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LETTER

Nutrient limitation constrains thermal tolerance in freshwater phytoplankton

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Scientific Significance Statement

Thermal performance curves are a crucial tool for predicting species responses to climate change. Recent studies have stressed the importance of species' thermal optima and critical thermal limits for predicting vulnerability to climate change. However, studies often fail to consider the potential for multiple stressors associated with global climate change and human activities such as decreases in nutrient availability or eutrophication to modulate thermal tolerance curves. Here, we studied how the thermal optimum of growth rate in five freshwater phytoplankton species varied across a spectrum of limiting to nonlimiting phosphorus concentration. We found that the thermal optimum increased with phosphorus availability in a saturating manner. These results imply that declines in nutrient availability could increase the vulnerability of phytoplankton to thermal stress from global warming.

Abstract

Thermal tolerance can depend critically on environmental context (e.g., resource availability and biotic interactions), yet it is often measured only under idealized conditions. Here, we investigated how the concentration of phosphate (a limiting resource for algal growth in freshwater ecosystems) influences the thermal optimum for growth rate in five species of freshwater phytoplankton. We found that low-phosphate concentrations led to a sharp decline in species' thermal optima, by up to 15°C relative to replete conditions, with the magnitude of the decline varying between species. Rapid global environmental change is expected to lead to rising temperatures, while nutrient concentrations in freshwaters are forecast to increase in waterbodies subject to eutrophication and decline in large lentic systems that become warmer and more stratified. Our findings suggest that phytoplankton that experience warming and nutrient limitation concurrently will be more vulnerable to environmental change.

The threat of climate change on biodiversity has renewed interest in the investigation of thermal physiology (Deutsch et al. 2008; Dillon et al. 2010; Thomas et al. 2012). In ectotherms, performance (e.g., locomotor speed, metabolism, or population growth rate) follows a left-skewed unimodal thermal performance curve (Fig. 1a; Deutsch et al. 2008). Small increases in temperature past the optimum translate into strong declines in performance, which in the context of global warming can lead to increased extinction risks (Dillon et al. 2010). However, studies often focus on individual environmental variables, without taking into account interactions with other drivers of global change (Deutsch et al. 2008; Dillon et al. 2010; Thomas et al. 2012), and consequently, very little is known about how the shape of thermal performance

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Author Contribution Statement: EB and GYD designed the study; EB performed the experiment, analyzed the data, and wrote the first draft; and all authors contributed to writing.

Data Availability Statement: Data are available in the zenodo repository at https://zenodo.org/record/1247453.

Additional Supporting Information may be found in the online version of this article.

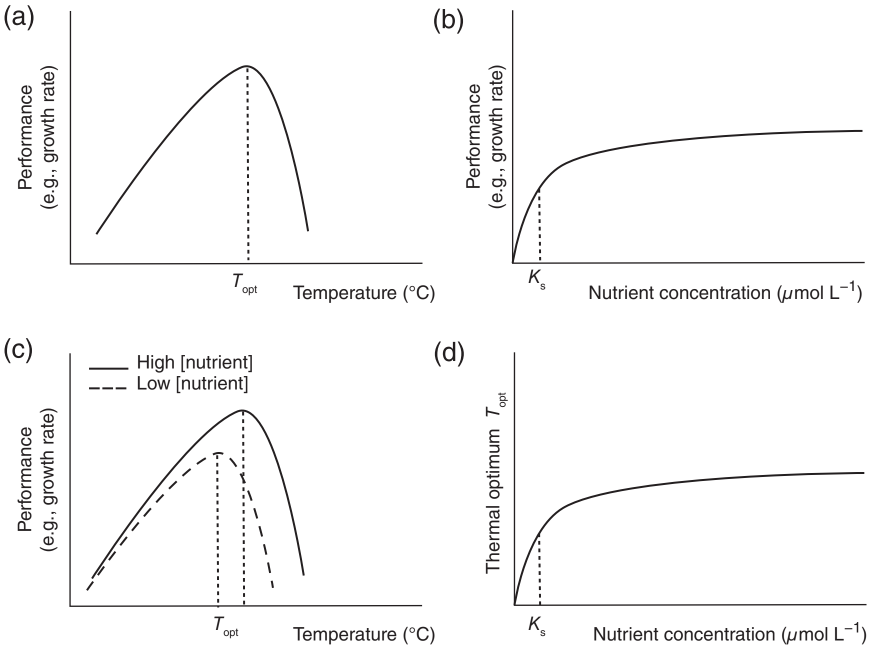

Fig. 1. (**a**) The thermal performance curve. Performance, which can be measured as growth rate or metabolism, increases with temperature until an optimum T_{opt} and then decreases sharply. (**b**) Monod curve for growth rate as a function of nutrient concentration. The half-saturation constant K_s is the nutrient concentration at which the growth rate is half of the maximum rate at saturating nutrient conditions. (**c**) Impact of both temperature and nutrients on growth rate following Thomas et al. (2017). At low nutrient concentration, the maximum growth rate is lower than at high nutrient conditions, and the thermal optimum shifts to lower temperatures. (**d**) The thermal optimum is a saturating function of nutrient concentration.

curves is modulated by other stressors (but see Verberk et al. 2016; Thomas et al. 2017).

In freshwater ecosystems, nutrient availability is a key driver of ecosystem functioning, influencing population growth rates (Monod 1949), interspecific competition (Tilman 1981), and community assembly (Bulgakov and Levich 1999). In addition to modifying water temperatures, global warming is expected to alter the nutrient availability through an increase in vertical stratification in lakes and oceans, reducing nutrient supply (Behrenfeld et al. 2006; Coma et al. 2009; Kraemer et al. 2015), or by increasing extreme precipitation events leading to greater nutrient run-off into freshwaters, resulting in eutrophication (Sinha et al. 2017). Furthermore, land-use change (e.g., for agricultural or urban development) frequently leads to eutrophication in both freshwater and coastal marine ecosystems (Bonsdorff et al. 1997; Ye et al. 2011). For instance, land-use changes are predicted to lead to increased eutrophication in most parts of the world and particularly in South Asia by 2030, while European freshwaters are predicted to see a decrease in eutrophication (Seitzinger et al. 2010). Consequently, climate change and increased human domination of Earth's ecosystems are likely to lead to complex impacts on nutrient supply, with both increases and decreases expected at local and regional scales depending on local management practices (Dokulil and Teubner 2010). It is therefore crucial to better understand how changes in nutrient availability and temperature will influence species' thermal tolerance in a warming world.

Interactions between temperature and nutrient availability have long been recognized to play a key role in shaping algal physiology (Rhee and Gotham 1981; Raven and Geider 1988). For instance, the half-saturation constant for growth (i.e., the nutrient concentration at which species grow at half the maximum rate under saturating nutrient conditions; Fig. 1b) increases with temperature in algae for nitrogen (Sterner and Grover 1998), silicate (Mechling and Kilham 1982) and phosphate (Bestion et al. 2018). Such temperature-dependent changes in nutrient physiology can also affect interspecific competition, leading to reversals in competitive advantages with warming (Tilman et al. 1981; Bestion et al. 2018). However, studies on the interaction between temperature and nutrients on phytoplankton have often focused on temperatures below the optimum temperature T_{opt} (Rhee and Gotham 1981; Tilman et al. 1981; Sterner and Grover 1998; Marañón et al. 2014).

In a recent study, Thomas et al. (2017) argued that the optimum temperature for growth rate should be a saturating function of increasing nutrient concentrations—i.e., the thermal optimum rises rapidly at low-nutrient concentrations and decelerates toward an asymptote under replete conditions (Fig. 1c,d). Thomas et al. (2017) used the coastal marine diatom *Thalassiosira pseudonana* to support their prediction and showed that the optimum temperature (T_{opt}) decreased by 3–6°C in this organism at low phosphorus and nitrogen concentrations relative to saturating nutrient conditions. Their

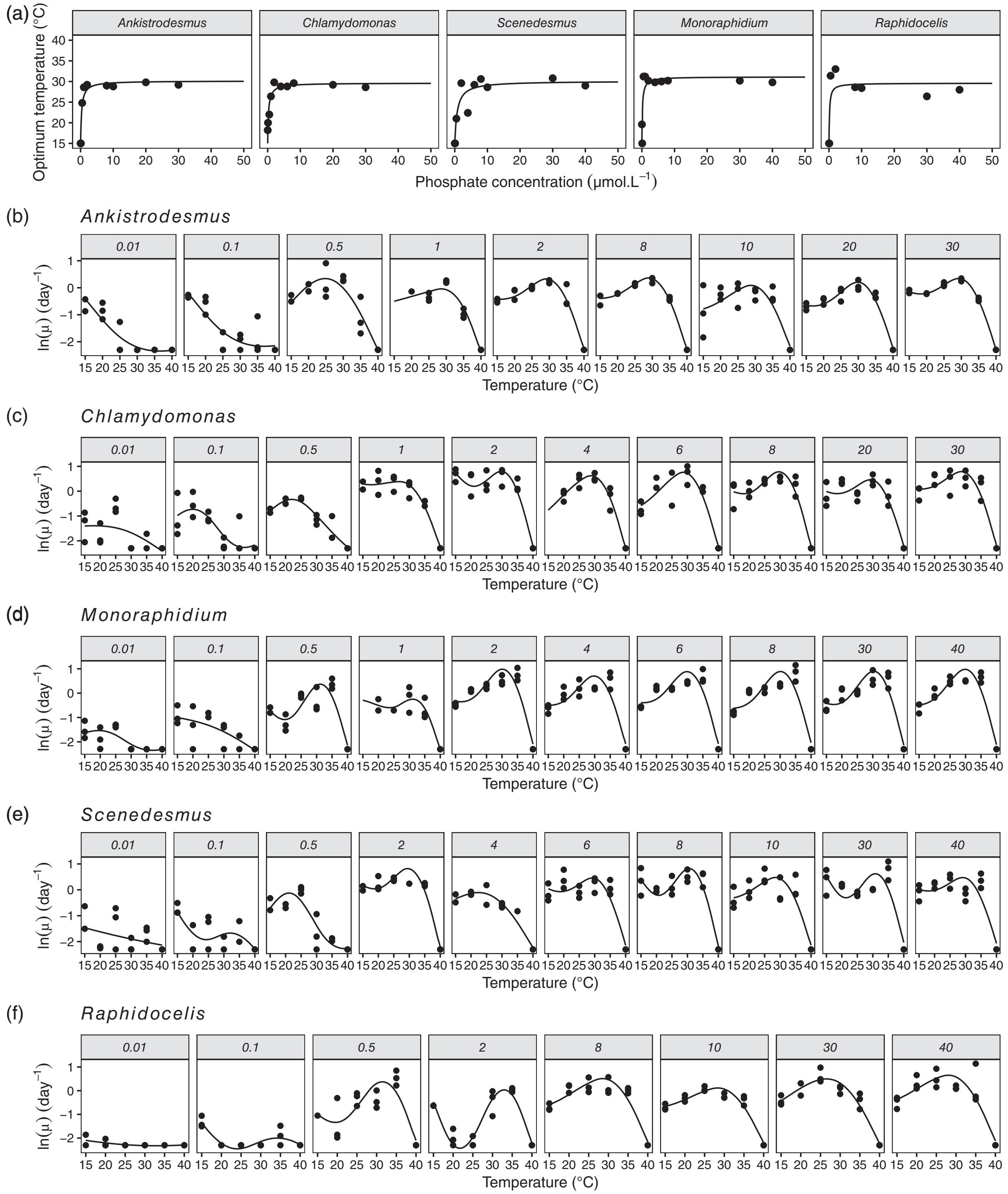

Fig. 2. (**a**) Thermal optimum T_{opt} is a saturating function of phosphate concentration for each species. (**b–f**) Growth rates as a function of temperature for each species by phosphate concentration. Lines are from the best fitting GAM model quantifying the coupling between the natural logarithm of growth rate as a function of temperature.

study highlighted the potential for other stressors to profoundly alter the way temperature change affects algal physiology; however, this proof of concept was only done on one marine species. It is now necessary to understand whether these findings can be generalized to other species of phytoplankton. Here, we address this gap by investigating how changes in phosphate concentrations affect the thermal tolerance of five species of freshwater phytoplankton.

Methods

Nonaxenic strains of five phytoplankton species, *Ankistrodesmus nannoselene, Chlamydomonas moewusii, Monoraphidium minutum, Scenedesmus obliquus,* and *Raphidocelis subcapitata*, were obtained from the Culture Collection of Algae and Protozoa (www.ccap.ac.uk, Supporting Information Table S1). Stocks of each strain were cultured in standard COMBO medium without animal trace elements (Kilham et al. 1998) in semi-continuous cultures in incubators at 15°C on a 12 : 12 light–dark cycle with 90 μmol m^{-2} s^{-1} light intensity. Cultures were transferred weekly to keep them in the exponential phase of growth. These conditions allowed healthy culturing of the samples under exponential, nutrient replete growth conditions until the start of the experiment. We then measured growth rates of each of the five species over a 1-month long experiment at 13 phosphate concentrations and six temperatures, each with three replicates, yielding a total of 1170 cultures. Due to the large number of cultures, we did not perform preacclimation of the cultures to each condition before measuring growth rate.

We created 13 solutions of different phosphate concentrations ranging from 0.01 μmol L^{-1} to 50 μmol L^{-1} of phosphate by mixing different amounts of COMBO medium with and without potassium phosphate dibasic (Supporting Information Table S2). This range is relevant to phosphate concentrations commonly found in North American and European temperate lakes (Downing and McCauley 1992; Cardoso et al. 2007; *see* Supporting Information Table S3), and to the nutrient physiology of these species (half-saturation constant for growth at 15°C ranged from 0.002 μmol L^{-1} to 0.274 μmol L^{-1} with all five species at saturating growth conditions by 10 μmol L^{-1}; Bestion et al. 2018). Because we focused on the impact of a limitation in phosphate concentration, we did not simultaneously vary nitrate concentrations to avoid confounding effects of complex colimitation. By design, this means that not only phosphate concentration but also the N : P stoichiometry covaried in the experiment. Small tissue culture flasks (Nunclon™) filled with 40 mL of each solution were inoculated with each species in monoculture at 100 cells mL^{-1}. To avoid potential-carry over, where phosphorus taken in excess by cells before the experiment would allow algae to grow even at low experimental phosphate concentrations, we inoculated cells at very low density and ensured that the increase in phosphate concentration due to the inoculum volume (8 μL of sample at 5 × 10^5 cells mL^{-1}) or to potential intracellular storage of phosphate was minimal (0.01 μmol L^{-1} P). Samples were incubated in Percival incubators at 15°C, 20°C, 25°C, 30°C, 35°C, and 40°C on a 12 : 12 light–dark cycle with 90 μmol m^{-2} s^{-1} light intensity. The range of temperatures was chosen to encompass the likely optimum temperature for growth at saturating nutrient conditions in these species, within the 25–35°C range commonly observed for freshwater green algae, including other strains of the same species or the same genus (Bouterfas et al. 2002; Hodaifa et al. 2010; Litchman et al. 2010; Lürling et al. 2013; Bestion et al. 2018). The light intensity was consistent with the long-term culture conditions of these strains. Cultures were manually shaken and their position in the incubator was randomly changed daily. Every 2 d, a 200 μL sample was taken, preserved by adding 10 μL of 1% sorbitol solution as a cryoprotectant, and frozen at −80°C. Cell density was estimated by counting 10 μL of each sample on fast flux settings (66 μL min^{-1}) on a flow cytometer (BD Accuri C6).

Statistical analyses

Specific growth rate, μ, for each sample was calculated by fitting the logarithm of population density $\log_{10}$(cells mL^{-1}) to the Buchanan three-phase linear growth model (Buchanan et al. 1997) using nonlinear least squares regression (*see* Supporting Information Methods for a more in-depth description of the statistics).

We used generalized additive models (GAMs) to quantify the thermal tolerance curves. For each species and phosphate level, we fitted a GAM of $\ln(\mu)$ with temperature as a smoother term (*see* Supporting Information Methods). Using these fits, we then estimated the optimal temperature, T_{opt}, as the temperature at which $\ln(\mu)$ was maximal.

We fitted T_{opt} for each species at each phosphate concentration against a modified Monod equation (Monod 1949)

$$T_{\text{opt}} = T_{\text{opt.min}} + \left(T_{\text{opt.max}} - T_{\text{opt.min}}\right) * \left(\frac{S}{K_s + S}\right)$$

where $T_{\text{opt.max}}$ is the temperature at which the specific growth rate is maximal (°C), $T_{\text{opt.min}}$ is the temperature at which the specific growth rate is the minimum when the concentration of nutrients S is zero (here fixed at 15°C as it was the minimum temperature in the assays), S the concentration of phosphate in the culture (μmol L^{-1}), and K_s the half-saturation coefficient for T_{opt} (μmol L^{-1}).

Results and discussion

Growth rate followed a unimodal function of temperature and a saturating function of phosphate concentration (Fig. 2a–f). Optimum temperatures for growth followed a saturating function of phosphate concentration in each species (Fig. 2). The saturating function was a better fit than either a linear model or an intercept-only (i.e., no nutrient-dependence of T_{opt}) model (ΔAICc >> 2 in both cases, Table 1). Under nutrient replete conditions, T_{opt} ranged from 29.6°C to 31.1°C (Table 1), falling within the 25–35°C range commonly observed for freshwater green algae (Bouterfas et al. 2002; Hodaifa et al. 2010; Litchman et al. 2010; Lürling et al. 2013). Studies on species of the same genera have for instance shown a 32.5°C optimum for *Ankistrodesmus falcatus*

(Lürling et al. 2013), a 27.5°C optimum for *Chlamydomonas reinhardtii*, *M. minutum*, and *Scenedesmus acuminatus* (Lürling et al. 2013) while *Selenastrum minutum* and *Scenedesmus maximus* had a 35°C optimum (Bouterfas et al. 2002; Lürling et al. 2013) and estimates for *Scenedesmus obliquus* varied between 27.5 and 29.5 depending on the study (Hodaifa et al. 2010; Lürling et al. 2013). However, under limiting phosphate concentrations, optimum temperature for growth drastically dropped to values as low as 15°C. The drop in T_{opt} with nutrient limitation may even be underestimated, as our measurements were carried out in the 15–40°C range and some T_{opt} for the lower nutrient concentrations were likely below 15°C. Indeed, in these cases, the highest performance was observed at 15°C, meaning we measured only the decreasing part of the performance curve. Thus our measured T_{opt} at 15°C represented the highest possible value for T_{opt} and the true T_{opt} value could be anywhere between 0°C and 15°C (Fig. 2b–f). A higher number of temperature levels would have yielded a more precise estimate of T_{opt}. However, given the magnitude of the decrease in T_{opt} under low-nutrient conditions, the low number of temperature treatments should not affect the general patterns we observe. Further, given the large scale of the experimental design, we were unable to preacclimate each species to each of the phosphate and temperature conditions. Although we took every precaution to avoid carry-over, where phosphate stocked in excess would allow cells to grow faster even at low temperature, this possibility cannot be discarded. However, potential for carry-over of phosphate would only lead to a reduced impact of phosphate limitation on thermal optimum, and thus to a higher than reported half-saturation constant. The half-saturation constants for T_{opt} varied between 0.18 μmol L^{-1} and 0.33 μmol L^{-1}, which suggests important effects on thermal physiology at nutrient concentrations relevant to phosphate concentration commonly found in northern hemisphere temperate lakes (approximately 0.01 μmol L^{-1} to 150 μmol L^{-1} in North American lakes, with a quarter of the lakes having a phosphate concentration below 0.12 μmol L^{-1}, below the observed half-saturation constant for T_{opt} (Downing and McCauley 1992; Downing et al. 2001), and 0–0.36 μmol L^{-1} in European lakes, with more than 50% of the lakes below 0.19 μmol L^{-1}, close to the minimum saturating concentration for T_{opt} (Cardoso et al. 2007; Supporting Information Table S3). Higher saturation constants would mean that the impacts of phosphate limitation on thermal optimum would arise even faster than expected.

Our results expand previous results on a marine species by Thomas et al. (2017). We investigated a different group of phytoplankton (green algae from two different orders (Sphaeropleales and Chlamydomonadales) from a different ecosystem type (freshwater vs. marine), and our findings suggest that decreases in optimum temperatures at low-nutrient concentrations are likely to be a general phenomenon (Downing et al. 2001). Interestingly, although the study from Thomas et al. (2017) assumed that the half-saturation constant for growth was independent of temperature, a previous study on the same strains showed that half-saturation constant varied with temperature (Bestion et al. 2018), suggesting that this condition is not needed for the nutrient-dependence of thermal optimum to arise. Over the range of phosphate concentrations investigated, optimum temperatures decreased by up to 15°C (Fig. 1, Supporting Information Table S4). This shift is substantially larger than observed in *T. pseudonana* (Thomas et al. 2017), where T_{opt} declined by 3.5°C under phosphate limitation and 6°C under nitrate limitation. This larger decrease could be due in part to the lower phosphate concentrations used in this study compared to the Thomas et al. study (the lowest concentrations being respectively 0.01 μmol L^{-1} and 1 μmol L^{-1}). Restricting our data to the

Table 1. Parameters returned from fitting the Monod model to the coupling between T_{opt} and the phosphate concentration. The table compares the small sample size corrected Akaike information criterion, AICc, of the Monod model to the AICc of a simple linear model and no nutrient-dependence of T_{opt}. The 95% confidence intervals for the parameters are given within brackets.

Species	$T_{\mathrm{opt.\ max}}$	K_s	AICc	Quasi R^2	AICc linear model $T_{\mathrm{opt}} \sim$ phosp	AICc linear model $T_{\mathrm{opt}} \sim 1$
Ankistrodesmus	30.14	0.33	43.99	0.92	65.10	63.09
	[27.98, 32.3]	[0.04, 0.62]				
Chlamydomonas	29.62	0.28	44.91	0.87	64.14	62.59
	[27.86, 31.39]	[0.05, 0.52]				
Monoraphidium	31.12	0.18	58.67	0.70	70.96	67.57
	[27.9, 34.34]	[−0.1, 0.46]				
Scenedesmus	30.11	0.75	54.55	0.84	70.58	69.80
	[26.85, 33.36]	[−0.27, 1.76]				
Raphidocelis	29.59	0.17	54.44	0.67	64.14	59.01
	[24.9, 34.29]	[−0.24, 0.57]				

same phosphate concentrations gave a 2.1–6.5°C decline in T_{opt} depending on species identity, higher than the drop found by Thomas et al. (2017) for two out of five species (Supporting Information Table S4). Alternatively, it might be due to a greater sensitivity of our freshwater green algae to phosphorus concentrations, as phosphate limitation is thought to be particularly important in freshwater ecosystems, specifically in lakes (Schindler 1977; Hecky and Kilham 1988; Elser et al. 2007), while nitrogen regulation has been thought to play a major role in oceanic systems (Falkowski 1997). Together, these results reveal striking declines in T_{opt} at phosphate concentrations that are commonly found in natural environments.

Reduced thermal tolerance under nutrient limited conditions may have important consequences for the impacts of environmental warming on phytoplankton communities. Indeed, in some locations, climate change is leading to longer periods of water stratification and thus nutrient depletion in lakes and oceans (Coma et al. 2009; Kraemer et al. 2015). In Lake Tahoe, warming waters led to nutrient depletion in the euphotic layer, causing a selection toward smaller cell sizes in diatom communities (Winder et al. 2009). Further, in Europe, the Water Framework Directive has led to 34% declines in soluble reactive phosphate (Dokulil and Teubner 2010), which are predicted to continue until 2030 (Seitzinger et al. 2010). On the other hand, some lakes and coastal marine ecosystems will see an increase in nutrient concentrations due to eutrophication (Bonsdorff et al. 1997; Ye et al. 2011), that will likely be exacerbated by extreme precipitation events brought about by climate change (Dokulil and Teubner 2010; Sinha et al. 2017). Furthermore, climate change might lead to changes in land use which could either reduce or increase eutrophication as changing climates will make some practices unsustainable (Heino et al. 2009). These complex socio-ecological interactions make impacts of climate change on water quality quite highly unpredictable and variable at the local scales (Heino et al. 2009; Dokulil and Teubner 2010). In locations where climate change is linked to lower nutrient availability (e.g., due to water stratification or land-use changes), or in oligotrophic systems (as the > 25% North American and > 50% European lakes where phosphate concentration is below K_S, Supporting Information Table S3), the combination of increased temperature and low nutrient availability might be strongly detrimental for some species. On the contrary, phytoplankton species in eutrophic systems (e.g., the 25% most eutrophic North American lakes, Supporting Information Table S3; where eutrophication is predicted to increase, Seitzinger et al. 2010) are likely to be less susceptible to warming.

Further; it should be noted that although all of the species were affected, the impact of nutrient limitation on T_{opt} varied between species, with some species showing a drop in T_{opt} at higher nutrient concentrations (higher K_s) than others (Fig. 1, Supporting Information Table S4). The combination of stressors might alter community composition through differential impacts on phytoplankton species. Together with the combined impacts of climate and nutrients on competitive interactions below T_{opt} (Tilman et al. 1981; Litchman et al. 2010; Bestion et al. 2018), these complex effects might also affect phytoplankton community structure.

Overall, we found consistent declines in thermal tolerance among six species of freshwater green algae that are in line with recent work on a marine diatom (Thomas et al. 2017). Together this work emphasizes the importance of considering the potential impact of multiple stressors when quantifying thermal tolerance. Indeed, this body of work suggests that phytoplankton are highly sensitive to a combination of high temperature and low nutrients. Trend of rising global temperatures are therefore particularly worrying when accompanied by nutrient limitation—e.g., when the vertical stratification in lakes and oceans reduces nutrient supply (Behrenfeld et al. 2006) or when land-use change lead to reoligotrophication (Anneville et al. 2005), or in already oligotrophic lakes (such as the 50% of European lakes where phosphate concentration is currently below 0.18 μmol L^{-1} [Supporting Information Table S3] and for which eutrophication is predicted to decrease; Seitzinger et al. 2010). Our results therefore suggest that failing to account for nutrient-temperature interactions might severely underestimate species' vulnerability to future environmental change.

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