SPECIAL FEATURE – ESSAY REVIEW
WHETHER IN LIFE OR IN DEATH: FRESH PERSPECTIVES ON HOW PLANTS AFFECT BIOGEOCHEMICAL CYCLING

Global biogeochemical impacts of phytoplankton: a trait-based perspective

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Summary

1. Phytoplankton are key players in the global carbon cycle, contributing about half of global primary productivity. Within the phytoplankton, functional groups (characterized by distinct traits) have impacts on other major biogeochemical cycles, such as nitrogen, phosphorus and silica. Changes in phytoplankton community structure, resulting from the unique environmental sensitivities of these groups, may significantly alter elemental cycling from local to global scales.

2. We review key traits that distinguish major phytoplankton functional groups, how they affect biogeochemistry and how the links between community structure and biogeochemical cycles are modelled.

3. Finally, we explore how global environmental change will affect phytoplankton communities, from the traits of individual species to the relative abundance of functional groups, and how that, in turn, may alter biogeochemical cycles.

4. *Synthesis*. We can increase our mechanistic understanding of the links between the community structure of primary producers and biogeochemistry by focusing on traits determining functional group responses to the environment (response traits) and their biogeochemical functions (effect traits). Identifying trade-offs including allometric and phylogenetic constraints among traits will help parameterize predictive biogeochemical models, enhancing our ability to anticipate the consequences of global change.

Key-words: aquatic plant ecology, biogeochemical cycles, cell size, functional groups, global change, phytoplankton community structure, trade-offs

Introduction

Understanding the links between the structure of primary producer communities and biogeochemistry is an important research frontier bridging community and ecosystem ecology.

Such research is especially important as rapid, human-driven changes in our environment affect primary producer communities and, ultimately, global biogeochemical cycles. Phytoplankton are major aquatic primary producers, responsible for about half of global primary productivity each year (Field *et al.* 1998). They are key contributors to biogeochemical cycles, both at present and over the long history of our planet,

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and are the subject of extensive experimental, observational and theoretical attention. Fully appreciating the role of phytoplankton in elemental cycling requires characterizing their diversity that encompasses two domains of life and several distinct functional groups. These groups differ in how the environment influences their growth, in the elements and their ratios that the groups consume and excrete, and, therefore, in their effects on biogeochemistry. We argue that establishing effective, mechanistic links between community and ecosystem ecology requires characterizing the traits that define these groups and their environmental sensitivities. Ultimately, this kind of trait-based approach can provide critical insights into the biogeochemical function of aquatic and terrestrial communities, both now and in our increasingly human-impacted world. In this review, we describe major phytoplankton groups (including their history, traits and involvement in biogeochemical cycling), how these groups have been incorporated in biogeochemical models, and discuss how they may be affected by global change.

What are the advantages of trait-based approaches? Traits capture aspects of physiology, morphology and life history that influence fitness and competitive success. Resource utilization traits connect species abundances and growth with the chemical compounds that are most limiting for metabolic processes, thereby linking ecological processes (species and community dynamics) with biogeochemical processes through species performance. For example, the rate at which a cell can take up phosphorus is an important determinant of its competitive ability in environments where phosphorus limits growth. Integrated over the community, these uptake rates feed back to influence external phosphorus concentrations. In other cases, the link between biogeochemistry and ecological success is less direct, and it may be useful to distinguish between traits that affect biogeochemical cycles (effect traits) and the traits that determine how abundances of these groups would respond to changing conditions (response traits) (Lavorel & Garnier 2002). Many phytoplankton traits are both response and effect traits, but many are only one or the other. For example, the optimal temperature for growth is a purely response trait (because temperature affects growth but not vice versa), and carbon export efficiency is an effect trait that is not tightly linked to a particular response trait. Understanding how response and effect traits are related will allow us to understand the links between the community structure of primary producers and biogeochemistry in a mechanistic way.

Many groups of primary producers differ both in their response and effect traits and, consequently, may have different impacts on biogeochemical cycling. For example, free living or symbiotic nitrogen-fixers can fix atmospheric nitrogen (N) and do not require other forms of N. Thus, their N response traits are distinct from those of non-N-fixers. While non-fixers consume available N, N-fixers can significantly increase N concentration in the environment (soil or water), thus having contrasting N effect traits as well. The N fixation response and effect traits are tightly linked, which is true for other resource acquisition traits.

Different traits are often not independent but connected by trade-offs, and these trade-offs determine how community structure and coexistence change under different conditions, with concomitant changes in biogeochemical processes. N-fixers are often thought to have high phosphorus requirements compared to other groups and thus exhibit a trade-off between N and P competitive abilities (Lenton & Klausmeier 2007). This trade-off can lead to coexistence of N-fixers and non-fixers and can explain shifts in community composition with changing N: P ratios. Similar trade-offs between N fixation and competitive abilities for light or iron may also be important (Agawin *et al.* 2007; de Tezanos Pinto & Litchman 2010; Ward *et al.* 2013). Whether N-fixers occur under particular conditions has many biogeochemical consequences, because it determines how much 'new' nitrogen is being added to the ocean, because it affects the stoichiometry of organic matter exported to the deep ocean and because fixed N can be released into the environment and consumed by other primary producers and other microbes.

In this review, we focus on biogeochemically relevant traits and trade-offs to discuss what is known about the feedbacks between phytoplankton community structure and biogeochemistry, with the hope that some of these ideas can also be applied to terrestrial plants. We begin by reviewing the distinct biogeochemical signatures and impacts of the major taxonomic groups of phytoplankton. Next, we discuss modelling approaches that link phytoplankton community structure and key traits to biogeochemical cycles. Finally, we describe major global change stressors in aquatic environments and discuss how they can change phytoplankton communities, selecting for groups and species with certain traits, with consequences for biogeochemistry.

Major phytoplankton groups and their biogeochemical signatures

Phytoplankton are a paraphyletic group of photoautotrophs with a complex evolutionary history extending across 2.5–3.5 billion years (Olson & Blankenship 2004; Yoon *et al.* 2004). Despite this paraphyly, they fall into evolutionarily distinct functional groups, including one major prokaryotic group (the cyanobacteria) and a number of eukaryotic groups (diatoms, green algae, coccolithophorids, dinoflagellates and others).

The evolution of oxygenic photosynthesis in cyanobacteria was a major advance in metabolic strategy that changed the fate of our planet forever. This major evolutionary innovation likely happened only once and changed the atmosphere of our planet from anoxic to oxygenic after two billion years in the former state (Knoll 2003). Vast amounts of solar energy were subsequently channelled into driving geochemical cycles (Rosing *et al.* 2006), reducing atmospheric carbon dioxide to a wide range of organic substances (Holmén 1992). Significant quantities of molecular oxygen started to accumulate in the atmosphere about 2.2–2.4 billion years ago (Catling & Zahnle 2002; Holland 2006). The timing of Earth's oxygenation coincided with the disappearance of large non-mass-dependent

sulphur isotope (^{33}S and ^{36}S) fractionations (Holland 2006) and of iron banded formations (Isley & Abbott 1999), showing the impacts of oxygenation on other element cycles.

This process of oxygenation was largely driven by the cyanobacteria, which remained the dominant phytoplankton for well over a billion years and strongly influence elemental cycles today. They are the only phytoplanktonic group with members capable of atmospheric nitrogen fixation (the absence of N fixation in eukaryotes is poorly understood, Schopf 1983) that has a major impact on global nitrogen cycle. Nitrogen fixation is one of the most metabolically expensive processes in biology (16 ATPs are hydrolysed per N_2 fixed) (Simpson & Burris 1984) and is crucial for Earth's nitrogen budget and primary productivity. The evolution of the ability to fix nitrogen is thought to be extremely ancient (Staley & Orians 1992), possibly older than oxygenic photosynthesis. Several authors infer that the nitrogenase family had already evolved in the last common ancestor of extant organisms (Normand *et al.* 1992; Fani, Gallo & Lio 2000), though another hypothesis suggests a later origin (see Raymond *et al.* 2004). Because nitrogen fixation is a process highly sensitive to the presence of oxygen, the evolution of oxygenic photosynthesis posed a major physiological burden on nitrogen fixation in cyanobacteria. This limitation was overcome by fixing nitrogen during the night (in the absence of oxygen production), hence separating N fixation and photosynthesis in time. Another strategy was the separation of photosynthesis and N fixation in space, by performing N fixation in anaerobic specialized cells, heterocysts, during daylight and photosynthesis in vegetative cells. There could still be other undiscovered strategies.

Marine cyanobacteria are responsible for 25–50% of natural (i.e. not anthropogenic via the Haber–Bosch process) global nitrogen fixation, or approximately $4.5–9 \times 10^{12}$ mol N year^{-1} (Mahaffey, Michaels & Capone 2005; Canfield, Glazer & Falkowski 2010; Zehr 2011). This spatial extent of nitrogen fixation is limited both by temperature (Staal, Meysman & Stal 2003) and by the availability of iron, which is needed for the production of the nitrogenase enzyme (Berman-Frank *et al.* 2001; Kustka *et al.* 2003). Consequently, nitrogen fixation occurs most strongly in the tropical and subtropical oceans, and in regions with high Fe: N ratios (Monteiro, Dutkiewicz & Follows 2011; Ward *et al.* 2013). The process of nitrogen fixation is leaky; between 50 and 90% of fixed nitrogen may be released to surrounding waters in the form of dissolved organic nitrogen (Glibert & Bronk 1994; Mulholland & Bernhardt 2005), thereby subsidizing non-fixers. The cyanobacteria possess the highest N: P ratio of any phytoplankton group, with an average N: P ratio of around 22:1, relative to 13:1 in eukaryotic taxa (data compiled from earlier studies by Deutsch & Weber 2012). This is considerably higher in the nitrogen-fixing *Trichodesmium* sp., which may be >40:1 due to the high nitrogen requirement for light-harvesting machinery (Letelier & Karl 1996; data compiled from earlier studies by Klausmeier *et al.* 2004). Although nitrogen fixation is a unique trait of cyanobacteria, not all cyanobacteria fix nitrogen. Among those that do not,

Prochlorococcus and *Synechococcus* play an important role in the carbon cycle, because they are major components of the photosynthetic biomass in the oligotrophic oceans (Johnson *et al.* 2006).

The eukaryotic taxa originated with the engulfment of a cyanobacterium by a heterotrophic protozoan, leading to the formation of a symbiotic relationship between the two, approximately 1.5 billion years ago (Yoon *et al.* 2004). The endosymbiotic cyanobacterium subsequently evolved into the contemporary chloroplast. Thereafter, this eukaryotic clade diverged into green and red lineages that differ based on their pigment composition (Delwiche 1999). Subsequent engulfment of these green and red eukaryotes by heterotrophs led to secondary and even tertiary endosymbioses: diatoms, for example, are the product of an endosymbiotic event between a heterotroph and a red alga (Archibald & Keeling 2002). As a consequence, contemporary eukaryotic phytoplankton are composed of two superfamilies. The green superfamily contains the green algae and groups formed by the engulfment of a green alga by a heterotroph, such as the euglenophytes. The red superfamily contains the red algae (now largely benthic) and groups containing red plastids, including diatoms, cryptophytes and coccolithophores. While both green and red superfamilies primarily use chlorophyll *a*, the former also possesses chlorophyll *b*, while the latter uses chlorophyll *c* and several accessory pigments that absorb blue and green wavelengths (Falkowski *et al.* 2004; Katz *et al.* 2004).

The eukaryotic superfamilies exhibit distinct stoichiometries from each other and the cyanobacteria. Members of the green superfamily possess higher C: P and N: P ratios than their counterparts in the red superfamily as well as higher requirements for some micronutrients (Fe, Cu and Zn) and lower requirements for others (Cd, Co and Mn; Quigg *et al.* 2003). These differences in stoichiometry are thought to be related to oceanic environmental conditions when these groups diversified, and have important implications for biogeographic patterns in ocean N: P ratios, which they both influence and are influenced by Weber & Deutsch (2010). Because functional groups also differ in their response to other environmental variables (characterized by their traits), environment-driven shifts in functional group composition are likely to drive changes in biogeochemical cycles due to shifts in the average cell stoichiometry. We discuss a few of the major eukaryotic groups here, but note that other less studied groups may be of considerable biogeochemical importance, though we lack data with which to draw broad conclusions. These include the non-calcifying haptophytes, chrysophytes, cryptophytes, raphidophytes, rhodophytes and euglenophytes, among others.

Green algae, the group that gave rise to terrestrial plants, evolved >1 billion years ago and comprised a large proportion of the phytoplankton community till the Mesozoic era, approximately 250 million years ago. Thereafter, they declined in abundance and diversity in the oceans, being apparently out-competed by members of the red superfamily groups that began to rise in prominence (Falkowski *et al.* 2004; Katz *et al.* 2004). This decline has been linked to changes in the redox state of the oceans, with their high trace

metal requirements possibly constraining their present marine distribution and diversity (they remain abundant, diverse and broadly distributed in freshwaters). Unlike the other groups described here, they perform no distinctive biogeochemical functions to our knowledge. They are thought to be exceptionally plastic in their biomass N: P ratio, but this is based largely on experiments with a single freshwater species, *Scenedesmus* sp. (Rhee 1978).

Coccolithophorids first occur in the fossil record approximately 220 million years ago and rose to prominence through the Mesozoic era and then declined in diversity as the diatoms diversified (Bown, Lees & Young 2004; Falkowski *et al.* 2004; Katz *et al.* 2004). They form a major portion of high latitude phytoplankton communities today, with massive blooms of one major species, *Emiliania huxleyi*, occurring over areas of hundreds of thousands of square kilometres (Brown & Podestá 1997). They play a dominant role among the phytoplankton in the marine calcium cycle through the formation of calcium carbonate plates (coccoliths), which are responsible for the formation of calcium carbonate rock formations across the globe. Although coccolith sinking may be expected to lead to considerable carbon export, the extent of the export is a function of sea floor depth and calcium compensation depth. If the ocean floor is lower than the compensation depth, coccoliths dissolve, returning carbon to the water. In total, they are thought to be responsible for approximately 10% of carbon export to the deep ocean (Jin *et al.* 2006). At the same time, calcification reduces total alkalinity, reducing the ability of the surface ocean to take up atmospheric CO_2 (Passow and Carlson 2012). Coccolithophores also produce dimethylsulfoniopropionate (DMSP), a precursor to dimethyl sulphide (DMS), a cloud condensation nucleus. Though there is a clear mechanistic link between coccolithophorid growth and climate in this case, the evidence for it as a regulator of climate is weak, though it may still play a minor role (Charlson *et al.* 1987; Ayers & Cainey 2007; Quinn & Bates 2011; Rap *et al.* 2013).

Diatoms are believed to have originated 160–200 million years ago and diversified strongly in the past 60 million years, at the expense of other groups (Kooistra & Medlin 1996; Falkowski *et al.* 2004; Sims, Mann & Medlin 2006). Their recent dominance may be a result of their ability to store pulses of nutrients in a large vacuole supported by the silica cell wall and/or protection from predation accorded by their silica shells (Smetacek 1999; Thingstad *et al.* 2005; Litchman, Klausmeier & Yoshiyama 2009). As other functional groups do not use silica, the ability to compete for this element does not contribute to their success against other functional groups, but may contribute towards determining which diatom species predominate. Globally, they play a dominant role in the carbon cycle, contributing an estimated 20–25% of global primary productivity (Nelson *et al.* 1995; Smetacek 1999). Their relatively large cell sizes lead to a high sinking rate which contributes to major portion of carbon export to the deep oceans (Nelson *et al.* 1995). They are also the primary phytoplankton group associated with the global silica cycle (with silicoflagellates playing a minor role). This uptake of silica is responsible for the undersaturation of silica in the surface oceans and leads to the burial of 6.3×10^{12} mol Si year^{-1} through sinking (Tréguer & De La Rocha 2013). They have low N: P ratios characteristic of the red superfamily, with an average of approximately 10:1 (Sarthou *et al.* 2005), and are most abundant in unstable, nutrient-rich waters with similarly low N:P ratios, typically at high latitudes and in coastal oceans (Arrigo 2005).

Dinoflagellates belong to the red superfamily and became a major component of the phytoplankton community over 200 million years ago, but have decreased in diversity over the past 40–60 million years (Katz *et al.* 2004). They exhibit exceptionally complex genomes and metabolic capabilities: members of this motile group exhibit mixotrophy (and even pure heterotrophy), toxin production, bioluminescence and tertiary endosymbiosis with complex symbionts such as diatoms and prasinophytes (Wisecaver & Hackett 2011). Despite belonging to the red superfamily, they also contain members that have appropriated plastids belonging to the green lineage (Falkowski *et al.* 2004). They possess among the largest phytoplankton cells and are typically poor competitors for nutrients and slow growers under autotrophic conditions (Litchman *et al.* 2007); mixotrophy allows them to persist despite this inefficiency, particularly in environments with high nutrient and organic matter concentrations.

Biogeochemical models of phytoplankton functional types

Biogeochemical models aim to explain how biogeochemical cycles operate today and operated in the past, and predict how they will respond to anthropogenic stressors such as climate change. Much of the foundational and current work on marine ecosystem models has used a NPZ (nutrient–phytoplankton–zooplankton) structure, where phytoplankton are modelled as a single population that consumes a single limiting nutrient (typically representing nitrogen) and are consumed by a single zooplankton population (Evans and Parslow 1985, Fasham *et al.* 1990, Franks 2002). NPZ models are formulated and parameterized by combining laboratory data on plankton traits, field observations of bulk stocks and rates, and theoretical considerations such as dynamical stability. Although they greatly simplify biological complexity, NPZ models are useful for theoretical exploration and have successfully represented ecosystem patterns in many situations (Franks 2002). More complex models have been developed to address questions such as the role of multiple limiting nutrients and their biogeochemical coupling, because iron, phosphorus and silicon may all limit phytoplankton growth in addition to nitrogen (Flynn 2003, Moore *et al.* 2013).

It has also become clear that incorporating the functional diversity of phytoplankton is important for modelling biogeochemical cycles, because community structure varies greatly in time and space, and different kinds of phytoplankton have distinct effects on carbon fixation and export, as well as the cycling of N and Si among other elements (Le Quéré *et al.* 2005, Hood *et al.* 2006). The most common way biogeo-

chemical models have incorporated functional diversity is by including multiple plankton functional types (PFTs) in the ecosystem (Le Quéré *et al.* 2005). These types are given parameters that represent response traits and effect traits, with values derived from laboratory and field experiments, guesses based on observed distributions and *post hoc* tuning to bring modelled distributions in line with the available data (Moore *et al.* 2002; Aumont *et al.* 2003; Gregg *et al.* 2003; Le Quéré *et al.* 2005; Litchman *et al.* 2006). We cannot review all approaches to modelling PFTs in this article, but we will compare a number of representative models to explain how trait variation is translated into model parameterization.

Plankton functional types models are an excellent first step to introducing trait diversity into biogeochemical models, due to the distinct roles of these types in biogeochemical cycles, but still neglect finer-scale diversity within each group. There are additional emerging trait-based modelling frameworks that can include greater trait diversity. These include random selections from a high-dimensional trait space (Follows *et al.* 2007), continuous trait distributions parameterized with putative trade-offs (Bruggeman & Kooijman 2007; Ward *et al.* 2012), flexible physiological allocation strategies (Klausmeier *et al.* 2004; Clark *et al.* 2013), optimality approaches (Smith *et al.* 2011) and approaches from evolutionary game theory (Litchman, Klausmeier & Yoshiyama 2009). The focus of these fully trait-based approaches shifts from modelling the dynamics and distribution of species or functional groups to modelling the distribution of traits. Synthesizing these more flexible approaches with distinct functional categories will likely be an important future direction, although realistic parameterization of multi-dimensional trait variation among multiple groups remains a significant empirical challenge.

A major form of functional diversity derives from phytoplankton cell size. Cell volume varies over nine orders of magnitude and is a 'master trait' that affects metabolic rates, light absorption, nutrient uptake, sinking rate and interaction with grazers (Chisholm 1992, Litchman and Klausmeier 2008, Finkel *et al.* 2010). Size plays a central role in biogeochemistry because phytoplankton of different sizes have distinct biogeographies and effects on the carbon cycle. Models often incorporate this variation by using two or three size classes (Moore *et al.* 2002; Aumont *et al.* 2003; Blackford, Allen & Gilbert 2004), or by using functional types whose parameterization is based in part on size differences (e.g. mixed phytoplankton, diatoms, coccolithophores; Le Quéré *et al.* 2005). Smaller size classes are typically given lower half-saturation constants for nutrient-limited growth or nutrient uptake (Moore *et al.* 2002; Dutkiewicz, Follows & Bragg 2009; Buitenhuis, Hashioka & Le Quere 2013). This has the effect of making smaller phytoplankton better competitors for nutrients under chronic limitation, that is they have a lower R* (Tilman 1982, Litchman 2007, Litchman *et al.* 2007, Dutkiewicz, Follows & Bragg 2009). In models, a lower R* allows smaller phytoplankton to dominate in permanently stratified or chronically iron-limited regions (Moore *et al.* 2002; Dutkiewicz, Follows & Bragg 2009).

The higher nutrient affinity of smaller cells has a sound theoretical basis (Pasciak & Gavis 1974) with empirical support (Edwards *et al.* 2012). What traits allow larger phytoplankton to prosper in seasonal environments, upwelling regions and productive continental shelves, and how are these traits incorporated into biogeochemical models? Interestingly, this appears to be a somewhat unresolved question, as there are multiple mechanisms that could allow larger phytoplankton to become abundant, and some or all of these have been incorporated in different models. We summarize these mechanisms as follows:

1. Larger phytoplankton experience a lower per capita grazing rate, which allows them to become relatively more abundant if resources are not strongly limiting (Kiørboe 1993; Smetacek 1999).
2. Some larger phytoplankton (e.g. diatoms) have a higher maximum growth rate, which allows them to capitalize on transiently high nutrient concentrations (Marañón 2014).
3. Large phytoplankton (diatoms) have greater nutrient (nitrate) storage capabilities that afford a competitive advantage under fluctuating nutrient regimes (Litchman, Klausmeier & Yoshiyama 2009).
4. Small and large phytoplankton are eaten by different grazer species (different size classes of grazers). As nutrient supply increases, small phytoplankton are controlled by their grazers, leaving sufficient remaining nutrients for larger phytoplankton to persist (Armstrong 1994).
5. Larger phytoplankton are eaten by slower-growing metazoan grazers, which allows them to transiently escape grazing control when nutrients and light are sufficient (Irigoien 2005).

Different combinations of these mechanisms appear in different models. For example, Follows *et al.* (2007) have a larger diatom-like class and a smaller picocyanobacteria-like class, and the former is given a higher mean maximum growth rate. This allows them to dominate under variable nutrient supply, that is as 'opportunists' as opposed to the small 'gleaners' (Grover 1991; Dutkiewicz, Follows & Bragg 2009; Litchman, Klausmeier & Yoshiyama 2009). Although the general allometric trend is for larger species to grow more slowly (Edwards *et al.* 2012), the smallest phytoplankton tend to grow more slowly than intermediate-sized diatoms and coccolithophores (Ward *et al.* 2012; Marañón 2014), which is consistent with this modelling approach. This model also has two size classes of grazers, which will allow mechanisms 3 and 4 to operate as well. In contrast, in the biogeochemical element cycling model of Moore *et al.* (2002), the diatoms and nanophytoplankton have the same maximum growth rate and are eaten by the same grazer, but the grazer feeds more slowly on diatoms. This implies that mechanisms 1 and 4 can operate in this model.

Although size is a master trait that affects many ecological processes, there are other kinds of functional variation that are important for biogeochemical models. Diatoms, in addition to being relatively large on average, require silica for growth. This dependency is often modelled as an additional

nutrient limitation term, and this can cause their regional patterns of growth limitation to be distinct from other phytoplankton types, due to variation in the supply of Si relative to other elements (Moore *et al.* 2002; Aumont *et al.* 2003; Blackford, Allen & Gilbert 2004). They are also thought to contribute disproportionately to carbon export from the euphotic zone, due to a number of potential factors: their larger size (on average), the boom-and-bust phenology of some species, the 'ballasting' effect of the silica frustule and reduced grazing rates (Smetacek 1999; Assmy *et al.* 2013). Some of these effects will emerge naturally if the functional type representing diatoms is given a higher maximum growth rate or lower grazing rate, as described above. The increase in export due to larger size or ballasting can be modelled with an increased sinking rate of non-grazed and/or grazed biomass (Moore *et al.* 2002; Litchman *et al.* 2006; Follows *et al.* 2007).

Coccolithophores play a distinct biogeochemical role due to calcification and ballasting of organic matter and have a distinct (and likely varied) ecology that is still being unravelled (Boyd *et al.* 2010). Their traits have been modelled in a variety of ways, although a general aim is to reproduce the fact that they bloom under more stratified conditions than diatoms, but are likely poorer nutrient competitors than picophytoplankton. Gregg & Casey (2007) give coccolithophores a half-saturation constant for nitrogen-limited growth that is higher than that of cyanobacteria but lower than that of diatoms, as well as an intermediate maximum growth rate (which is highest for diatoms in this case) and a relatively high irradiance requirement. In this formulation, they essentially have an intermediate position on a gleaner–opportunist trade-off axis (Margalef 1978; Kudela 2010; Edwards, Klausmeier & Litchman 2013). In contrast, the PlankTOM10 model gives coccolithophores a relatively slow maximum growth rate, intermediate nutrient affinity traits and a minimum temperature threshold that is lower than that of the picocyanobacteria that are the best nutrient competitors (Kwiatkowski *et al.* 2014, http://lgmacweb.env.uea.ac.uk/green_ocean/model/code_description/PFT/fluxes.html). An increased efficiency of carbon export for coccolithophores, due to ballasting, can be implemented with a higher sinking rate (Moore *et al.* 2002; Gregg & Casey 2007).

Diatrophs (nitrogen-fixers) are an important functional type, due to their unique role in the nitrogen cycle. They are thought to prosper under extreme nitrogen limitation, while suffering a number of disadvantages described earlier. They are often modelled as having a relatively high iron requirement, which makes them poor competitors when iron supply is low relative to N and P (Moore *et al.* 2002; Ward *et al.* 2013). They are also typically given a low maximum growth rate, which means they cannot take advantage of variable nutrient supply (Tyrell 1999, Moore *et al.* 2002; Monteiro, Dutkiewicz & Follows 2011). It may also be important for diazotrophs to be poor P competitors (Tyrrell 1999; Lenton & Klausmeier 2007; Ward *et al.* 2013), although a relatively low P stoichiometry will at least partially offset this (Moore *et al.* 2002). In combination, these traits will lead to diazotroph occurrence in stably stratified regions with a low supply ratio of N: Fe and N: P (Ward *et al.* 2013). Although most ocean biogeochemical models represent diazotrophs by a single group, some models include different diazotroph types with distinct traits, such as filamentous *Trichodesmium*, unicellular N-fixers and symbiotic N-fixers living inside diatoms (e.g. Monteiro, Follows & Dutkiewicz 2010).

Responses of phytoplankton communities to global environmental change and implications for biogeochemistry

The many dimensions of global change are increasingly affecting marine environments and the phytoplankton communities that inhabit them. In the following section, we briefly summarize the most important aspects of the ocean that are changing, including temperature, acidity and nutrient availability. The traits and functions of phytoplankton groups and species determine both how they are affected by global change and how their responses in turn alter global biogeochemistry. In the remaining text, we discuss how global change stressors influence phytoplankton across different levels of biological organization from functional groups to species.

Global change is multifaceted and includes not just CO_2 emissions and climate change, but also anthropogenic effects that are independent of these factors. Acidification, rising temperatures and changes in the supply of nutrients and light will pose the greatest challenges for marine ecosystems and phytoplankton communities. Several reviews have examined these effects in greater detail (e.g. Hoegh-Guldberg & Bruno 2010; Boyd and Hutchins 2012, Doney *et al.* 2012), so our summary is brief. World-wide, oceans act as a major sink for both the rising levels of atmospheric CO_2 and the increased amount of heat trapped by this CO_2 and other greenhouse gasses. Nearly 1/3 of anthropogenic CO_2 is being absorbed into the oceans, where it interacts with water, altering seawater carbonate chemistry and driving ocean acidification (Riebesell 2004; Doney *et al.* 2009; Hoegh-Guldberg & Bruno 2010). Temperatures have risen by ~0.6 °C over the last 100 years within the surface layers of the ocean (Hoegh-Guldberg & Bruno 2010) and are predicted to increase by another 1–3 °C by the end of the century (IPCC; Collins *et al.* 2013). Temperature plays an important role in physical ocean processes, driving mixing, vertical stratification and currents. In tropical and temperate regions, warmer temperatures lead to stronger stratification and shallower mixed layers, simultaneously intensifying nutrient limitation and reducing light limitation (as plankton avoid being mixed to deeper, darker regions) (Beardall, Stojkovic & Larsen 2009). Regionally, warming may strengthen coastal upwelling and nutrient supply and alter the depth of mixing in polar oceans (Hoegh-Guldberg & Bruno 2010). Temperature and pH also influence the chemistry of seawater; changes in both of these variables will alter the solubility and oxidation state of trace metals such as iron in ways that are not yet fully understood (Hoffmann *et al.* 2012). These changes will be significant for marine organisms requiring these trace metals

often as catalysts for critical biochemical processes. The supply of more abundant (though no less important) nutrients such as nitrogen and phosphate is also being altered by human activities. This occurs most dramatically in coastal regions, through the influx of agricultural run-off and sediments from rivers, but also includes atmospheric deposition of dust and combustion by-products. Ultimately, these nutrients affect microbial communities producing areas of hypoxia, especially in coastal regions (Diaz & Rosenberg 2008), and altering biogeochemical processes. Finally, climate-driven changes in weather patterns and cloud cover, among other factors, alter the amount of light (and especially ultraviolet radiation) reaching and penetrating the ocean surface (Beardall, Stojkovic and Larsen 2009).

Adding to the complexity of global change is the fact that few environments will experience only one of these changing stressors: marine organisms may simultaneously face rising temperatures, changing nutrient levels and acidification (Halpern *et al.* 2008). The combined effects of multiple stressors can be non-additive and nonlinear, so global change studies for most environments or species must consider the effects of a suite of stressors (Crain, Kroeker & Halpern 2008; Boyd 2013; Boyd *et al.* 2015). Many aspects of global change also exhibit significant regional variability on top of underlying global trends (Hansen *et al.* 2006).

As complex as global change is, understanding its effects on phytoplankton and marine ecosystems presents an even greater challenge, because these ecological systems, composed of diverse and interacting species, are exceedingly complex in their own right. We can organize this complexity by considering how global change affects phytoplankton at different ecological resolutions, ranging from the collective response of the phytoplankton as a whole to the fine-scale reactions of individual species (Fig. 1). These categories roughly correspond to the level of detail included in different biogeochemical models of phytoplankton communities as discussed in 'biogeochemical models of phytoplankton functional types', which range from as coarse as one or a few functional groups, to dozens of species. Determining the appropriate level of detail to resolve is a critical open research question, which likely depends on which ecological or biogeochemical features are of interest, and the degree of precision required. The following discussion examines each of these categories in turn, starting with the broadest and most simplified view.

At the coarsest scale, briefly setting aside the particulars of species or functional group identity, photoautotrophs such as phytoplankton are united in their requirement for light, nutrients and CO_2 to support their growth and productivity. If basic requirements are either not met or dramatically exceeded (e.g. photoinhibition or nutrient toxicity), whether through regional variation or global change, growth and productivity are limited (Fig. 1a). Modelling studies that include a generic phytoplankton component, with parameters based on these requirements, improve biogeochemistry models and can reproduce empirical patterns of nutrient distributions (Kriest, Khatiwala & Oschlies 2010). They may also be able to crudely predict global
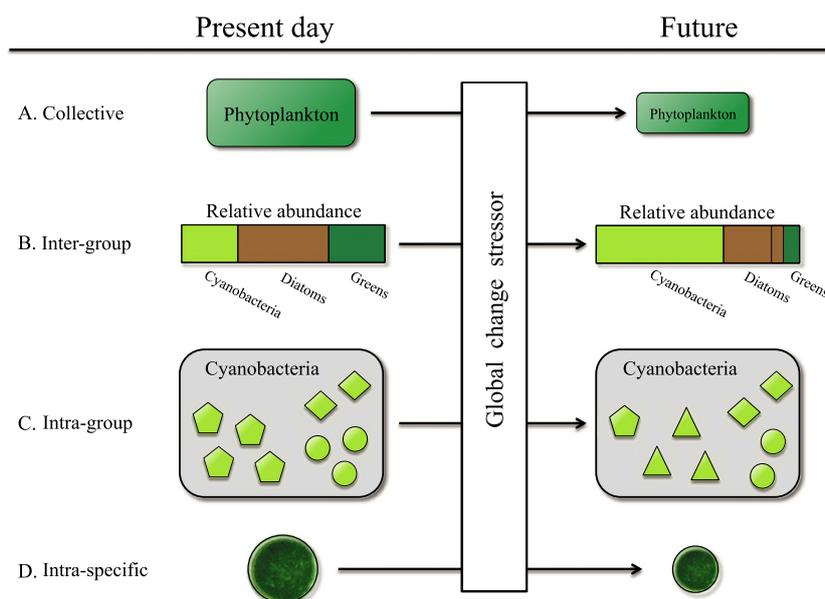

Fig. 1. The effects of global change on phytoplankton span nested levels of biological organization influencing the function of phytoplankton, including their contributions to biogeochemical cycles. For example, we can consider the consequences of increased nutrient limitation, at each scale: (a) Collective. Changes in bulk properties of phytoplankton, such as their productivity, can alter energy fluxes and carbon cycling. Increasing stratification can reduce productivity in temperate and tropical oceans. (b) Intergroup. Functional groups within phytoplankton communities can respond differently to shared stressors, altering their relative abundance. Diazotrophs may become more common in nitrogen-limited waters, altering N cycling. (c) Intragroup. Turnover in the identity and abundance of particular species within a group may alter its functioning. Nutrient limitation favours small-celled species, influencing rates of zooplankton predation and carbon export to the deep ocean. (d) Intraspecific. Individual species may change their traits and function as a result of global change, through plasticity or rapid evolution. As with C, this could lead to smaller cell sizes in the case of nutrient limitation.

change-driven shifts in the abundance, productivity and function of phytoplankton as a whole. Empirical evidence of such broad trends is actively being sought and evaluated. For example, studies combining *in situ* and satellite measurements of chlorophyll have shown a negative relationship between sea surface temperature and net primary productivity (from 1999 to 2004, Behrenfeld *et al.* 2006), and potential declines in productivity over the last 100 years (Boyce, Lewis & Worm 2010; but see McQuatters-Gollop *et al.* 2011 and Mackas 2012). The former result holds across three quarters of the world's permanently stratified oceans and is hypothesized to be driven by increases in stratification and nutrient limitation (Behrenfeld *et al.* 2006). However, these trends are debated; they are influenced by changes in instrumentation (Beaulieu *et al.* 2013) and may not be large enough to exceed the range of 'natural' background variability (Henson *et al.* 2010). If such trends hold, isolating and determining their causes may still require a more detailed description of phytoplankton communities. We next consider trait differences at the functional group level, highlighting how variation influences their response to different stressors, highlighting acidification and nutrient limitation as examples.

The distinct traits of different functional groups may cause functional groups to respond differently to global change stressors, altering their relative abundances, community function and ultimately global biogeochemical cycling (Fig. 1b) (Doney *et al.* 2009; Hoegh-Guldberg & Bruno 2010; Litchman *et al.* 2012). Functional groups differ in their ability to compete for CO_2, ranging from passive CO_2 uptake to sophisticated mechanisms for actively collecting CO_2 and bicarbonate (HCO_3^-). While many groups (including diatoms) are not carbon limited, others, such as the coccolithophorids, show dramatic increases in photosynthetic rate with increases in CO_2 (Rost *et al.* 2003; Riebesell 2004; Doney *et al.* 2012). Such trait differences likely explain shifts from diatom to coccolithophorid dominance due to CO_2 enrichment in mesocosm experiments (Riebesell 2004; Hoegh-Guldberg & Bruno 2010). Shifting elemental ratios within sedimenting particles in the North Atlantic suggest that abundances of diatoms and coccolithophores are already changing (Antia *et al.* 2001; Beardall, Stojkovic and Larsen 2009). While increased CO_2 appears to favour coccolithophorid growth, ocean acidification increases the difficulty and energetic costs of forming the calcium carbonate plates after which they are named. The ecological consequences of producing thinner, deformed shells due to acidification (Riebesell 2004; Hoegh-Guldberg & Bruno 2010) are not conclusively known, but may include increased susceptibility to predation. Ultimately, the net effect of these organisms on carbon cycling depends on the balance between carbon export to deep waters and carbon emissions during calcification, determined by interactions between their sensitivity to CO_2, acidification and competition with other groups (Riebesell 2004; Beardall, Stojkovic and Larsen 2009, Hoffmann *et al.* 2012).

Acidification is not the only stressor influencing the relative abundance of functional groups. Nutrient limitation, intensified by stratification due to rising temperatures, favours functional groups with traits required to compete effectively for nutrients or access unique resources. Major functional groups differ in their sizes: diatoms and dinoflagellates typically have cell volumes that are orders of magnitude larger than cyanobacteria, while green algae and haptophytes are intermediate in size (Diaz & Rosenberg 2008; Finkel *et al.* 2009). Large diatoms and other large-celled species perform well in seasonal environments with significant, albeit periodic, supplies of nutrients (Beardall, Stojkovic and Larsen 2009, Litchman, Klausmeier & Yoshiyama 2009). However, as stratification intensifies and nutrient-limited ocean regions expand with global change (Behrenfeld *et al.* 2006; Halpern *et al.* 2008; Irwin & Oliver 2009), smaller-celled species and groups and nitrogen-fixing cyanobacteria will be competitively favoured and increase in abundance at the expense of other groups, such as diatoms (Bopp *et al.* 2005; Crain, Kroeker & Halpern 2008; Morán *et al.* 2010). Potential increases in the abundances of nitrogen-fixers would have obvious, direct effects on nitrogen cycling. Changes in the size-structure of phytoplankton communities may be just as significant for biogeochemical cycling. Smaller phytoplankton, especially those without hard shells, are less likely to sink, limiting their direct contributions to carbon export. Indeed, Bopp *et al.* (2005) found that as oceans warm, small phytoplankton replaced diatoms in an ocean biogeochemical model, leading to increased rates of carbon and nutrient recycling and decreased export ratios. These results are supported by another modelling study documenting increases in groups of phytoplankton species that are small (and good nutrient competitors) due to nutrient limitation, with regional exceptions driven by iron supply (Dutkiewicz, Scott & Follows 2013).

The effects of global change on size-structure and subsequently on productivity and biogeochemistry can also be amplified by trophic interactions (Hansen *et al.* 2006; Stock, Dunne & John 2014). Smaller phytoplankton support different zooplankton predators, primarily smaller crustaceans and gelatinous species (micro- and mesozooplankton) compared to the larger crustaceans that dominate in seasonal and polar regions (Redfield 1958; Richardson 2008). This alters food chain length, leading to less productive zooplankton communities that provide a poorer resource for higher trophic levels. It can also influence the amount of carbon export resulting from predation; some zooplankton groups produce faecal pellets that rapidly sink from the surface exporting carbon, while others excrete more labile forms of carbon that persist in the water column. Rising temperatures associated with stratification and nutrient limitation may also alter the stoichiometry of phytoplankton, changing their value as a resource for zooplankton (Kriest, Khatiwala & Oschlies 2010; Yvon-Durocher *et al.* 2015).

Functional groups themselves are composed of many individual species representing significant amounts of trait variation and subject to trade-offs between traits. Global change has the potential to affect both the presence/absence and abundance of particular species within a functional group in a given location or environment (Fig. 1c). Environmental conditions and competitive interactions winnow out some species, while creating opportunities for others. When changing

community composition alters the functional contributions of a group, global change can affect biogeochemistry at the intragroup level. Such dynamics occur in response to climate change within an intermediate complexity Earth system model, as the ranges of individual species expand and contract based on their trait differences (including growth rates, temperature optima, size and half-saturation constants), leading to substantial turnover in the composition of local communities (Dutkiewicz, Scott & Follows 2013). Several examples exist of between-species trait variation with the potential to produce intragroup level biogeochemical effects, limited seemingly only by the number of traits and environmental factors studied so far. Biogeochemical rates are fundamentally linked to biological rates, such as growth rate. Growth rates are strongly linked to temperature, yet individual species often differ dramatically in their temperature dependence (Thomas *et al.* 2012; Boyd *et al.* 2013). In turn, these differences lead to predicted range shifts as oceans warm (Thomas *et al.* 2012). Looking beyond temperature, different coccolithophorid species and strains engage in calcification to varying degrees, with important consequences for productivity and carbon cycling. In nitrogen-fixing cyanobacteria, responses to CO_2 are diverse: elevated CO_2 stimulated growth and N_2 fixation in *Trichodesmium* species and *Crocosphaera watsonii*, important open ocean diazotrophs (Behrenfeld *et al.* 2006; Beardall, Stojkovic and Larsen 2009, Hutchins *et al.* 2013), but inhibited these processes in coastal *Nodularia spumigena* (Czerny, Barcelos e Ramos & Riebesell 2009; Boyce, Lewis & Worm 2010). In this case, turnover in cyanobacteria species driven by rising CO_2 might actually support consistent levels of function (N_2 fixation) in the face of global change. Overall, the effects of species turnover within functional group will depend on which species are favoured by the combinations of global change stressors experienced by communities regionally and how these species contribute to ecosystem function.

Finally, within a functional group, individual species need not have fixed traits (Fig. 1d). Even within primarily asexual phytoplankton, species consist of multiple strains with different traits, representing standing genetic and phenotypic variation. In addition to between-species differences in the sensitivity of N fixation rates to pCO_2, Hutchins *et al.* (2013) demonstrated significant strain-level variation. Given this variation, increasing CO_2 concentrations may select for particular strains, influencing future biogeochemistry in complex ways. The traits of species also respond to environmental changes through physiological, behavioural and evolutionary mechanisms. For example, the lipid content of several species of Antarctic diatom (in the genus *Navicula*) declines with increasing temperature, making them a poorer resource for zooplankton (Teoh, Phang & Chu 2012). Many phytoplankton are capable of nutrient storage and exhibit variable stoichiometries through a variety of physiological mechanisms. Changes in the stoichiometry of individual species can be of similar magnitude to effects driven by turnover between species (Behrenfeld *et al.* 2006; Finkel *et al.* 2009). This can influence their value as a food resource as mentioned

previously. In addition to physiological changes, evolutionary responses are likely within the phytoplankton due to their small size, huge populations and rapid generation times. These responses might allow species to adapt to conditions imposed by global change, suggesting that (over longer time-scales) communities might recover from short-term perturbations. Understanding the effects of evolutionary responses to global change is a complex process, requiring detailed, specific knowledge of how environments will change, how quickly phytoplankton can adapt and what genetic constraints or trade-offs limit them. Experiments designed to investigate these questions are becoming more common, but much work remains to be done.

Ultimately, understanding how the effects of global change will propagate through phytoplankton communities to influence biogeochemical cycling requires understanding the individual and combined effects of stressors on phytoplankton from species to functional groups. The key to obtaining this knowledge rests on elucidating the links between environment, species traits and trade-offs, and their performance and function.

Conclusions

Understanding the feedbacks between phytoplankton community structure and biogeochemistry is a burgeoning area of research. Distinct functional groups have been shaping the biogeochemistry of our planet, from the period of oxygenation ushered in by the cyanobacteria to contemporary patterns of N fixation and carbon cycling in the oceans. Understanding the physiology and ecology of these groups is continuing. We are still learning about new members of the phytoplankton (Cuvelier *et al.* 2010), the environmental sensitivities and traits of even the well-studied groups (Boyd *et al.* 2010), approaches for efficiently modelling diverse plankton communities and multiple element cycles (Stock, Dunne & John 2014), and methods for conceptually managing complex global change (Boyd *et al.* 2015). These are crucial problems in an era of global change. Quantifying the traits and trade-offs that affect functional group composition will help connect community responses to biogeochemical causes and effects.

A challenging empirical aspect of this approach is the number of important traits that must be gathered, especially given trait variation between functional groups, species and populations. Which traits do we need to measure in order to predict functional group dynamics? Predicting the outcome of competition between two populations requires knowledge of traits relating to competition for resources (macronutrients, micronutrients and light) and avoidance of predators, all of which differ between groups (Litchman and Klausmeier 2008; Boyd *et al.* 2010; Edwards *et al.* 2012, 2015). However, this task is made easier because of several fundamental constraints, including both allometric and phylogenetic relationships. Many traits scale strongly with cell size and temperature, including cellular stoichiometry (Yvon-Durocher *et al.* 2015). Due to the physical constraints that size and shape place on cells' ability to obtain nutrients, cell size cor-

relates extremely strongly with nutrient competitive traits (Litchman *et al.* 2007, Edwards *et al.* 2012; Marañón *et al.* 2012). Although there are undoubtedly biochemical differences between functional groups, they possess overlapping but distinct size distributions (Edwards *et al.* 2012), and differences in nutrient competitive abilities are driven at least in part by size differences. Cellular and environmental stoichiometric ratios are temperature-dependent, with N: P ratios in particular increasing with temperature (Yvon-Durocher *et al.* 2015). Many traits also show significant phylogenetic conservatism. Cell volume, nutrient competitive traits and grazer susceptibility are more similar among closely related species (Bruggeman 2011). In combination with empirically derived allometric relationships, this allows us to infer traits of unmeasured species with some success (Bruggeman 2011). These relationships can dramatically simplify the task of collecting the requisite data to parameterize models.

A complicating factor is that the traits of species, and, therefore, the functional groups, are not constant through time. We know that trait distributions within functional groups have shifted along with the environment over evolutionary time-scales (Finkel *et al.* 2005). With the short generation time and vast population sizes of phytoplankton species, evolutionary time-scales may in fact be remarkably short. This implies that future biogeochemical processes may be influenced by trait values that do not exist today, limiting our ability to make predictions in a rapidly changing world. To address this challenge, we must understand evolutionary constraints and trade-offs within different functional groups. Targeted evolutionary experiments may offer us a powerful tool to explore this matter, exposing phytoplankton species to one or more environmental stressors and observing trait changes over time. In addition, many unintentional experiments are ongoing in the form of decades-old laboratory cultures of phytoplankton. Comparisons of strains from natural environments with their laboratory-grown counterparts commonly show signs of adaptation to a high-resource, low-variability lifestyle (Swan *et al.* 2013). As biogeochemical models become more sophisticated, they may begin to incorporate the results of such studies, considering the joint effects of community ecology and evolution on ecosystem-level patterns, such as biogeochemistry.

Acknowledgements

Data accessibility

This review does not use any new data.

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