nature communications

Article

https://doi.org/10.1038/s41467-024-54926-3

Global lake phytoplankton proliferation intensifies climate warming

Received: 29 May 2023

Accepted: 25 November 2024

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In lakes, phytoplankton sequester atmospheric carbon dioxide (CO_2) and store it in the form of biomass organic carbon (OC); however, only a small fraction of the OC remains buried, while the remaining part is recycled to the atmosphere as CO_2 and methane (CH_4). This has the potential effect of adding CO_2-equivalents (CO_2-eq) to the atmosphere and producing a warming effect due to the higher radiative forcing of CH_4 relative to CO_2. Here we show a 3.1-fold increase in CO_2-eq emissions over a 100-year horizon, with the effect increasing with global warming intensity. Climate warming has stimulated phytoplankton growth in many lakes worldwide, which, in turn, can feed back CO_2-eq and create a positive feedback loop between them. In lakes where phytoplankton is negatively impacted by climate warming, the CO_2-eq feedback capacity may diminish gradually with the ongoing climate warming.

In lakes, phytoplankton can uptake carbon dioxide (CO_2) from the atmosphere and convert it to organic carbon (OC) throughout photosynthesis. Severe CO_2 limitation is therefore often observed in the water during phytoplankton blooms[1–3]. Thus, phytoplankton have been considered as a potent atmospheric CO_2 mitigator to combat climate warming[4–6]. However, in inland waters, much of the OC is ultimately recycled as CO_2 and methane (CH_4) back to the atmosphere by phytoplankton respiration and microbial activities, with a small remainder buried in the sediment bed over geological timescales[7–9]. Phytoplankton blooms in eutrophic lakes have been observed to significantly increase CO_2 and CH_4 emissions through the efficient recycling of phytoplankton biomass into greenhouse gases[10–12]. Since the higher radiative forcing of CH_4 relative to CO_2, the conversion of sequestered CO_2 to CH_4 has the potential to add CO_2-equivalents (CO_2-eq) to the atmosphere and produce a warming effect[13,14]. Until now, the CO_2-eq feedback of lake phytoplankton still remains unclear.

The earth's surface has been warming steadily since the mid-19th century concurrent with climate change[14,15]. In global lakes, phytoplankton exhibit varied responses to climate warming[16–21]. In many lakes, the growth of phytoplankton was stimulated by elevated temperatures, leading to an increase in phytoplankton biomass[18]. In these lakes, the increased phytoplankton biomass can, in turn, feed back more CO_2-eq, and there is a potential for amplification of global warming through a positive feedback loop between climate warming and eutrophication. In contrast, in other lakes, phytoplankton biomass shows a decrease under climate warming possibly due to that the stable water layer formed under climate warming, hindering the entrainment of deep water nutrients into surface water where they are available to support phytoplankton growth, especially in nutrient-poor

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aquatic environments[22,23]. In these lakes, the CO_2-eq feedback capacity of phytoplankton may diminish gradually with the ongoing climate warming. Here, we quantified the CO_2-eq feedback capacity of phytoplankton, assessed this feedback at a global scale, and predicted the extent of this response under future warming scenarios.

Results and discussion

CH_4 is a potent climate forcer and the second most important greenhouse gas. On the same mass basis, CH_4 can produce higher radiative forcing than CO_2 within a specific time[13], which is equivalent to 80.8 CO_2 over a 20-year horizon, 27.2 CO_2 over a 100-year horizon, and 7.3 CO_2 over a 500-year horizon according to the latest Sixth Assessment Report by the Intergovernmental Panel on Climate Change[14]. Thus, the conversion of CO_2 to CH_4 by phytoplankton has the potential to increase CO_2-eq and produce a warming effect, which depends on the mineralization efficiency of the fixed OC and the ratio of CH_4 to CO_2 that is recycled back to the atmosphere (Fig. 1). Our literature meta-analysis of global studies (Supplementary Data 1) shows that the mineralization efficiency of OC in lake environments (x) varies from 0.60–0.95 (mean = 0.74, median = 0.81), and the proportion of CH_4 in CO_2 and CH_4 emissions (x_1) varies from 0.015 to 0.37 (mean = 0.17, median = 0.025). The CO_2-eq changes (ΔCO_2-eq) across all ranges of x and x_1 are shown in Fig. 1.

When $\Delta CO_2\text{-eq} > 0$, it signifies that phytoplankton add CO_2-eq into the atmosphere. As shown in Fig. 2, CO_2-eq is almost unanimously increased by phytoplankton, especially on shorter time horizons due to the recycling of OC as CH_4, with this effect growing as more OC is mineralized and recycled as CH_4 (Fig. 2a–f). The probability of $\Delta CO_2\text{-eq} > 0$ reaches up to 99.9% on the 20-year horizon (Fig. 2a, d), indicating phytoplankton can increase CO_2-eq at almost all the phytoplankton decomposition scenarios. The probability of $\Delta CO_2\text{-eq} > 0$ is still 94.1% on the 100-year horizon (Fig. 2b, e), and 57.2% on the 500-year horizon (Fig. 2c, f). Our global meta-analysis revealed that on average 74.0% of OC ($x = 0.74$) entering lakes will be decomposed, 17.0% of which ($x_1 = 0.17$) is recycled as CH_4. In inland waters, allochthonous OC derived from lake catchment is generally considered to be more recalcitrant than autochthonous OC from planktonic plants, i.e., OC fixed by phytoplankton is more readily mineralized and has a higher x value[24–26]. According to the estimate described above, after a unit mass of carbon was introduced into lakes by phytoplankton, CO_2-eq will be increased by 12.0, 3.1 and −0.2 times over the 20-,100- and 500-year horizons, respectively (Fig. 2a–c), even when the low global average x is employed. This suggests that, although there is always some residual burial of carbon from phytoplankton biomass, this requires ΔCO_2-eq to be neutral or negative over the long 500-year scale when the CH_4 effect is small. Over short timescales, lake phytoplankton feed more CO_2-eq back to the atmosphere throughout the conversion of CO_2 to more potent CH_4 than what is fixed from the atmosphere. It implies that eutrophication control will help reduce CO_2-eq over the short timescales.

Our model provides evidence that despite phytoplankton assimilation of CO_2 from the atmosphere, ultimately more CO_2-eq is emitted back to the atmosphere (Fig. 1), suggesting that phytoplankton are net "CO_2-eq emitters". Highly productive lakes have a particular strong CO_2-eq feedback capacity. In oligotrophic, mesotrophic and eutrophic lakes, the CO_2-eq feedback is estimated to 166.5–999.0, 832.5–3330.0, and > 3330.0 g CO_2-eq/m^{2}d over the 100-year horizon, respectively. Over the past four decades, severe phytoplankton blooms in eutrophic lakes may have had large cumulative impacts on the climate. According to the chlorophyll-specific productivity (Supplementary Data 2), the CO_2-eq feedback capacity of phytoplankton over a 100-year horizon in global lakes is estimated (Fig. 3a). The feedback capacity generally decreases from the low (9.23 g CO_2-eq/m^{2}d) to the high (~0 g CO_2-eq/m^{2}d) latitude zone, but exhibits regional variation globally. The feedback size is the highest in North America (3.57×10^6 t CO_2-eq/d, Fig. 3a) and the 40°–50°N zone (3.55×10^6 t CO_2-eq/d, Fig. 3b), likely due to the presence of a large lake area (Supplementary Data 3).

In global lakes, phytoplankton display varied responses to climate warming, and the trends in their CO_2-eq feedback capacity may differ under future warming. In lakes where phytoplankton growth is stimulated by climate warming[16,27,28], the increased phytoplankton productivity can, in turn, feed back more CO_2-eq (Fig. 2), creating a positive feedback loop between them. In contrast, in lakes where phytoplankton growth is negatively impacted by climate warming, the CO_2-eq feedback capacity may diminish gradually with the ongoing climate warming. Here, we projected the changes in the CO_2-eq feedback of phytoplankton under future climate warming:

$$F = \Delta PP * \Delta CO_2 - eq \qquad (1)$$

where F represents the CO_2-eq feedback of phytoplankton, g CO_2-eq/m^{2}d; ΔPP refers to the changes in phytoplankton productivity under future climate warming. We employed a dataset of 11,857 time series historical records from LAGOS database to analyze the relationship between lake phytoplankton and air temperature (Supplementary Data 4), and then analyzed the changes in Chl-a concentration and the corresponding CO_2-eq feedback capacity under future warming scenarios.

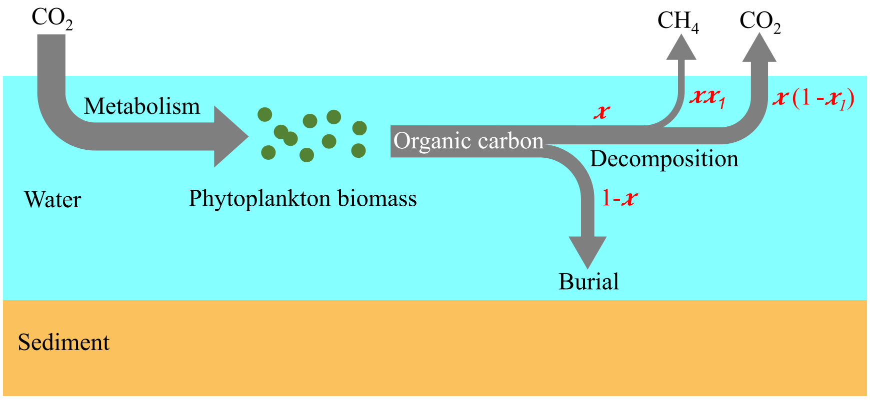

Fig. 1 | Conceptual model of carbon budget throughout the life cycle of phytoplankton in lakes. During their growth, phytoplankton sequester atmospheric CO_2 and store it in the form of biomass OC. Upon death, a portion of this OC remains buried, while the remaining part is recycled to the atmosphere as CO_2 and CH_4. The x is the mineralization efficiency of OC in lake environments, and the x_1 is the proportion of CH_4 in CO_2 and CH_4 emissions. OC, CO_2 and CH_4 represent organic carbon, carbon dioxide and methane, respectively.

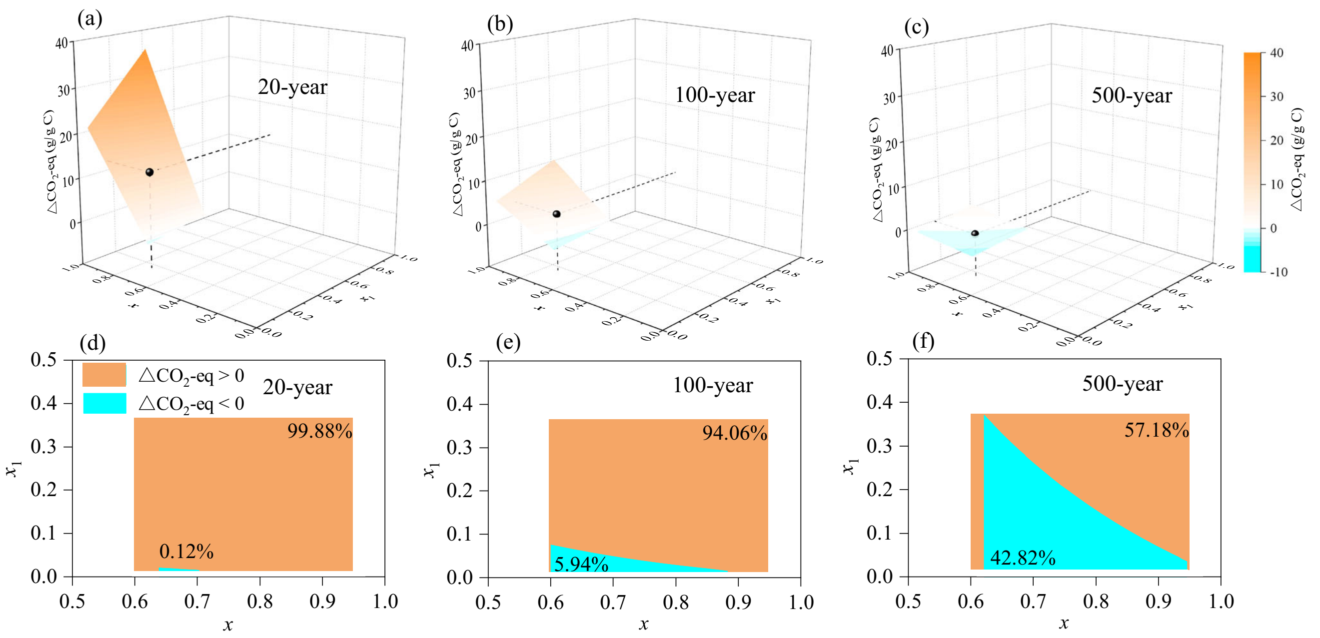

Fig. 2 | CO_2-eq changes throughout the life cycle of phytoplankton. a ΔCO_2-eq on the 20-year horizon; (**b**) ΔCO_2-eq on the 100-year horizon; (**c**) ΔCO_2-eq on the 500-year horizon; (**d**) x and x_1 values at different ΔCO_2-eq on the 20-year horizon; (**e**) x and x_1 values at different ΔCO_2-eq on the 100-year horizon; (**f**) x and x_1 values at different ΔCO_2-eq on the 500-year horizon. The x is the mineralization efficiency of OC in lake environments, and the x_1 is the proportion of CH_4 in CO_2 and CH_4 emissions. The black circles in (**a**–**c**) indicate average ΔCO_2-eq caused by phytoplankton in global lakes. The inserted data in (**d**–**f**) are the probability of ΔCO_2-eq < 0 and > 0 on different time horizons for CH_4. The 20, 100, and 500 years are the time scales that are employed by the Intergovernmental Panel on Climate Change to assess the radiative forcing of greenhouse gases. OC, CO_2, CH_4, CO_2-eq and ΔCO_2-eq represent organic carbon, carbon dioxide, methane, CO_2-equivalents and the changes of CO_2-equivalents, respectively.

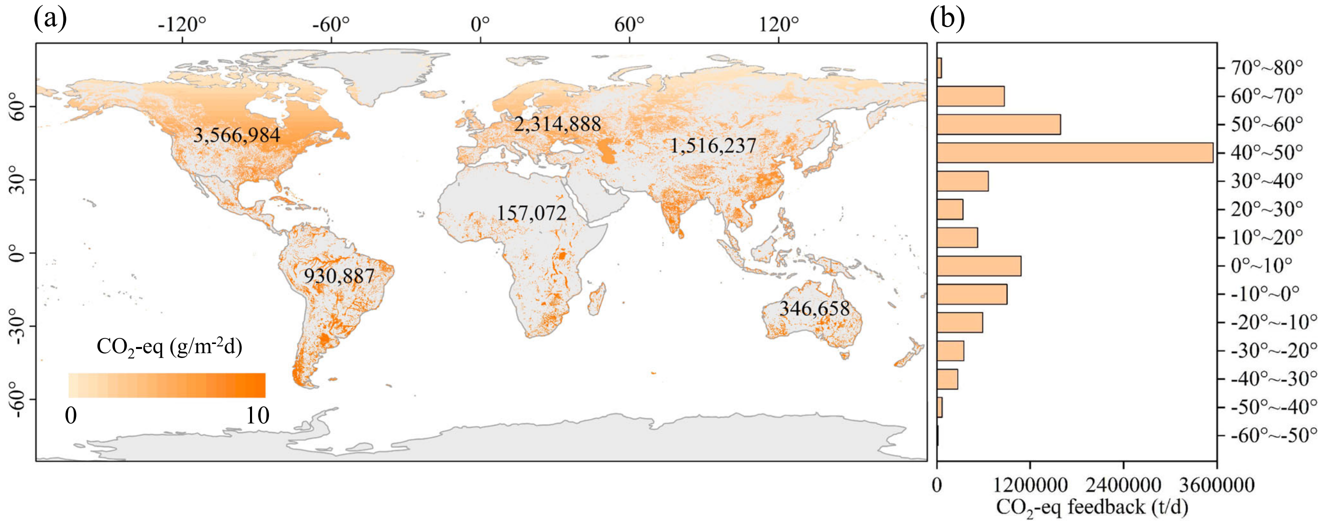

Fig. 3 | The CO_2-eq feedback of phytoplankton in global lakes. a The regional pattern of the CO_2-eq feedback capacity; (**b**) the feedback size across a span of 10 degrees of latitude; The data in (**a**) are the feedback extent (t/d) of phytoplankton in various continental lakes. The CO_2-eq is calculated on the 100-year horizon. CO_2-eq represents CO_2-equivalents.

The results indicated that among 235 lakes, 62 lakes exhibit a significant positive correlation between Chl-a levels and air temperature ($p < 0.05$), while 15 lakes show a significant negative correlation ($p < 0.05$) (Supplementary Data 5). In lakes where phytoplankton growth is stimulated by climate warming, the CO_2-eq feedback of phytoplankton will be increased by 0.16, 0.27, 0.40, 0.57 and 0.66 times under the SSP1-1.9, SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5 warming scenarios, respectively, by the end of the 21st century (Fig. 4a). Nevertheless, this is a conservative estimate, as (i) phytoplankton derived autochthonous OC is more readily mineralized and facilitates oxygen depletion compared to allochthonous OC from landscape[24–26], resulting in a larger proportion of OC being recycled as CH_4[10]; (ii) warmer temperature can increase OC mineralization efficiency as this process is mainly mediated by microbes[29], and has the potential to make a larger proportion of OC recycled as CH_4 than CO_2[8]. All these scenarios lead to a higher feedback capacity for phytoplankton in these lakes (Fig. 1). In contrast, in lakes where phytoplankton is negatively impacted by climate warming, the CO_2-eq feedback capacity of phytoplankton is expected to be decreased by 0.36, 0.51, 0.76, 1.08 and 1.29 times under the SSP1-1.9, SSP1-2.6, SSP2-

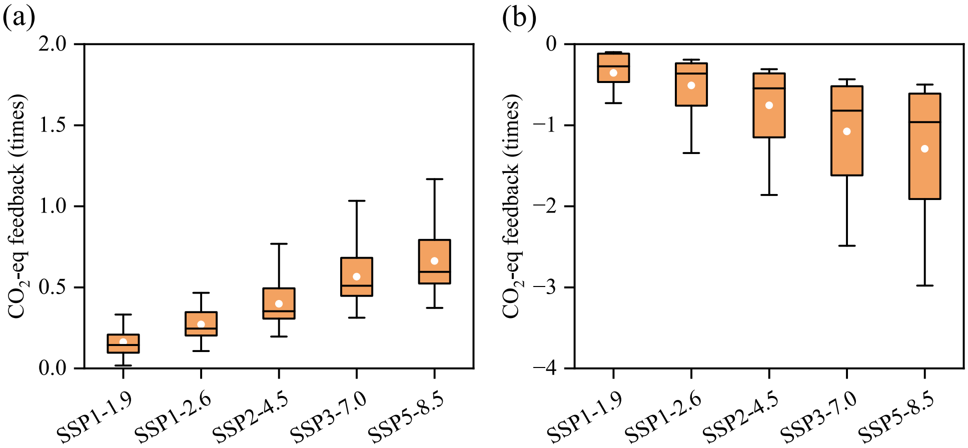

Fig. 4 | The changes in the CO_2-eq feedback capacity of lake phytoplankton under future climate warming. a The phytoplankton CO_2-eq feedback in lakes where phytoplankton growth is stimulated by climate warming ($n = 62$). **b** The phytoplankton CO_2-eq feedback in the lakes where phytoplankton is negatively impacted by climate warming ($n = 15$). The SSP1-1.9, SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5 are warming scenarios outlined in the latest Sixth Assessment Report by the Intergovernmental Panel on Climate Change. CO_2-eq represents CO_2-equivalents. Box plot with center line = median, hollow circle = mean, box limits = upper and lower quartiles, whiskers = min to max. Data are presented as mean values ± SD.

4.5, SSP3-7.0 and SSP5-8.5 warming scenarios, respectively, by the end of the 21st century (Fig. 4b).

In lakes, phytoplankton sequester atmospheric CO_2 and store it in biomass organic OC. The high biodegradability of this endogenous OC, however, can generate anaerobic conditions and facilitate CH_4 production. The conversion of sequestered CO_2 to potent CH_4 contribute to the greenhouse effect. Consequently, efforts to reduce the greenhouse effects through the control of carbon emissions would be undermined by the widespread phytoplankton proliferation. Therefore, there is an urgent need for aggressive nutrient management to mitigate severe eutrophication in global lakes. In lakes where phytoplankton is stimulated by climate warming, there exists a positive feedback loop between phytoplankton and climate warming, which can be further intensified by increasing climate warming, while, in lakes where phytoplankton is negatively impacted by climate warming, the CO_2-eq feedback capacity of phytoplankton will decrease with the ongoing climate warming.

In lakes, the PP is influenced by various factors such as Chl-a concentration, light radiation intensity, and air temperature[30,31]. Although Chl-a itself explains these variables, with high Chl-a concentration often associated with rich nutrients, high light radiation intensity and high temperatures, the estimation of PP using the Chl-a-based empirical model still remains uncertainties due to the lack of global-scale multiple parameters. In the future, there is a need for additional global-scale datasets to address these gaps. While quantifying the relationship between Chl-a concentration and air temperature using lake time series historical data with a significance level of $p < 0.05$, the average explanatory power of air temperature for Chl-a is only 16%. This might be attributed to the predominant influence of nutrient limitations on the growth of phytoplankton. Despite using a 10-year dataset, it still requires longer time series data for a more comprehensive understanding of the relationship between Chl-a concentration and air temperature.

Methods

CO_2-eq budget throughout the life cycle of phytoplankton

Phytoplankton-derived OC is the product of phytoplankton metabolism. When it reaches lakes, a portion of the OC becomes buried in sediment beds while the remaining fraction is mineralized into CO_2 and CH_4. The changes of CO_2-eq can be quantified by subtracting the fixed CO_2 from the total CO_2-eq of subsequent CO_2 and CH_4 emissions. Assuming that m gram of carbon is fixed by phytoplankton, the fraction x is ultimately decomposed, with x_1 as CH_4 and $(1 - x_1)$ as CO_2, as shown in Fig. 1. The resulting net impact on CO_2-eq emissions can be approximated as:

$$\Delta CO_2 - \mathrm{eq} = \frac{m * x * x_1 * 1.33 * k + m * x * (1 - x_1) * 3.67 - m * 3.67}{m} \tag{2}$$

where ΔCO_2-eq represents the changes in CO_2-eq emissions that occur when a unit mass of carbon is introduced into lakes via phytoplankton (g CO_2-eq/g C); 1.33 and 3.67 are the transfer coefficients from a unit mass of carbon to CH_4 and CO_2, respectively; k represents the transfer coefficient from CH_4 to CO_2, with the values of 80.8, 27.2 and 7.3 CO_2-eq given for 20-,100- and 500-year horizons, resepectively[14]. The model (2) can be simplified even further to the more streamlined model (3) presented below:

$$\Delta CO_2 - \mathrm{eq} = 1.33k * x * x_1 - 3.67 * x * x_1 + 3.67x - 3.67 \tag{3}$$

To access the mean ΔCO_2-eq in global lakes, the globally averaged x and x_1 were utilized in this study. These values were obtained from previously published literatures (Supplementary Data 1).

Estimation of phytoplankton CO_2 feedback in global lakes

The CO_2 feedback capacity of phytoplankton was estimated as:

$$F = \mathrm{PP} * \Delta CO_2 - \mathrm{eq} \tag{4}$$

where F is the CO_2-eq feedback capacity of phytoplankton in lakes, g CO_2-eq/m^{2}d; PP is the phytoplankton productivity, which was estimated using an empirical model based on Chl-a standing stock according to Morin et al. (1999)[32]:

$$\mathrm{PP} = 10^{(1.3 + 0.98 * \mathrm{Log}_{10}^{\mathrm{Chla}})} \tag{5}$$

where PP represents phytoplankton productivity, mg C/m^{2}d; Chl-a represents the areal concentration of Chl-a, mg/m^2, which was obtained by integrating the cubic value over the reported photic depth in the original paper. The Chl-a concentrations were obtained from an open-access data repository (https://doi.org/10.5063/F1RV0M1S) that was published by Filazzola et al. in 2020[33]. The data repository contained multiple measurements of Chl-a concentrations taken at different locations within the same lake, or at different times. To obtain a representative value for each lake, these measurements were averaged in this study. The unavailable euphotic depth data were estimated from Chl-a ($r^2 = 0.85$) according to Tilzer (1988)[34]:

$$Z_{eu} = \frac{4.61}{0.021 * \text{Chla} + 0.27} \tag{6}$$

where Z_{eu} is the euphotic depth, m. If the estimated Z_{eu} value was larger than lake depth, the lake depth was used. The CO_2 feedback capacity of phytoplankton in 1649 lakes was evaluated, and a model was established (Supplementary Data 2) for analyzing the feedback size of global lakes (1,427,688 records in Global Lakes and Wetlands Database, Supplementary Data 3).

The whole-lake feedback size was calculated as the product of the CO_2 feedback capacity of phytoplankton and lake area. Likewise, the regional feedback size was estimated by summing this value across all lakes in the region (Supplementary Data 3).

Projection of phytoplankton CO_2 feedback responses to climate warming

In global lakes, phytoplankton exhibit diverse responses to climate warming, and the trend of changes in their CO_2-eq feedback capacity may vary under future warming. After establishing the relationship between Chl-a concentration and air temperature, we projected the changes in Chl-a concentration for each lake under different warming scenarios and subsequently estimated the alterations in CO_2-eq feedback capacity resulting from the variations in Chl-a concentration.

To avoid the potential disturbance arising from a space for time substitution, we used time series historical data from 235 lakes in the LAGOS database (https://portal.edirepository.org/nis/mapbrowse?packageid=edi.101.2)[35]. The time-series data on Chl-a concentration were required to cover a period of at least 10 years in order to identify long-term trends rather than short-term, potentially misleading fluctuations. There is a total of 11,857 datasets after successfully matching them with air temperature (Supplementary Data 4). The correlation between Chl-a concentration and air temperature was examined using linear regression analysis, with a threshold set for p-values less than 0.05 to ensure statistical significance. A two-sided test was applied, and no adjustments were made for multiple comparisons. The air temperature data that was matched with Chl-a was obtained from ERA5-Land monthly average data (https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land-monthly-means?tab=form)[36]. The nearest neighbor interpolation method was employed to match the coordinates of lakes and extract the temperature values for the corresponding date[37].

Considering the variations in baseline temperatures and responses to climate warming across different lake locations, we selected the historical average temperatures (1950-present) for each lake location as their respective baseline temperatures. Historical temperature data were also sourced from ERA5-Land land surface temperature data. The warming values for 2081-2100 under SSP1-1.9, SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5 scenarios, which are outlined in the latest Sixth Assessment Report by the Intergovernmental Panel on Climate Change, were obtained from https://climate-scenarios.canada.ca/?page=cmip6-scenarios. The difference between future temperatures and baseline values was considered as the warming magnitude for each lake location.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data used in this study are available on Figshare (https://doi.org/10.6084/m9.figshare.27174948.v1).

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Acknowledgements

This study was supported by National Natural Science Foundation of China (No. 42422605 to W.S., and 42220104010 to B.Q.), Jiangsu Provincial Carbon-peak and Carbon-neutralization Technology Innovation Project (BK20220041 to B.Q.), and the US National Science Foundation (No. 1840715 and 1831096 to H.P). We thank Prof. Yonglong Lu from Xiamen University (China) and Dr. Benjamin M. Kraemer from Department of Ecosystem Research, IGB Leibniz-Institute of Freshwater Ecology and Inland Fisheries (Germany) for their valuable comments on this manuscript, and thank M.S. Boyi Liu, Liping Hu, Xueru Mao, Ziqian Li and Zuqiang Zhang for data analysis using ArcGIS 10.8.1.

Author contributions

W.S. wrote the initial manuscript; B.Q. conducted the analysis in discussion with W.S., B.D. H.P. and E.J.; C.Z. and Q.Z. contributed to interpreting results and improvement of this paper.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41467-024-54926-3.

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Peer review information *Nature Communications* thanks Benjamin Kraemer, and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. A peer review file is available.