

**Thermophilization but weak phosphorus-affinity shifts in freshwater phytoplankton communities**

Running title: Phytoplankton thermophilization

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## Abstract

Climate warming and nutrient enrichment are reshaping many freshwater lakes, yet their relative roles in driving directional changes in phytoplankton communities across broad geographic gradients remain poorly understood. Using data from lakes repeatedly surveyed by the U.S. National Lakes Assessment in 2012, 2017, and 2022, we examined whether warming and phosphorus enrichment produced comparable shifts in phytoplankton community composition, environmental affinities, and cell size structure. Temporal compositional change increased with the magnitude of temperature change but was not significantly associated with changes in phosphorus concentration. Communities showed thermophilization, shifting toward taxa associated with warmer conditions as temperature increased, primarily through gains of warmer-affinity taxa. In contrast, phosphorus-affinity shifts were not significantly related to phosphorus change. Average community-level phytoplankton cell size declined with warming but did not respond to phosphorus change. These results suggest that temperature change drive more consistent taxonomic and functional reorganization than phosphorus change in freshwater phytoplankton communities.

**Keywords:** Community phosphorus index, community temperature index, phosphorus, phytoplankton, thermophilization, temperature.

## Introduction

In recent decades, increasing concern about anthropogenic impacts on ecological communities has been driven by multiple global environmental stressors, including climate change, eutrophication, land use change, biological invasions, and pollution (IPBES 2019; Sala *et al.* 2000; Vitousek *et al.* 1997). Freshwater lakes, which provide habitat for diverse aquatic taxa and support important ecosystem functions and services to humanity (Sterner *et al.* 2020), are particularly sensitive to these anthropogenic stressors as they are influenced by processes occurring in both their surrounding watersheds and the atmosphere. In freshwater lakes, climate warming and eutrophication are among the most important and widely studied anthropogenic stressors, with warming affecting lake physical and chemical properties (Adrian *et al.* 2009; Williamson *et al.* 2009) and eutrophication altering nutrient availability and water quality (Carpenter *et al.* 1998), with ensuing consequences for the biotic components of lake ecosystems (Adrian *et al.* 2009; Smith 2003; Williamson *et al.* 2009). In many lake ecosystems, phytoplankton are the dominant primary producers and play a key role in supplying energy for pelagic food webs (Reynolds 2006). Thus, studying phytoplankton may provide important insights into the ecological impacts of climate change and eutrophication on freshwater ecosystems.

A growing number of studies have observed changes in community structure as a result of warming, often through thermophilization, where warm-affinity species increase in relative abundance under warming. Evidence for thermophilization is particularly well documented in terrestrial systems, although the rate and magnitude of community change often vary across ecosystems (Bertrand *et al.* 2011; Borderieux *et al.* 2024; Yue *et al.* 2026; Zhu *et al.* 2024). For example, lowland forests in France exhibited lagged responses to climate warming, likely

reflecting the long-term persistence of adult trees and dispersal limitation of their propagules (Bertrand *et al.* 2011). On the other hand, grassland communities, which are dominated by shorter-lived herbaceous species, can shift more rapidly towards species associated with warmer conditions (Zhu *et al.* 2024). Recent work also suggests that alpine summit vegetation may respond more strongly to warming than forest and grassland communities (Yue *et al.* 2026). By comparison, evidence for thermophilization in freshwater phytoplankton communities remains scarce, with the few existing studies reporting either cryophilization or no detectable shift toward warm-affinity phytoplankton taxa (Khaliq *et al.* 2024; Mäkinen *et al.* 2025). Furthermore, no study, to our knowledge, has evaluated phytoplankton thermophilization while simultaneously considering eutrophication that often co-occur with warming in freshwater ecosystems.

Phosphorus plays a central role in freshwater ecosystem dynamics, often being the primary limiting nutrient in lakes and reservoirs (Schindler 1977; Schindler *et al.* 2008). Anthropogenic inputs of phosphorus from agricultural fertilizers, wastewater effluent, urban runoff, and detergent use have altered natural phosphorus cycles, contributing to eutrophication and changes in phytoplankton biomass and community structure (Carpenter *et al.* 1998; Smith 2003). Previous studies have shown that phosphorus enrichment can increase phytoplankton biomass and chlorophyll concentrations and promote shifts toward cyanobacteria and other taxa associated with eutrophic conditions (Rigosi *et al.* 2014; Schindler *et al.* 2016). Although broad-scale studies have examined relationships between phosphorus and phytoplankton communities across lakes (e.g., Verspagen *et al.*, 2022), comparisons of the relative influence of phosphorus enrichment and climate warming on phytoplankton community structure across large geographic and environmental gradients remain scarce. In particular, it remains unclear whether phosphorus enrichment produces directional temporal shifts in phytoplankton community composition in a

manner analogous to thermophilization under warming, or whether phosphorus effects are more context dependent across lakes. Evaluating the relative influence of phosphorus and temperature is therefore essential for more accurate predictions of ecological change in lake ecosystems under ongoing environmental change.

A trait-based approach may be useful for understanding phytoplankton responses to environmental change because functional traits provide a more direct link to individual performance and ecosystem function than species identity or composition (Litchman & Klausmeier 2008; McGill *et al.* 2006). In phytoplankton, cell size represents one of the most important functional traits, influencing various processes such as resource uptake, metabolism, growth, and grazer evasion (Chisholm 1992; Finkel *et al.* 2010; Hillebrand *et al.* 2022). Phytoplankton cell size structure may therefore provide insight into the relative effects of climate warming and phosphorus enrichment: warming is often associated with shifts toward smaller organisms, whereas phosphorus enrichment may alter cell size structure by relaxing nutrient limitation and changing competitive dynamics among phytoplankton size classes (Daufresne *et al.* 2009; Irwin *et al.* 2006; Zohary *et al.* 2021). Thus, examining phytoplankton cell size structure can help understand functional shifts in lake communities and evaluate whether these shifts are more strongly associated with changes in temperature or phosphorus availability.

In this study, we used phytoplankton data from the United States Environmental Protection Agency's National Lakes Assessment (NLA), a standardized survey designed to assess the ecological condition of lakes across the continental United States. From 2012 to 2022, the NLA surveyed more than 2,500 lakes to assess water quality and the composition and abundance of aquatic taxa, including phytoplankton. Over the course of the survey, many lakes experienced temporal changes in temperature and phosphorus concentration, providing an

opportunity to evaluate how phytoplankton communities respond to these two important environmental drivers. Our study therefore aims to assess how warming and phosphorus enrichment shape freshwater phytoplankton community structure, with particular emphasis on whether these drivers promote thermophilization and shifts toward phosphorus-affinity taxa.

## **Materials and Methods**

### **Data Sources**

Data on lake phytoplankton and nutrient used in this study were obtained from the U.S. Environmental Protection Agency's (EPA) National Lakes Assessment (NLA) program. The NLA program began in 2007 and surveys freshwater lakes, ponds, and reservoirs across the continental US every five years. Given changes in the survey design, including changes in the criterion for the selected lakes and differences in some measured variables and sampling protocols, between 2007 and 2012, we elected to focus on data collected in 2012, 2017, and 2022. For our selected years of study, the survey operated under standardized collection and laboratory protocols for physiochemical and biological analysis, with detailed methods publicly available in the EPA's field and laboratory manuals.

The NLA survey identified phytoplankton species to the lowest practical taxonomic level, often genus or species depending on the taxa, and quantified their abundances present in each water sample using standardized optical microscopy techniques. Total phosphorus concentrations were determined from depth-integrated water samples collected from the euphotic zone and analyzed using persulfate digestion followed by automated colorimetric analysis with the molybdate–ascorbic acid method. We focused on phosphorus as the nutrient of interest because it is often the primary limiting nutrient in freshwater ecosystems. A total of 2,502 unique lakes were assessed across 2012, 2017, and 2022 surveys. To examine temporal change among

repeatedly sampled lakes, we identified the subset of lakes that were sampled in all three surveys (n = 33; Fig. S1), and focused on these lakes in subsequent analyses. Data from the remaining lakes were used to estimate phytoplankton niches with respect to temperature and phosphorus (see Data Analyses below).

Environmental temperature data were obtained from Terraclimate, which houses monthly climate data for global terrestrial surfaces at approximately 1/24° spatial resolution from 1950 to the present (Abatzoglou *et al.* 2018). We used the geographic coordinates from the NLA to match each lake to the corresponding grid cell in the Terraclimate dataset. For each lake and survey year, we extracted the relevant temperature values to use as the environmental temperature metric in subsequent analyses.

## **Data Analyses**

As phytoplankton exhibit strong seasonal dynamics and are most active within the warmer months of the year, we used the average summer temperature as our primary temperature metric. However, since a substantial portion of the NLA surveys were conducted in the early summer, temperature conditions later in the season would not have influenced phytoplankton communities at the time of sampling, rendering the average summer temperature of the current year a less suitable metric. To avoid incorporating post-sampling thermal conditions, we used the average summer temperature from the year preceding each year of NLA survey in our analysis. This approach is consistent with evidence that lake and phytoplankton dynamics can reflect prior seasonal conditions through ecological memory and carryover in community state from the previous growing season (Padisák 1992). For the entirety of this study, temperature is defined as the average summer temperature of the year prior to NLA data collection unless otherwise noted. Monthly average temperatures were calculated as the mean of the monthly maximum and

minimum temperatures. Summer average temperatures were calculated as the mean of the monthly averages from May through September.

Phytoplankton temporal community compositional change was quantified using beta diversity. For each repeatedly sampled lake, beta diversity was calculated as Bray–Curtis dissimilarity between samples from the same lake across each survey interval, 2012–2017 and 2017–2022.

For each phytoplankton taxon observed in the 33 repeatedly sampled lakes (Fig. S1), we estimated its temperature niche and phosphorus niche using NLA survey data collected between 2012 and 2022, excluding observations from the 33 repeatedly sampled lakes to avoid circularity. For each taxon, we identified all lakes in which it was present (Fig. S2a) and calculated the median temperature and median total phosphorus concentration across those lakes (Fig. S2b). These median values were used to represent the species' temperature niche and phosphorus niche, respectively (Fig. S2c).

The Community Temperature Index (CTI) was calculated following established approaches that characterize communities as the abundance-weighted mean temperature niche of their constituent taxa (Bowler *et al.* 2017; Devictor *et al.* 2008). We applied the same community-weighted framework to phosphorus by calculating a Community Phosphorus Index (CPI), defined as the abundance-weighted mean phosphorus niche of all taxa observed in a lake. Thus, CTI and CPI describe the average temperature and phosphorus affinities of each phytoplankton community, respectively. CTI and CPI were calculated for each of the 33 repeatedly sampled lakes separately for each survey year.

To quantify the contribution of taxonomic turnover to changes in community thermal composition, we decomposed changes in CTI for each lake across the two study phases (2012–

2017 and 2017–2022) into the contributions of gained, lost, and resident taxa. For each phase, taxa were classified as gained if they were absent in the initial year but present in the final year, lost if they were present in the initial year but absent in the final year, and residents if they were present in both years. For each taxon, we calculated its contribution to CTI change as the product of its change in relative abundance and the difference between its thermal niche and the lake's initial CTI. Contributions were then summarized by turnover category to evaluate the relative roles of gained species, lost species, and abundance change among resident taxa.

Community-weighted mean (CWM) cell volume for each lake-year sample was calculated as the abundance-weighted mean of taxon-level cell biovolumes, with weights based on each taxon's relative abundance. Phytoplankton taxa were assigned to size classes based on equivalent spherical diameter (ESD), which was calculated from cell biovolume assuming a spherical shape. Taxa were classified as picoplankton ( $ESD < 2 \mu m$ ), nanoplankton ( $2-20 \mu m$ ), or microplankton ( $20-200 \mu m$ ) following the conventional plankton size classification (Sieburth *et al.* 1978).

All statistical analyses were conducted in R version 4.2.2 (R Core Team 2022). Bray–Curtis dissimilarity was calculated using the `vegdist` function in the `vegan` package (Oksanen *et al.* 2026). Temporal Bray–Curtis dissimilarity, CTI, CPI, CWM cell volume, and CTI contributions from gained, lost, and resident taxa were analyzed using linear mixed-effects models, with lake identity treated as the random effect. Models tested associations between Bray–Curtis dissimilarity and changes in temperature or phosphorus, CTI and temperature, CPI and phosphorus, and CWM cell volume and temperature or phosphorus. LMMs were also used to assessed relationships between taxon-specific cell volume and temperature niche within each phytoplankton size class. Models were fitted using the `lmer` function in the `lme4` package (Bates *et al.* 2015).

## Results

Temporal changes in phytoplankton community composition were associated with changes in temperature but not phosphorus. Temporal Bray-Curtis dissimilarity as a metric of community compositional change, calculated between the beginning and end of each study phase for each repeatedly sampled lake, increased with the magnitude of temperature change. Lakes experiencing larger temperature shifts, both positive and negative, exhibited greater compositional dissimilarity between sampling endpoints (Fig. 1a). By contrast, no significant relationship was found between Bray-Curtis dissimilarity and changes in total phosphorus concentration (Fig. 1b).

Community-level niche indices showed a similar pattern. Across the 33 repeatedly sampled lakes, changes in CTI were positively associated with changes in environmental temperature, indicating that phytoplankton communities shifted toward warmer-affinity taxa in lakes that experienced warming and toward cooler-affinity taxa in lakes that experienced cooling (Fig. 2a). In contrast, changes in CPI were not significantly related to changes in total phosphorus concentration (Fig. 2b).

The contribution of gained species to CTI changes was positively associated with temperature change, indicating that increases in CTI were linked to the addition of warmer-affinity taxa (Fig. 3a). In contrast, contributions from both lost and resident taxa varied across lakes and time periods, but were not associated with temperature change (Fig. 3b, c).

To investigate whether phytoplankton thermal niches were associated with functional traits, we examined the relationship between taxon-specific temperature niche and cell volume within each size class. No significant relationship was detected for picoplankton or microplankton. On the other hand, nanoplankton, which comprised the majority of observations,

exhibited a significant negative relationship between temperature niche and cell volume (Fig. 4a), indicating that nanoplankton taxa associated with warmer thermal niches tended to have smaller cell volumes.

At the community level, changes in CWM cell volume were negatively related to changes in temperature, with greater warming associated with larger decreases in average cell volume (Fig. 4b). By contrast, changes in CWM cell volume showed a weak positive, non-significant relationship with changes in phosphorous concentration (Fig. S3).

## **Discussion**

Phytoplankton are the main primary producers in many freshwater lakes, yet the relative role of climate change and eutrophication, as two key anthropogenic stressors, in driving directional changes in phytoplankton communities remains poorly understood. Across U.S. lakes repeatedly surveyed in 2012, 2017, and 2022, we found that phytoplankton community structure showed discernible responses to temperature change, but not to phosphorus change. Larger thermal shifts were associated with greater temporal changes in phytoplankton community composition, and CTI tracked the direction of temperature change, indicating shifts toward warmer-affinity taxa under warming and cooler-affinity taxa under cooling. By contrast, changes in total phosphorus were not significantly associated with changes in either community composition or CPI. Changes in CTI were primarily driven by taxon gains, rather than taxon losses or changes in the relative abundance of resident taxa. Temperature also influenced phytoplankton cell size structure, with warming linked to decreasing community-weighted mean cell volume, a pattern largely driven by nanoplankton taxa. Overall, these findings suggest that temperature is a more important driver of directional taxonomic and functional change in the freshwater phytoplankton communities that we studied.

Our study extends evidence for directional climate tracking to freshwater phytoplankton communities, for which broad-scale evidence remains scarce. The observed thermophilization is consistent with a growing body of literature documenting positive CTI responses to warming in terrestrial systems, including forests, grasslands, and birds (Borderieux *et al.* 2024; Bowler *et al.* 2017; Devictor *et al.* 2008; Zhu *et al.* 2024). However, our findings contrast sharply with Khaliq *et al.* (2024), who reported cryophilisation in phytoplankton communities, indicating increased prevalence of cold-affinity taxa under warming. This discrepancy may reflect methodological differences between studies: our analysis estimated thermal affinities from NLA lake occurrences and used abundance-weighted community indices that captured changes in relative abundance, whereas Khaliq *et al.* (2024) estimated thermal affinities from occurrence data and used occurrence-based indices. Our findings also contrast with studies reporting lagged responses to climate change in terrestrial systems, such as lowland forests in France (Bertrand *et al.* 2011), but align with other studies reporting rapid community responses to warming in terrestrial systems dominated by shorter-lived taxa, such as grasslands in the California Floristic Province (Zhu *et al.* 2024). More generally, our results lend support to the idea that the speed of a community's response to climate change may depend on the longevity of the species that make up the community (Compagnoni *et al.* 2021; Zhu *et al.* 2024). Rapid phytoplankton responses to warming may reflect their short generation times and high dispersal potential via wind, water, and animal vectors, which allow for faster population turnover.

We found that the observed thermophilization was primarily driven by the gain of warmer-affinity taxa, rather than the loss of cooler-affinity taxa or shifts in the relative abundance among resident taxa. This pattern is consistent with gain-driven thermophilization reported in some terrestrial plant communities, where increases in thermophilic or mesophilic

species contributed more strongly than losses of cold-affinity species (e.g., Kiebach et al. 2023). However, it contrasts with other terrestrial plant studies in which the loss of cold-affinity species was the main driver of thermophilization (e.g., Borderieux et al., 2024). This discrepancy may reflect differences in life history and dispersal between long-lived terrestrial plants and short-lived planktonic organisms. In phytoplankton, taxon gains may occur more readily through colonization, recruitment from resting stages, or increases from rare taxa that were previously below detection thresholds. We hypothesize that thermophilization in phytoplankton communities through gains of warm-affinity taxa may be a fairly general phenomenon, which should be further tested as more data become available.

In contrast to warming, increases in phosphorus concentration did not produce a clear directional shift toward phosphorus-affinity taxa. This result, however, should not be interpreted as evidence that phosphorus is unimportant for phytoplankton, as phosphorus is a primary limiting nutrient in many freshwater lakes and a major driver of eutrophication, phytoplankton biomass, and harmful cyanobacterial blooms (Carpenter *et al.* 1998; Rigosi *et al.* 2014; Schindler 1977; Schindler *et al.* 2008, 2016; Smith 2003). Indeed, total phosphorus was a significant predictor of spatial variation in phytoplankton community composition among our study lakes (Fig. S4), echoing similar findings from other studies (e.g., Verspagen *et al.* 2022). These results highlight the limits of space-for-time inference (Blois *et al.* 2013; Johnson & Miyanishi 2008; Pickett 1989): phosphorus may structure differences among lakes, but temporal phosphorus change within lakes may not move communities predictably along the same cross-lake phosphorus gradient, at least across the decadal scale (2012-2022) within our study lakes.

Our results also provide evidence that temperature plays an important role in shaping phytoplankton functional traits. Warmer-affinity nanoplankton taxa tended to have smaller cell

volumes, and community-weighted mean cell volume declined with warming. These patterns are consistent with widely reported negative temperature-size relationships in aquatic ecosystems (Daufresne *et al.* 2009), including freshwater phytoplankton (Zohary *et al.* 2021). In phytoplankton, smaller cells may be favored under warmer conditions because their higher surface-area-to-volume ratios can enhance nutrient uptake, while cell size may further influence metabolism, growth, sinking, grazing susceptibility, and trophic transfer (Hillebrand *et al.* 2022; Litchman & Klausmeier 2008). Thus, warming-associated declines in cell volume suggest that temperature-driven phytoplankton reorganization may have functional consequences beyond taxonomic turnover, potentially affecting pelagic food web structure, sedimentation, and carbon cycling.

Several limitations of our study should be noted. First, although the National Lakes Assessment provides standardized phytoplankton and environmental data for a large number of lakes across broad geographic gradients, only 33 lakes were sampled in all three survey years. Therefore, caution should be exercised when generalizing our findings, which should be further evaluated as longer temporal data from more repeatedly sampled lakes become available. Second, our study focused on summer temperature preceding each NLA survey year, because many lakes were sampled in early summer and phytoplankton communities may reflect antecedent environmental conditions. The significant associations between antecedent summer temperature and shifts in community composition, thermal affinity, and cell size thus suggest a lagged effect of thermal conditions, consistent with ecological memory previously reported for phytoplankton communities (Padisák 1992). As a sensitivity analysis, we examined whether changes in average spring temperature during the survey year explained changes in CTI, but found no significant relationship (Fig. S5). This result suggests that the observed

thermophilization patterns may be better captured by antecedent thermal conditions than by spring temperature during the survey year. Third, total phosphorus was measured at the time of sampling. Although it explained a significant fraction of spatial variation in phytoplankton community structure (Fig. S4b), contemporaneous phosphorus concentration may not fully capture the nutrient conditions most relevant to temporal phytoplankton community changes. This may have limited our ability to detect community responses to phosphorus change, particularly if phytoplankton communities respond more strongly to cumulative nutrient history or nutrient availability prior to sampling. Future studies with higher-frequency measurements of both thermal and nutrient conditions would help clarify how warming and phosphorus enrichment jointly shape phytoplankton community reorganization in freshwater lakes.

Despite these caveats, our results suggest that warming is associated with directional taxonomic and functional reorganization in freshwater phytoplankton communities, including greater community turnover, shifts in thermal affinity, and declines in average cell volume. By contrast, phosphorus enrichment did not produce comparable community-level shifts. These findings suggest that warming may generate more consistent community responses than phosphorus enrichment across environmentally diverse lakes, with potentially important implications for pelagic food webs, trophic transfer, and biogeochemical cycling.

## **Author Contributions**

**Eric Jiang:** Formal analysis, Data curation, Visualization, Writing – original draft.

**Yiping Zuo:** Conceptualization, Methodology, Supervision, Writing – review & editing.

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#### **Data Availability Statement**

The data and code supporting the findings of this study are openly available in Figshare at <https://figshare.com/s/a804566d7a1a77df50f1>.

#### **Conflicts of Interest**

The authors declare no conflicts of interest.

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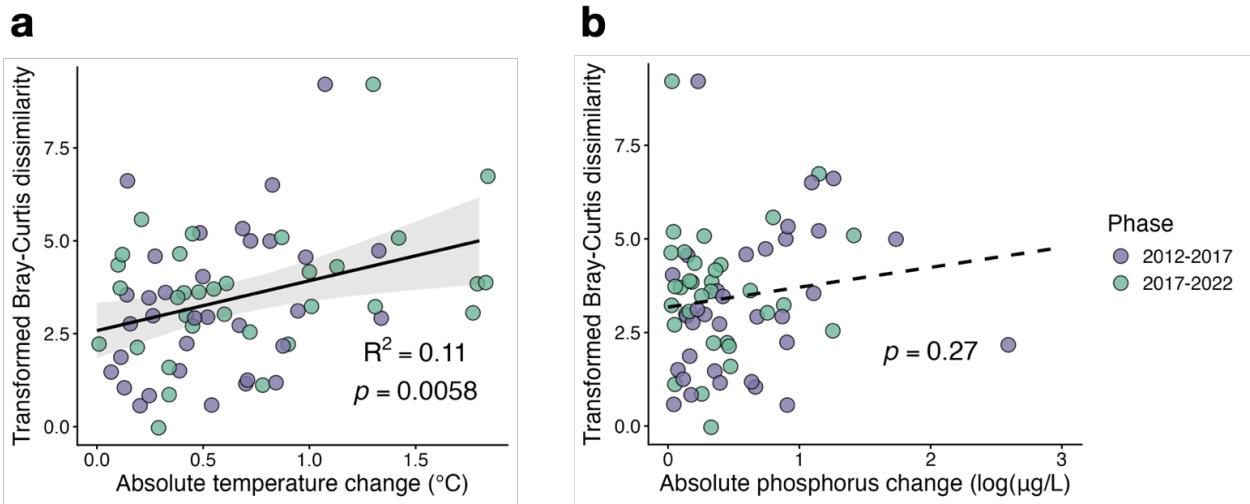
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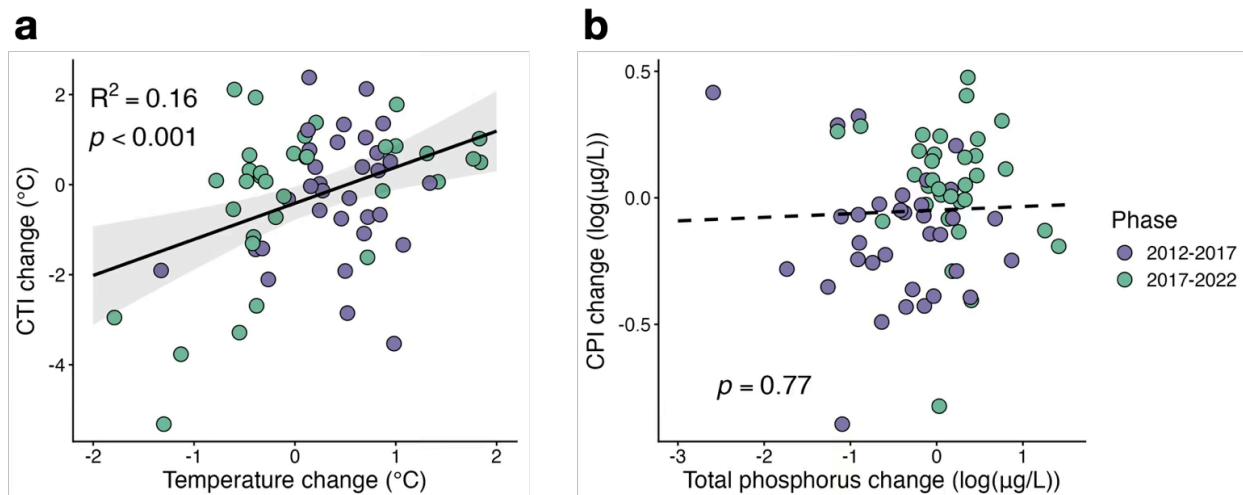
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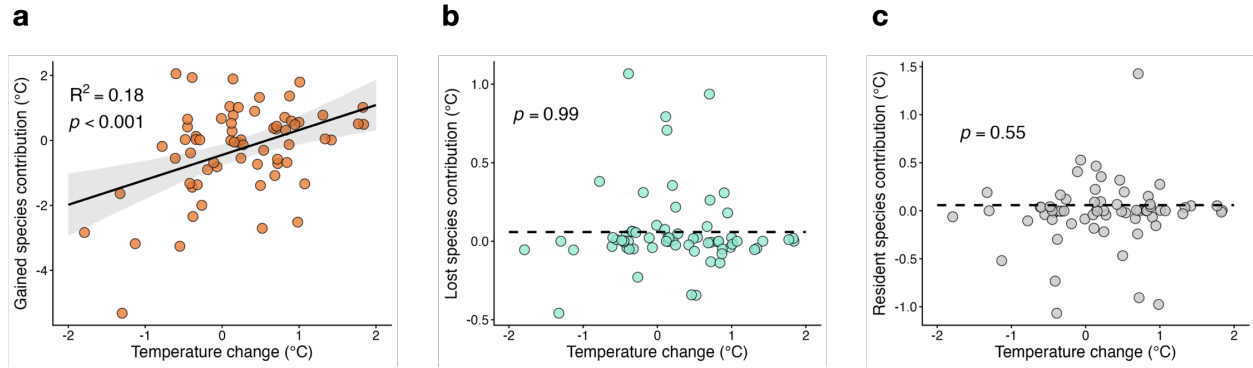
Figures



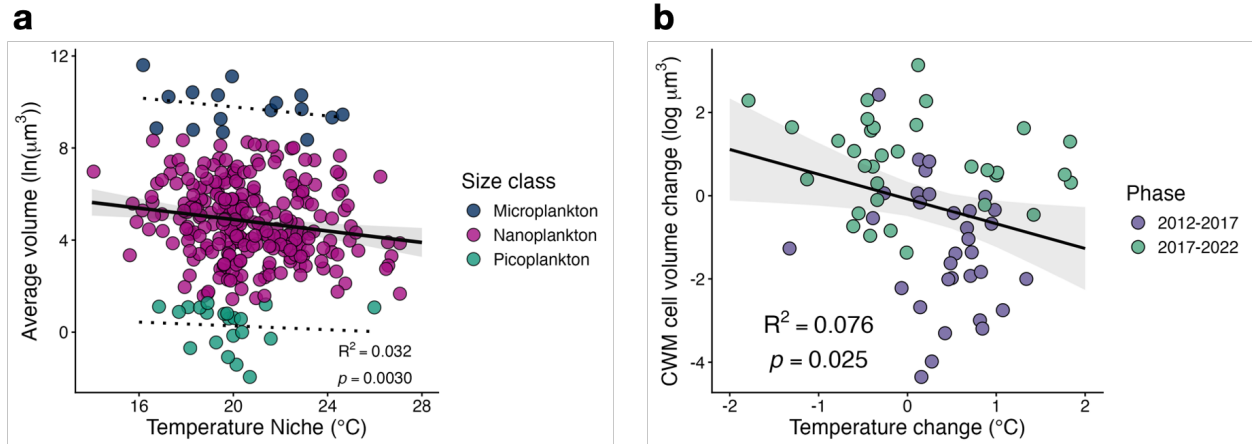
**Fig. 1 | Relationships between changes in lake environmental conditions and temporal beta diversity.** **a**, Temporal beta diversity, measured as Bray-Curtis dissimilarity, as a function of temperature change; **b**, Temporal beta diversity as a function of total phosphorus change. Each point represents a lake observed during a single survey interval, with point color denoting the sampling period. The solid line indicates the fitted linear regression, and the shaded band shows the 95% confidence interval; the dashed line indicates non-significant regressions.



**Fig. 2 | Relationships between changes in lake environmental conditions and phytoplankton community affinity indices. a,** Change in CTI as a function of temperature change. **b,** Change in CPI as a function of changes in total phosphorus concentration. Each point represents a single lake within a single survey interval, with point color denoting the sampling period. The solid line indicates the fitted linear regression, and the shaded band shows the 95% confidence interval; the dashed line indicates non-significant regressions.

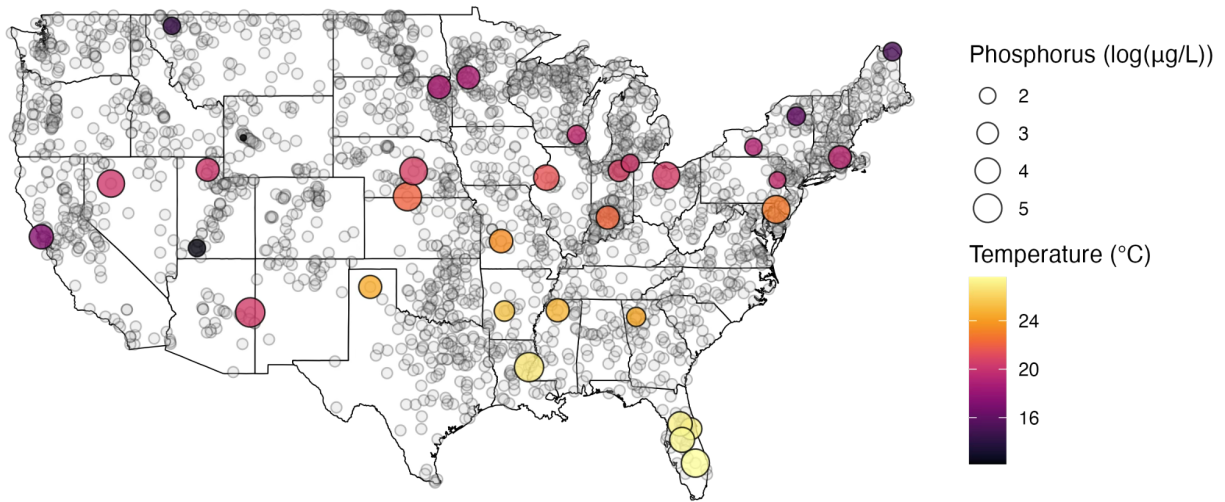


**Fig. 3 | Taxon turnover contributions to changes in phytoplankton community thermal affinity.** **a**, Contribution of gained taxa to CTI as a function of temperature change. **b**, Contribution of lost taxa to CTI as a function of temperature change. **c**, Contribution of resident taxa to CTI as a function of temperature change. Each point represents a single lake. The solid line indicates the fitted linear regression, and the shaded band shows the 95% confidence interval; the dashed line indicates non-significant regressions.

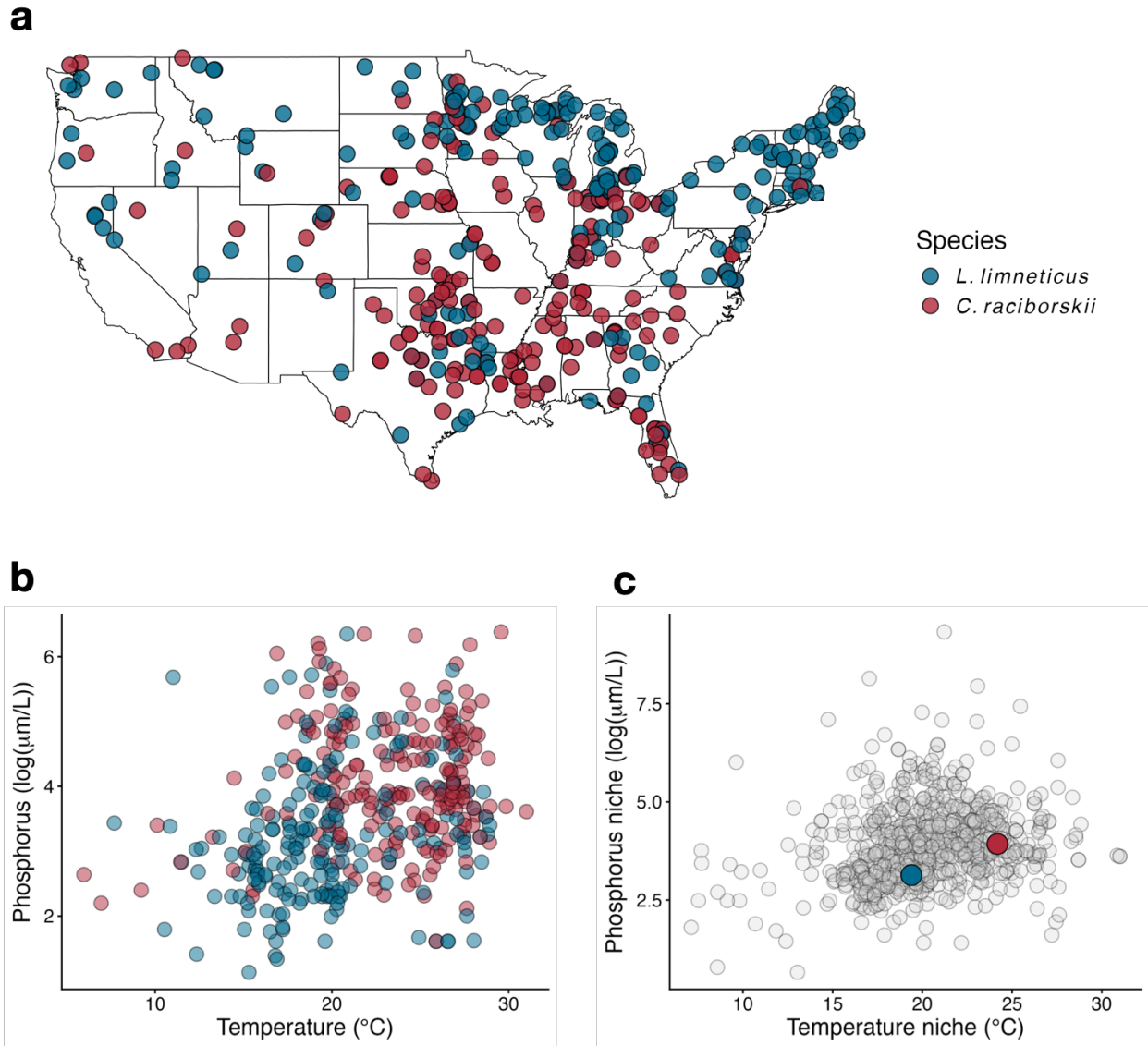


**Fig. 4 | Phytoplankton cell size responds to environmental temperature change. a**, Taxon-level average cell volume as a function of temperature niche, with colors corresponding to phytoplankton size class. Each data point represents one phytoplankton taxon. The solid line and reported statistics correspond to the fitted linear regression for nanoplankton only, and the shaded band denotes the 95% confidence interval. The dotted lines correspond to non-significant regressions for microplankton and picoplankton. **b**, Community-weighted mean (CWM) cell volume as a function of environmental temperature change. Each point represents a lake during a single survey interval. The solid line represents the fitted linear regression, and the shaded band denotes the 95% confidence interval.

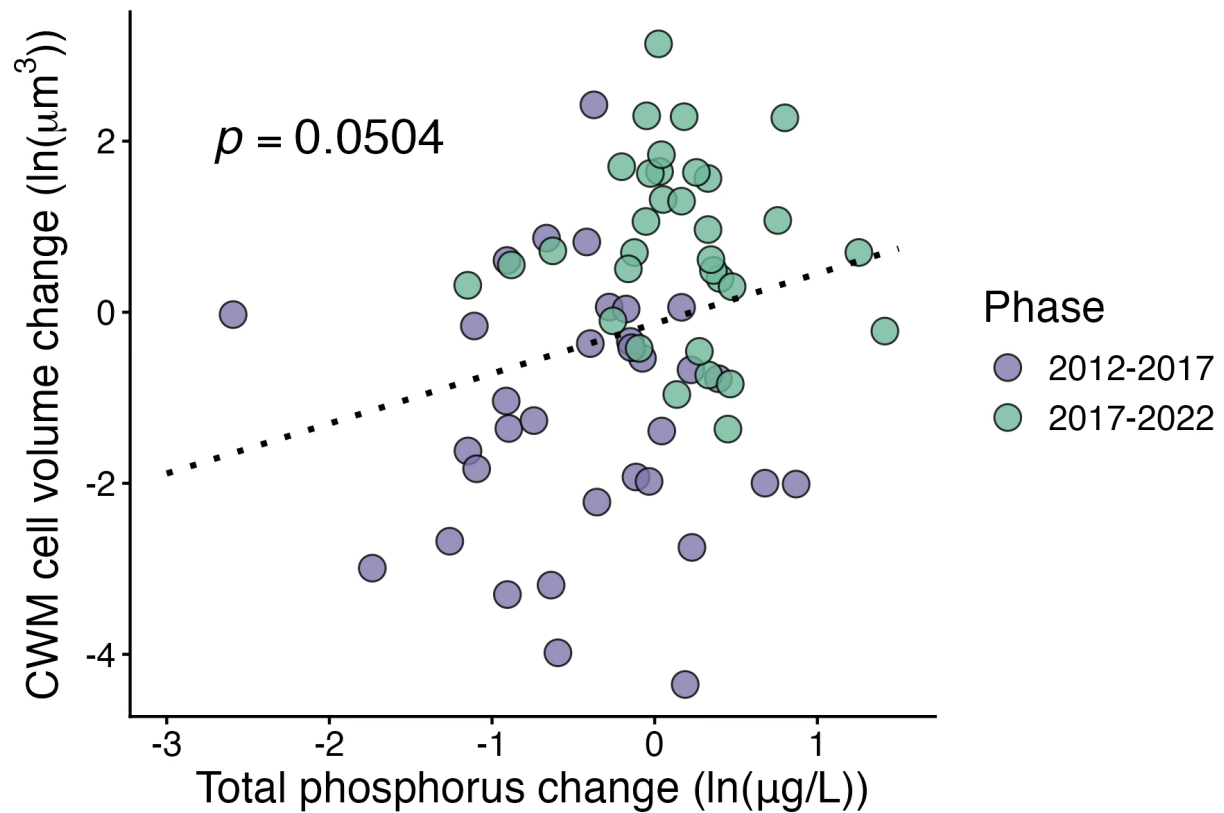
## Supplementary materials



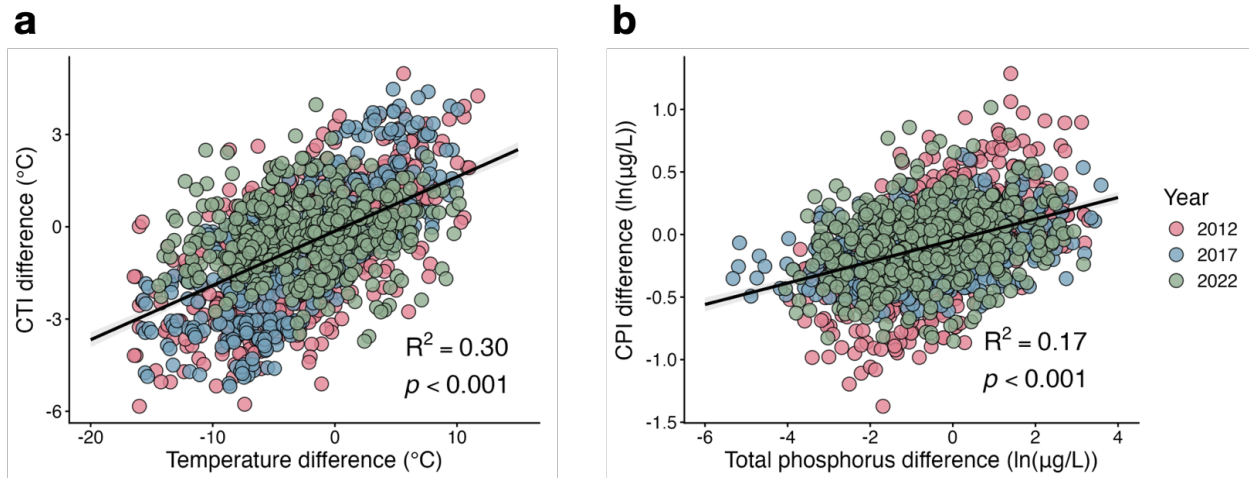
**Fig. S1 | Geographic distribution of sampled lakes.** Colored points indicate repeatedly sampled lakes, with color representing environmental temperature and point size representing total phosphorus concentration. Gray points indicate lakes used to estimate taxon temperature and phosphorus niches.



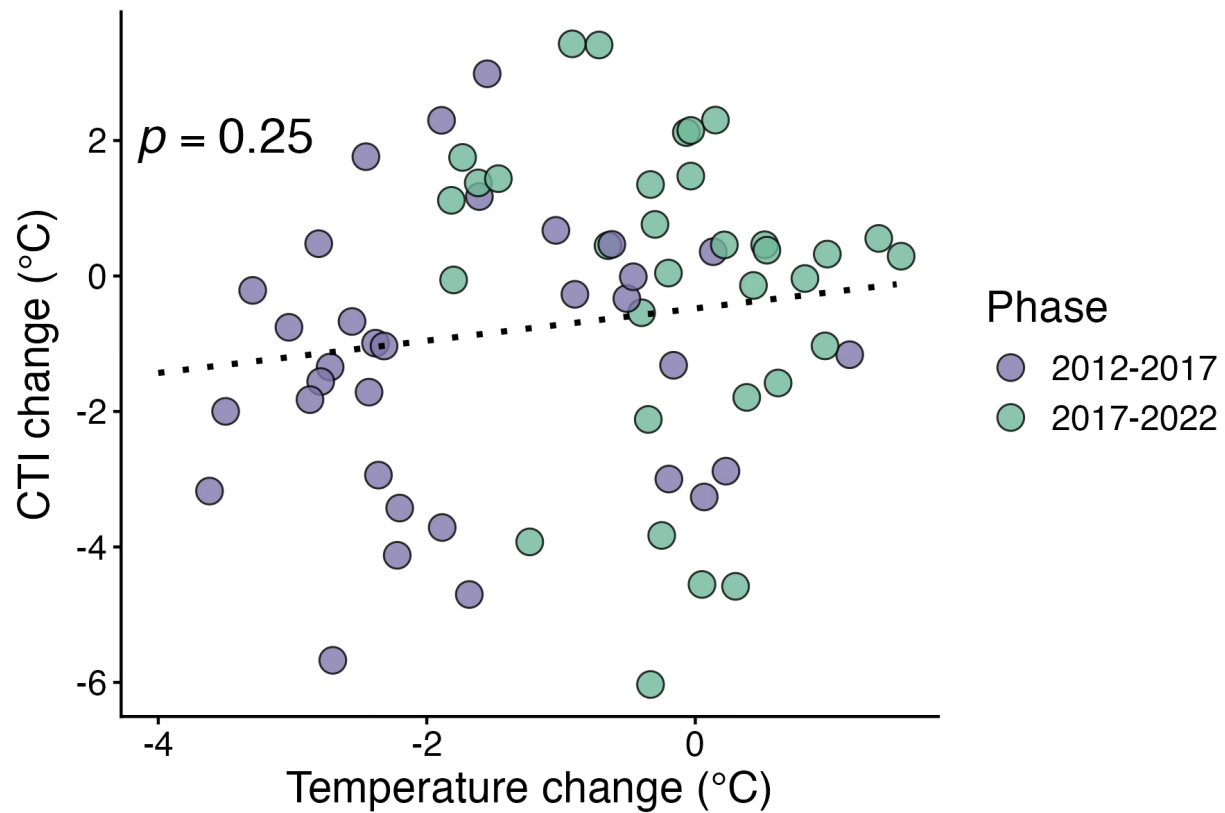
**Fig. S2 | Estimation of phytoplankton temperature and phosphorus niches.** **a**, Occurrences of two example taxa, *Limnococcus limneticus* and *Cylindrospermopsis raciborskii*, used to illustrate niche estimation. **b**, Temperature and total phosphorus concentration of lakes in which either example taxon occurred; each point represents one lake. **c**, Estimated temperature and phosphorus niches of the two example taxa plotted with the niches of all other taxa analyzed in the study, shown as gray points.



**Fig. S3 | The relationship between changes in community-weighted mean (CWM) cell volume and changes in total phosphorus concentration.** Each point represents a lake during a single survey interval. The dashed line indicates non-significant regressions.



**Fig. S4 | Relationships between pairwise spatial differences in environmental conditions and phytoplankton community indices.** **a**, pairwise differences in phytoplankton community temperature index (CTI) between lakes as a function of pairwise differences in water temperature. **b**, pairwise differences in phytoplankton community phosphorus index (CPI) between lakes as a function of pairwise differences in total phosphorus concentration. Each point represents a pair of lakes. Each colored point represents one lake–lake pair from a given survey year (2012, 2017, or 2022).



**Fig. S5 | The relationship between changes in spring temperatures and phytoplankton community temperature index (CTI).** Spring average temperatures were calculated as the mean of the monthly average temperatures from March through May of the sampling year. Phytoplankton temperature niches and lake CTI were then recalculated using these spring averages. Each point represents a single lake within a single survey interval, with point color denoting the sampling period. The dashed line indicates non-significant regressions.