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Phytoplankton stoichiometry

Abstract Because phytoplankton live at the interface between the abiotic and the biotic compartments of ecosystems, they play an important role in coupling multiple nutrient cycles. The quantitative details of how these multiple nutrient cycles intersect is determined by phytoplankton stoichiometry. Here we review some classic work and recent advances on the determinants of phytoplankton stoichiometry and their role in determining ecosystem stoichiometry. First, we use a model of growth with flexible stoichiometry to reexamine Rhee and Goldman's classic chemostat data. We also discuss a recent data compilation by Hall and colleagues that illustrates some limits to phytoplankton flexibility, and a model of physiological adaptation that can account for these results. Second, we use a model of resource allocation to determine the how the optimal nitrogen-to-phosphorus stoichiometry depends on the ecological conditions under which species grow and compete. Third, we discuss Redfield's mechanism for the homeostasis of the oceans' nitrogen-to-phosphorus stoichiometry and show its robustness to additional factors such as iron-limitation and temporal fluctuations. Finally, we suggest areas for future research.

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Introduction

Phytoplankton have played an important role in the development of the field of ecological stoichiometry (Sterner and Elser 2002). This can be attributed to two causes. First, phytoplankton make an ideal model system for studying both the biochemistry (Calvin and Benson 1948) and the ecological interactions of photosynthetic organisms (Tilman 1977). Second, phytoplankton are responsible for approximately half of the world's primary production (Field et al. 1998), and therefore play an important role in coupling global biogeochemical cycles (Sarmiento and Gruber 2006; Falkowski and Raven 2007). For these reasons, phytoplankton stoichiometry has received extensive attention, including the seminal studies of Droop, Rhee, and Goldman in the 1970s. After that, research in the area diminished. Perhaps it was thought that the subject was completely understood (a comment we've received in reviews of some of our recent manuscripts on the topic). However, recently research in phytoplankton stoichiometry has revived, supporting some parts of the accepted wisdom, while overturning other parts. In this article we give an overview of the subject, including both historical and recent research (but biased towards our own work), and suggest areas of future research, using a framework of mathematical models to unify concepts. We focus on the physiological and ecosystem levels and, due to space, neglect the manifold effects of phytoplankton stoichiometry on higher trophic levels (Urabe and Sterner 1996; Loladze et al. 2000) as well as the feedbacks from higher trophic levels on phytoplankton stoichiometry (Sterner 1990; Hessen and Andersen 1992).

Any discussion of phytoplankton stoichiometry should start with the work of Alfred Redfield (1934, 1958; Falkowski 2000). Based on work by Fleming (1940), Redfield (1958) declared the average atomic

C:N:P ratio of phytoplankton to be 106:16:1, a ratio which has since been enshrined as the "Redfield ratio". Recent work has extended the Redfield ratio to include trace elements (Quigg et al. 2003); the average composition of phytoplankton in this study was found to be $C_{124}N_{16}P_1S_{1.3}K_{1.7}Mg_{0.56}Ca_{0.5}Fe_{0.0075}Zn_{0.0008}Cu_{0.00038}Cd_{0.00021}Co_{0.00019}$. While expanding our knowledge of phytoplankton stoichiometry to include trace elements, the original Redfield trio of C:N:P remained markedly unchanged.

A more fundamental change in our conception of the phytoplankton stoichiometry has been a greater appreciation of its variability (Michaels et al. 2001; Karl et al. 2001). Although originally designated as an average, the Redfield ratio has sometimes been misconstrued as the universal and constant stoichiometry of phytoplankton. Recent research has emphasized the variability of phytoplankton stoichiometry in space and time and between different species (Michaels et al. 2001; Karl et al. 2001).

The Droop curve relating growth rate to the intracellular quota (Q) of an element provides a useful construct for thinking about variability in phytoplankton stoichiometry (Droop 1968; Caperon 1968; Fig. 1; see also the historical review by Leadbeater 2006). Growth rate is zero at the minimum quota (Q_{min}), and increases with additional nutrient supply, asymptotically approaching a theoretical maximum growth rate (μ_∞) at infinite quota. We can interpret the minimum quota as the element used in cellular structure and machinery, and all quota above the minimum quota as nutrient stored for future growth (Caperon 1968). This is a gross oversimplification of reality, but allows us to investigate two levels of variability in phytoplankton stoichiometry: that of overall stoichiometry (question 1 below) and that of cellular machinery (resource needs) (question 2 below).

Question 1: What determines overall stoichiometry (structure + stores)?

Classic chemostat experiments in the 1970s identified two key factors that interact to affect overall phytoplankton stoichiometry: nutrient supply ratio (Rhee 1978) and
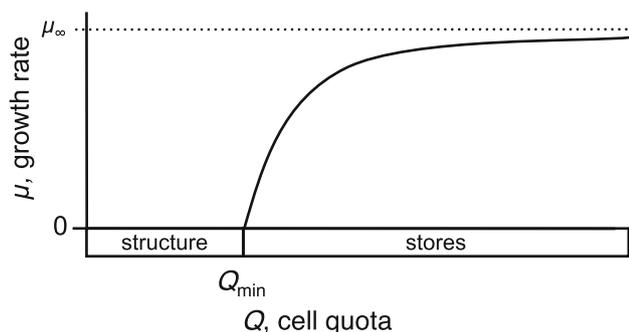
growth rate (Goldman et al. 1979). Rhee fixed the dilution (growth) rate and varied the N:P supply ratio. He found that *Scenedesmus* stoichiometry matched the N:P supply ratio over a range from 5 to 80. Goldman and colleagues (1979) performed an orthogonal set of experiments: they fixed the N:P supply ratio and varied the dilution (growth) rate. They found that phytoplankton N:P matched the N:P supply at low growth rates (as Rhee found), but high growth rates converged on a single N:P ratio, regardless of the identity of the limiting nutrient. They interpreted this single ratio at high growth rates as the Redfield ratio (although the numerical value from their experiments was clearly not 16:1).

We set out to understand these results using a simple mathematical model of phytoplankton growth on two essential nutrients with flexible stoichiometry (Klausmeier et al. 2004a). All the components were available "off the shelf": chemostat nutrient supply, Michaelis–Menten uptake kinetics, and Droop growth functions linked by Liebig's law of the minimum. Surprisingly, this model was not investigated until 1997 (Legović and Cruzado 1997) and not in the context of controls of phytoplankton stoichiometry. The model's dynamics are not particularly interesting: it has a unique, globally stable equilibrium point (De Leenheer et al. 2006). What is biologically interesting is that the model captures both Rhee's and Goldman's classical chemostat results (Fig. 2). Of course there are limits to the flexibility of phytoplankton stoichiometry, leading this model to not fit well at extreme N:P supplies (Klausmeier et al. 2004a; Smith and Yamanaka 2007).

The flexibility of overall phytoplankton stoichiometry as exemplified by Rhee's *Scenedesmus* has been taken as one of the fundamentals of ecological stoichiometry (Sterner and Elser 2002). Recently, Hall and colleagues reexamined the generality of this result and found it much more restricted than previously assumed (Hall et al. 2005). In natural lakes and experimental mesocosms, the N:P of seston did not match N:P supply, but was much more constant. Even more surprising, laboratory cultures also deviated from perfect N:P flexibility in the same way. It turns out that Rhee's results were the exception rather than the rule.

There are a number of possible explanations for this discrepancy (Hall et al. 2005). First, as Goldman's experiments (1979) and our model results (Fig. 2b, Klausmeier et al. 2004a) show, at high growth rates we do not expect a perfect correspondence between phytoplankton N:P and supply N:P. Second, there may be an inhibition of nutrient uptake at high internal concentrations, a result known from experimental work (Gotham and Rhee 1981). When incorporated into models, this uptake inhibition can prevent perfect flexibility, either instantaneously (Hall et al. 2005; Smith and Yamanaka 2007) or with a time lag (Klausmeier et al. 2007).

Our model (Klausmeier et al. 2004a) also clarified the meaning of the N:P ratio converged upon at high dilution rates. Goldman and colleagues called it the Redfield

Fig. 1 Droop function relating growth rate to cellular quota (nutrient per cell)
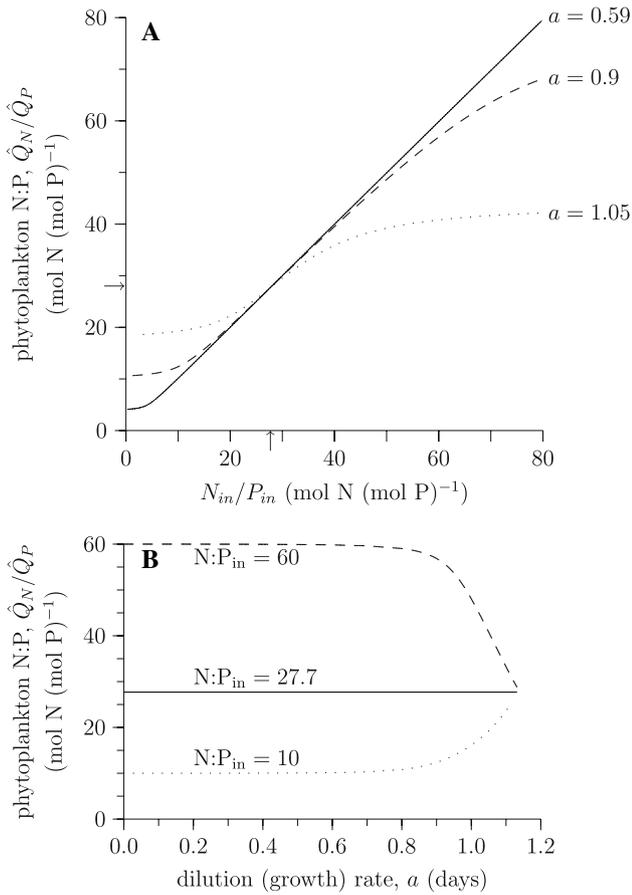
Fig. 2 Overall phytoplankton N:P as a function of **a** N:P supply and **b** dilution (growth) rate a, as determined by a simple model (Table 1) (after Klausmeier et al. 2004a)

Table 1 Model of phytoplankton with flexible stoichiometry of two essential resources, (after Legović and Cruzado 1997, Klausmeier et al. 2004a,b)

Variable	Equation
Available resource i	$\dfrac{\mathrm{d}R_i}{\mathrm{d}t} = a(R_{in,i} - R_i) - \dfrac{v_{\max,i}R_i}{R_i + K_i}B, i = 1, 2$
Nutrient quota i	$\dfrac{\mathrm{d}Q_i}{\mathrm{d}t} = \dfrac{v_{\max,i}R_i}{R_i + K_i} - \mu_\infty \min\left(1 - \dfrac{Q_{\min,1}}{Q_1}, 1 - \dfrac{Q_{\min,2}}{Q_2}\right)Q_i,$ $i = 1, 2$
Biomass	$\dfrac{\mathrm{d}B}{\mathrm{d}t} = \mu_\infty \min\left(1 - \dfrac{Q_{\min,1}}{Q_1}, 1 - \dfrac{Q_{\min,2}}{Q_2}\right)B - mB$

Parameter/ variable	Meaning
R_i	Concentration nutrient i available
Q_i	Quota nutrient i
B	Biomass
a	Chemostat dilution rate (day^{-1})
$R_{in,i}$	Input concentration nutrient i
$v_{\max,i}$	Maximum uptake rate nutrient i
K_i	Uptake half-saturation constant nutrient i
μ_∞	Growth rate at infinite quota
m	Mortality rate
$Q_{\min,i}$	Minimum quota resource i
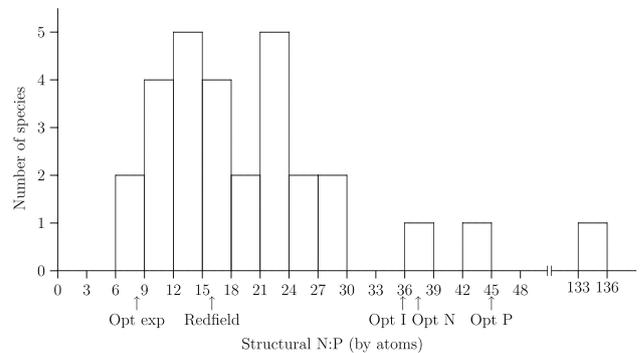
Fig. 3 Interspecific variation in optimal N:P ratios and model predictions during exponential growth and at competitive equilibrium (after Klausmeier et al. 2004b)

ratio, but we found it to be the ratio of the minimum quotas of N and P. Recall that these can be interpreted as the elemental requirements of a species. This ratio of minimum quotas has also been called the "optimal N:P" ratio of a species (Rhee and Gotham 1980). Because it causes equality in the minimum function that sets the growth rate, this ratio can be proven to be optimal, in that phytoplankton that adjust their nutrient uptake machinery to match this ratio will outcompete all others (see details in Klausmeier et al. 2007). The importance of this ratio of elemental needs leads to our next question.

Question 2: What determines structural stoichiometry (optimal N:P)?

It has long been recognized that species differ in their elemental needs (Fig. 3, Rhee and Gotham 1980; Klausmeier et al. 2004b), although this interspecific variation in structural stoichiometry is more limited than the intraspecific variation in overall stoichiometry that depends on growing conditions. This is empirical evidence that there is nothing intrinsically special about the Redfield N:P ratio of 16:1.

We sought to explain this variation in optimal N:P ratios by adding a layer of interpretation to our simple model (Klausmeier et al. 2004b). We imagined a phytoplankton cell as a factory equipped with two different types of machinery: uptake machinery, responsible for bringing raw ingredients into the cell, and assembly machinery, responsible for assembling those raw ingredients to form new cells. Each type of machinery was given its own N:P stoichiometry. The uptake machinery represents proteins and chloroplasts, and the assembly machinery represents ribosomes. Proteins are N-rich but have little P (Sterner and Elser 2002). According to the Growth Rate Hypothesis (Sterner and Elser 2002), ribosomes have abundant N but also represent a major pool of intracellular P. Because a cell cannot have everything, we assigned a trade-off between these two

types of cellular machinery. A species allocation strategy determines its structural stoichiometry as well as its ecophysiological parameters. Thus, the problem of calculating structural N:P needs could be reduced to finding the optimal allocation between ribosomes and proteins (Falkowski 2000; Geider and La Roche 2002).

But what is optimal? It depends on the conditions under which species grow and compete. We examined two extreme cases that bracket the range of possibilities. In a nonequilibrium, high-resource environment, the optimal strategy is one that maximizes its exponential growth rate μ_{max}. In a steady-state, low-resource environment, the optimal strategy is one that can reduce the limiting resource to the lowest level (R^*) (Tilman 1982). Since we have algebraic expressions for both of these fitness measures, it is easy to find the optimal allocation strategy and therefore the optimal structural N:P in each case. When parameterized, the model predicts structural N:P ratios to vary from 8.2 during exponential growth to 35.8, 37.4, and 45.0 at competitive equilibrium depending on the limiting resource (light, N, or P, respectively) (Klausmeier et al. 2004b). These values are close to the range of observed structural N:P ratios (Fig. 3), lending theoretical support to the idea that the Redfield ratio is not intrinsically special. If the mix of exponential growth and equilibrium phases would change in the ocean, then so would the average N:P composition of the phytoplankton.

As an aside, we note the terminological train wreck concerning the word "optimal" that we have been party to (Leonardos and Geider 2004). The ratio of minimum quotas is known as an "optimal ratio" because a species that achieves this ratio outcompetes others that do not (Rhee and Gotham 1980; Klausmeier et al. 2007), at least if we assume that species have a single μ_∞ value for both elements (Terry et al. 1985). Another use of the phrase "optimal ratio" is "the elemental ratio of species growing during their optimal conditions" (e.g., Hillebrand and Sommer 1999). These are identical given our theoretical results (Fig. 1b), given the same proviso concerning μ_∞ values. Finally, what we have done here (Klausmeier et al. 2004b) is derive the best possible ratio of minimum quotas, that is, the *optimal* optimal N:P ratio. Although this phrase is more accurate, it is probably better disregarded.

Question 3: Why do phytoplankton and ocean N:Ps (almost) match?

The final question we would like to address brings us back to Redfield (1934, 1958). That is, why is the average N:P ratio of phytoplankton and that of the ocean as a whole so similar? Redfield offered three explanations: (1) over long time scales, phytoplankton have adapted to thrive on the chemical composition of the ocean; (2) over long time scales, the ocean has changed to match what phytoplankton require; and (3) it is just a coincidence (Redfield 1958). The third hypothesis is hard to test. The first hypothesis is intuitively appealing, while the second seems non-Darwinian. Despite this, Redfield favored the second hypothesis of biotic control over oceanic N:P, which is now considered to be true (Falkowski 2000).

What mechanism could account for this counterintuitive explanation? Redfield (1958) suggested that competition between nitrogen-fixing and non-fixing phytoplankton could determine the N:P ratio of the ocean. If the ocean's N:P ever became too low, nitrogen-fixing species would dominate by fixing atmospheric N, and increase the ocean's N:P ratio as they die and decompose. Recently, two simple models of the ocean demonstrated that this mechanism could operate as Redfield suggested (Tyrell 1999; Lenton and Watson 2000). This explanation can be recast in terms of Tilman's (1982) graphical approach to resource competition (Fig. 4, Schade et al. 2005). Non-fixing species have a right-angled zero net growth isocline (ZNGI) typical of essential resources, while the nitrogen-fixer has a vertical ZNGI because it can grow with no nitrate available. Consumption vectors reflect that non-fixers consume both phosphate and nitrate while N-fixers consume only phosphate. This sets a wedge-shaped region of supply points that lead to coexistence. Finally, in a completely closed system, the supply point corresponds to the N:P ratio in deep waters. Over long time scales this point moves up as nitrogen-fixers die and increase the deep water N pool. In a closed system, this process would continue until the supply point reached the upper boundary of the coexistence region, set by the N:P needs of the non-fixer. The continual N loss due to denitrification and sedimentation prevents the nitrogen-fixers from fixing themselves out of existence.

Fig. 4 Graphical model of the regulation of N:P in the ocean by competition between N-fixing and non-fixing phytoplankton (after Schade et al. 2005)
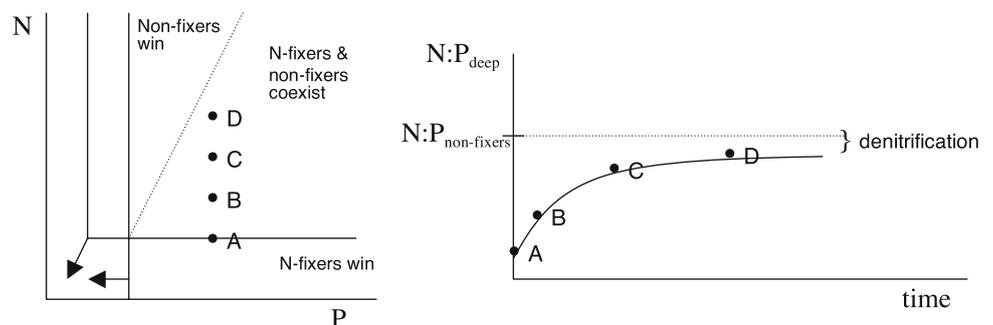
One argument that could be made against this model is that recent evidence shows that nitrogen-fixers are often limited by light or iron (Falkowski 2000; Berman-Frank et al. 2001; Hood et al. 2004; Mills et al. 2004). To see if the widespread limitation of N-fixers by factors other than P would break Redfield's homeostatic mechanism, we modified Tyrell's (1999) model to include two upper ocean boxes, one where both N-fixers and non-fixers can live and one where N-fixers are excluded (Lenton and Klausmeier 2007). We found that Redfield's homeostatic mechanism was remarkably robust to this complication. When N-fixers were restricted to a small part of the ocean's surface, their density there increased to mostly compensate. Even when N-fixers were restricted to 20% of the ocean's surface, the deep ocean N:P was kept between 11 and 14.6. We also found that the N:P stoichiometry of N-fixers had very little effect on the ocean's N:P, but the N:P stoichiometry of the non-fixers had a large effect (Lenton and Klausmeier 2007).

One complication that we uncovered was that Tyrell's (1999) model coupling the N-and P-cycles did not always reach a stable equilibrium point, but could give rise to sustained large-scale oscillations with an approximately 300-year period (Lenton and Klausmeier 2007). The ocean's N:P ratio and overall abundance of N-fixers do not oscillate at this frequency, so something needs to be done to account for this behavior. It is likely that, if this dynamic were embedded in a spatially-explicit model, spatiotemporal oscillations would result, leading to local instability but global stability (Pascual and Levin 1999; Durrett and Levin 2000), but we will not know for sure until such a model is constructed. These self-sustained oscillations may permit the coexistence of more phytoplankton species than possible at equilibrium (Huisman and Weissing 1999; T. Daufresne et al., manuscript in preparation.).

Future directions

Here we briefly outline some directions for future research that might prove fruitful.

Derive the Droop model from individual behavior

The way in which we and others have used the Droop function (Fig. 1) is to treat nutrient quota as the independent variable and growth rate as the dependent variable, that is to say that quota determines growth rate. This is actually the opposite of how Droop (1968) and Caperon (1968) originally discovered this relationship, which was by running a series of chemostats with varying dilution rates and measuring the nutrient quota at equilibrium. At steady state, the results are identical, but an important use of the variable internal stores models is understanding dynamics away from equilibrium (Grover 1991; Ducobu et al. 1998) where this

discrepancy may become important. We suggest that an important open problem is to put the Droop model on a firm foundation, starting from an individual-based model and scaling up to population dynamics (Metz and Diekmann 1986; Pascual and Caswell 1997) to derive the steady-state relationship between the growth rate and quota.

Include energy

The models we have discussed have focused on chemical resources, yet light energy is obviously also important to phototrophs. The balance between light and nutrients is known to affect many aspects of ecosystem structure (Sterner et al. 1997) and the effect of light supply on nutrient stoichiometry is becoming understood (Diehl et al. 2005; Jäger et al. 2008). To what extent carbon/light be modeled in a similar way to the Droop model (Zonneveld et al. 1997)? How do light supply and fluctuations affect elemental stoichiometry (Litchman et al. 2004)? There has been much work on modeling photoadaptation of chlorophyll (e.g., Geider et al. 1996; Zonneveld 1997), but less work coupling chlorophyll and nutrient dynamics (but see Geider et al. 1998 and Armstrong 1999). This remains an area in need of further work, perhaps based on Kooijman's DEB theory (Kooijman 2000).

C-limitation

Free CO_2 can often be limiting in the water, especially in marine environments (Stumm and Morgan 1981). Many species of phytoplankton, including cyanobacteria, possess mechanisms to increase the efficiency of photosynthesis by taking up different forms of inorganic carbon (CO_2, HCO_3^-) and concentrating CO_2 around Rubisco, the main photosynthetic (carbon fixation) enzyme (Badger et al. 2002; Raven 2003). High concentration of inorganic carbon around Rubisco inhibits the oxygenase function (photorespiration) of this enzyme and hence decreases inhibition of photosynthesis by oxygen. Carbon-concentrating mechanisms (CCMs) thus influence the resulting C:nutrient stoichiometries of phytoplankton cells. Nutrient limitation can, in turn, down-regulate CCMs (Beardall et al. 2005), further modulating C:nutrient ratios.

Consider multiple constraints and dynamics of acclimation

In our studies, we have considered only a single constraint between uptake of two resources (Klausmeier et al. 2007) or uptake of resource and cellular assembly (Klausmeier et al. 2004b). Phytoplankton require multiple resources and they also face multiple constraints that restrict the metabolic strategies they can employ to

obtain these resources. For example, there are the nested constraints of allocation of multiple elements, energy for assembly and operation of cellular machinery, and physical space to put the machinery (Aksnes and Egge 1991). It would be instructive to simultaneously consider multiple constraints on phytoplankton metabolic strategies. Initial attempts in this direction have been quite complex (Flynn 2003). Perhaps ideas could be borrowed from ecology's sister field of economics, where multiple constraints are also the rule, or from models of terrestrial primary producers (Rastetter and Shaver 1992).

Spatiotemporal variability as a mechanism of coexistence

In our work in deriving the optimal N:P ratio of phytoplankton (Klausmeier et al. 2004b) we considered two extreme ecological scenarios: competition to exclusion and maximal exponential growth. Implicitly, we assumed that the real world is a mixture of these extremes that would select for an intermediate community N:P ratio. Whether that community consists of a single best-adapted type or a more diverse collection of species was unaddressed, but is a classic question of plankton community ecology (Hutchinson 1961). It is well known that spatial (Levin 1974), temporal (Armstrong and McGehee 1980; Huisman and Weissing 1999; Litchman and Klausmeier 2001), and spatiotemporal variability [externally-forced (Snyder 2007) and generated by patchy nutrient recycling by grazers (Kato et al. 2007)] can all contribute to species diversity. How these mechanisms of diversity and the physiological trade-offs between ecological strategies interact to determine the stoichiometric diversity of phytoplankton communities is still an open question.

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