Feedbacks between phytoplankton and nutrient cycles in a warming ocean

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Climate warming increasingly drives changes in large-scale ocean physics and biogeochemistry, and affects the kinetics of biological reactions. Together these factors govern phytoplankton productivity, thereby shaping the responses of ocean carbon and nutrient cycles to global change. Here we bring together results from experimental, observational and modelling studies to highlight how interactive feedbacks between warming and nutrient limitation can affect the responses of biogeochemically critical marine primary producers. The availability of many bioactive elements in seawater will be altered markedly in the future, thereby shifting resource deficiencies. These modifications to nutrient limitation when compounded by concurrent warming can change phytoplankton optimum growth temperatures and elemental use efficiencies in group-specific and nutrient-specific ways. The biogeochemical impacts of these nutrient and warming interactions reflect a distinction between the thermal reactivity of major cellular structural elements like nitrogen (N) and catalytic micronutrients like iron (Fe). Integrating the mechanistic feedbacks between warming, nutrient availability and primary productivity into Earth system models is necessary to improve confidence in projections of ocean biogeochemical cycle transformations in a changing climate.

Planktonic primary producers underpin key ocean ecosystem services because they play a central role in supporting marine nutrient cycling, carbon sequestration and biological resources. Accordingly, phytoplankton primary producers are critical to the grand challenge of forecasting, managing and mitigating the impacts of climate change on ocean ecosystem services. Moreover, there is growing interest in responding to insufficient cuts in fossil fuel emissions via ocean carbon dioxide removal approaches such as alkalinity enhancement, ocean afforestation and iron fertilization, which raises the urgency of understanding the implications of downstream impacts on phytoplankton[1,2]. Phytoplankton growth rates, abundance and productivity in a changing climate will integrate environmental drivers including temperature and key resources such as nitrogen (N), phosphorus (P) and iron (Fe), alongside feedbacks associated with factors like grazing, light limitation and ocean acidification[3–5]. Most Earth system models (ESMs) have emphasized the role of physically driven changes due to a

warming climate[6]. Here we focus instead on the role of phytoplankton as lynchpins of ocean biogeochemistry, and specifically on how their physiological responses to warming may shape nutrient cycles, with implications for improved forecasting of changing marine ecosystems using ESMs.

Climate warming and nutrient supply

The Intergovernmental Panel on Climate Change (IPCC) sixth assessment reports that sea surface temperatures (SSTs) have been increasing since the 1950s[7], with isotherms moving generally poleward at a rate of over 20 km per decade since the 1960s[8]. Future projections vary with the emissions scenario, ranging from 1 to 3 °C greater for low and high emissions scenarios, respectively[7]. Importantly, the inter-model agreement for SST changes is high, especially relative to net primary productivity (NPP)[9]. This progressive anthropogenic warming of the upper ocean is augmented by episodic marine heatwaves that are

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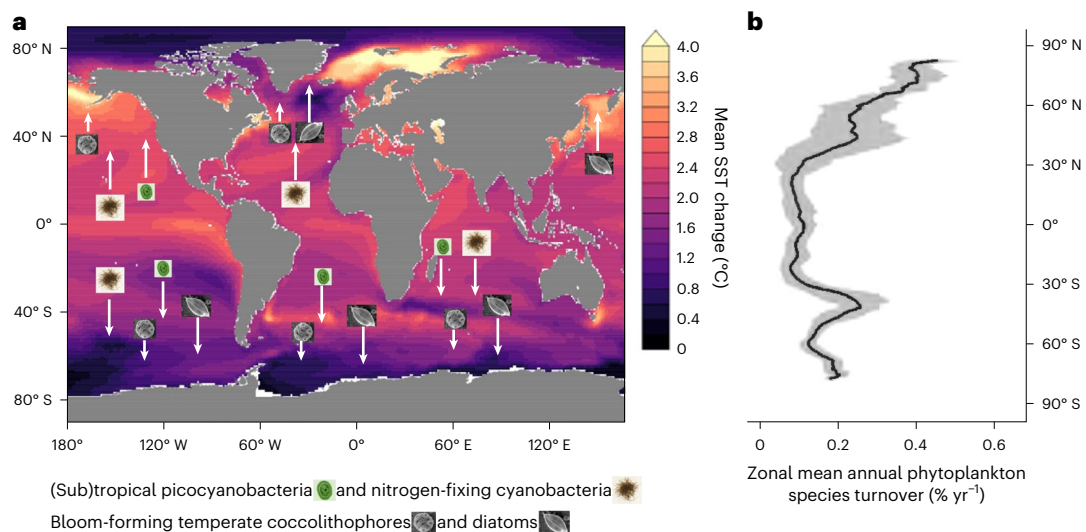
Fig. 1 | Projected poleward shifts in distributions of biogeochemically important phytoplankton functional groups with extreme warming.
a, Projected phytoplankton biogeographic trends[23,34] superimposed on an IPCC Atlas multi-model projection[17] of mean SST change (°C) in 2081–2100 relative to 1850–1900. Most phytoplankton groups will move towards higher latitudes in a warmer ocean, but the nature of these shifts will differ. Poleward migration of temperate coccolithophores may be constrained by ocean acidification in the polar oceans, while temperate diatoms may more successfully invade these highest latitudes. Tropical picocyanobacteria and nitrogen-fixing cyanobacteria expand into warming temperate regimes, but may be displaced from lower latitudes by excessive warming. **b**, Projected zonal average annual phytoplankton species turnover (% per year), based on the Jaccard dissimilarity index between 2012–2031 and 2081–2100 (from ref. 31). Grey shading indicates the standard deviation around the mean value (black line). Panel **b** reproduced with permission from ref. 31, Springer Nature Ltd.

increasing in their frequency, intensity and duration[7,10], with implications for marine ecosystems and microbial biodiversity[8,11]. These ongoing and future changes in ocean warming will directly impact phytoplankton, but will also interact with other climate forcings such as wind and freshwater fluxes to affect nutrient supplies to upper ocean ecosystems via the depth of mixing and stratification, a measure of the vertical density gradient. Synthesis of observations across 1970–2018 shows summertime mixed-layer depths are both stratifying and getting deeper (especially in the Southern Ocean) in response to parallel changes in warming and winds[12]. These results imply quantitative and qualitative alterations in the supply routes by which nutrients are transferred to surface biological communities from deeper nutrient reserves that operate alongside warming SSTs. Climate models project that stratification will strengthen further in response to rising emissions, but there is less confidence in the projections of shallower mixed-layer depths in the future, especially at high latitudes[7] that are also affected by changes in the cryosphere[13]. In parallel, there are changes to N and Fe supplies due to anthropogenic inputs from the atmosphere in many marine regimes[14,15], and Fe supplies from wildfires have become more important in recent decades[16].

Ultimately, being able to confidently forecast changes in ocean biogeochemistry requires us to link environmental shifts such as changing SSTs and nutrient levels with phytoplankton metabolisms. Both direct changes in temperature[17] and indirect impacts on resource availability due to warming will vary between tropical, temperate and polar ecosystems (Fig. 1). At present, ESMs take broadly similar approaches in their representation of the responses of microbial growth and primary production to environmental change[4,18,19] (Supplementary Information). These models, which are a focus of this Review, usually assume that the traits governing the responses of key functional groups (for example, nutrient affinities or thermal limits) are fixed. Changes in key metabolisms such as primary production and N_2 fixation are then driven by how SST directly affects growth rates, or via modifications to the ocean physical mixing that alters resource limitation[4,6,19]. Not accounting for microbial adaptation and acclimation of both thermal sensitivities and nutrient requirements is thus a crucial knowledge gap[20] that contributes to the current overall low confidence in future projections of NPP and biogeochemical cycles[4].

Phytoplankton responses to warming

Inherent differences in the thermal sensitivities of dominant microbial groups will greatly affect how ocean biogeochemical cycles respond to a warming climate. Photosynthetic diatoms dominate the marine silicon cycle, support productive fisheries and are especially efficient at exporting fixed carbon from surface to deep water via sinking particles (the 'biological pump')[21]. Although distributed worldwide, diatoms are most often the dominant phytoplankton group in cool, nutrient-rich environments such as high- and mid-latitude upwelling systems. This may be owing to the notable temperature sensitivity of the nitrate reductase enzyme they use to access this predominant form of bioavailable N in these regions[22]. Thus, these mid- and high-latitude diatom groups may be disadvantaged under the warmer, lower-NO_3 conditions that will become more widespread in the future temperate and subpolar oceans[9,23], and diatom nutrient stress may be further exacerbated by parallel declines in the availability of silicon[24] (Fig. 1).

The precipitation of calcium carbonate shells by the coccolithophore phytoplankton group has an important influence on the global carbon cycle. Although coccolithophore species diversity is highest in the warm oceans[25], remote sensing calcite reflectance imagery shows that major bloom-forming species are commonly associated with cooler SSTs in regions such as the North Atlantic, the Bering Sea and the sub-Antarctic Ocean[23] (Fig. 1). Recently these dense regional coccolithophore blooms have shifted poleward, probably in response to moderate SST warming trends[26–28]. However, projected extreme temperature increases of 3 °C or more may also result in the loss of some of these bloom-forming coccolithophore species from lower latitudes[23], as documented for many coccolithophores during past greenhouse warming events such as the Palaeocene–Eocene Thermal Maximum[29]. The high-density calcium carbonate plates that cover coccolithophore cells provide ballast when they become incorporated into detrital aggregates, thereby increasing the sinking rates and export of organic carbon. Thus, more coccolithophores at high latitudes and/or fewer

at low latitudes may cause basin-scale changes in the distributions of both organic and inorganic carbon export to the deep ocean by the biological pump (Fig. 1). Coccolithophore biomineralization sometimes exceeds their production of organic carbon by photosynthesis and thereby causes a net consumption of seawater alkalinity[30], suggesting that declining coccolithophore abundance could act to mitigate ocean acidification to some extent.

Thus, many currently dominant diatoms and coccolithophores are likely to experience substantial poleward shifts under accelerated warming scenarios. Future phytoplankton community changes are consequently likely to be greatest at high latitudes[31] (Fig. 1b), and the influences of these functional groups on the ocean biogeochemical cycles of silicon, carbon and alkalinity will be displaced closer to the margins of the Arctic and Southern Oceans. Impacts on coccolithophores may be exacerbated further as the polar seas are especially prone to altered saturation states of calcium carbonate due to ocean acidification[13], inhibiting formation of their mineral shells[32] and so potentially constraining their ability to migrate into truly polar regimes.

In contrast to the ecological dominance of many bloom-forming diatoms and coccolithophores in cooler waters, tiny but abundant picocyanobacteria are typically favoured by warm temperatures[23]. Picocyanobacteria play a dominant role in nutrient recycling throughout the vast central gyres of the ocean. Other cyanobacteria specialize in fixing atmospheric nitrogen gas (diazotrophy), and so provide critical supplies of this essential nutrient to nitrogen-depleted subtropical marine ecosystems[33]. Like other phytoplankton groups, both diazotrophic and non-N_2-fixing cyanobacteria are also experiencing poleward range shifts in response to ocean warming (Fig. 1a), extending the area where they strongly influence the ocean nitrogen and carbon cycles to higher latitudes[23,34,35]. Nevertheless, even some warmth-loving cyanobacteria may find the future low-latitude tropical ocean to be too hot for their thermal tolerances, and they could potentially decline in the warmest parts of their current ranges[34,36,37] (Fig. 1a).

However, such broad generalizations about biological responses to greenhouse warming can sometimes be misleading, as some populations of diatoms[38] and cyanobacteria[39] possess a surprising amount of previously unsuspected thermal microdiversity. Thus, strains or ecotypes that will have an advantage under future warmer conditions may already exist unrecognized within today's phytoplankton. Microorganisms can also acquire new adaptations quickly due to their rapid generation times and very large population sizes, and experimental evolution studies demonstrate increases in thermal tolerance under long-term selection by elevated temperature in diatoms[40], coccolithophores[32,41] and nitrogen-fixing cyanobacteria[42]. Either existing thermal diversity or selection for novel high-temperature adaptations could help phytoplankton populations to cope with a warmer climate, while still maintaining their ecological niches and key functional roles in ocean biogeochemical cycles. This would imply that assessments of the exclusion of nitrogen fixation from the warmest parts of the ocean predicted by ESMs[34] and culture experiments[36,37] may be overly pessimistic.

Warming and phytoplankton nutrient requirements

The relationship between rising temperatures and nutrient limitation of phytoplankton remains uncertain, even as it underpins modelled projections of changes in biogeochemical cycles and marine ecosystems[4,6,9]. Marine primary productivity throughout ~60–70% of the ocean is limited by availability of the major nutrient nitrogen (N), while the micronutrient iron (Fe) is the main limiting nutrient in most other marine ecosystems, including the biogeochemically important Southern Ocean[3]. Phosphorus (P) can limit phytoplankton communities in a few areas such as the Mediterranean Sea[3], while both Fe and P limitations are common and widespread for nitrogen-fixing cyanobacteria[33]. Phytoplankton seldom entirely escape nutrient limitation in most

Table 1 | The relative thermal sensitivity of cellular metabolic pathways in cyanobacteria

Cellular components and metabolic pathways	Nitrogen-enriched (N:C)	Phosphorus-enriched (P:C)	Iron-enriched (Fe:C)
Cell membrane (phospholipids[a])		↑	
Storage compounds (cyanophycin[a], ferritin[a] or phosphate granules[a])	↑	↑	↑
Nucleic acids (DNA[a], messenger RNA[a])	↑	↑	
Photosynthesis and carbon fixation (antennae pigments[b], electron carriers[a], enzymes[b])	↑		↑
Respiration (electron carriers[a], enzymes[b])			↑
Enzyme catalysis (nitrogenase[b], nitrate/nitrite reductase[b], superoxide dismutase[b])	↑		↑
Protein synthesis (ribosomes[b])	↑	↑	
Energy metabolism (adenosine triphosphate hydrolysis[b])	↑	↑	

[a]Relatively thermally resilient cellular components. [b]Metabolic pathways with potentially thermally sensitive rates. Listed are macromolecular or ultrastructural components that are notably enriched in the nutrients N, Fe or P in cyanobacteria, and whether they are primarily involved in [b]relatively temperature-sensitive catalytic processes or [a]relatively thermally resilient structural, storage, genetic and electron transfer uses. Arrows illustrate that their synthesis or increased abundance should tend to increase cellular N:C, P:C or Fe:C ratios, as well as demand for uptake of these nutrients. Some cellular pathways and components are different in eukaryotic phytoplankton, but the distinction between 'structural' and 'catalytic' nutrients is similar. Data summarized from refs. 20,45,50,51,80–84.

oceanic environments[3], though, raising questions about the results of classic temperature response experiments that used nutrient-replete phytoplankton cultures[43].

Our understanding of marine biogeochemistry has historically revolved around phytoplankton elemental stoichiometry, particularly the idealized Redfield ratio[44] of 106 C:16 N:1 P. However, large deviations from the Redfield ratio are the rule rather than the exception[3], and this considerable stoichiometric flexibility provides insights into temperature and nutrient limitation relationships. Phytoplankton community C:N, C:P and N:P ratios are often twice as high in the warm, oligotrophic central gyres as in cold, nutrient-rich high-latitude regions[45]. These latitudinal trends in plankton stoichiometry may be largely temperature-driven[46], suggesting they may shift spatially in a warming ocean. However, other work highlights nutrient supply variability as a major driver in addition to temperature[47]. In observational studies, it can be difficult to distinguish the effects of temperature on phytoplankton elemental ratios from those of co-varying nutrient availability[48].

Thermally mediated changes in elemental ratios are also linked to the macromolecular composition of phytoplankton. Thermal effects on requirements for the catalytic micronutrient Fe, which is located largely in temperature-sensitive enzymes[22,49], can differ considerably from the interactions of temperature with major nutrients such as N that are used to a larger extent in relatively thermally resilient ultrastructural, storage and genetic macromolecules (Table 1). Phosphorus can behave much like Fe in this respect due to its major requirement for ribosomal RNA in protein-synthesizing ribosomes[50,51] (Table 1). The protein translation rates of ribosomes are thermally dependent, so phytoplankton require fewer ribosomes and thus less cellular P as temperatures rise[51]. This 'temperature-dependent translation efficiency model' has been invoked to explain lower phytoplankton P:C
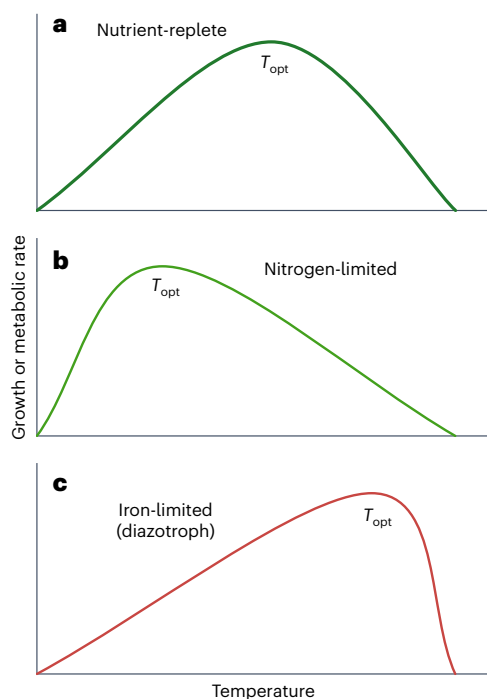
Fig. 2 | Idealized temperature response curves for growth and metabolic rates relative to nutrient availability in phytoplankton. a–c, Typical curves for nutrient-replete cells[51,56,62] (**a**), nitrogen-limited cells[56] (**b**) and iron-limited cells (specifically for the diazotrophic cyanobacterium *Trichodesmium*; **c**)[62]. Decreasing trends in T_{opt} under N limitation and increasing trends in T_{opt} under Fe limitation in the diazotroph are depicted.

ratios at higher temperatures[48,51] (Table 1). Phytoplankton N:P ratios also tend to rise with warming, probably due to both less demand for P-rich ribosomal RNA and greater production of N-rich proteins as temperatures rise[47,52,53].

Recently, marine microbiologists have moved away from nutrient-replete experiments and have instead tested the biological effects of warming under more realistic nutrient-limited conditions. For the major nutrient N, the temperature and nutrient relationship is often an antagonistic one, with N limitation diminishing the positive effects of warming on phytoplankton growth rates[54]. Conversely, warming can magnify the growth-inhibiting effects of N limitation in phytoplankton communities[55,56]. However, the physiological context of increasing temperature matters greatly. Warming is typically beneficial up to a species' thermal optimum for growth (T_{opt}), but quickly becomes deleterious above this temperature (Fig. 2). N or P limitation can reduce this optimum growth temperature tipping point[56], potentially making phytoplankton more susceptible to thermal stress (Fig. 2a,b). Similarly, both the optimum growth point and maximum thermal limit of many Southern Ocean diatoms can be lower under prevailing Fe-limited conditions, making them more vulnerable to warming[57].

Some ecologically dominant diatoms require less cellular Fe under moderate levels of warming[58–60], allowing them to substantially increase their cellular iron use efficiencies (IUEs, the rate of carbon fixation per unit of cellular iron; Fig. 3). These positive thermal responses of diatom IUEs may be a competitive advantage in Fe-limited regimes, with potentially large consequences for carbon export and nutrient cycling[61]. As the polar ocean warms, it remains to be seen how lower thermal growth optima in Fe-limited Southern Ocean diatoms[57] may interact with simultaneously increased IUEs[59,60] (Fig. 3) to affect elemental cycling.

N₂-fixing (diazotrophic) cyanobacteria must frequently contend with Fe limitation, as the nitrogen-fixing nitrogenase enzyme has a very high catalytic Fe content[22,33]. However, the responses of

diazotrophic cyanobacteria to combined Fe stress and warming are distinct from those of N-limited phytoplankton. Under simultaneous Fe limitation and warming, the optimum growth temperature of the globally distributed colonial *Trichodesmium* increases rather than decreases[62] (Fig. 2c), while that of the unicellular *Crocosphaera* remains unchanged[63]. This could be because both of these biogeochemically prominent N₂ fixers greatly increase their IUEs at higher temperatures[62,63] (Fig. 3), which may help them to cope with future warmer, Fe-limited oceans[19]. Whether other lesser-studied marine diazotrophs such as symbiotic cyanobacteria and non-photosynthetic N₂-fixing bacteria will respond similarly remains to be determined[33].

These positive interactions between Fe and warming in diazotrophic cyanobacteria may be due to this element's main catalytic role in their nitrogenase enzyme. Enzyme substrate turnover rates typically increase with temperature up to some maximum rate, without any need for increases in catalytic co-factor content[22]. N is, however, a major structural component of amino acids comprising all of the proteins in the cell[22,50]. This may make cellular N quotas and use efficiencies less sensitive to warming than those of Fe. A fundamental distinction between catalytic and structural elements may be a useful way to consider the responses of nutrient biogeochemistry in a warmer ocean (Table 1).

Phosphorus is required for synthesis of nucleic acids (especially ribosomal RNA), adenosine triphosphate, cell membranes and some proteins[50,51] (Table 1). As for N, the ability of phytoplankton to grow at elevated temperatures can be compromised by P limitation[56]. Like IUEs, though, phosphorus use efficiencies (PUEs; carbon or nitrogen fixation rate per unit of cellular P) of phytoplankton generally increase with warming up to their thermal optimum[63–65]. In fact, PUE increases with temperature in a strikingly linear fashion for N₂ fixation in the cyanobacterium *Trichodesmium*[64] (Fig. 4a) as well as for CO₂ fixation by the coccolithophore *Emiliana huxleyi*[65] (Fig. 4b), possibly lending itself to straightforward parameterization in models. Like Fe, the ability to use cellular P more efficiently may offer some photosynthetic microorganisms relief from nutrient limitation as the ocean warms. For the frequently P-limited nitrogen-fixing cyanobacteria, this advantage will probably be especially significant for major biogeochemical cycles[33,63].

Improving ESMs

Along with altered physical nutrient supplies, the influence of warming on the physiology and thermal niches of phytoplankton will operate to change nutrient biogeochemistry in a changing climate. Thermal effects on nutrient utilization will vary depending on the groups of microorganisms involved, and thereby influence specific
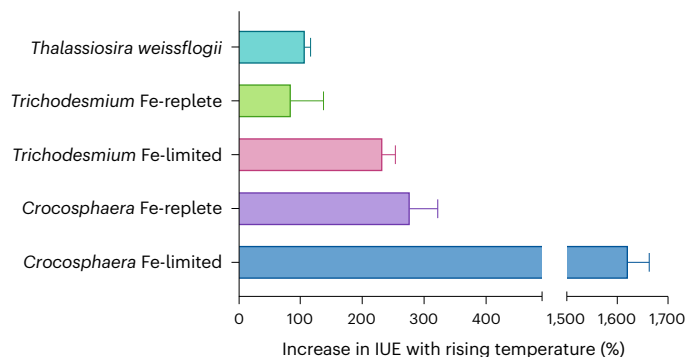

Fig. 3 | Effects of warming on phytoplankton IUEs. Per cent increase in IUE (mol C fixed h⁻¹ mol cellular Fe⁻¹) with temperature increase for the temperate diatom *Thalassiosira weissflogii* (from 10 to 20 °C)[60], and in Fe-replete and Fe-limited cultures of the diazotrophic cyanobacteria *Trichodesmium* (from 27 to 32 °C)[62] and *Crocosphaera* (from 22 to 27 °C)[63]. Bars and error bars represent means and standard deviations of per cent change in triplicate cultures, respectively. Data from refs. 60,62,63.
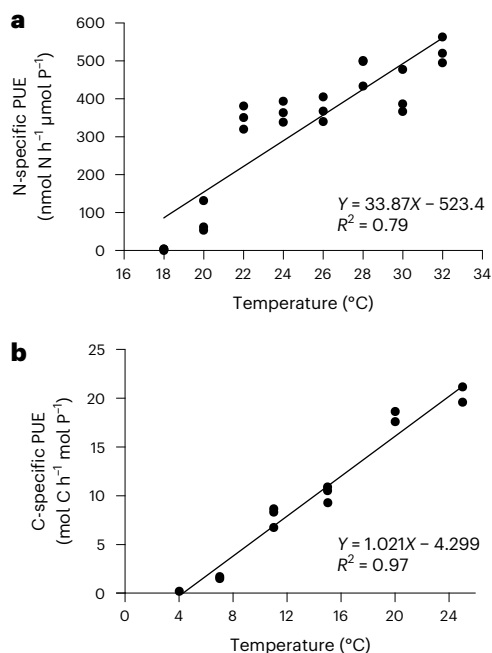
Fig. 4 | Phytoplankton PUEs increase linearly with temperature.
a, N_2-fixation-specific PUE (mol N fixed h^{-1} mol cellular P^{-1}) of the diazotrophic cyanobacterium *Trichodesmium erythraeum* from 18 to 32 °C. Data from ref. 64.
b, C-fixation-specific PUE (mol C fixed h^{-1} mol cellular P^{-1}) of the coccolithophore *Emiliana huxleyi* from 4 to 24 °C. Data points represent the PUEs of three replicates for each temperature treatment, and the lines and equations represent multiple linear regressions. Data from ref. 65.

biogeochemical processes such as primary production, nitrogen fixation, silicification, calcification and carbon export. Although this Review focuses on phytoplankton due to their central importance in both nutrient and carbon biogeochemistry, rising temperature and changes in substrate availability will also affect the metabolisms of other key microbial groups such as nitrifying and denitrifying bacteria and archaea, with additional biogeochemical implications that are still being explored[33]. Other limiting factors, such as light or inorganic carbon chemistry, may also come into play. Thus, we need to better constrain how phytoplankton physiology will be altered in response to feedbacks between temperature and nutrient availability (Fig. 5). In the short term, a promising pathway towards first-order quantifications of the large-scale implications for biogeochemical cycles is to focus on aspects of physiology already represented in some of the more advanced ESMs such as required resource quotas, and parameterize their sensitivity to other modelled properties like temperature or nutrient limitation.

One general principle for nutrient-limited phytoplankton is that their optimum growth temperatures often decline, so warming may particularly displace nutrient-stressed populations to cooler regimes. Such biogeographic shifts will occur alongside climate-driven displacements of isotherms[31,66,67], resulting in poleward shifts in the characteristic roles of specific biogeochemical functional groups (Fig. 1). A meta-analysis shows that temperatures in the regimes where tropical phytoplankton species grow are already very close to their upper thermal limits, and that future extreme warming could thus exclude them from the lowest, hottest latitudes[36]. If so, how and when these biogeochemical niches in the tropics will be filled remains speculative at this stage. However, it is unlikely that critical microbially mediated elemental cycling processes will disappear abruptly, as might be expected from nutrient limitation or thermal limits thresholds used in ESMs[68]. Instead, natural selection and rapid microbial evolution[20,40–42,69] will enable new, more thermally tolerant variants or species, and

thus maintain functional redundancy for key steps in future ocean biogeochemical cycles. Of course, there is no guarantee that the novel marine assemblages that emerge from these adaptive replacements will retain their current societal resource value.

Although ESMs are now integral to our understanding of the global carbon cycle, progress is required before they can reliably quantify the broader carbon and biogeochemical consequences of the interactions between warming and nutrients raised in this Review. This is important because it indicates that we have an incomplete understanding regarding the future of the key biogeochemical cycles mediated by phytoplankton. Nevertheless, the ocean components of ESMs are excellent tools to assess how detailed aspects of phytoplankton physiology may make contributions to elemental cycling and important carbon cycle fluxes such as NPP and export. In the context of a changing climate, ESMs can quantify the sensitivity of these key biogeochemical functions to specific modelled processes. For example, model sensitivity experiments have shown the importance of shifts in nitrogen fixation[68] and Fe and N limitation feedbacks[70] to climate-driven trends in NPP for climate scenarios. In addition, sensitivity tests focusing on present-day and end-of-century climate states have been used to assess interactions between CO_2 and either light or temperature, particularly for modelled phytoplankton functional types[71]. As described above, there is the potential for similar targeted sensitivity studies to begin to assess the interactive influences of warming and changing nutrient availability. However, the outcome of these exercises depends entirely on the structure of the model concerned, and we currently lack insight into whether the sensitivity to a given process is similar for models of different structural complexity.
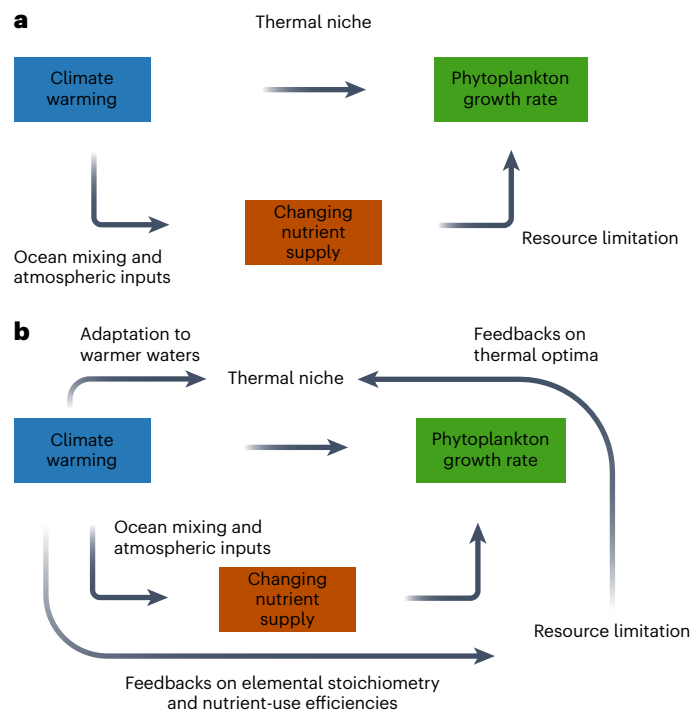

Fig. 5 | Developing improved ESMs of ocean warming and nutrient interactions. a, Standard ESM treatment of temperature and nutrient controls on phytoplankton growth and biogeochemistry, showing currently recognized direct links between warming and physical changes in nutrient supply, and phytoplankton thermal niches and nutrient responses modelled as fixed traits. **b**, Evolving ESM approach highlighting the dynamic interplay between warming and nutrient availability, including flexible elemental stoichiometry, variable nutrient-use efficiencies, modulation of thermal optima by nutrients and evolution of phytoplankton in a warmer ocean. Resulting positive and negative feedbacks can govern the responses of phytoplankton growth and productivity, leading to major shifts in global biogeochemistry.

Here we have emphasized issues related to how ESMs represent phytoplankton physiology and its interaction with rising temperatures, but of equal importance may be their simplification of ecological interactions. ESMs often present very coarse granularity in their resolution of specific taxa, and so lack explicit representation of biogeochemically and ecologically important phytoplankton groups such as dinoflagellates, coccolithophores and diazotrophs. ESMs that consider only generic groups of 'diatoms' or 'picophytoplankton', or that present only rudimentary treatments of grazing and competition, may undermine their representation of the complex communities that make up ecosystems.

The evidence presented here argues that ESMs using thermal performance curves that ignore feedbacks between nutrient limitation and thermal responses may neglect important aspects of the impacts of future climate change on biogeochemistry. Modelling experiments are needed to quantify the potential importance of shifts in thermal optima due to nutrient limitation across different functional groups, and to incorporate evolutionary processes for different climate change scenarios. Greater focus on how ESMs represent nutrient limitation in a changing ocean in particular may be facilitated by newly emerging large-scale biogeochemical and molecular datasets[72–74]. Overall, progress is required in terms of our conceptual understanding of key mechanisms in order to develop tools of appropriate complexity that are capable of addressing the issues at hand. Ultimately it may be that the inherent structure of ocean biogeochemical models and their broad reliance on concepts such as fixed stoichiometry and the 'law of the minimum', and on inflexible traits such as inherent thermal limits and nutrient affinities, is simply too rigid to accommodate the complexity emerging from observations and experiments. Clearly, innovation beyond the state of the art will be required[75].

Integrating climate, nutrients and primary productivity

Meeting the grand challenge of predicting the responses of microbially mediated marine elemental cycling to climate change will require biogeochemists and modellers to work across disciplinary boundaries. Exciting recent developments in ocean observing[76] and large-scale sampling programmes for bioactive elements[77] have provided a greatly expanded overview of global ocean biogeochemistry. Molecular biological techniques also now offer unprecedented observations of the regulatory machinery of key microbial nutrient and carbon transformation processes[78]. Critically, renewed emphasis on manipulative experiments will be needed to put these macro- and microscale correlational approaches into perspective, by providing unambiguous cause-and-effect mechanistic evidence[79]. Expanded observational capacity is needed, but it cannot come without the parallel expansion of process-oriented understanding that is particularly lacking in the areas emphasized in this Review. Ultimately, the mechanistic insights gained from all these diverse approaches will need to be integrated into improved climate projections and ESM assessments[6,9]. Looking forward, advancements may include greater development of coupled metabolic- or genome-based modelling efforts at global scales[47,74,80,81], and the generation of mechanistically informed parameterizations of the key tradeoffs that can be embedded in current ESM structures. This integrated approach is uniquely suited to make rapid progress via efficient co-design across the modelling, observational and experimental communities, and provide holistic projections of the impacts of climate change on biogeochemistry at the level of uncertainty required by policymakers.

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Competing interests

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