seAs, and it is a multi-pollutant watershed model. The model quantifies, amongst other, nutrient inputs to rivers from point (e.g. sewage systems and direct manure discharges) and diffuse sources (e.g. livestock manure, synthetic fertiliser applications, atmospheric N deposition) by sub-basin. See Supplementary Information (SI) A for model descriptions. We used three types of input parameters to estimate the lake Chl-*a* concentration in PCLake+ (Fig. 1): morphological (depth, fetch and sediment type), climate (wind speed, albedo, water temperature and water balance) and nutrient (nitrogen and phosphorus loads) (Janssen et al., 2019b). All the other parameters existing in PCLake+ (i.e., the algal growth rate, mortality rate etc.) were left at their calibrated default values, and constant between representative lakes and scenarios. We used a combination of the ISIMIP2b (Lange and Büchner, 2017; Marcé et al., 2022) and the HydroLAKES datasets (Messager et al., 2016) to describe the morphological and climate factor parameters (Section 2.2). We performed none or minor spatial adjustments to these datasets before we use them as inputs for PCLake+. To describe the nutrient factor parameters, we soft-coupled the MARINA-Multi model with the PCLake+ model (Fig. 1). We coupled the models by converting the nutrient input to rivers output data from the MARINA-Multi model to lake nutrient loads as required for PCLake+ (Section 2.2.4). This new model system allowed us to assess future trends in algal blooms in lakes globally, considering the attribution of both nutrient and climate factors.

2.2. Study area

2.2.1. Representative lakes included in this study

Dividing the world into 0.5° × 0.5° cells results in 720 cells longitudinally and 360 cells latitudinally, for a total of >200000 grid-cells. However, lakes are not equally distributed on Earth, resulting in grid-cells that do not contain any lake. Yet, some large lakes may be covering multiple grid-cells. Based on the HydroLAKES database (Messager et al., 2016), we know there are no less than 41708 grid-cells with at least one lake. Since each of these cells potentially contains multiple lakes with different characteristics (e.g., depth, area, etc.), it is impossible to fully capture their heterogeneity at a 0.5° × 0.5° scale. Therefore, as recommended by the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP) 2b protocol (Frieler et al., 2017), we defined a ‘representative lake’ for each cell. Each representative lake was described with the average of the parameters and characteristics of all the lakes within its cell; as defined by ISIMIP 2b (Frieler et al., 2017), which provided several datasets (Lange and Büchner, 2017; Marcé et al., 2022; Vanderkelen and Schewe, 2020; Volkholz and Müller, 2020). The representative lakes approach is beneficial in three ways: (1) it improves the global representativeness of lakes, especially in data-poor areas, allowing us to assess lakes in all climate zones and continents (2) it increases computational feasibility, and (3) it allows for model intercomparison as we follow the ISIMIP2b protocol for defining representative lakes. The first point especially holds for data on nutrient inputs to the lakes, which availability is limited at a lake-specific resolution for large-scale analysis. Yet, global water quality models, such as the MARINA-Multi model (Micella et al., 2024; Strokal et al., 2021), can provide nutrient inputs to sub-basins globally. With an elegant downscaling approach such models can provide data for the representative lakes. The representative lakes approach has been commonly used for large-scale studies (e.g. La Fuente et al., 2024; Wang et al., 2018; Woolway et al., 2022; Zhou et al., 2021).

Out of the 41708 grid-cells that contain at least one lake, we only included 3563 representative lakes in this study. We only ran the representative lakes with complete sets of input parameters, which brought the number of representative lakes down to 4224. We further reduced the sample to 3994, excluding all the Arctic and Antarctic Circles lakes. Finally, since the TSI-Chl*a* needs a minimum concentration of 0.045 mg/m^3 to be calculated, we excluded lakes with a Chl-*a* concentration below this threshold.

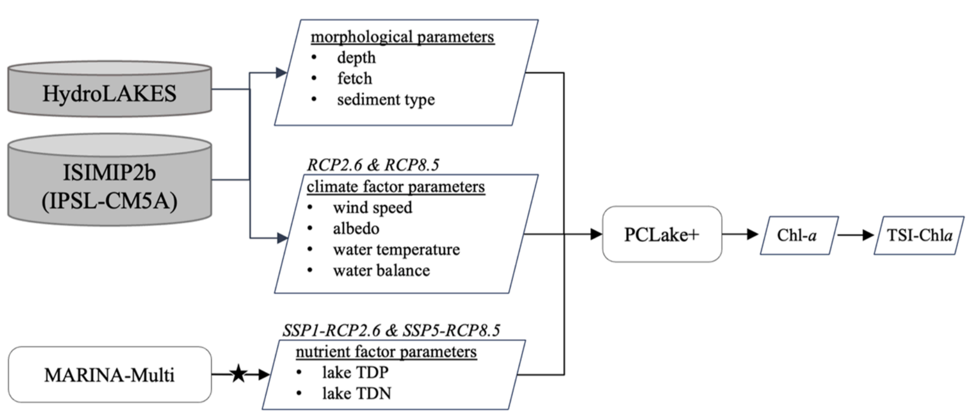

Fig. 1. Overview of the newly soft-coupled model system. Grey cans represent database or model outputs used in this study; adjustments to spatial scales were minor or non-existent. Parallelograms represent input/output data for the PCLake+ model. Rounded rectangles represent models. The star indicates that major data modifications were made regarding spatial and temporal scales. HydroLAKES refers to the database of Messager et al. (2016). ISIMIP2b refers to the Inter-Sector Impact Model Intercomparison Project simulation round 2b. IPSL-CM5a refers to the IPSL Climate Model version 5a. MARINA-Multi represents the Model to Assess River Inputs of pollutaNts to seAs for multiple pollutants. SSP represents the Shared Socioeconomic Pathways. RCP represents the Representative Concentrations Pathways. TDN represents the total dissolved nitrogen. TDP is short for total dissolved phosphorus. Chl-a represents chlorophyll-a. TSI-Chl*a* represents the Trophic State Index for chlorophyll-*a*.

2.2.2. Morphological parameters

Each representative lake was described in terms of (1) depth, (2) fetch, and (3) sediment type. Even though the morphological characteristics (size and depth) of specific lakes may change significantly over time (Pekel et al., 2016), we kept them unvaried throughout the development scenarios (Section 2.3). We believe that changes are mostly limited temporally and spatially and will therefore have a limited impact on the global pattern. We used the datasets of Vanderkelen and Schewe (2020), Messager et al. (2016) and Fischer et al. (2008) to determine the morphological parameters for the 3563 representative lakes, see SI B for details.

2.2.3. Climate factor parameters

To describe the climate parameters of wind (Lange and Büchner, 2017), albedo (Marcé et al., 2022) and lake water temperature (Marcé et al., 2022) in the representative lakes in the baseline and two development scenarios (see Section 2.3), the datasets from ISIMIP2b (GCM IPSL-CM5A) were used (see Table C.1 in SI). These datasets were already provided at a $0.5^\circ \times 0.5^\circ$ spatial resolution and needed no further conversion. Also, in this case, the dataset for the lake water temperature showed an average value for the representative lakes.

For the baseline and the two development scenarios, the daily average of a 30-year period (2000–2029 for 2010 and 2040–2069 for 2050) was used to represent the climate forces (e.g., average of the 1st of January of the years 2040–2069). To describe the water fluxes in the representative lakes, a simple water balance was used (Eq. (1)). We ran the model keeping the lake depth unvaried over time (as we do for all other morphological parameters) and excluding the groundwater flow:

$$Qin + Pr = Qout + E \tag{1}$$

where: Qin is the lake inflow (mm/d); Pr is the precipitation over the lake (mm/d); Qout is the lake outflow (mm/d); and E is the evaporation of the lake water (mm/d).

The daily precipitation data were taken from ISIMIP (Lange and Büchner, 2017), whilst the daily evaporation data were estimated using the Thornthwaite equation (Thornthwaite, 1948). The lake outflow was calculated starting from HydroLAKES data on discharge (m^3/s) and surface area (m^2) (Messager et al., 2016), upscaling to a $0.5^\circ \times 0.5^\circ$ spatial resolution by taking the mean value for each cell. The lake outflow was assumed to be the same for every day of the year, as HydroLAKES does not provide a time series. The daily lake inflow was then derived from the water balance equation (Eq. (1)).

2.2.4. Nutrient factor parameters

To estimate the nutrient loads, including total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP), into the representative lakes the output datasets from the MARINA-Multi model were used (Li et al., 2022; Strokal et al., 2021). The data for nutrient inputs coming from point sources were available at a $0.5^\circ \times 0.5^\circ$ scale (Strokal et al., 2021), whilst the data coming from the diffuse sources were only available at a sub-basin scale (Li et al., 2022). Therefore, we estimated the nutrient inputs from diffuse sources at a cell scale ($0.5^\circ \times 0.5^\circ$) using the ratio between point and diffuse sources in the sub-basin ($I_{\text{point-sub}}$ and $I_{\text{diff-sub}}$) and the point sources at a $0.5^\circ \times 0.5^\circ$ scale ($I_{\text{point-cell}}$) (Eq. (2)). The total TDN or TDP loads in each cell ($I_{\text{TDN/TDP-cell}}$ in kg/y/cell) were then calculated by adding the cell's TDN or TDP loads from diffuse ($I_{\text{TDN/TDP-diff-cell}}$) and point sources ($I_{\text{TDN/TDP-point-cell}}$).

$$I_{\text{TDN/TDP}-\text{diff}-\text{cell}} = \frac{I_{\text{TDN/TDP}-\text{point}-\text{sub}}}{I_{\text{TDN/TDP}-\text{diff}-\text{sub}}} \times I_{\text{TDN/TDP}-\text{point}-\text{cell}} \tag{2}$$

where $I_{\text{TDN/TDP-diff-cell}}$ are the TDN or TDP inputs from diffuse sources to rivers in the cell (kg/y); $I_{\text{TDN/TDP-point-sub}}$ are the TDN or TDP inputs from point sources to rivers at the sub-basin scale (kg/y); $I_{\text{TDN/TDP-diff-sub}}$ are the TDN or TDP inputs from diffuse sources to rivers at the sub-basin scale (kg/y); and $I_{\text{TDN/TDP-point-cell}}$ are the TDN or TDP inputs from point sources to rivers in the cell (kg/y).

Since the MARINA-Multi model output represents the nutrient input to rivers, only cells with a river had an I_{cell} value. This meant that the I_{cell} values for the cells of the representative lakes expanding beyond the cells of the incoming rivers were missing. Therefore, for lakes bigger than one cell, the sum of all the cells with I_{cell} values within it (i.e., all the incoming rivers) was assigned to the whole lake. Then, the I_{cell} value was divided by the cell's area to obtain the I_{cell} value in kg/y/km^2 of the lake. Finally, since the area of each cell was known, the nutrient inputs were regridded to kg/y for each cell that the lake covered.

To estimate the actual nutrient load in the representative lakes, we calculated the nutrient input at a watershed level (kg/y/catchment) for each cell. To do this, we assumed that the nutrient input is regularly distributed in the lake watershed, and we used the watershed area data from HydroLAKES (Messager et al., 2016) to convert kg/y/cell to kg/y/watershed. The nutrient load in PCLake+ is described in g/m^2 lake/d; however, this does not equal the nutrient inputs (Icell in kg/yr/cell); but refers to the actual nutrient load in the lakes, which accounts for processes such as sedimentation, denitrification etc. The actual nutrient load of the lake's watersheds was calculated by applying the statistical model developed by Behrendt and Opitz (1999) to the kg/y/watershed. Finally, by dividing the actual load in kg/y/watershed by the lake area, the 365 days in a year, and converting from kg to g, we arrived at the nutrient load in g/m^2/d for each representative lake. The top and bottom 2.5 % values of the nutrient load datasets were excluded, as the extremely high or low nutrient loadings may have resulted from artefacts due to the global modelling approach and the combination of several assumptions made, leaving data for 95 % of the representative lakes.

2.3. Baseline and scenarios description

We use data for the year 2010 as the baseline and two opposite future climate and socio-economic development scenarios for 2050: "fossil-fuelled development" (RCP8.5-SSP5) and "sustainable development" (RCP2.6-SSP1). In the fossil-fuelled development scenario, it is assumed that human activities will result in globally high nutrient loads (Beusen et al., 2022; Strokal et al., 2021) and high greenhouse gas emissions in 2050 (Beusen et al., 2022; Riahi et al., 2011). In the sustainable development scenario, it is assumed that human activities will result in globally low nutrient loads (Beusen et al., 2022; Strokal et al., 2021) and limited greenhouse gas emissions in 2050 (Beusen et al., 2022; Riahi et al., 2011). See SI D for details on how nutrient and climate factors are affected by the two development scenarios.

2.4. Assessing future trends in algal blooms

2.4.1. Chlorophyll-a

We ran PCLake+ for 3563 representative lakes to simulate their Chl-*a* concentrations (mg/m^3). We performed seven model runs for each representative lake: once to set the baseline and then three times for each development scenario (one run considering both projected climate and nutrient factors, another run considering only the projected climate factor, and a third run considering only the projected nutrient factor).

When providing PCLake+ with time series, it interpolates linearly between the days with data, which means that the greater the daily variation, the longer the run time. To shorten the run time, the time series describing the climate in the representative lakes fed to PCLake+ had monthly averages (all days in January had the same mean value and so on). The built-in functions of PCLake+ were used to calculate the stratification and light intensity in the lakes (Janssen et al., 2019b). To make sure the ecosystem was stable, the model was run for 25 years, starting from a clear-state lake.

2.4.2. Trophic State Index

Chl-*a* is used as a proxy for the algal concentration, as it is the most abundant pigment in algae cells. The higher the Chl-*a* concentration, the more severe the algal blooms. Different lakes have different reference trophic states (Poikāne et al., 2010), dependent on regional climatic and geographical characteristics; this implies that implications of increased Chl-*a* concentrations are lake-specific. Hence, setting global water quality standards ignores this local-scale variety. There is no universally adopted system to interpret the Chl-*a* concentrations in terms of water quality standards (Poikane et al., 2014). In this study, we applied the TSI-Chl*a* to interpret the yearly mean Chl-*a* levels modelled by PCLake+ following Eq. (3) (Carlson, 2007, 1977):

$$\mathrm{TSI} - \mathrm{Chl}a = 9.81\ln(\mathrm{Chl} - a) + 30.6 \tag{3}$$

where: TSI-Chl*a* is the Trophic State Index for chlorophyll-*a* (0–100), and Chl-*a* is the yearly mean chlorophyll-*a* concentration (mg/m^3).

Accordingly, representative lakes can be classified as “oligotrophic” (0.045–2.6 mgChl-*a*/m^3, or with a TSI-Chl*a* <40), “mesotrophic” (2.6–7.3 mgChl-*a*/m^3, or with a TSI-Chl*a* of 40–50), “eutrophic” (7.3–55.5 mgChl-*a*/m^3, or with a TSI-Chl*a* of 50–70), and “hypertrophic” (>55.5 mgChl-*a*/m^3, or with a TSI-Chl*a* >70 mgChl-*a*/m^3). Based on this classification, we intend to capture lake eutrophication. This is challenging for the global scale because of the spatial variability in ecological limits and reference conditions among lakes (e.g. Poikane et al., 2010, 2019, 2014). Nevertheless, we take a pragmatic and simplified approach that can be applied to all representative lakes. For this, we use a threshold of 7.3 mgChl-*a*/m^3 or a TSI-Chl*a* of 50 that should be considered as a proxy to reflect the potential of lake eutrophication. In general, it is considered that with this TSI-Chl*a* value, the characteristics of the classical eutrophic lake are as follows: a lake with decreased transparency, anoxia in the hypolimnion and considerable macrophyte problems according to Carlson and Simpson (1996). When this illustrative threshold is crossed, the lake is considered to be more likely to be algal bloom dominated. To account for the uncertainty and variability of the threshold, besides the value of 50, we also analysed the results for TSI-Chl*a* threshold values of 55 (=12 mg/m^3) and 60 (=20 mg/m^3) (see Table F.1 in SI).

2.5. Attribution analysis

The change in Chl-*a* from the baseline is caused by the effect of the change in nutrients, the change in climate and the interaction effect of the two. To assess how each of these factors attributed to the change, we quantified the difference from the median Chl-*a* of the baseline (2010), with the results of the model run with exclusively the climate or the nutrient factors of the two future development scenarios (Eq. (4)).

$$Echla_{C/N.FFD/SD} = Mchla_{C/N.FFD/SD.50} - Mchla_{baseline} \tag{4}$$

where: $Echla_{C/N.FFD/SD}$ is the effect (E) of the attribution of either climate (C) or nutrient (N) factors to the change in chlorophyll-*a* concentration (chla) in the fossil-fuelled development (FFD) or sustainable development (SD) scenario compared to the baseline (-); $Mchla_{C/N.FFD/SD.50}$ is the median (M) chlorophyll-*a* concentration accounting for only C or N factors in the FFD or SD scenario for 2050 (mg/m^3). $Mchla_{baseline}$ is the median chlorophyll-*a* concentration of the baseline (mg/m^3).

To assess the extent of the combined factor (Eq. (5)), we summed what the impact of only the climate or only the nutrients was and then accounted for the difference with the median of the run with the combined factors.

$$Echla_{C\&N.FFD/SD} = Mchla_{C\&N.FFD/SD.50} - \left(Mchla_{C.FFD/SD.50} + Mchla_{N.FFD/SD.50}\right) \tag{5}$$

where: $Echla_{C\&N.FFD/SD}$ is the interaction effect (E) of the attribution of both climate (C) and nutrient (N) factors to the change in chlorophyll-*a* concentration (chl*a*) in the fossil-fuelled development (FFD) or sustainable development (SD) scenario compared to the baseline (−); $Mchla_{C\&N.FFD/SD.2050}$ is the median (M) chlorophyll-*a* concentration accounting for both C and N factors in the FFD or SD scenario for 2050 (mg/m^3). $Mchla_{C/N.FFD/SD.50}$ is the median chlorophyll-*a* concentration accounting for only C or N factors in the FFD or SD scenario for 2050 (mg/m^3).

Next to our global attribution analysis, we performed a second analysis that only considers lakes ($N = 2010$) that were non-eutrophic (<7.3 mg Chl-*a*/m^3) in the baseline scenario (2010). This allows us to study the effect on lakes with a current relatively good water quality regarding algal blooms (non-eutrophic). Subsequently, to establish whether the effect was significant, we performed a pairwise permutation test (threshold <0.05, adjustment method = false discovery rate with the Benjamini–Hochberg method).

3. Results

3.1. Algal blooms in the future

In the *baseline (2010)*, 56 % of lakes are below the eutrophication threshold (oligotrophic and mesotrophic lakes), whilst the remaining 44 % are above the threshold (eutrophic and hypereutrophic lakes). More specifically, the model calculates that 34 % of the lakes are oligotrophic, 22 % are mesotrophic, 42 % are eutrophic, and 2 % are hypereutrophic (Fig. 2a). The eutrophic and hypereutrophic lakes dominate the majority of the United States, Europe, and South-East Asia. Whilst the areas dominated by mesotrophic and oligotrophic lakes are those in Canada, the very north of Europe and Asia, Patagonia, and Tibet (Fig. 2b).

In the *fossil-fuelled development scenario* for 2050, a TSI-Chl*a* increase is projected for the vast majority of representative lakes (91 %) compared to the baseline scenario. The highest increases are projected for lakes in South–East Asia, Africa, and South America (Fig. 2c). The 9 % of the representative lakes that showed a decrease in TSI-Chl*a* are evenly distributed around the globe. The share of lakes that is projected to exceed the eutrophication threshold (eutrophic and hypereutrophic lakes) grows from 44 % in the baseline to 55 % under fossil-fuelled development. More specifically, the model projects that 21 % of the lakes are oligotrophic, 24 % are mesotrophic, 50 % are eutrophic, and 5 % are hypereutrophic (Fig. 2a). Under fossil-fuelled development, there is thus a clear shift from a world dominated by “non-eutrophic lakes” (56 % of lakes below the eutrophication threshold) in the baseline to a world dominated by “eutrophic lakes“ (55 % of lakes above the eutrophication threshold) (Fig. 2a).

Contrarily, in the *sustainable development scenario* for 2050, a TSI-Chl*a* decrease is projected for more than half of representative lakes (63 %) compared to the baseline. The United States and Europe, where most lakes exceeded the eutrophication threshold in the baseline, are amongst the regions that show a decrease in TSI-Chl*a* (Fig. 2d). Other regions include South America, Oceania, and northern Asia. The model projected a TSI-Chl*a* increase in 37 % of the lakes compared to the baseline. Although TSI-Chl*a* increases are distributed over the globe, a relatively greater share of TSI-Chl*a* increases are projected for representative lakes in south Asia and central Africa (Fig. 2d). The share of lakes that is projected to stay below the eutrophication threshold grows from 56 % in the baseline to 62 % under sustainable development scenario. More

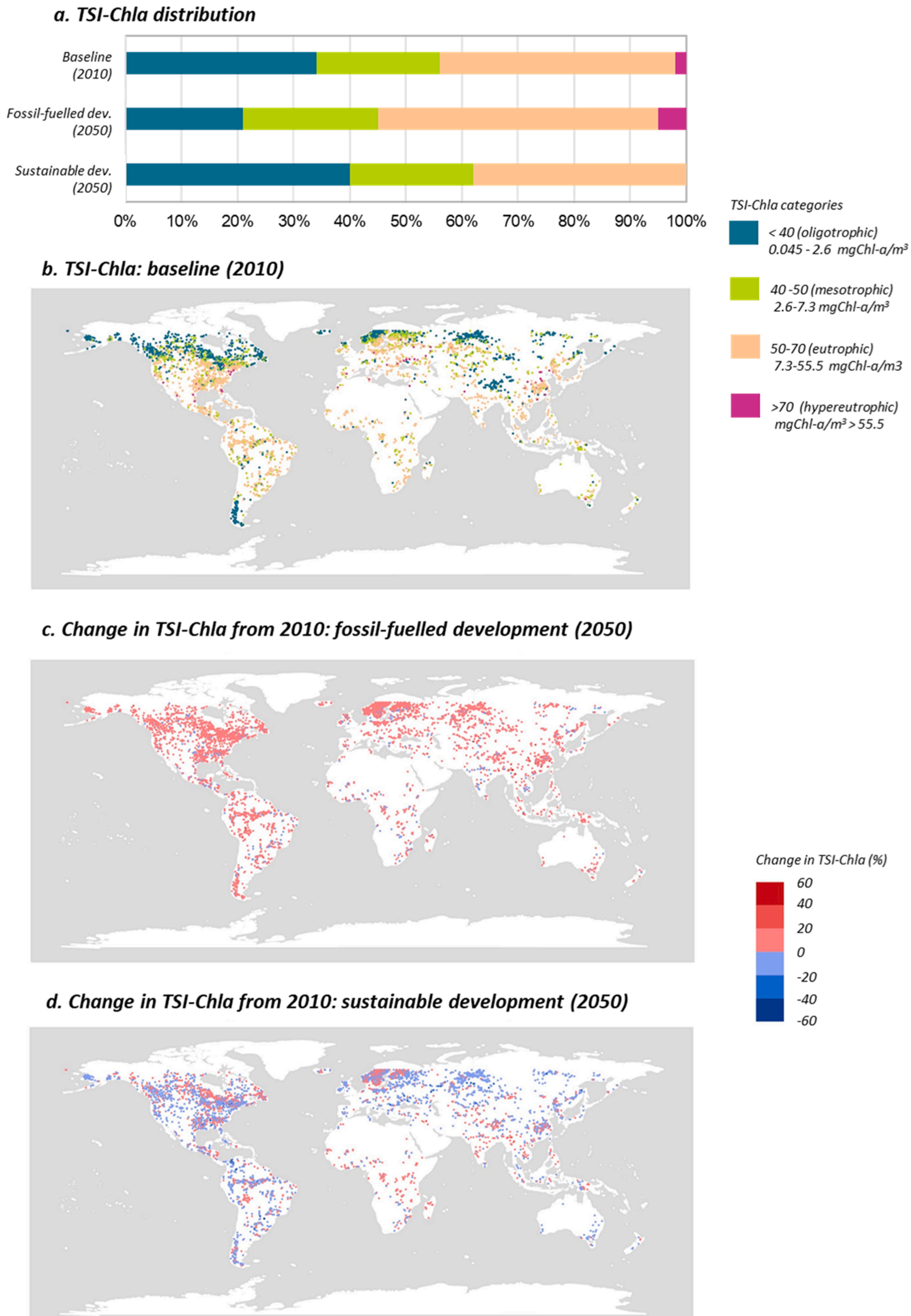

Fig. 2. Projected changes in Trophic State Index for chlorophyll-a (TSI-Chla) for representative lakes in 2050 scenarios compared to the baseline of 2010. a. distribution of TSI-Chla in the scenarios. b. TSI-Chla calculations for the baseline (2010). c. projected change in TSI-Chla in the fossil-fuelled development scenario for 2050. d. projected change in TSI-Chla in the sustainable development scenario for 2050. Chl-a is short for chlorophyll-a.

specifically, the model projects that 40 % of the lakes are oligotrophic, 22 % are mesotrophic, 38 % are eutrophic and none are hypereutrophic (Fig. 2a). Under the sustainable development scenario, there is thus a clear downward trend in lake eutrophication levels compared to the baseline (from 56 % of lakes under eutrophication threshold to 62 %).

Supplementary Table F.1 shows the results for different TSI-Chl*a* thresholds. Regardless of the threshold, we find that the share of eutrophic lakes in the fossil-fuelled development scenario increases compared to the baseline (2010) whilst it decreases in the sustainable development scenario (see the Discussion section).

3.2. *Attribution analysis: climate vs. nutrient factors*

In the *fossil-fuelled development scenario*, the nutrient factors increased the median Chl-*a* concentration by 2.44 mg/m^3 (Fig. 3a). The attribution of the climate factors increased the median Chl-*a* concentration too, however, only by 0.55 mg/m^3. The interaction effect of the nutrient and climate factors decreased the median Chl-*a* concentration by 0.05 mg/m^3. Altogether, the nutrient factors, climate factors, and their interaction effect increase the median Chl-*a* concentration by 2.94 mg/m^3.

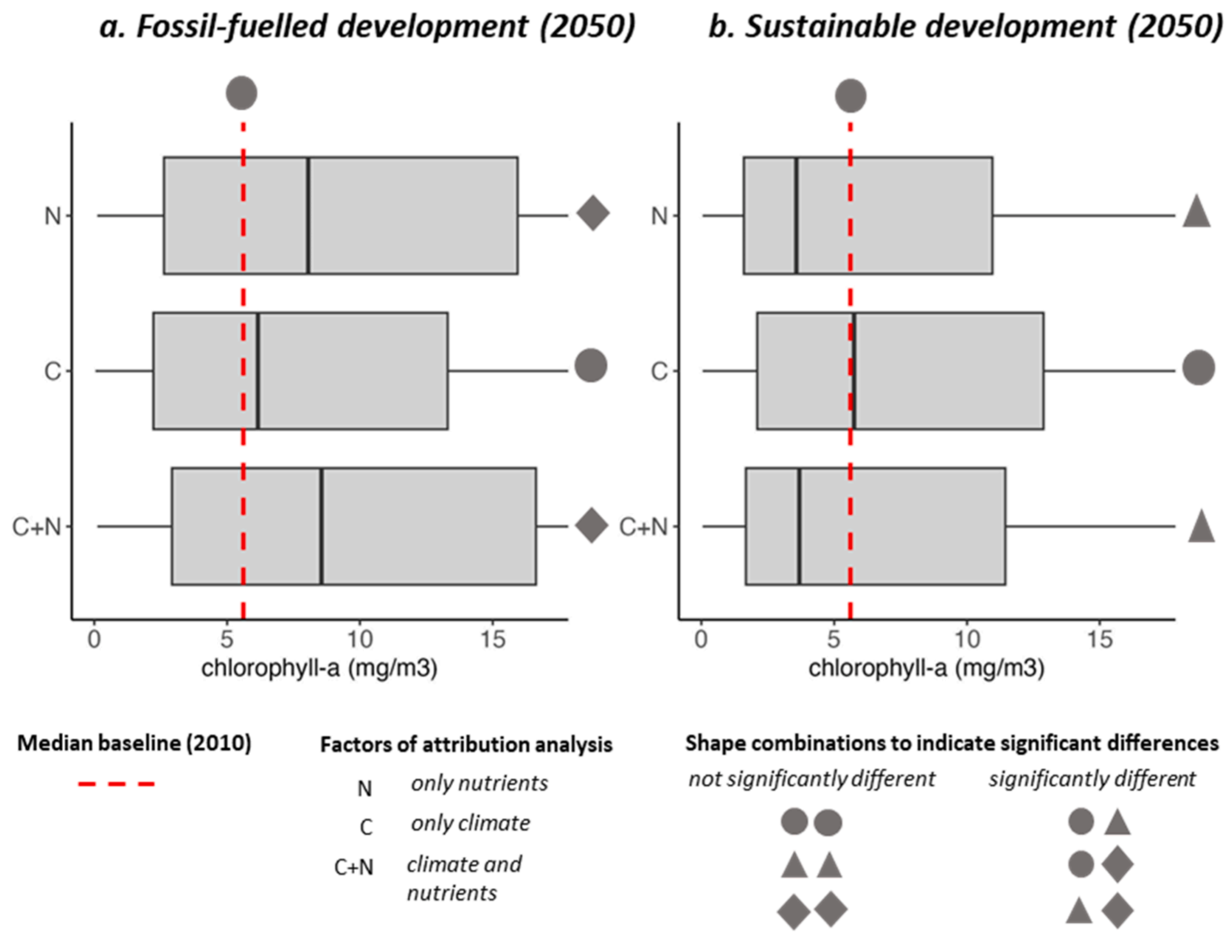

Fig. 3. Attribution analysis of nutrient and climate factors on the median chlorophyll-a concentration (mg/m^3) in (a) the fossil-fuelled development scenario and (b) the sustainable development scenario for the year 2050. The attribution is relative to the baseline for the year 2010 (red dashed line). N refers to nutrient factors. C refers to climate factors. N + C refers to the interaction effect of nutrient and climate factors. The shapes on the right side of each bar indicate whether the factors had a significant impact (e.g., circle and diamond) or not (e.g., two triangles) compared to the other scenarios. We used a pairwise permutation test to test significance, $P < 0.05$ (see Section 2.5 for details on the attribution analysis).

In the *sustainable development scenario*, the nutrient factors decreased the median Chl-*a* concentration by 2.03 mg/m^3 (see Fig. 3b). Contrarily, the attribution of climate factors increased the median Chl-*a* concentration by 0.14 mg/m^3. The interaction effect of the nutrient and climate factors decreased the median Chl-*a* concentration by 0.03 mg/m^3. Altogether, the nutrient factors, climate factors and their interaction effect decrease the median Chl-*a* concentration by 1.92 mg/m^3.

The effect of nutrient factors alone significantly ($P < 0.05$) impacted the Chl-*a* concentration (circle vs. diamond in Fig. 3a, and circle vs. triangle in Fig. 3b). The effect of climate factors alone in both scenarios did not significantly impact the Chl-*a* levels compared to the baseline (also a circle in Fig. 3a and b). In both scenarios, when combined, the two factors impact the Chl-*a* concentration significantly compared to the baseline (neither is a circle in Fig. 3a and b); however, the result is not significantly different from the impact of the nutrient factors alone, meaning that the additional interaction effect was overall not significant (both diamonds in Fig. 3a, and both triangles in Fig. 3b).

When only the lakes that were non-eutrophic in the baseline scenario (2010) are considered, the results are different (Fig. E.1 in SI). Firstly, the attribution of the climate factor, although still smaller than that of the nutrients factor, significantly impacts the Chl-*a* concentration under fossil-fuelled development (pentagon vs. star in Fig. E.1c and d in SI). Secondly, the interaction effect of climate and nutrients is +0.14 mg Chl-*a*/m^3 in the fossil-fuelled development scenario and +0.02 mg Chl-*a*/m^3 in the sustainable development scenario (Fig. E.1c and d in SI). This means that in both scenarios, there was a positive synergetic effect of nutrients and climate that increased the Chl-*a* concentrations; however, in the fossil-fuelled development scenario, this was seven times greater than in the sustainable development scenario.

4. Discussion

Our study is the first to project future trends in algal blooms in lakes at a global scale, accounting for nutrient and climate factors under different climatic and socio-economic developments using a process-based ecosystem model. Herewith, we show that the pathway chosen by humans can impact the global algal bloom status of lakes significantly, even in a relatively short time (i.e., 40 years). Our projections revealed that by 2050, the TSI-Chl*a* in lakes globally may rise from a mean of 47 (category: mesotrophic) of the baseline to a mean of 51 (category: eutrophic) under a fossil-fuelled development (RCP8.5-SSP5), yet under sustainable development the mean TSI-Chl*a* will decrease to 44 (category: mesotrophic). Globally, this implies a rising trend in algal blooms under fossil-fuelled development and a declining trend under sustainable development.

We use a threshold of 7.3 mg Chl-*a*/m^3 or a TSI-Chl*a* of 50 that should be considered as a proxy to reflect the potential lake eutrophication. We consider that when this illustrative threshold is crossed, the lake is considered to be more likely to be algal bloom-dominated. This threshold could be debatable and vary among lakes, climate and basin characteristics (Suman et al., 2023). For example, Poikane et al. (2014) define distinct thresholds for Central European lakes, setting good status thresholds at 21–23 mgChl-a/m^3 for lakes with depth less than 3 m, and at 10–12 mgChl-a/m^3 for lakes 3–15 m deep. The thresholds could also be defined based on either ecosystem-oriented or health-oriented focus. For example, WHO defines the 'Vigilance level' at 3–12 mgChl-a/m^3 and the `Alert level 1′ for health risks due to algal blooms as 12–24 mgChl-$a$/m$^3$ (Chorus and Welker, 2021). A threshold of 7.3 Chl-$a$ is between the lowest end of 'Vigilance level' (3 mg/m$^3$) and the highest end of the `Alert level 1′ (23 mg/m^3), and it is comparable to the ecosystem-oriented nutrient threshold values between 'moderate' and 'good' biodiversity status (Poikane et al., 2019), which correspond to those equivalent to TSI values around 50 for some lake types and ~60 for others. To account for uncertainty and variability of our threshold, we also show the results for TSI-Chl$a$ threshold values of 55 (=12 mg/m^3) and 60 (=20 mg/m^3) in Table F.1 in the SI. Generally, we find that, regardless of the threshold, the share of eutrophic lakes increases under fossil-fuelled development compared to the baseline whilst it decreases under sustainable development. If the TSI-Chl$a$ threshold is considered to be 55 or 60, there is $a + 12$ % or +8 % share of eutrophic representative lakes in the fossil-fuelled development scenario compared to the 2010 baseline, respectively (for reference, +11 % for TSI-Chl$a$ of 50). Similarly, in the sustainable development scenario, there is a −3 % or −3 % share of eutrophic representative lakes compared to the baseline for TSI 55 or 60, respectively (for reference, −6 % for TSI-Chl$a$ of 50). We also find that in all cases, the impact in the sustainable development scenario is generally lower than that in the fossil-fuelled development scenario. Our threshold may seem too simple. However, it is transparent and enabled us to execute this study on a global scale for representative lakes. Thus, our analysis should be interpreted as large-scale analysis for representative lakes worldwide and should not be used to analyse individual lakes. For individual lakes, we argue for more in-depth analysis with targeted thresholds that will represent better lake characteristics, climatic and geographical factors influencing those lakes.

The change in nutrient loads to lakes has the largest impact on future trends in algal blooms. Nonetheless, under fossil-fuelled development, climate change has a significant impact on the Chl-a of lakes that were "non-eutrophic" in 2010. For lakes that are currently 'eutrophic', climate change impacts might become significant with intensified climate extremes as are expected for the end of the 21st century (Tewari, 2022). Reasons for this could be (water) temperature increases, which also lead to prolonged stratification periods (Woolway et al., 2021b), reduced lake ice coverage (Sharma et al., 2019) and increased soil nutrient mineralization rates (Havens and Paerl, 2015), consequently impacting the Chl-a concentration in lakes, regardless of their starting state. For individual lakes (Istvánovics et al., 2022; Sharma et al., 2019), the impact of climate change on algal blooms may already be significant to-date or in the near future. Yet, uncertainties remain due to the complexity of biogeochemical-climate interactions for algal bloom types and locations (Tewari, 2022). Hence, it is of utmost importance to consider the effects of climate change on algal blooms.

Nutrient inputs to lakes show opposite trends in the two future development scenarios. The mean TDN load of 0.15 g/m^2/d in the baseline increases to 0.32 in 2050 with the fossil-fuelled development scenario, and decreases to 0.064 in the sustainable development scenario. The TDP load increases from 0.065 g/m^2/d in the baseline to 0.23 in 2050 with the fossil fuel development scenario, and decreases to 0.013 in the sustainable development scenario. Globally, this led to an increase in Chl-a, and therefore increased TSI-Chl$a$, in the fossil-fuelled development scenario and a decrease in Chl-a in the sustainable development scenario. Our study focussed on TDN and TDP inputs to lakes under different socio-economic and climate scenarios (rather than lake-specific management options). The scenarios cover both TDN and TDP emissions. Hence, local studies are required to indicate which lake-specific management options are effective in a "sustainability" or "fossil-fueled development" scenario.

Several factors may contribute to the greater attribution of the nutrient factor on future trends in global algal blooms compared to the climate factors. First, this may be due to the relatively short period between the baseline and the 2050 scenarios considered in this study (i.e., 40 years). Since the change in climate under fossil-fuelled development was severe enough to cause a significant difference in Chl-a concentration by 2050, we must consider that climate may have a bigger attribution if a more extended period is being analysed (i.e., after 2050) (Woolway et al., 2021b). For instance, in RCP8.5 (the climate in the fossil-fuelled development), lakes will continue to become warmer in 2070 and 2099, whilst in RCP2.6 (the climate in the sustainable development), the temperature stabilises from 2050 on (Grant et al., 2021). For 2100, the two scenarios are thus expected to have an opposite outcome regarding climate factors. In that respect, SSP1 and SSP5 were chosen deliberately to provide insight into opposing possible futures. Second, using a different global climate model will likely affect climate factor attributions. However, in this study we only used the ISPL-CM5A climate model, which includes the most comprehensive datasets (Frieler et al., 2017), to reduce computation time. Thirdly, the nutrient factors in our study simultaneously account for climate impacts related to hydrology (e.g. changes in surface runoff from land to surface waters). Hence, the attribution of the two factors is not fully separated and, consequently, we may have underestimated the attribution of climate change.

Additionally, the attribution analysis showed an interaction effect of nutrient and climate factors, however, in our study these were not significant ($P > 0.05$) and limited (−0.051 mg Chl-a/m^3 under fossil-fuelled development and −0.03 mg Chl-a/m^3 under sustainable development). This contradicts our expectations, as algal blooms generally "like it hot" (Paerl and Huisman, 2008). Hence, we expected that the combination of nutrient loads and climate change would have mutually reinforced algal blooms in lakes and thus would worsen the water quality further (Moss et al., 2011). For example, climate change, besides causing a rise in water temperature, is affecting precipitation patterns, which may alter the water levels in lakes and, consequently, the nutrient concentrations, which are strongly linked to algal growth (Moss et al., 2011). We do see that blooms "like it hot" in the lakes with initially lower Chl-a concentrations, in particular in the fossil-fuelled scenario, which is where climate change was represented the most (RCP 8.5). This suggests that, when looking at the global scale, lakes with lower Chl-a concentrations (non-eutrophic) tend be more impacted by interaction effects of climate change and nutrients in the future. Although further research is needed as other studies suggest that climate change has a more intense effect in eutrophic waters than in oligotrophic waters (Rigosi et al., 2014). Future studies could look at individual lakes to better understand the impact of climate change.

We encountered limitations related to the high input demand for process-based models such as PCLake+. For example, the availability of lake-specific discharge data was limited in space and time (see SI F for implications on the results). This restricted our study pool significantly. Nevertheless, we consider the 3563 representative lakes in this study to be a copious sample, not only numerically but also because they are scattered throughout both hemispheres and all continents. We see the benefits of using a process-based model as it allows for a wider prediction domain compared to empirical approaches (Janssen et al., 2019a). This is due to the inclusion of essential parameters such as the optimal temperature of the algae, growth rate and prey-predator relationships. Hence, we foresee that our attempt will open opportunities for new studies to better understand the projections and management of algal blooms in lakes globally. The use of representative lakes allows us to project global trends, limiting the inputs needed for the model, but it also has limitations. First, representative lakes can be defined in multiple ways. For example, in this study, data from ISIMIP2b (Frieler et al., 2017) are used, where the values of representative lakes are simply an average of all the lakes within the particular grid cell. An alternative is the weighted average approach used in ISIMIP3 (Golub et al., 2022) where larger lakes within a grid cell account for more than smaller lakes.

However, this approach may be underrepresenting small lakes that are overcast by, for example, one big lake. Secondly, the usage of representative lakes may generalise local lake's ecosystem responses to climate change and nutrient inputs. Thirdly, the validation of results is extremely hard and somewhat unfair when comparing data of "real world" lakes with representative lakes.

Lakes are complicated ecosystems, and even the most detailed ecosystem models inevitably oversimplify reality. Hence, it is important to interpret model results carefully and assess their uncertainties via model evaluation. In this study, we used two well-evaluated models: PCLake+ and MARINA-Multi. The PCLake+ model is calibrated, and applied to >125 lakes and reservoirs in various world regions with the evaluation results. Some examples for model validations are: in Europe (Janse et al., 2010), China (Hu et al., 2019; Janssen et al., 2017; Kong et al., 2019; Li et al., 2019; Qin et al., 2022; Shi et al., 2023; Yang et al., 2022), South America (Fragoso Jr et al., 2008), and Africa (Goshu et al., 2020). Moreover, PCLake+ is a process-based model that accounts for detailed in-lake processes, and therefore, it is broadly applicable (Janssen et al., 2019b). The MARINA-Multi model has been evaluated in various ways for many regions in the world. For example, the first version of the model was validated for the Chinese rivers (Strokal et al., 2016) with the validation results of RP2 at 0.84. The next version was validated for river streams in China annually (Chen et al., 2022) and for sub-basins seasonally (Chen et al., 2019). The model was also evaluated globally for over 10000 rivers (Strokal et al., 2021, 2019) using the "building trust approach". This approach goes beyond validation and applies options to evaluate the model inputs (comparisons with other independent datasets), model approaches (sensitivity analysis) and model outputs (comparisons with other studies and expert knowledge). Recently, the updated version of the model was validated for river mouths for over 10000 rivers (Micella et al., 2024) again observations for different nutrient forms. Their validation results are with R^2 with the range of 0.57–0.73 depending on nutrient form. All of this gives us trust to use the MARINA-Multi model in our study. We used model evaluation approaches to build trust in this pioneer global assessment by comparing the baseline as modelled by our soft-coupled model system and two global datasets, one of satellite-derived chlorophyll-a values (Carrea et al., 2022), and one of measured chlorophyll-a concentrations (Filazzola et al., 2020) (see SI F for details). When excluding the outliers, the average lower and upper quartile of the two datasets are slightly higher with 3.9 and 15 mgChl-a/m^3 versus the 2.3 and 11.9 mgChl-a/m^3 in this study (Fig. G.1a in SI). This is also reflected in the median, with 7.6 mgChl-a/m^3 from the other datasets and the 6 mgChl-a/m^3 of this study. All things considered; we believe that the estimates of our model are in accordance with the results of these two other studies. However, it should be noted that evaluating Chl-*a* concentrations for (representative) lakes at a global scale is challenging due to of three reasons. First, as mentioned previously, comparing representative lakes with data from "real world" lakes is extremely hard and somewhat unfair. Not only because the representative lakes are an average representation of all lakes in a 0.5-degree grid cell, but also because the input data used to simulate the representatives lake's water quality are based on 30-year averages. Second, field data using consistent measurement methods are hard to retrieve and a dataset that is equally distributed over space and time is non-existent. For example, even the most extensive in situ datasets available (e.g., Filazzola et al., 2020) use data that are collected and published in different ways: different sensors and calibration techniques, different sampling depths, independent papers, different sampling programmes, and very European Union and North America centric (with scarce availability in the Southern Hemisphere as a whole). Datasets that are based on satellite images, such as the CEDA dataset (Carrea et al., 2022), could serve as an alternative to estimate chlorophyll-*a* concentrations in lakes. However, data uncertainties may occur as the lake's sediments and vegetation can interfere with the remote sensing estimates (Feng et al., 2021). Third, even though PCLake+ is an intermediately complex process-based model, it still does not capture the full complexity of factors affecting the development of algal blooms (e.g., species differences, spatial inhomogeneities, food web differences, sediment composition, etc.). Considering these challenges, we believe that our model results are in accordance with other Chl-*a* studies (see SI F for details).

We took a first step in simulating future trends in algal blooms in lakes globally accounting for the attribution of nutrient and climate factors. Yet, further research is needed. We see opportunities in five aspects. First, we see the need to overcome data limitations. For example, global hydrology and water quality models could be used to generate scenario-dependent lake water balances and lake nutrient loads (Janssen et al., 2019a). Second, we can use model ensembles for both input and output data (Golub et al., 2022; Semenov and Stratonovitch, 2010). Third, additional analysis could further improve our understanding of the impact of different societal choices on future trends in algal blooms. For example, extending the modelled period and the attribution analysis up to the year 2100 and including more SSP-RCP scenarios could further enhance our understanding of the attribution of nutrient and climate factors on Chl-*a* concentration in lakes. Fourth, it would be useful to conduct an ecosystem services impact assessment (Sousa et al., 2020) for each representative lake to assess the impacts of water quality changes on society. Fifth, we see opportunities to advance the new model system by replacing the soft coupling with dynamic coupling. Dynamic coupling would allow us to include feedback loops between river-lake water quality.

Lakes in clear conditions are vital as they support more ecosystem services than algal bloom-dominated ones (Janssen et al., 2021). This study showed that the future status of algal blooms in lakes globally is in our hands. Hence, responsible climate and nutrient measures should be strongly considered on national and international policy agendas. It is advisable that actions towards sustainable development, as opposed to fossil-fuelled development, are preferred, and promoted globally, as this will improve water quality. Sustainable development includes management strategies addressing both nutrient management (via socio-economic choices) and climate change mitigation. Special attention is required for regions such as South Asia and Central Africa as, even with sustainable development, water quality is likely threatened by algal blooms here. Although nutrient management had a greater impact on water quality in the short term (i.e., 40 years), climate change mitigation is assumed to become more relevant in the long term (i.e., up to 2100). Yet, challenges exist in adapting lake management to climate change. Examples are the frequencies and severity of extreme events that affect lake quality (e.g. increase of algal blooms by warming, increased nutrient loading by extreme rain events, decreased water levels due to droughts). In addition, the water quality thresholds for nutrients may also change because of climate change (Mooij et al., 2007). In our study, climate change impacts are reflected in the two future scenarios: RCP2.6 (low global warming with less frequent and severe extremes) and RCP8.5 (high global warming with more frequent and severe extremes. Our results, generally, point out that more impacts on lake eutrophication are under the scenario with RCP8.5. This indicates that lake managers may need to increase management efforts to adapt to climate change impacts under that scenario. Adaptation strategies will likely differ among lakes because of differences in their characteristics and pollution sources. For future localised studies on this topic, we recommend using our modelling framework, which links a watershed model (MARINA for pollution sources) and a lake ecosystem model (PCLake+) using local input data to explore adaptation strategies suitable for individual case studies.

It is pivotal that agencies with a global influence, such as the World Water Quality Alliance (WWQA) and the Intergovernmental Panel on Climate Change (IPCC), support this research agenda. By providing snapshots for two opposite development scenarios, this study allows us to understand lake algal bloom dynamics at a global scale. This may aid international organisations such as the United Nations Environment Programme (UNEP), European Union (EU), and the Global Alliance on

Health and Pollution (GAHP) to support policy development that acts "on time".

5. Conclusions

We developed a new model system that soft-couples a process-based lake ecosystem model (PCLake+) and a watershed nutrient model (MARINA-Multi) to, for the first time, explore future trends in algal blooms in lakes globally for >3500 representative lakes for the year 2050, considering the attribution of both nutrient and climate factors. Here, we summarise the three main findings:

1. In the fossil-fuelled development scenario for 2050, a chlorophyll-*a* concentration-based Trophic State Index increase is projected for an extensive majority of representative lakes (91 %) compared to the baseline scenario. This implies a rising algal bloom trend.
2. In the sustainable development scenario, a chlorophyll-*a* concentration-based Trophic State Index decrease is projected for more than half of representative lakes (63 %) compared to the baseline scenario. This implies a declining algal bloom trend. Regardless, the improvement is not "evenly distributed" across the globe, and in regions such as South-East Asia and Central Africa, algal blooms will continue to be a rising issue.
3. In both development scenarios explored, the nutrients were the defining factor that led to a change in chlorophyll-*a* concentrations ($P < 0.05$) and, thus, trends in algal blooms. The climate factor and interaction effect of nutrients and climate factors have shown to be unfavourable in 2050 for lakes starting with low chlorophyll-*a* concentrations, potentially exacerbating lake water quality in the long run (e.g., for 2100).

Overall, our study shows that the pathway chosen by humans can impact the state of lakes significantly ($P < 0.05$), even in a relatively short period (i.e., 40 years), and it should therefore serve as motivation to establish responsible nutrient and climate management policies globally.

CRediT authorship contribution statement

Maddalena Tigli: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mirjam P. Bak:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Conceptualization. **Jan H. Janse:** Writing – review & editing, Methodology, Conceptualization. **Maryna Strokal:** Writing – review & editing, Supervision, Methodology. **Annette B.G. Janssen:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Data curation, Conceptualization.

Declaration of competing interest

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

Data availability

The data that support the findings of this study are openly available at: https://doi.org/10.17026/PT/R2QITK.

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Supplementary materials

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