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REVIEW

The role of phytoplankton diversity in the emergent oceanic stoichiometry

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Marine phytoplankton are a taxonomically and functionally diverse group of organisms that are key players in the most important biogeochemical cycles. Phytoplankton taxa show different resource utilization strategies (e.g. nutrient-uptake rates and cellular allocation) and traits. Therefore, acknowledging this diversity is crucial to understanding how elemental cycles operate, including the origin and dynamics of elemental ratios. In this paper, we focus on trait-based models as tools to study the role of phytoplankton diversity in the stoichiometric phenomenology observed in the laboratory and in the open ocean. We offer a compilation of known empirical results on stoichiometry and summarize how trait-based approaches have attempted to replicate these results. By contrasting the different ecological and evolutionary approaches available in the literature, we explore the strengths and limitations of the existing models. We thus try to identify existing gaps and challenges, and point to potential new directions that can be explored to fill these gaps. We aim to highlight the potential of including diversity explicitly in our modeling approaches, which can help us gain important knowledge about changes in local and global stoichiometric patterns.

KEYWORDS: stoichiometry; trait-based models; redfield; phytoplankton

INTRODUCTION

Phytoplankton play a crucial role in some of the most important biogeochemical cycles ([A Sea of Microbes \[Theme Issue\], 2007](#)): for instance, the carbon (C) cycle, by performing >50% of the global (terrestrial and marine) primary production; and the nitrogen (N), phosphorus (P), iron (Fe) and silicon (Si) cycles. Phytoplankton cells capture these resources, assimilate them and use them for vital processes. Afterwards, these elements are introduced back into the environment as (particulate or dissolved) organic matter, which is either remineralized by heterotrophs and thus made available for other organisms, or sinks thus contributing to the elemental composition of deeper waters. Therefore, understanding how phytoplankton take up these nutrients and allocate the available resources to carry out key physiological processes, that is, changes in phytoplankton stoichiometry, is key to understanding the past, present and future linkages of these important biogeochemical cycles.

For decades, models and theoretical work remained within the Redfield ratio paradigm that marine phytoplankton stoichiometry (and thus the deep ocean elemental composition) is remarkably constant across environments ([Redfield, 1934; Redfield, 1958](#)). Initially set to 106 : 16 : 1 for C : N : P, it has been subsequently argued that other important elements such as Fe or Si should be included in this paradigm ([Quigg et al., 2003](#)). Today, we know that marine phytoplankton actually show a variety of stoichiometric patterns and strategies that vary across taxa and environmental conditions [see review in Geider and La Roche ([Geider and La Roche, 2002](#))], and the proposed fixed ratios of such key elements comprise only one possibility within a wide distribution of possibilities ([Klausmeier et al., 2004a](#)). Phytoplankton stoichiometry changes across taxa and varies in time and space.

Phytoplankton stoichiometry is determined by the relative elemental composition of the different macromolecules present in the cell. For instance, most of the cell's N can be found in proteins, whereas most of the P is used for rRNA or phospholipids ([Geider and La Roche, 2002](#)). Because different species show a different macromolecule distribution and availability, stoichiometry differs across species. In addition, size, a master trait for phytoplankton ([Litchman and Klausmeier, 2008](#)), also influences stoichiometry indirectly, as bigger cells have vacuoles to store an additional amount of these elements.

Due to these interspecific differences in elemental ratios, phytoplankton biogeography and community composition

may be important drivers for spatial (local and global) patterns. Phytoplankton N : P ratios sampled in different parts of different oceans, for instance, revealed a strong latitudinal pattern by which the ratio of N and P is inversely correlated with latitude ([Martiny et al., 2013](#)) (see Fig. 5A), a trend that has also been reported for terrestrial vegetation ([Reich and Oleksyn, 2004](#)). Thus, the stoichiometry of a specific region depends largely on which species are present in such regions ([Geider and La Roche, 2002](#)); in other words, phytoplankton diversity plays a key role in ultimately determining the observed stoichiometry.

Additionally, local and global stoichiometries change with time. The composition of the community changes during the year due to changes in the availability of each of these nutrients, along with diurnal and seasonal variations in light, temperature and predatory pressures. Moreover, phytoplankton can react to environmental changes by changing resource allocation to the different physiological processes, thus altering their stoichiometry. These acclimation responses are controlled by organismal traits and, in consequence, are shaped and constrained by evolution. Furthermore, because phytoplankton have short generation times, their populations are subject to rapid evolutionary events in response to quickly changing and/or stressing environments; rapid evolution can, in turn, influence ecological interactions ([Lennon and Martiny, 2008; Litchman et al., 2012; Lomas et al., 2014](#)). In consequence, ecological responses may be intertwined with evolutionary strategies.

Therefore, emergent local and global stoichiometries are the highly dynamic, non-trivial result of interactions across spatial scales, and across temporal scales, in which diversity plays a crucial role. Thus, if we want to understand and replicate the different stoichiometric patterns that are observed in the open ocean, we need to devise empirical methods and theoretical models that go beyond assuming a constant ratio for C, N and P and acknowledge the changeable character of cell-level and population-level stoichiometries and the importance of diversity in determining the emerging stoichiometry of the community.

In this paper, we argue that trait-based models (TBM) are a powerful tool to this end. As discussed below, the formalism of TBM is specifically conceived to represent biodiversity in a simple yet reliable way. These models have been the focus of recent development for phytoplankton ([Litchman and Klausmeier, 2008; Follows and Dutkiewicz, 2011](#)), representing macroscopic patterns such as basic phytoplankton biogeography ([Follows et al., 2007](#)) to more

sophisticated physiological aspects (Bruggeman and Kooijman, 2007; Lomas *et al.*, 2014). We will specifically center on N:P, because this ratio has been the focus of intense research in the last few decades, but we will also offer some additional insight and results related to C:N and C:P. First, we collect some of the most important experimental results providing the key laboratory and field observations on phytoplankton N:P under a variety of environmental and growth conditions. Then, we provide a brief introduction to TBM, followed by a compilation of ecological and evolutionary TBM and applications to phytoplankton stoichiometry, at the local and the global levels. Finally, we propose future directions and outline the important challenges that lie ahead and possible ways to tackle them.

QUANTIFYING STOICHIOMETRY

Intraspecific variation

There is a growing emphasis on the importance of intra-specific variation in community and food web ecology in general (Bolnick *et al.*, 2011). The intraspecific variation in stoichiometry is a key aspect of this variation. Therefore, understanding the extent and the drivers of intraspecific stoichiometric variation, and its proper characterization, is important for our mechanistic understanding of food web dynamics and ecosystem functioning.

Intraspecific variation in stoichiometry can originate from either differences in genotypes or plasticity of individual cells/colonies, even within a single genotype, or a combination of both phenomena. Phytoplankton have highly plastic macroelemental ratios (N:P, C:N and C:P) that depend on the nutrient supply ratio, light and temperature, and growth rate, among other factors [(Rhee, 1978; Goldman *et al.*, 1979; Hall *et al.*, 2005; Hillebrand *et al.*, 2013; Yvon-Durocher *et al.*, 2015); see Fig. 4 for an illustration of some of these correlations]. Nutrient supply ratio changes phytoplankton stoichiometry, so that at high N:P supply ratios phytoplankton N:P ratio increases and vice versa (Rhee, 1978). However, phytoplankton stoichiometry usually does not match the N:P supply perfectly, especially at high growth rates (Goldman *et al.*, 1979; Klausmeier *et al.*, 2004b; Bonachela *et al.*, 2013). Irradiance also affects stoichiometry of phytoplankton species: experiments with a diatom showed that the C:N ratio in the stationary phase increased and C:P ratio decreased with increasing irradiance, while they did not change during the early exponential phase (Leonardos and Geider, 2004). The C:N ratio in a different diatom species also increased under high light (Norici *et al.*, 2011). Less is known about how temperature may influence

stoichiometry. A recent data compilation analysis shows that increasing temperature may increase N:P and C:P (Yvon-Durocher *et al.*, 2015). This behavior may be due to a lower demand for P-rich ribosomes at higher temperatures, which may occur if the rate of biosynthesis increases with temperature more quickly than the rate of photosynthesis (Daines *et al.*, 2014).

In addition, it is likely that species or functional groups differ in the degree of plasticity of their stoichiometries (Klausmeier *et al.*, 2008). For example, species with a high storage potential [e.g. large vacuole, (Litchman *et al.*, 2009)] may have higher variability in N:P ratios. The evolution and cost of plasticity is poorly understood, but studying it could provide insights into the origin and maintenance of stoichiometric diversity.

While the plasticity of an individual genotype stoichiometry in response to different environmental factors has been studied experimentally, much less is known about the genotypic differences in stoichiometry in phytoplankton. We know, however, that different genotypes can have significantly different growth rates (Rynearson and Armbrust, 2004). Consequently, according to the Growth Rate Hypothesis (Sterner and Elser, 2002), we may expect different C:P and N:P ratios, with faster growing genotypes potentially having higher P content and lower C:P and N:P ratios than the slower growing genotypes. A recent study (Lind and Jeyasingh, 2015) investigated two different genotypes of the green alga *Chlamydomonas*, a wild type and a mutant that lacks the *psr1* gene that is involved in the responses to low P supply. The two genotypes had different C:P ratios, and there was a significant genotype by P-level interaction. Interestingly, the two *Chlamydomonas* genotypes had different effects on the zooplankter *Daphnia* growth, highlighting the effects of intraspecific variation in producer stoichiometry on food web dynamics.

Interspecific variation

As stated above, there is ample evidence that elemental composition varies across phytoplankton species. Because stoichiometry is plastic within species, interspecific variation is necessarily quantified in different ways.

Often, elemental content is measured for nutrient-replete, exponentially growing cultures. Stoichiometry under nutrient-replete growth is affected in part by nutrient storage and biochemical acclimation to high nutrient supply. Comparative analyses of nutrient-replete cultures have found that C:N, C:P and N:P all vary substantially across species, although C:N varies less than N:P and C:P (Geider and La Roche, 2002; Quigg *et al.*, 2011). The average N:P across species may be less than the Redfield ratio of 16 (Geider and La Roche, 2002) or slightly higher

(Quigg *et al.*, 2011), while C : N tends to be similar to the Redfield ratio of 6.625 (Geider and La Roche, 2002; Quigg *et al.*, 2011).

Quigg *et al.* (Quigg *et al.*, 2003, 2011) found that some of this interspecific variation can be explained by phylogeny, with members of the green plastid superfamily tending to have higher C : P and N : P than members of the red plastid superfamily. They also found differences in trace element stoichiometry that may reflect the origin of the plastids of these lineages through different endosymbiotic events. Bertilsson and Berglund (Bertilsson and Berglund, 2003) found that *Prochlorococcus* and *Synechococcus* from the oligotrophic ocean tend to have relatively high C : P and N : P. The ratios for these species are higher than the Redfield ratios and, compared with the results of Quigg *et al.* (Quigg *et al.*, 2003), similar to those of prasinophytes and chlorophytes (green plastid superfamily).

Measurements of stoichiometry in field populations also demonstrate interspecific variation. Martiny *et al.* (Martiny *et al.*, 2013) found in the subtropical North Atlantic that *Prochlorococcus* had the highest C : P and N : P, and that small eukaryotes had the lowest ratios, with *Synechococcus* intermediate. Arrigo (Arrigo, 2002) found that *Phaeocystis*-dominated waters in the Ross Sea had C : P and N : P drawdown ratios higher than Redfield, while diatom-dominated waters had ratios lower than Redfield, and matter exported to sediment traps had C : P differences consistent with the differences in drawdown ratio. Twining *et al.* (Twining *et al.*, 2004) found that flagellates had a C : P ratio 30% lower than that of diatoms in the Southern Ocean.

Species differences in N : P (or other potentially limiting nutrients) can also be quantified in terms of the cellular N : P at which growth switches from N- to P-limitation, which has been termed the “optimal” (Rhee and Gotham, 1980) or “critical” (Terry *et al.*, 1985) N : P ratio. Under relatively low growth rates, this ratio is equal to the ratio of the minimum subsistence quotas [Q_{\min} ; (Droop, 1968)] for N and P. For any growth rate, phytoplankton at the optimal ratio can match the environmental elemental ratio and therefore grow by drawing down all the available resources. Models have provided additional insight on this switching point for higher growth rates and possible interactions between the two nutrients around this point (see below). Compilations of lab experiments have found that the optimal N : P ratio varies substantially across species [from ~6 to >100; (Klausmeier *et al.*, 2004b; Edwards *et al.*, 2012); Fig. 1] and that the median ratio is somewhat higher for freshwater (median = 27.2) than marine species (median = 16.9).

In spite of this quantification of phytoplankton stoichiometric diversity observed in the laboratory and the field, we currently have relatively little understanding of the

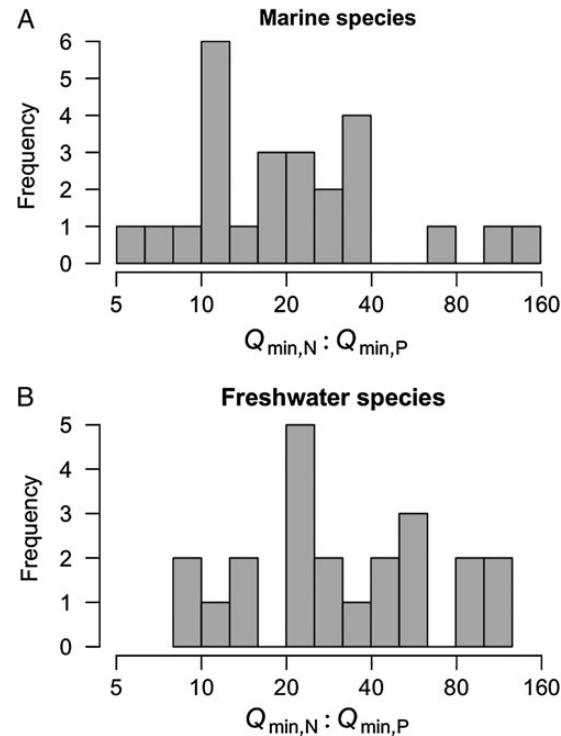


Fig. 1. Interspecific variation in N : P, measured as the ratio of the minimum subsistence quotas for N and P. **(A)** Marine species, **(B)** freshwater species. Reproduced from Edwards *et al.* (Edwards *et al.*, 2012), updated with data from Edwards *et al.* (Edwards *et al.*, 2015a).

causes of this interspecific variation, in terms of either the underlying biochemistry or the evolutionary causes of these differences. Although genotypes can acclimate their biochemical composition to environmental conditions, for example by increasing chlorophyll content under low irradiance, there are still large differences between species in mean Chl : C across irradiances (Dubinsky and Stambler, 2009). These differences presumably represent strategies adapted to different environmental conditions, in the face of underlying tradeoffs. Quigg *et al.* (Quigg *et al.*, 2011) argue that stoichiometric differences among major lineages reflect differences over geological time in the oxidation state of the ocean and the relative availability of different elements at the time when the lineages originated. However, if stoichiometric differences reflect ancient evolutionary events, the question remains why this stoichiometric diversity persists in the current ocean.

In terms of ecological strategies, species may diverge in adapting to conditions of resource limitation versus rapid growth. The low N : P content of ribosomes, relative to proteins for nutrient uptake and photosynthesis, may cause rapidly growing species to have low structural N : P (Klausmeier *et al.*, 2004b). There is some evidence that faster growth under low irradiance leads to a high N demand (low C : N) even when N (not light) is limiting

growth (Edwards *et al.*, 2015b), which is consistent with a cost of investment in photosynthetic machinery. Strzepek and Harrison (Strzepek and Harrison, 2004) found that an oceanic diatom reduced demand for iron, relative to a coastal congener, by reducing the content of iron-rich photosystem components. This led to faster growth under iron limitation, perhaps at the expense of tolerance to fluctuating irradiance.

Ecosystem-level variation

Stoichiometry also varies spatially and temporally at the ecosystem level, often quantified using elemental ratios of bulk particulate matter. In a global compilation, Martiny *et al.* (Martiny *et al.*, 2013) found latitudinal trends in C : P and N : P, such that P content was lower than Redfield in warm, nutrient-depleted, low latitude regions and higher than Redfield in cold, nutrient-rich, high latitude regions (see N : P case in Fig. 5A). Sterner and Andersen (Sterner and Andersen, 2008) found that within regions, samples with higher total biomass tended to have higher nutrient content (lower C : N and C : P). In the subtropical North Pacific, particulate N : P varies within years by 50–100% and tends to be higher in the summer fall, additionally showing a long-term increase away from the Redfield 16 : 1 (Karl *et al.*, 2001). The observation of some of these patterns also in terrestrial ecosystems (Reich and Oleksyn, 2004) points to the existence of fundamental mechanisms beyond simple environmental factors that contribute to the emergence of such patterns.

Plasticity, within-species genetic variation, and variation in community composition likely play a role in these stoichiometric patterns, and causes of variation may include variation in the magnitude and ratio of nutrient supply as well as temperature (Yvon-Durocher *et al.*, 2015). Regional variation in nutrient supply ratios may be driven by the differential lability of DON versus DOP, regional variation in denitrification and regional variation in nitrogen fixation (Deutsch and Weber, 2012). Globally and over long timescales, N : P in the ocean is thought to be regulated by competition between diazotrophic cyanobacteria and non-diazotrophic phytoplankton (Redfield, 1958; Tyrrell, 1999). The removal of N from the ocean by microbial denitrification will tend to favor diazotrophs by making N scarce relative to P. At the same time, the metabolic and material costs of nitrogen fixation are thought to make diazotrophs poor competitors for other resources, such as phosphorus. Simple theoretical arguments also lead to the conclusion that this dynamic causes diazotrophs effectively to fertilize the ocean with N until N : P is high enough that they are almost competitive excluded (Tyrrell, 1999). This scenario is, however, complicated by variation across regions

and over geological eras in iron supply (which likely limits diazotrophs) and the magnitude denitrification, but mixing between regions may maintain a homeostatic N : P in the face of regional variation in the abundance of nitrogen fixers (Lenton and Klausmeier, 2007; Deutsch and Weber, 2012).

Thus, documenting the patterns above, and understanding the mechanisms underlying them, is still in the early stages. Models are proving to be an essential tool for the latter task.

MODELING BIODIVERSITY AND STOICHIOMETRY

Modeling biodiversity

Diversity exists at all organizational levels: behavioral and phenotypic plasticity within individuals, genetic variation within species and species richness within communities. Aside from interest in its own right, diversity is important, because it allows biological systems to respond to environmental changes. However, representing diversity is a challenging task.

In phytoplankton ecology, the traditional way to implement the dynamics of plankton communities has been by means of the paradigmatic NPZD models, which keep track of the temporal changes in nutrients, phytoplankton, zooplankton and detritus, using one single box with fixed trait values for each of the biotic components [(Riley, 1946; Franks, 2002); Fig. 2A]. Such a simple setup is computationally economical, but does not capture the wide variety of phytoplankton characteristics and stratagies that are observed in the ocean.

To represent such diversity with NPZD approaches, every distinct species requires an additional dynamic equation, which in the case of phytoplankton can mean the need of hundreds of new equations. Incorporation of genetic diversity within species compounds the problem. In addition to the certain simulation slowdown, the main problem associated with such large (diverse) systems is that of parameterization: there are simply too many unknown parameters, leaving models hopelessly unconstrained.

Similarly to the Lagrangian versus Eulerian conundrum (Hellweger and Bucci, 2009), one suggested solution is the use of a “mesoscopic scale” or coarser representation in which the thousands of possibilities are grouped into functional groups attending to the distinct role of each of these groups in the biogeochemical cycles [(Moore *et al.*, 2002; Le Quéré *et al.*, 2005; Litchman *et al.*, 2006; Follows and Dutkiewicz, 2011); Fig. 2B]. Thus, phytoplankton diversity can be represented by using a small number of functional groups with some common basic physiological features, which differ in specific abilities such as being motile

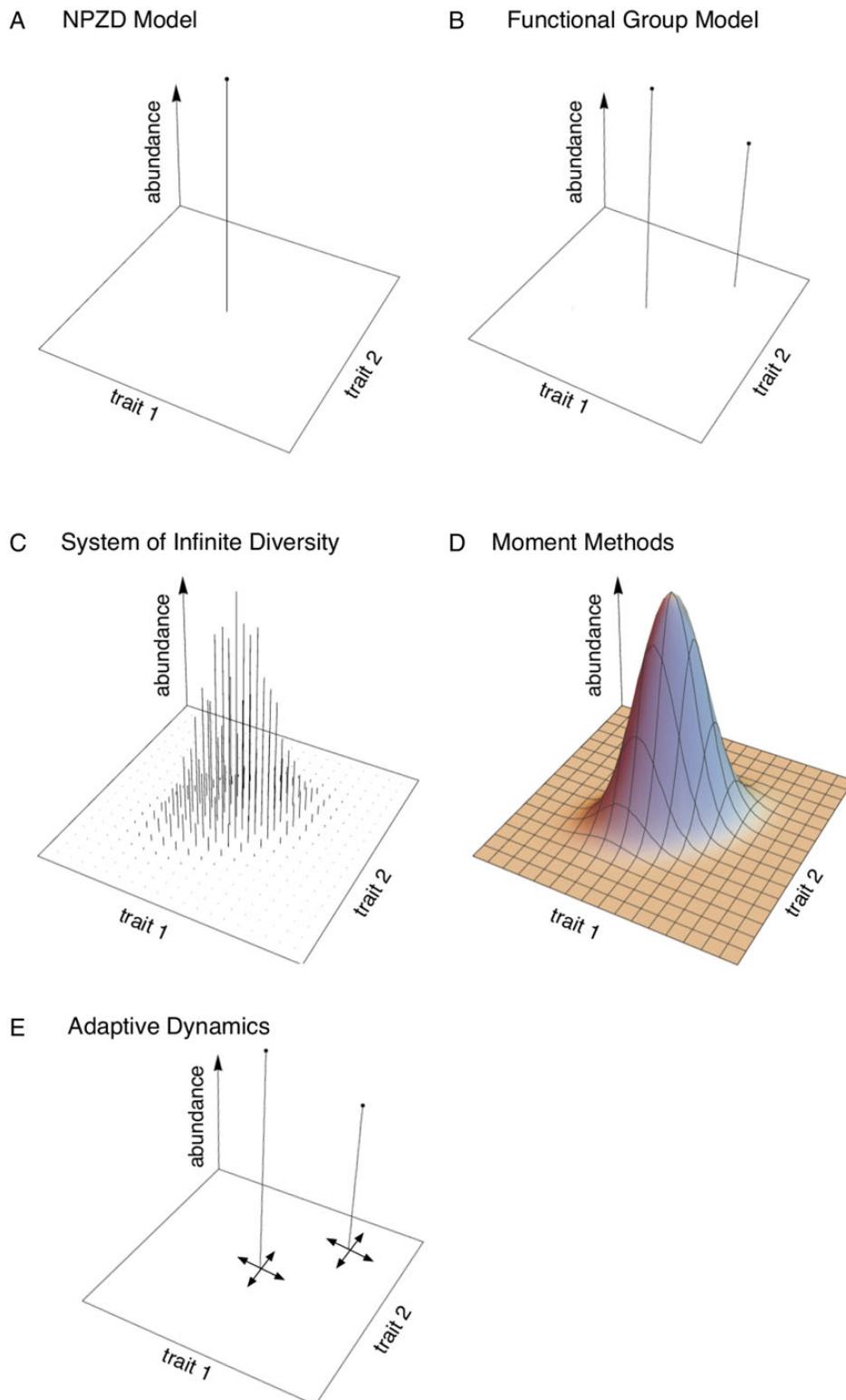


Fig. 2. A comparison of plankton modeling approaches. **(A)** In traditional NPZD models, there is one species per trophic level, with fixed traits. **(B)** Plankton Functional Group models represent functional groups as a single species, with fixed traits. **(C)** The System of Infinite Diversity (SID) approach considers a large number of species approximating a continuum. **(D)** Moment methods attempt to tame the complexity of SID models by reducing them to mean traits and their variances and covariances. **(E)** Evolutionary frameworks such as Quantitative Genetics and Adaptive Dynamics allow species traits to vary over time.

and/or mixotrophs (dinoflagellates), silica sequestration (diatoms) or nitrogen fixation (diazotrophic cyanobacteria). All these functional groups share the same basic terms in their respective dynamic equations, but also have additional group-specific terms that capture the distinct strategies of each group. Still, these Functional Group models omit much diversity and neglect the fact that, while they differ in mean traits, these groups often have overlapping trait distributions (Edwards *et al.*, 2012, 2015b).

TBM provide an alternative way to incorporate biodiversity into simulations of ecosystem dynamics (Litchman and Klausmeier, 2008; Follows and Dutkiewicz, 2011). TBM consider a universe of possible strategies (or, more generally, ecotypes) defined by a set of functional traits. Tradeoffs between traits limit the spectrum of possible combinations among those traits, avoiding the curse of parametric dimensionality and preventing non-plausible combination of traits from occurring, such as the so-called superspecies (or “superbugs,” unrealistic combination of traits so advantageous that could outcompete any other ecotype in the system) (Litchman and Klausmeier, 2008; Follows and Dutkiewicz, 2011; Flynn *et al.*, 2015). Allometries provide one relatively easy way to incorporate these tradeoffs. Because size is one of the most important traits for phytoplankton, it is linked to many of the traits that are involved in the most important physiological processes such as growth or nutrient uptake (Litchman *et al.*, 2007; Litchman and Klausmeier, 2008). Therefore, known allometric relationships may be used to reduce the need for specific parameterizations.

A variety of closely related TBM frameworks exist (Abrams, 2001; Abrams, 2005), differing in how they interpret diversity, where new strategies come from, and what approximations they make to reduce model complexity. Many TBM frameworks do not specify at which hierarchical level trait variation occurs (intraspecific versus interspecific). This strategic approach has benefits (greater simplicity and generality) and costs (less realism). New strategies can arise from small mutation of existing ones [Adaptive Dynamics (Geritz *et al.*, 1998; Dercole and Rinaldi, 2008)] or invasion from a broader meta-community [community assembly, e.g. (Louille and Loreau, 2005)], or be maintained as standing genetic variation [Quantitative Genetics, e.g. (Jiang *et al.*, 2005)].

Thus, although some TBMs include genetic dynamics (via, e.g. Adaptive Dynamics or Quantitative Genetics), other TBMs do not implement genetic change at the level of the organism, relying on the assumption that the initial population represents all possible genetic variability and the environment selects that genotypes survive in each location [“everything is everywhere” paradigm (Baas-Becking, 1934; Follows and Dutkiewicz, 2011)]. Local genotypic distributions can be, nonetheless, very

dynamic with extinctions via competition but also innovation, that is, new genotypes, through genotype immigration from different regions of the system (Baas-Becking, 1934; Follows and Dutkiewicz, 2011). Ultimately, however, innovation is constrained to the initial genotype distribution and, therefore, genotypic resolution depends on the degree of exhaustiveness with which the initial condition or community composition samples the genotype space.

One possible downside of both functional group and some TBM approaches is, precisely, the lack of clear indications as to what an optimal number of functional groups or ecotypes is for this initial distribution. The answer is probably question- and situation-specific. It is always tempting to use as many groups as the available computational power allows. However, doing so is not only arbitrary, but also may sometimes be unnecessary and ineffective as increasing the number of ecotypes may not result in any additional improvement or change in the outcome of the model (Follows and Dutkiewicz, 2011). In addition, representing diverse regional strategies for a group may require the use of multiple duplicate versions of such groups, properly parameterized using group-specific or ecotype-specific features specific of each region. Some TBM frameworks (e.g. those incorporating evolutionary adaptation) allow diversity to emerge based on species interactions, providing a potential resolution to this conundrum.

The most straightforward representation of diversity is a separate equation for each population’s density, either approximating a continuum of strategies [System of Infinite Diversity *sensu* (Bruggeman and Kooijman, 2007); Fig. 2C] or a large number of randomly chosen strategies to sample a higher dimensional trait space [the Darwin model (Follows *et al.*, 2007)]. Moment-based methods ([Wirtz and Eckhardt, 1996; Norberg *et al.*, 2001]; Fig. 2D] reduce the dimensionality by following various moments of the trait distribution (total population size, mean traits, trait variance and covariances), while optimality methods (Smith *et al.*, 2011) assume that traits instantaneously reach their optimal values. At equilibrium, these differences may not matter, but in spatially and temporally variable environments, they may affect trait dynamics and acclimation responses (Norberg *et al.*, 2001; Kremer and Klausmeier, 2013).

Including acclimation responses offers, in turn, a realistic way to increase the spectrum of possible responses without increasing the number of groups or ecotypes. Phenotypic plasticity confers the organism with flexibility to react to various environmental changes without any genetic alteration. Therefore, including such responses allows the same functional group or ecotype to show a different phenotype, e.g. photosynthetic rate under different irradiance conditions, or different number of uptake proteins under different nutrient availabilities. These

responses can be implemented by using phenomenological expressions that, based on data or field observations, link trait values to physiological observables [e.g. maximum photosynthetic rate to chlorophyll to carbon ratio, or maximum uptake rate, proportional to the number of nutrient-uptake proteins, to the internal content of the focal nutrient (Geider *et al.*, 1998)]; or more mechanistic approaches in which it is the changes in trait values that depend on those observables [i.e. the response itself is what is triggered by physiological changes, see, e.g. (Klausmeier *et al.*, 2007; Bonachela *et al.*, 2011)]. These ecophysiological models usually center on one single species; however, because the organism's dynamics are mostly driven by the main traits of the cell in these models, they have the potential to capture diversity and be adapted to the TBM framework. Thus, we will consider these models indistinguishable from TBM henceforth.

TBM have been used to explore a variety of phytoplankton-related aspects, from the specifics of nutrient-uptake kinetics and tradeoffs using one single ecotype (Fiksen *et al.*, 2013), to evolution of optimal N:P stoichiometry or cell size under different environmental conditions (Klausmeier *et al.*, 2004a; Litchman *et al.*, 2009; Daines *et al.*, 2014), to global biogeographic patterns (Follows *et al.*, 2007) or regional community structure (Bruggeman and Kooijman, 2007) using dozens of ecotypes. Theoretical issues that are yet to be resolved concern the maintenance of trait variation and whether trait distributions can become multimodal, invalidating some of the assumptions of moment-based and optimality methods. Nonetheless, TBM are a powerful way to include diversity that can be combined with functional groups (for instance, by informing the trait initialization using group-specific values and/or providing groups with a variety of intraspecific variability or ecotypes).

In summary, including biodiversity in phytoplankton models is a non-trivial task that is receiving more and more attention due to its importance. Once a starting point for the implementation of a variety of distinct strategies has been identified in functional groups or ecotypes, and simple ways to initialize these groups (e.g., using allometries) have been found, now modelers are starting to include more mechanistic approaches to more sophisticated questions, such as the inclusion of acclimation responses, evolution or dynamic changes in each of phytoplankton's resource pools.

Modeling stoichiometry

The approaches with which modelers have tried to replicate the experimental observations of phytoplankton stoichiometry are diverse, but have some important points in common. All these models focus on a particular species

and share, of course, the need for the internal content of the different nutrients that are resolved (typically N and P) to change with time. Therefore, these models leave behind the fixed Redfield stoichiometry paradigm and keep track of the dynamics of these quotas, using to this end simple balance equations in which the focal pools increase via nutrient uptake and decrease via assimilation. The main difference between the models below is how they approach the link between growth and these quotas.

A first group of models use the quota (or Droop) model to represent cell growth (Droop, 1968) in combination with Liebig's law of the minimum; thus, cell or population growth depends in a hyperbolic way on the most limiting of the suite of possible resources (Legovic and Cruzado, 1997). For instance, if N and P are the only limiting resources and μ represents the population growth rate:

$$\mu = \mu_{\max} \min(f(Q_N), f(Q_P)),$$

where μ_{\max} is the maximum growth rate, and f is a hyperbolic function that depends on the limiting resource; if the normalized version of the Droop model is considered, then (Flynn, 2008):

$$f(Q_i) = \frac{(1 - Q_{\min,i}/Q_i)}{(1 - Q_{\min,i}/Q_{\max,i})},$$

where $Q_{\min,i}$ represents the maximum amount of nutrient i the cell can store, and $Q_{\min,i}$ the minimum that the cell needs to survive. Thus, in these models the functional form associating growth rate with the most limiting nutrient is common to all possible limiting nutrients (note that we used the same function, f , for all the terms into the min function) and, therefore, is qualitatively similar among situations regardless of the specific resource that limits growth. Differences in growth introduced by specific nutrients are thus implemented through differences in the physiological limits for each of the nutrient quotas, Q_{\max} and Q_{\min} . These models are called threshold models, because the cell can be only limited by one resource at a time except for one specific threshold, the co-limitation point mentioned in the previous section, at which cell growth can be limited by multiple resources at the same time (Legovic and Cruzado, 1997; Klausmeier *et al.*, 2004a,b, 2007; Bougaran *et al.*, 2010).

Another group of models detach themselves from the Droop model by constructing the growth rate using mechanistic arguments (Ågren, 2004; Pahlow and Oschlies, 2009; Bonachela *et al.*, 2013). These models are arguably more mechanistic, although more parameter expensive as well. In addition, all these models introduce in one way or another interactions among the limiting

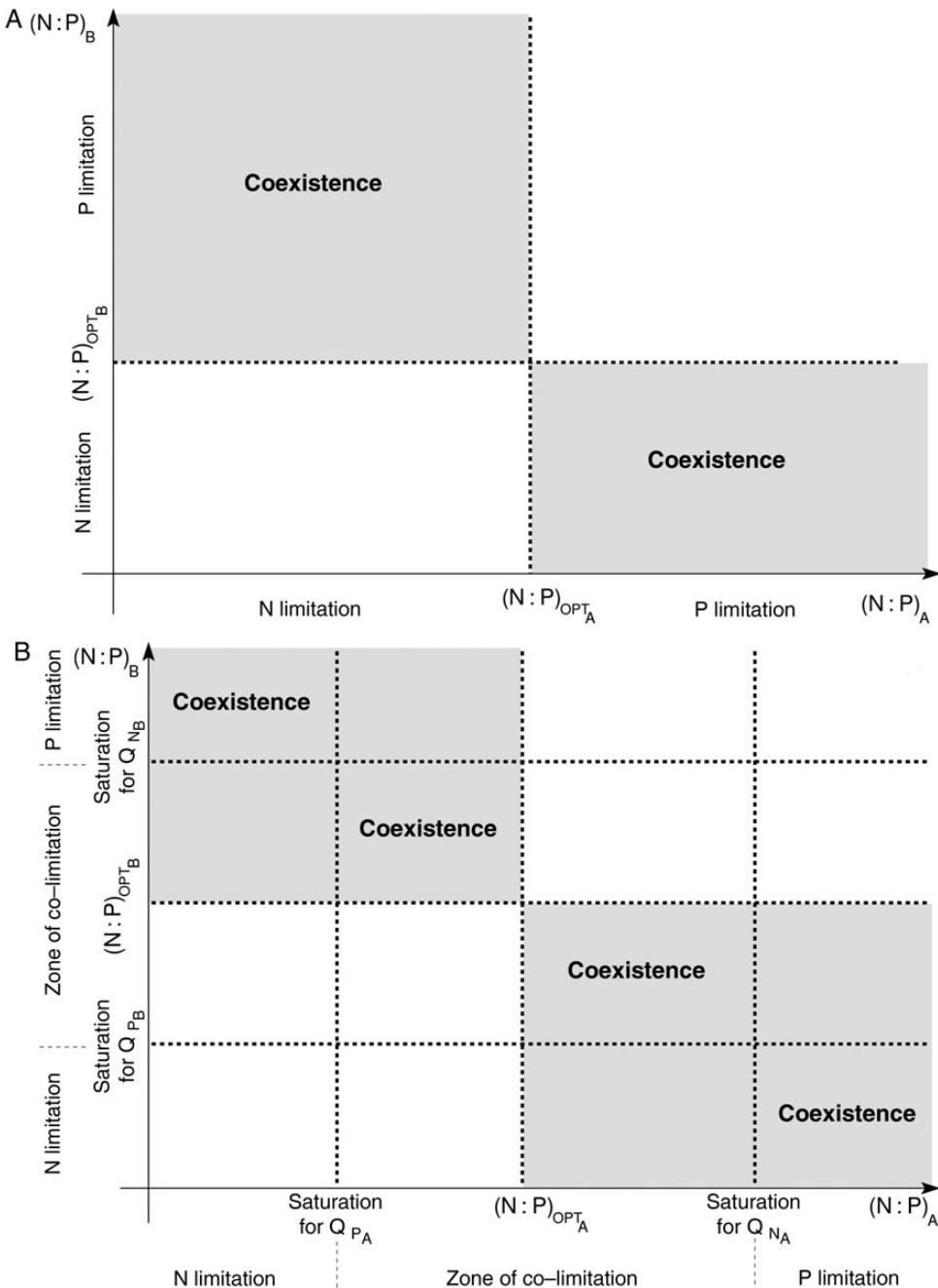


Fig. 3. Expected outcome of simulated competition between hypothetical species A and B, resulting from threshold models (**A**) and models in which interactions between nutrients are considered (**B**), for the specific case of N and P potential limitation. In the upper panel, coexistence only occurs when each of the competitors is limited by a different nutrient. The latter models, however, show co-limitation in a wide range of environmental conditions, the spectrum of possibilities is larger than in the former case, and the outcome depends on the degree of co-limitation. Reproduced from Bonachela *et al.* (Bonachela *et al.*, 2013) with permission from the authors.

resources that may affect the growth rate. These models can replicate the same phenomenology that threshold models replicate, for instance the expected behavior of the cell's N : P with respect to changes in growth rate or input N : P (see Fig. 3); in addition, interactions among nutrients affect the conditions under which co-limitation

occurs (generally transforming the co-limitation point into a co-limitation region) and, in consequence, the competitive abilities of the focal organism (Bonachela *et al.*, 2013) (see Fig. 4).

Among the model groups above, it is possible to find examples in which acclimation responses are included,

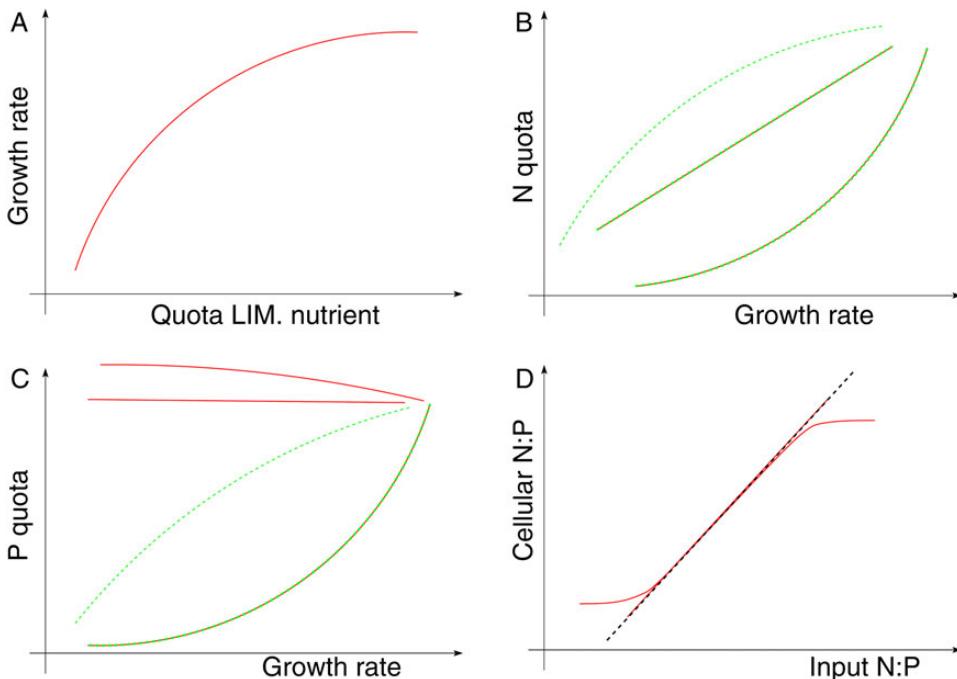


Fig. 4. Compilation of the qualitative behavior observed in stoichiometric experiments and replicated by models in the groups mentioned above. (A) Growth rate shows a hyperbolic dependence on cell quota; (B) N quota shows convexity or concavity dependence on growth rate depending on N availability; (C) P quota shows a similar phenomenology, but there is an asymmetric response with respect to that observed for the N quota; (D) the cell's stoichiometry mimics the environmental elemental ratio, but this strategy can be prevented by the cell's physiological limits. In A–C, dashed lines indicate P limitation and solid lines, N limitation; the dashed line in D indicates $N:P = [N]_0/[P]_0$. Adapted from Bonachela *et al.* (Bonachela *et al.*, 2013) with permission from the authors.

either by using phenomenological expressions (Pahlow and Oschlies, 2009) or explicit dynamic equations [(Klausmeier *et al.*, 2007; Loladze and Elser, 2011; Bonachela *et al.*, 2013), see above]. These responses necessarily introduce additional interactions between the two nutrients, either directly (for instance, with one nutrient limiting specific physiological responses linked to the alternative nutrient such as protein or ribosome synthesis (Pahlow and Oschlies, 2009; Bonachela *et al.*, 2013)] or indirectly [for instance, through the competition between the respective uptake proteins for space on the cell surface (Klausmeier *et al.*, 2007; Bonachela *et al.*, 2013)]. These acclimation responses provide the cells with an additional flexibility that allows these models potentially to replicate highly dynamic growth conditions, as well as a wider spectrum of stationary possibilities.

There are some remarkable differences between these approaches in key aspects such as the asymmetric response of the N and the P quotas to changes in growth rate, or the existence of an effective minimum value for quota (Q_{min} , quota such that $\mu = 0$, see above) that changes with the input elemental ratio. However, with the empirical information available, it is difficult to discern which group of models represents phytoplankton single or simultaneous limitation in a more realistic way.

More experimental information is required to discern to what extent there exists an interaction between N and P such that mutual limitation conditions growth under a diverse spectrum of environmental conditions. On the other hand, the choice of whether to include acclimation responses may be in this case a more subtle issue beyond resolving single-organism lifetime strategies as adding phenotypic plasticity may introduce, as explained above, potential interactions between resources.

Importantly, all the ecophysiological models above can, in turn, potentially be used for the study of the diversity in phytoplankton stoichiometry, as they all highlight traits as main drivers of the cell's stoichiometric dynamics. For example, threshold models have been used to show that the structural N:P that maximizes growth varies depending on whether resources are plentiful, or whether growth is limited by light, N or P, showing that the optimal strategies for elemental ratios under diverse conditions differ from Redfield significantly (Klausmeier *et al.*, 2004a).

Stoichiometry at a global scale

Until very recently, global-level biogeochemical models relied on the Redfield paradigm to represent stoichiometry.

A fixed ratio of the most important elements is a computationally helpful feature, because it allows the models to keep track of one single nutrient while the pools of the rest of the nutrients are calculated by means of this fixed number. This approach has been used successfully in the past to answer a variety of questions not directly related with phytoplankton stoichiometry (Follows *et al.*, 2007; Stock *et al.*, 2014).

As we stated above, however, phytoplankton stoichiometry is highly dynamic and diverse, and affects global biogeochemical cycles in a very non-trivial way. The constantly changing inorganic elemental ratios and variable phytoplankton stoichiometry that occur in the oceans lead to dynamic feedbacks between phytoplankton and environment that will influence phytoplankton physiology and population growth and can thus potentially cascade to the rest of trophic levels in the marine food web. Therefore, reliable biogeochemical models should include variable phytoplankton elemental pools in their description. One approach is to allow the stoichiometry of each functional group to vary, as determined by a quota model for each potentially limiting nutrient, and in addition, a variable Ch 1:C ratio can be controlled by the supply of nitrogen and light (Moore *et al.*, 2002). Using such an approach, Ayata *et al.* (Ayata *et al.*, 2013) found using a 1D ecosystem model of BATS to show that variable Ch 1:C and C:N allow the model to better represent the deep chlorophyll maximum and primary production over time, compared with models with either of the variable terms removed. Models with variable nutrient quotas and Ch 1:C are often formulated in terms of physiological acclimation and nutrient storage of a single phytoplankton population, but in reality there are likely different genotypes and species dominating at different depths and seasons, and this species turnover leads to variation in bulk Ch 1:C and C:N. Therefore, models of physiological acclimation may implicitly capture trait diversity across species and its consequences.

Although there are extended NPZD marine ecosystem models that include N, P and other pools for various phytoplankton functional groups at the regional level, only recently have models started to consider more mechanistically grounded physiological models to include a flexible description of phytoplankton stoichiometry at a global level. One example is given by (Daines *et al.*, 2014), a pool model reminiscent of the classic Shuter model (Shuter, 1979) for phytoplankton physiology which in this case includes simple acclimation and genetic adaptation rules, coupled to a physical global circulation model. Although the C:N ratio for each compartment is fixed, the variable P pool and data-inferred parameterization allow this mechanistic TBM to replicate the most important global patterns for phytoplankton N and P (see Fig. 5B).

Similarly, in Arteaga *et al.* (Arteaga *et al.*, 2014), the dynamics of the phytoplankton component are provided by the so-called chain model. This is a mechanistic model for flexible quotas that include interactions between nutrients at the growth-rate level, but also at the nutrient-uptake level by using a sequential limitation of processes by the different resources: P limits rRNA synthesis, which limits protein production, in turn limited by N availability, which may affect photosynthesis (Pahlow and Oschlies, 2009). Although not strictly a TBM, it relies on optimality assumptions which, implicitly, necessarily take into account diversity in phytoplankton strategies. Acclimation responses are included using phenomenological expressions, which also account for interactions between the different resources. Instead of an underlying global circulation model, in this approach the global map is subdivided into cells in which stationary environmental conditions are imposed and informed from the World Ocean Atlas. Although the N:P ratios are far from observations, C:P ratios are closer to reality. Interestingly, this model points to the possibility of co-limitation as being much more extended than previously thought, with low latitudes mostly dominated by N-P co-limitation, whereas high latitudes would be mostly co-limited by light and N availability.

Although most of the models above have included diversity in one way or another as a necessary ingredient, none have studied to what extent is diversity responsible for the observed stoichiometric patterns. To answer this question, TBM offer an unrivaled tool. For example, the Darwin model [see above and Follows *et al.* (Follows *et al.*, 2007)] is specifically devised to represent diversity in an efficient way by using a stochastic trait initialization for ecotypes, thus reducing substantially the information needed. In a recent modification, the Darwin model incorporated a one-nutrient version of the quota model focused on top-down controls of the phytoplankton community (Ward *et al.*, 2013); thus, modifications to the Darwin that include additional, variable quota pools are potentially powerful ways to assess global stoichiometry. Current ongoing efforts, for example, attempt to bridge the different mechanistic models above by including phytoplankton acclimation responses to changes in nutrient availability (Bonachela *et al.*, 2013) into the Darwin model.

In summary, although phytoplankton stoichiometry has been the focus of intense experimental and theoretical research, only recently have empirical and theoretical approaches come together in a synergistic effort to replicate and predict global stoichiometric patterns. However, very few of those efforts consider the role of diversity in determining such patterns. Because we now have the necessary computational power, we need to assess and decide on the level of detail suitable for these global TBM, in terms of both physiological mechanisms and

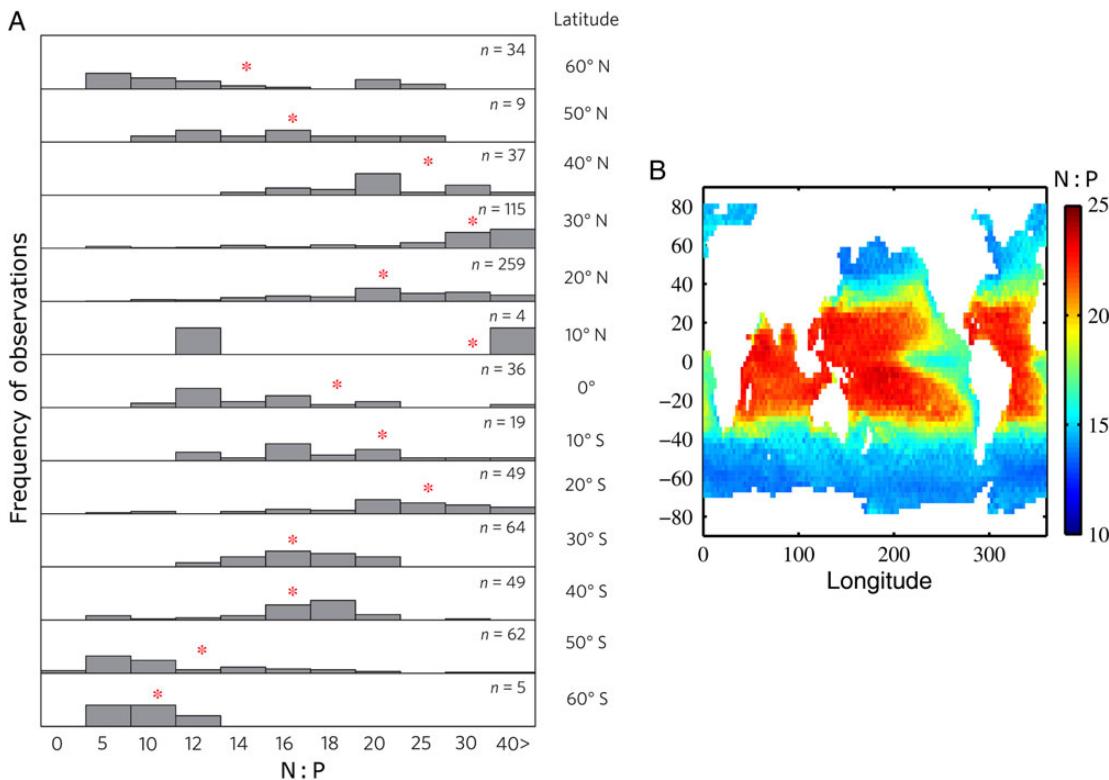


Fig. 5. Latitudinal N:P pattern found in Martiny *et al.* (Martiny *et al.*, 2013) (A) and global map representing phytoplankton N:P obtained with the trait-based model introduced in Daines *et al.* (Daines *et al.*, 2014) after weighting using net primary productivity (B). The emergent ratios in this model reproduce the latitudinal pattern described in Martiny *et al.* (Martiny *et al.*, 2013). The asterisk in A represents the lognormal average of the distribution, and *n* the number of sampling stations. Reproduced from original article with permission from the authors.

ecological interactions, and how much diversity in both would be required to properly describe regional and global patterns. Accommodating diversity and providing a better link between the fluid dynamics and the biology represent the greatest remaining challenges. But they are not the only ones.

FUTURE CHALLENGES AND DIRECTIONS

After decades of phytoplankton stoichiometry research, and according to the compilation presented above, much is known at the organismal level. In consequence, current research is now shifting to understanding the ecological consequences of diversity in cellular stoichiometry under a diversity of environmental conditions. Although these aspects are of course important, we are still far from a complete understanding of key aspects of phytoplankton stoichiometry at many other levels.

For instance, there is very little knowledge about the physiological ranges for the quotas of any element different from N, although they are a key part of the Droop model

and, therefore, used in most TBM (see above). There is very little experimental work reporting well-defined values for, e.g., the maximum P quota. Furthermore, these physiological ranges will certainly be affected by the ratio of the available nutrients and/or the growth rate of the cell; for example, the vast majority of theoretical models available predict that the minimum quota at which growth can be sustained, or the quota at which the growth rate reaches its maximum (points normally used as reference to measure Q_{min} and Q_{max} , respectively), change when the input ratio is changed in a simulated chemostat. Thus, new experiments are needed that investigate systematically how growth and the pools of the different elements react to changes in environmental conditions; for example, changes in light and nutrient concentrations, but also temperature.

Similarly, a logical argument establishes that the N and P pools interact when N- and P-uptake transporters compete for space on the cell's surface. On the other hand, N and P are classically non-interchangeable resources for plants (Tilman, 1982) and therefore are treated independently (e.g., using Liebig's law of the minimum). Available data are not detailed enough to discern to what extent this

interaction is important for the stoichiometric behavior of the cell and whether there is a co-limitation point in the input ratio axis, or a wide co-limitation range (with a single optimum, see above).

On the other hand, the answers to these questions and the information and models presented in previous sections are based on the classic assumption that phytoplankton populations are clonal, with very little intraspecific variability. It would be very interesting to study to what extent that assumption is correct by characterizing intraspecific diversity in, for instance, elemental ratios.

Furthermore, a (similar) exercise of scaling up population-level phenomena to the community level, while considering interspecific variability, would benefit from a more precise way to assess what species (or ecotypes or functional groups) should be added, as opposed to including them as a number set by the available computational power or modeling method. For example, it is well known that there is a significant functional redundancy in the marine ecosystem that contributes to its stability; the existence of several ecotypes/species belonging to groups that play similar functions ensures that the focal function remains present in the ecosystem even if several of these species go extinct. However, introducing redundancy (several ecotypes with similar characteristics) may be seen as an unnecessary complication for the focal theoretical model or experiment.

Similarly, some functional groups have also been exceedingly simplified in models so far. At the global scale, competition between diazotrophs and phytoplankton that do not fix nitrogen is the most prominent hypothesis for global regulation of N:P (Redfield, 1958; Tyrrell, 1999; Lenton and Klausmeier, 2007). Models that implicitly or explicitly include continuous trait variation of phytoplankton do not typically include diazotrophy, or the rate of diazotrophy, as a trait axis. However, diazotrophy could be incorporated into trait-based models by using putative tradeoffs to describe the cost of N fixation and then asking when diazotrophy can evolve or invade an ecosystem, as a function of environmental conditions such as nutrient supply ratios [e.g. (Pahlow *et al.*, 2013; Dutkiewicz *et al.*, 2014) are recent efforts in this direction].

Finally, models are more and more concerned with including the structure of the lower trophic levels of the marine food web as a way to increase the precision of these models, thus highlighting top-down regulation as an important control of, for instance, community structure (Ward *et al.*, 2013). Similarly to the previous case, to include this structure in a reliable way we need to understand how to assess which are the keystone species or functional groups in these food webs, and which species contribute to the (functional or structural) redundancy of the trophic network.

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