

The role of phytoplankton diversity in the emergent oceanic stoichiometry

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Abstract:

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 in order to fill these gaps. We aim to highlight the potential of including diversity explicitly in our modelling approaches, which can help us gain important knowledge about changes in local and global stoichiometric patterns.

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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 more than 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 in order 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, e.g. (Geider & La Roche 2002)), and the proposed fixed ratios of such key elements comprise only one possibility within a wide distribution of possibilities (Klausmeier, Litchman, Daufresne & Levin 2004). 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 & 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 & 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 & Oleksyn 2004). Thus, the

stoichiometry of a specific region depend largely on which species are present in such regions (Geider & 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 & 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, nontrivial 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 (Follows & Dutkiewicz 2011, Litchman & Klausmeier 2008), representing macroscopic patterns such as basic phytoplankton biogeography (Follows et al. 2007) to more sophisticated physiological aspects (Bruggeman & 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 intraspecific 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 ((Goldman et al. 1979, Hall et al. 2005, Hillebrand et al. 2013, Rhee 1978, 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 (Bonachela et al. 2013, Goldman et al. 1979, Klausmeier et al. 2008, Klausmeier, Litchman & Levin 2004). Irradiance also affects stoichiometry of phytoplankton species: experiments with a diatom species 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 & 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 (Ryneckson & Armbrust 2004). Consequently, according to the Growth Rate Hypothesis (Sterner & 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 & 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 & La Roche 2002, Quigg et al. 2011). The average N:P across species may be less than the Redfield ratio of 16 (Geider & 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 & La Roche 2002, Quigg et al. 2011).

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 et al.

(Bertilsson & 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 to the results of (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 et al. (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 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 & 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 varies substantially across species (from ~6 to >100; (Edwards et al. 2012, Klausmeier, Litchman & Levin 2004); 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 causes of this interspecific variation, either in terms of 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 & 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 vs. 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, Litchman & Levin 2004). 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. 2015), which is consistent with a cost of investment in photosynthetic machinery. Strzepek and Harrison (Strzepek & 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 et al. (Sterner & 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 & 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 vs. DOP, regional variation in denitrification, and regional variation in nitrogen fixation (Deutsch & 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 (Deutsch & Weber 2012, Lenton & Klausmeier 2007).

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 ((Franks 2002, Riley 1946); Fig. 2A). Such a simple setup is computationally economical, but does not capture the wide variety of phytoplankton characteristics and strategies 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 & 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 ((Follows & Dutkiewicz 2011, Litchman et al. 2006, Moore et al. 2002, Quéré et al. 2005); 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 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, Edwards et al. 2015).

Trait-based models (TBM) provide an alternative way to incorporate biodiversity into simulations of ecosystem dynamics (Follows & Dutkiewicz 2011, Litchman & Klausmeier 2008). TBM consider a universe of possible strategies (or, more generally, ecotypes) defined by a set of functional traits. Trade-offs 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) (Flynn et al. 2015, Follows & Dutkiewicz 2011, Litchman & Klausmeier 2008). Allometries provide one relatively easy way to incorporate these trade-offs. 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 & Klausmeier 2008, Litchman et al. 2007). 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 vs. 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 (Dercole & Rinaldi 2008, Geritz et al. 1998)) or invasion from a broader metacommunity (community assembly, e.g. (Louille & 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 which genotypes survive in each location (“everything is everywhere” paradigm (Baas-Becking 1934, Follows & 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 & 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 & 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 & 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 ((Norberg et al. 2001, Wirtz & Eckhardt 1996); 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 (Kremer & Klausmeier 2013, Norberg et al. 2001).

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. (Bonachela et al. 2011, Klausmeier et al. 2007)). 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 (Daines et al. 2014, Klausmeier, Litchman, Daufresne & Levin 2004, Litchman et al. 2009), to global biogeographic patterns (Follows et al. 2007) or regional community structure (Bruggeman & 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 intra-specific 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 & Cruzado 1997). For instance, if N and P are the only limiting resources and μ represents the population growth rate:

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

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):

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

where $Q_{\max,i}$ 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 (Bougaran et al. 2010, Klausmeier, Litchman, Daufresne & Levin 2004, Klausmeier, Litchman & Levin 2004, Klausmeier et al. 2007, Legovic & Cruzado 1997).

Another group of models detach themselves from the Droop model by constructing the growth rate using mechanistic arguments (Ågren 2004, Bonachela et al. 2013, Pahlow & Oschlies 2009). 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 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, either by using phenomenological expressions (e.g. (Pahlow & Oschlies 2009)) or explicit dynamic equations ((Bonachela et al. 2013, Klausmeier et al. 2007, Loladze & Elser 2011), 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 (Bonachela et al. 2013, Pahlow & Oschlies 2009)) or indirectly (for instance, through the competition between the respective uptake proteins for space on the cell surface (Bonachela et al. 2013, Klausmeier et al. 2007)). 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 in order to discern to what extent there exists an interaction between, e.g. 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, Litchman, Daufresne & Levin 2004).

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 (e.g. (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 nontrivial 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 Chl:C ratio can be controlled by the supply of nitrogen and light (e.g. (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 Chl:C and C:N allow the model to better represent the deep chlorophyll maximum and primary production over

time, compared to models with either of the variable terms removed. Models with variable nutrient quotas and Chl: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 Chl: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 models have 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. 2014), the dynamics of the phytoplankton component are provided by the so-called *chain model*, a mechanistic model for flexible quotas that includes 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 & 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. 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 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 about phytoplankton stoichiometry 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 modelling 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 (Lenton & Klausmeier 2007, Redfield 1958, Tyrrell 1999). 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. (Dutkiewicz et al. 2014, Pahlow et al. 2013) 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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References

- Ågren, G. (2004), 'The C:N:P Stoichiometry of Autotrophs - Theory and Observations', *Ecol. Lett.* **7**, 185–191.
- Abrams, P. A. (2001), 'Modelling the adaptive dynamics of traits involved in inter- and intraspecific interactions: an assessment of three methods', *Ecology Letters* **4**, 166–175.
- Abrams, P. A. (2005), 'Adaptive dynamics vs. adaptive dynamics', *Journal of Evolutionary Biology* **18**, 1162–1165.
- Arrigo, K. R. (2002), 'Taxon-specific differences in C/P and N/P drawdown for phytoplankton in the Ross Sea, Antarctica', *Geophysical Research Letters* **29**(19), 1938.
<http://doi.wiley.com/10.1029/2002GL015277>
- Arteaga, L., Pahlow, M. & Oschlies, A. (2014), 'Global patterns of phytoplankton nutrient and light colimitation inferred from an optimality-based model.', *Global Biogeochemical Cycles* **28**, 648–661.
- A Sea of Microbes [Theme Issue]* (2007), *Oceanography* **20**(2), 16–171.
- Ayata, S.-D., Levy, M., Aumont, O., Sciandra, A., Sainte-Marie, J., Tagliabue, A. & Bernard, O. (2013), 'Phytoplankton growth formulation in marine ecosystem models: Should we take into account photo-acclimation and variable stoichiometry in oligotrophic areas?', *Journal of Marine Systems* **125**, 29 – 40.
- Baas-Becking, L. (1934), *Geobiology of inleiding tot de milieukunde*, van Stockum and Zoon, Le Hague, Netherlands.
- Bertilsson, S. & Berglund, O. (2003), 'Elemental composition of marine prochlorococcus and synechococcus: Implications for the ecological stoichiometry of the sea', *Limn. Oceanogr.* **48**, 1721–1731.
- Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C. & Vasseur, D. A. (2011), 'Why intraspecific trait variation matters in community ecology', *Trends in Ecology & Evolution* **26**(183-192).

- Bonachela, J., Allison, S., Martiny, A. & Levin, S. (2013), 'A model for variable phytoplankton stoichiometry based on cell protein regulation', *Biogeosciences* **10**, 4341–4356.
- Bonachela, J., Raghib, M. & Levin, S. (2011), 'Dynamic Model of Flexible Phytoplankton Nutrient Uptake', *Proc. Nat. Acad. Sci. USA* **108**, 20633–20638.
- Bougaran, G., Bernard, O. & Sciandra, A. (2010), 'Modeling Continuous Cultures of Microalgae Colimited by Nitrogen and Phosphorus', *J. Theor. Biol.* **265**, 443–454.
- Bruggeman, J. & Kooijman, S. (2007), 'A Biodiversity-Inspired Approach to Aquatic Ecosystem Modeling', *Limnol. Oceanogr.* **52**, 1533–1544.
- Daines, S., Clark, J. & Lenton, T. (2014), 'Multiple environmental controls on phytoplankton growth strategies determine adaptive responses of the n : P ratio', *Ecol.Lett.* **17**, 414–425.
- Dercole, F. & Rinaldi, S. (2008), *Analysis of Evolutionary Processes: the Adaptive Dynamics Approach and its Applications*, Princeton University Press, Princeton, NJ.
- Deutsch, C. & Weber, T. (2012), 'Nutrient ratios as a tracer and driver of ocean biogeochemistry.', *Annual review of marine science* **4**, 113–41. <http://www.ncbi.nlm.nih.gov/pubmed/22457971>
- Droop, M. R. (1968), 'Vitamin B₁₂ and Marine Ecology IV: the Kinetics of Uptake, Growth and Inhibition in *monochrysis lutheri*', *J. Mar. Biol. Assoc. UK* **48**, 689–733.
- Dubinsky, Z. & Stambler, N. (2009), 'Photoacclimation processes in phytoplankton: mechanisms, consequences, and applications', *Aquatic Microbial Ecology* **56**(September), 163–176. <http://www.int-res.com/abstracts/ame/v56/n2-3/p163-176/>
- Dutkiewicz, S., Ward, B., Scott, J. & Follows, M. (2014), 'Understanding predicted shifts in diazotroph biogeography using resource competition theory', *Biogeosciences* **11**, 5445–5461.
- Edwards, K. F., Thomas, M. K., Klausmeier, C. a. & Litchman, E. (2012), 'Allometric scaling and taxonomic variation in nutrient utilization traits and maximum growth rate of phytoplankton', *Limnology and Oceanography* **57**(2), 554–566. http://www.aslo.org/lo/toc/vol_57/issue_2/0554.html

Edwards, K. F., Thomas, M. K., Klausmeier, C. a. & Litchman, E. (2015), 'Light and growth in marine phytoplankton: allometric, taxonomic, and environmental variation', *Limnology and Oceanography* **60**, 540–552. <http://doi.wiley.com/10.1002/lno.10033>

Fiksen, O., Follows, M. & Aksnes, D. (2013), 'Trait-based Models of Nutrient Uptake in Microbes Extend the Michaelis-Menten Framework', *Limnol. Oceanogr.* **58**, 193–202.

Flynn, K. J. (2008), 'Use, Abuse, Misconceptions and Insights from Quota Models - The Droop Cell Quota Model 40 Years On', *Oceanogr. Mar. Biol. Ann. Rev.* **46**, 1–23.

Flynn, K., St. John, M., A., R. J., Skibinski, D., Allen, J. I., Mitra, A. & Hofmann, E. E. (2015), 'Acclimation, adaptation, traits and trade-offs in plankton functional type models: reconciling terminology for biology and modelling', *J. Plankton Res.* **under review**.

Follows, M. & Dutkiewicz (2011), 'Modeling Diverse Communities of Marine Microbes', *Annu. Rev. Mar. Sci.* **3**, 427–451.

Follows, M., Dutkiewicz, S., Grant, S. & Chisholm, S. (2007), 'Emergent Biogeography of Microbial Communities in a Model Ocean', *Science* **315**, 1843–1846.

Franks, P. (2002), 'NPZ models of plankton dynamics: their construction, coupling to physics, and application', *Journal of Oceanography* **58**, 379–387.

Geider, R. & La Roche, J. (2002), 'Redfield Revisited: Variability of C:N:P in Marine Microalgae and its Biochemical Basis', *Eur. J. Phycol.* **37**, 1–17.

Geider, R., MacIntyre, H. & Kana, T. (1998), 'A Dynamic Regulatory Model of Phytoplanktonic Acclimation to Light, Nutrients, and Temperature', *Limnol. Oceanogr.* **43**, 679–694.

Geritz, S. A. H., Kisdi, E., Meszéna, G. & Metz, J. A. J. (1998), 'Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree', *Evolutionary Ecology* **12**, 35–57.

Goldman, J. C., Mccarthy, J. J. & Peavey, D. G. (1979), 'Growth rate influence on the chemical composition of phytoplankton in oceanic waters.', *Nature* **279**, 210–215.

- Hall, S., Smith, V., Lytle, D. & Leibold, M. (2005), 'Constraints on Primary Producer N:P Stoichiometry Along N:P Supply Ratio Gradients', *Ecology* **86**, 1894–1904.
- Hellweger, F. L. & Bucci, V. (2009), 'A Bunch of Tiny Individuals - Individual-Based Modeling for Microbes', *Ecol. Modell.* **220**, 8–22.
- Hillebrand, H., Steinert, G., Boersma, M., Malzahn, A., Meunier, C. L., Plum, C. & Ptacnik, R. (2013), 'Goldman revisited: Faster-growing phytoplankton has lower n : P and lower stoichiometric flexibility.', *Limnology and Oceanography* **58**, 2076–2088.
- Jiang, L., Schofield, O. M. E. & Falkowski, P. G. (2005), 'Adaptive evolution of phytoplankton cell size', *American Naturalist* **166**, 496–505.
- Karl, D., Björkman, K. & Dore, J. (2001), 'Ecological nitrogen-to-phosphorus stoichiometry at station ALOHA', *Deep Sea Research* **48**, 1529–1566.
<http://www.sciencedirect.com/science/article/pii/S09670664500001521>
- Klausmeier, C., Litchman, E., Daufresne, T. & Levin, S. (2004), 'Optimal Nitrogen-to-Phosphorus Stoichiometry of Phytoplankton', *Nature* **429**, 171–174.
- Klausmeier, C., Litchman, E., Daufresne, T. & Levin, S. (2008), 'Phytoplankton stoichiometry.', *Ecological Research* **23**(479-485).
- Klausmeier, C., Litchman, E. & Levin, S. (2004), 'Phytoplankton Growth and Stoichiometry under Multiple Nutrient Limitation', *Limnol. Oceanogr.* **49**, 1463–1470.
- Klausmeier, C., Litchman, E. & Levin, S. (2007), 'A Model of Flexible Uptake of Two Essential Resources', *J. Theor. Biol.* **246**, 278–289.
- Kremer, C. T. & Klausmeier, C. A. (2013), 'Coexistence in a variable environment: eco-evolutionary perspectives', *Journal of Theoretical Biology* **339**, 14–25.
- Legovic, T. & Cruzado, A. (1997), 'A model of phytoplankton growth on multiple nutrients based on the Michaelis-Menten-Monod uptake, Droop's growth and Liebig's law', *Ecol. Model.* **99**, 19–31.

- Lennon, J. & Martiny, J. (2008), 'Rapid evolution buffers ecosystem impacts of viruses in a microbial food web', *Ecol. Lett.* **11**, 1178–1188.
- Lenton, T. & Klausmeier, C. (2007), 'Biotic stoichiometric controls on the deep ocean N:P ratio', *Biogeosciences* **4**, 353–367. <https://hal.archives-ouvertes.fr/hal-00297869/>
- Leonardos, N. & Geider, R. J. (2004), 'Effects of nitrate: Phosphate supply ratio and irradiance on the C:N:P stoichiometry of *Chaetoceros Muellieri.*', *European Journal of Phycology* **39**(173-180).
- Lind, P. & Jeyasingh, P. (2015), 'Genotypic differences in phosphorus use physiology in producers (*Chlamydomonas reinhardtii*) and consumers (*Daphnia pulex*) interact to alter primary and secondary production.', *Evolutionary Ecology* pp. 1–13.
- Litchman, E., Edwards, K. F., Klausmeier, C. A. & Thomas, M. K. (2012), 'Phytoplankton niches, traits and eco-evolutionary responses to global environmental change.', *Marine Ecology Progress Series* **470**, 235–248.
- Litchman, E. & Klausmeier, C. (2008), 'Trait-Based Community Ecology of Plankton', *Annu. Rev. Ecol. Evol. Syst.* **39**, 615–639.
- Litchman, E., Klausmeier, C. A., Miller, J. R., Schofield, O. M. & Falkowski, P. G. (2006), 'Multi-nutrient, multi-group model of present and future oceanic phytoplankton communities', *Biogeosciences* **3**, 585–606.
- Litchman, E., Klausmeier, C. A. & Yoshiyama, K. (2009), 'Contrasting size evolution in marine and freshwater diatoms', *Proc. Natl. Acad. Sci. USA* **106**, 2665–2670.
- Litchman, E., Klausmeier, C., Schofield, O. & Falkowski, P. (2007), 'The Role of Functional Traits and Trade-Offs in Structuring Phytoplankton Communities: Scaling From Cellular to Ecosystem Level', *Ecology Letters* **10**, 1170–1181.
- Loladze, I. & Elser, J. J. (2011), 'The origins of the redfield nitrogen-to-phosphorus ratio are in a homeostatic protein-to-rRNA ratio', *Ecology Letters* .
- Lomas, M., Bonachela, J., Levin, S. & Martiny, A. (2014), 'Impact of ocean phytoplankton diversity on phosphate uptake', *Proc. Nat. Acad. Sci. USA* **111**, 17540–17545.

- Louille, N. & Loreau, M. (2005), 'Evolutionary emergence of size-structured food webs', *Proc. Nat. Acad. Sci. USA* **102**, 5761–5766.
- Martiny, A. C., Pham, C. T. A., Primeau, F. W., Vrugt, J. A., Moore, J. K., Levin, S. A. & Lomas, M. W. (2013), 'Strong latitudinal patterns in the elemental ratios of marine plankton and organic matter', *Nature Geoscience* **6**, 279–283.
- Moore, J. K., Doney, S. C., Kleypas, J. A., Glover, D. M. & Fung, I. Y. (2002), 'An intermediate complexity marine ecosystem model for the global domain.', *Deep-Sea Research II* **49**, 403–462.
- Norberg, J., Swaney, D. P., Dushoff, J., Lin, J., Casagrandi, R. & Levin, S. A. (2001), 'Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework', *Proc. Nat. Acad. Sci. USA* **98**, 11376–11381.
- Norici, A., Bazzoni, A. M., Pugnetti, A., Raven, J. A. & Giordano, M. (2011), 'Impact of irradiance on the C allocation in the coastal marine diatom *Skeletonema marinoi* sarno and zingone', *Plant Cell and Environment* **34**, 1666–1677.
- Pahlow, M., Dietze, H. & A., O. (2013), 'Optimality-based model of phytoplankton growth and diazotrophy', *Mar. Ecol. Prog. Ser.* **489**, 1–16.
- Pahlow, M. & Oschlies, A. (2009), 'Chain model of phytoplankton P, N and light co-limitation', *Marine Ecology Progress Series* **376**, 69–83.
- Quéré, C. L., Harrison, S. P., Colin Prentice, I., Buitenhuis, E. T., Aumont, O., Bopp, L., Claustre, H., Cotrim Da Cunha, L., Geider, R., Giraud, X., Klaas, C., Kohfeld, K. E., Legendre, L., Manizza, M. and Platt, T., Rivkin, R. B., Sathyendranath, S., Uitz, J., Watson, A. J. & Wolf-Gladrow, D. (2005), 'Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models.', **11**, 2016–2040.
- Quigg, A., Finkel, Z., Irwin, A. & Rosenthal, Y. (2003), 'The evolutionary inheritance of elemental stoichiometry in marine phytoplankton', *Nature* **425**, 291–294.
<http://www.nature.com/articles/nature01953>
- Quigg, A., Irwin, A. & Finkel, Z. V. (2011), 'Evolutionary inheritance of elemental stoichiometry in phytoplankton', *Proceedings of the Royal Society B: Biological Sciences* **278**, 526–534.

- Redfield, A. (1934), On the Proportions of Organic Derivatives in Sea Water and their Relation to the Composition of Plankton, in 'James Johnstone Memorial Volume', University of Liverpool, pp. 176–192.
- Redfield, A. (1958), 'The Biological Control of Chemical Factors in the Environment', *Am. Sci.* **46**, 205–221.
- Reich, P. & Oleksyn, J. (2004), 'Global patterns of leaf n and p in relation to temperature and latitude', *Proc. Nat. Acad. Sci. USA* **101**, 11001–11006.
- Rhee, G. (1978), 'Effects of N:P Atomic Ratios and Nitrate Limitation on Algal Growth, Cell Compositions, and Nitrate Uptake', *Limnol. Oceanogr.* **23**, 10–25.
- Rhee, G. & Gotham, I. J. (1980), 'Optimum N:P ratios and coexistence of planktonic algae', *Journal of Phycology* **16**, 486–489.
- Riley, G. A. (1946), 'Factors controlling phytoplankton population on Georges Bank', *J. Mar. Res.* **6**, 54–73.
- Rydgren, T. A. & Armbrust, E. V. (2004), 'Genetic differentiation among populations of the planktonic marine diatom *Ditylum brightwellii* (Bacillariophyceae)', *Journal of Phycology* **40**, 34–43.
- Shuter, B. (1979), 'A model of Physiological Adaptation in Unicellular Algae', *J. Theor. Biol.* **78**, 519–552.
- Smith, S. L., Pahlow, M., Merico, A. & Wirtz, K. W. (2011), 'Optimality-based modeling of planktonic organisms', *Limnology and Oceanography* **56**, 2080–2094.
- Sterner, R. & Andersen, T. (2008), 'Scale-independent carbon:nitrogen:phosphorus seston stoichiometry in marine and freshwaters', *Limnology and Oceanography* **53**(3), 1169–1180. <http://onlinelibrary.wiley.com/doi/10.4319/lo.2008.53.3.1169/abstract>
- Sterner, R. & Elser, J. (2002), *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*, Princeton University Press, Princeton, NJ.

Stock, C. A., Dunne, J. P. & John, J. G. (2014), 'Global-scale carbon and energy flows through the marine planktonic food web: An analysis with a coupled physical-biological model', *Progress in Oceanography* **120**, 1–28.

Strzepek, R. & Harrison, P. (2004), 'Photosynthetic architecture differs in coastal and oceanic diatoms', *Nature* **403**(August 2003), 689–692.

<http://www.nature.com/nature/journal/v431/n7009/abs/nature02954.html>

Terry, K. L., Hirata, J. & Laws, E. A. (1985), 'Light-, nitrogen-, and phosphorus-limited growth of *Phaeodactylum tricornutum* Bohlin Strain TFX-1: Chemical composition, carbon partitioning, and the diel periodicity of physiological processes', *Journal of Experimental Marine Biology and Ecology* **86**, 85–100.

Tilman, D. (1982), *Resource Competition and Community Structure*, Princeton University Press, Princeton, NJ.

Twining, B. S., Baines, S. B. & Fisher, N. S. (2004), 'Element stoichiometries of individual plankton cells collected during the Southern Ocean Iron Experiment (SOFeX)', **49**(6), 2115–2128.

Tyrrell, T. (1999), 'The relative influences of nitrogen and phosphorus on oceanic primary production', *Nature* **400**, 525–531. <http://www.nature.com/nature/journal/v400/n6744/abs/400525a0.html>

Ward, B. A., Dutkiewicz, S., Jahn, O. & Follows, M. J. (2013), 'A size-structured food-web model for the global ocean', *Limn. Oceanogr.* **57**, 1877–1891.

Wirtz, K.-W. & Eckhardt, B. (1996), 'Effective variables in ecosystem models with an application to phytoplankton succession', *Ecological Modelling* **92**, 33–53.

Yvon-Durocher, G., Dossena, M., Trimmer, M., Woodward, G. & Allen, A. P. (2015), 'Temperature and the biogeography of algal stoichiometry.', *Global Ecology and Biogeography* **24**, 562–570.

Figure captions

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. After (Edwards et al. 2012), updated with data from Edwards et al. (in press).

Fig. 2: (Color online). 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.

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. In panels a-c, dashed lines indicate P limitation and solid lines, N limitation; the dashed line in panel d indicates $N:P=[N]_0:[P]_0$. Reproduced from (Bonachela et al. 2013) with permission from the authors.

Fig. 4: (Color online). 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. Adapted from (Bonachela et al. 2013) with permission from the authors.

Fig. 5: (Color online). Latitudinal N:P pattern found in (Martiny et al. 2013) (**a**) and global map representing phytoplankton N:P obtained with the trait-based model introduced in (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. 2013). The asterisk in panel a) represents the lognormal average of the distribution, and n the number of sampling stations. Reproduced from original article with permission from the authors.

Figures

Figure 1:

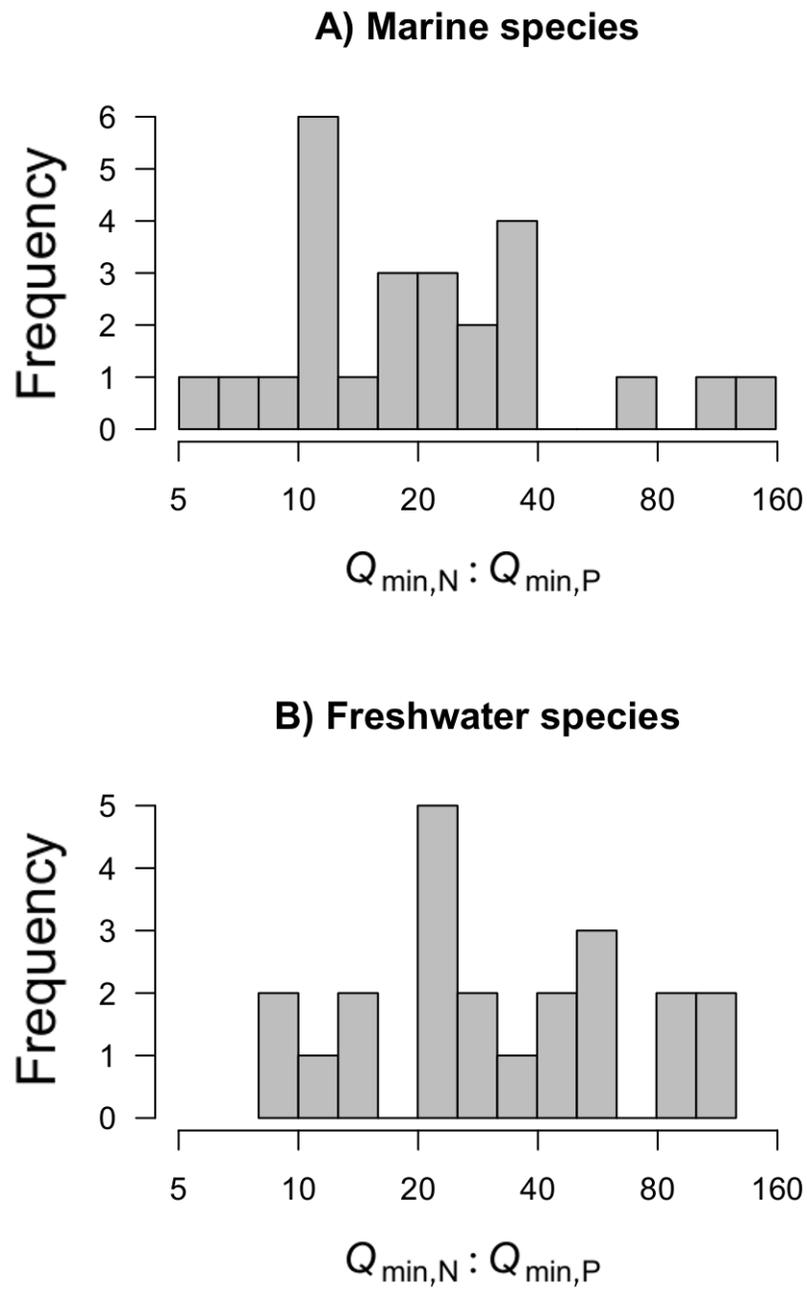
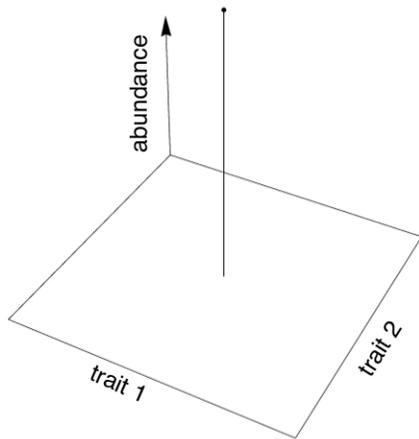
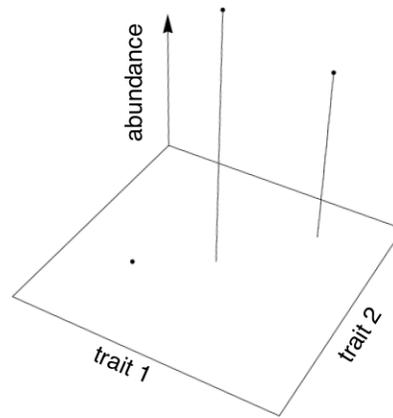


Figure 2:

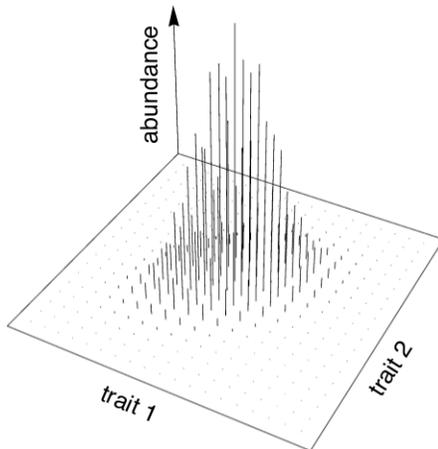
A) NPZD Model



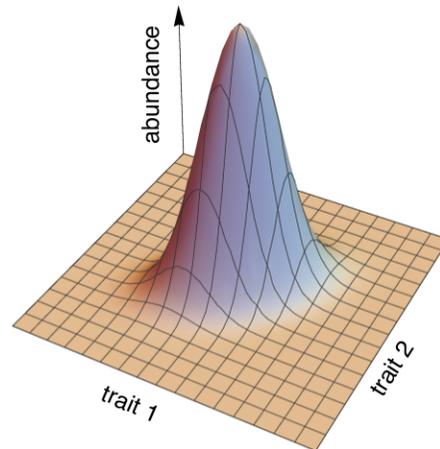
B) Functional Group Model



C) System of Infinite Diversity



D) Moment Methods



E) Adaptive Dynamics

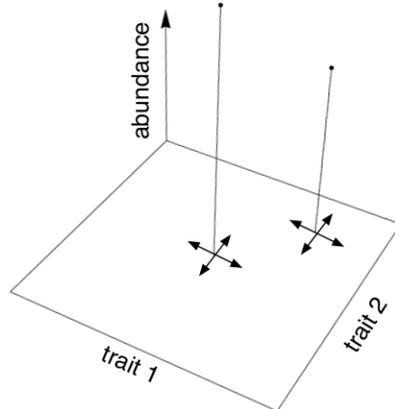


Figure 3:

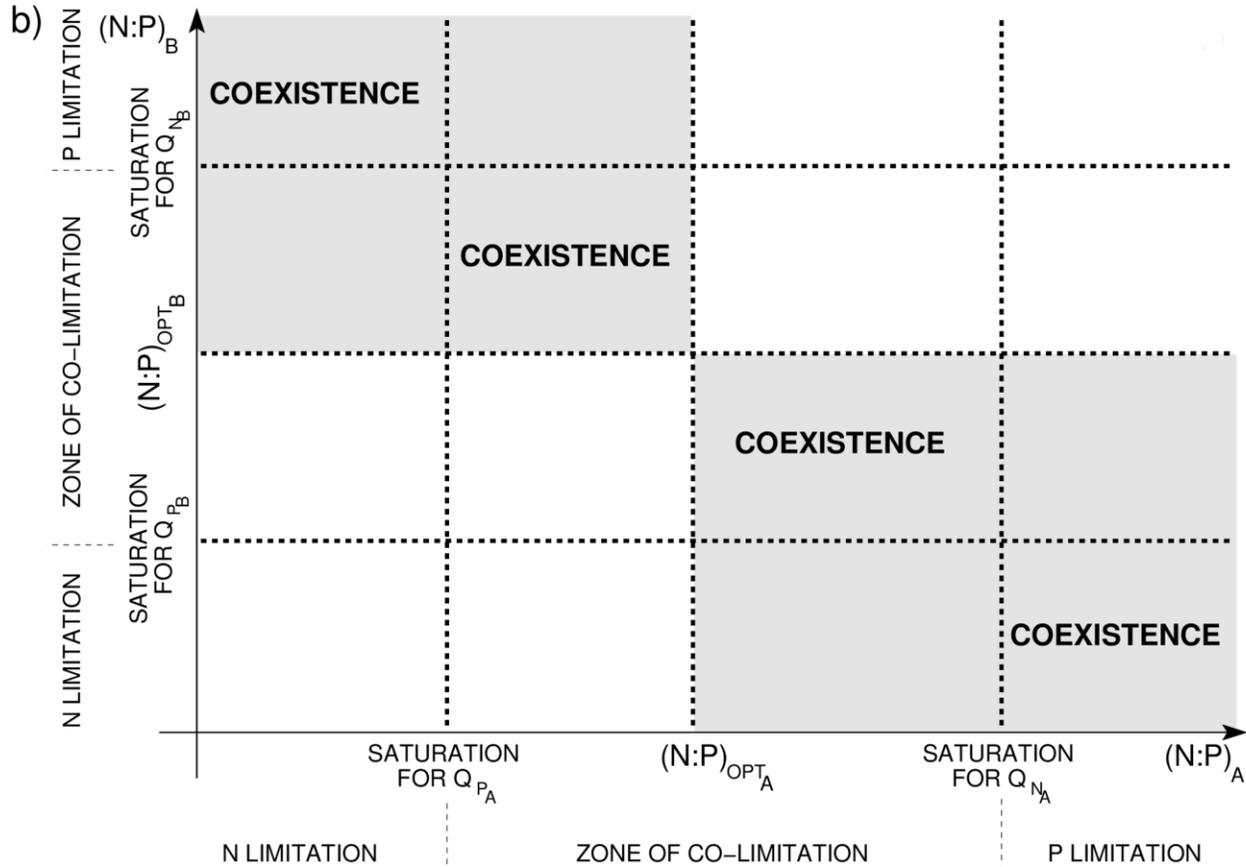
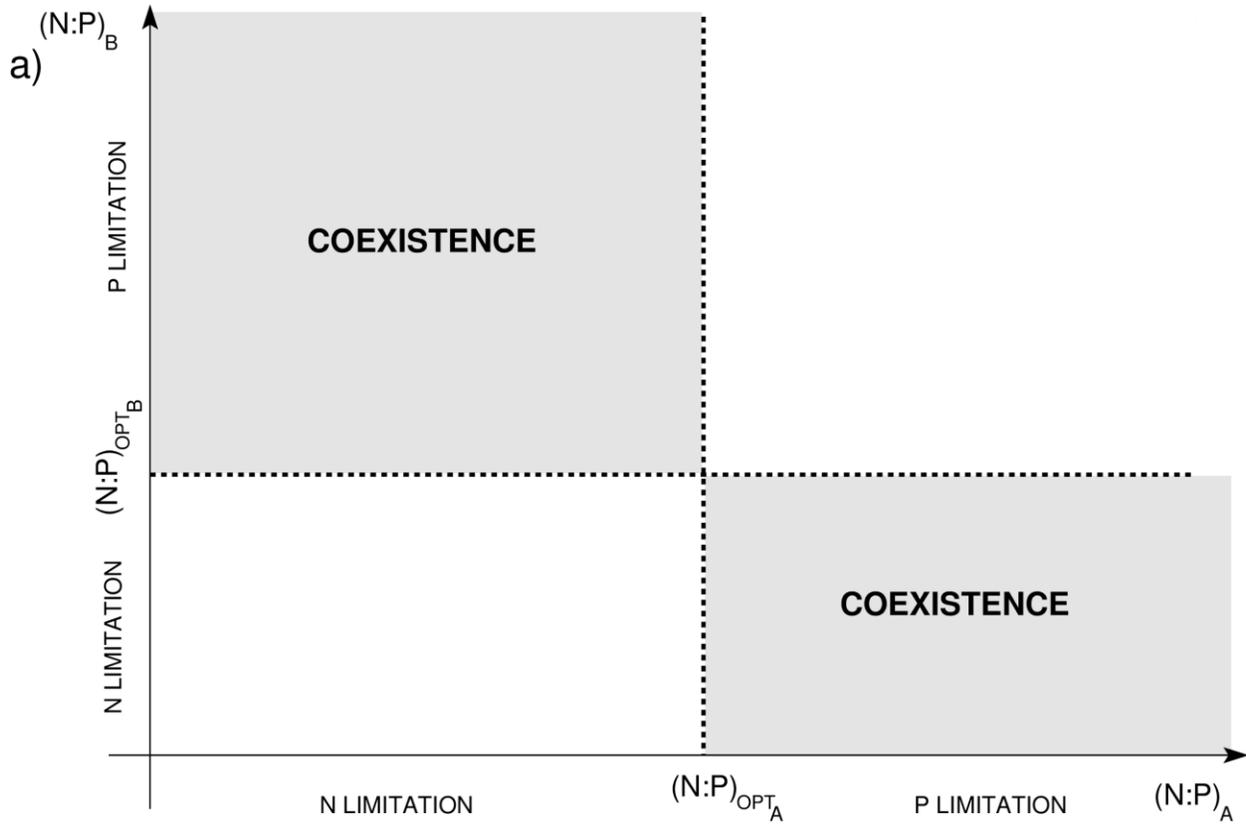


Figure 4:

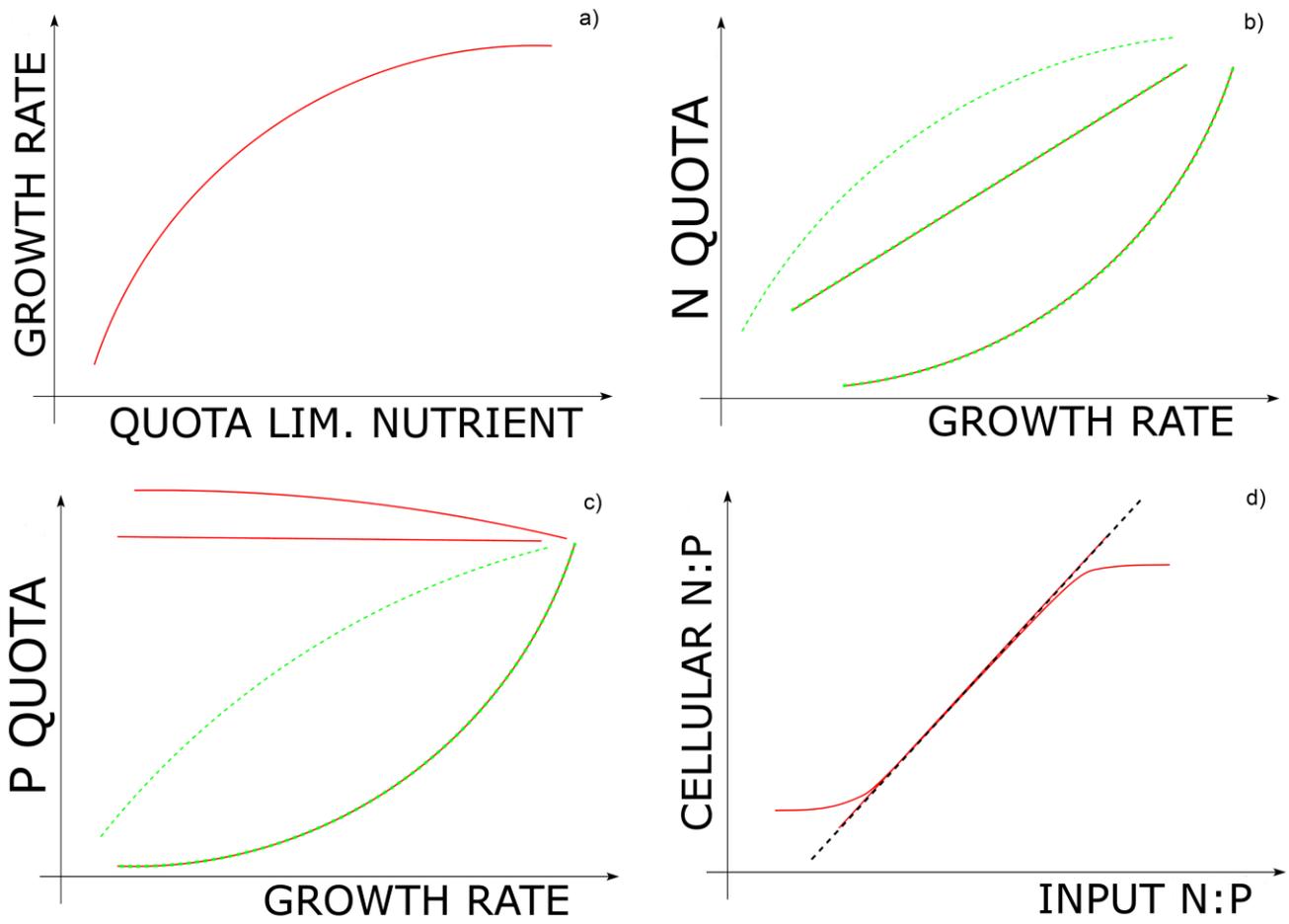
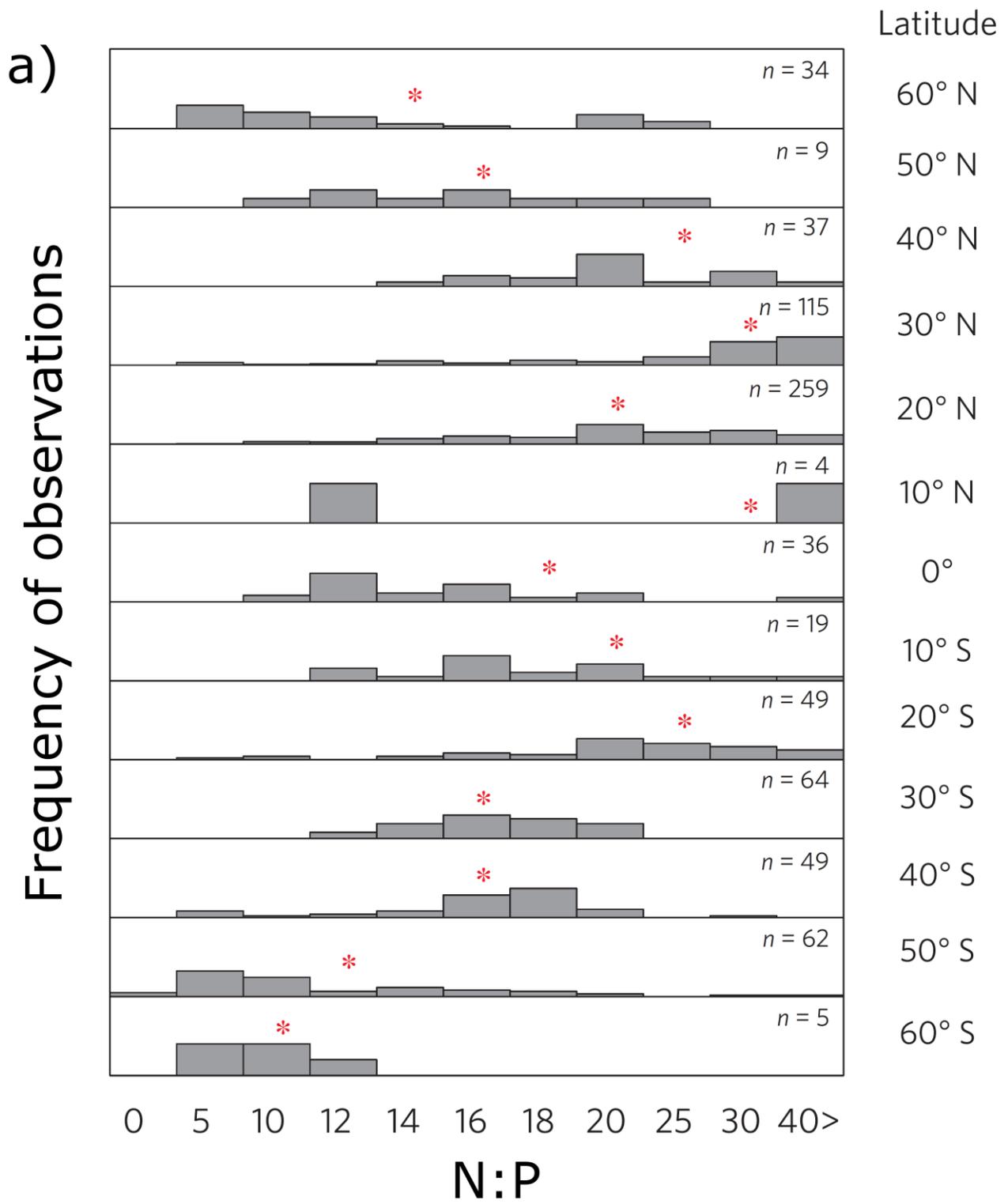


Figure 5:



b)

