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A meta-analysis on environmental drivers of marine phytoplankton C:N:P

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Abstract. The elemental stoichiometry of marine phytoplankton plays a critical role in the global carbon cycle through carbon export. Although extensive laboratory experiments have been carried out over the years to assess the influence of different environmental drivers on the elemental composition of phytoplankton, a comprehensive quantitative assessment of the processes is still lacking. Here, we synthesized the responses of P:C and N:C ratios of marine phytoplankton to five major drivers (phosphate and nitrate, irradiance, temperature, and iron) by meta-analysis of laboratory experimental data available in the literature. Our results show that the response of the ratios to changes in macronutrients is consistent across all the studies, where the nutrient availability is positively related to changes in P:C and N:C ratios. We found that diatoms are more sensitive to the changes in macronutrients compared to other eukaryotes and cyanobacteria, possibly due to their larger cell size and their abilities to quickly regulate their gene expression patterns required for nutrient uptake. The effect of irradiance on P:C was mixed and not significant, but the same effect on N:C was significant and constant across all studies where an increase in irradiance decreased N:C. The response to temperature changes was mixed by species, except warming consistently decreased P:C ratio in cyanobacteria. This may explain why P:C is consistently low in the cyanobacteria-dominated subtropical oceans. The effect of iron on P:C and N:C for cyanobacteria were statistically significant but the small sample size precludes drawing firm conclusions. Overall, our findings highlight the high stoichiometric plasticity of diatoms and the importance of macronutrients in determining P:C and N:C ratios, which both provide us insights on how to understand and model plankton diversity and productivity.

1 Introduction

Elemental stoichiometry of biological production in the surface ocean plays a crucial role in cycling of elements in the global ocean. The elemental ratio between carbon and the key limiting macronutrients, nitrogen (N) and phosphorus (P), in exported organic matter expressed in terms of C:N:P ratio helps determine how much atmospheric carbon is sequestered in the deep ocean with respect to the availability of limiting nutrients. On geologic timescale, N:P ratio reflects the relative availability of nitrate with respect to phosphate, both of which are externally supplied from atmosphere via nitrogen-fixation and/or continents via river supply (Broecker, 1982; Lenton and Watson, 2000; Redfield, 1958; Tyrrell, 1999). On shorter timescales the average stoichiometry of exported bulk organic matter reflects elemental stoichiometry of phytoplankton (Bonachela et al., 2016; Garcia et al., 2018a; Martiny et al., 2013b) with additional influences of biological diversity and secondary processing of organic matter by zooplankton and heterotrophic bacteria. In the face of global change, understanding and quantifying the mechanisms that leads to variability in C:N:P ratio are crucial in order to have an accurate projection of future climate change.

A key unresolved question is what determines C:N:P of individual phytoplankton? Phytoplankton grow in the upper light-lit layer of the ocean where the amount of inorganic nutrients, light, and temperature vary spatially and temporally. Laboratory studies show that these fluctuations trigger responses at the cellular level, whereby cells modify resource allocation in order to adapt optimally to their ambient environment (Geider and La Roche, 2002; Moreno and Martiny, 2018). For example, phytoplankton may alter resource allocation between P-rich biosynthetic apparatus, N-rich light-harvesting apparatus, and C-rich energy storage reserves. Under a typical future warming scenario, the global ocean is expected to undergo changes in nutrient availability, temperature, and irradiance (Boyd et al., 2010). These changes are likely to have profound effects on physiology of phytoplankton (Finkel et al., 2010; van de Waal et al., 2010) and observations show that competitive phytoplankton species are able to acclimate and adapt to changes in temperature, irradiance, and nutrients on decadal timescales (Irwin et al., 2015). Over 100 laboratory and field experiments have been conducted thus far to study the relationship between C:N:P ratio of phytoplankton and environmental drivers. It is however challenging to synthesize those studies and generalize the response of phytoplankton C:N:P to changes in environmental drivers. One reason for the challenge is that the acclimation and adaptation strategies as well as genetic composition differ amongst different species, and so the response of phytoplankton differs by species even if the experiment is conducted at otherwise identical conditions. In addition, individual studies employ different sets of statistical analyses to characterize effects of environmental driver(s) on elemental ratios, ranging from a simple t-test to more complex mixed models, which makes interstudy comparisons challenging.

Meta-analysis/systematic-review is a powerful statistical framework for synthesizing and integrating research results obtained from independent studies and for uncovering general trends (Gurevitch et al., 2018). It has a number of advantages over narrative review and "vote counting" because it compares the common measure of outcome (effect size) that includes information on both the sign and magnitude of an effect of interest from each study. Effect size from individual studies can be combined across studies to estimate the grand mean effect size and its confidence interval, which are then used to test whether overall effect is statistically significant. In addition, with its comprehensive and rigorous procedure for study inclusion criteria, meta-analysis avoids the pitfall of "cherry-picking" data aimed toward supporting particular hypothesis.

We present results from a systematic literature review and subsequent meta-analysis to quantify how five key environmental drivers affect P:C and N:C ratios of marine phytoplankton. Unlike previous meta-analyses on elemental stoichiometry of phytoplankton that strictly synthesized the effect of a single environmental driver, our study assessed the effects of five drivers, specifically for marine phytoplankton species. Importantly, we use a unique newly defined measure of effect size, a *stoichiometry sensitivity factor* (Tanioka and Matsumoto, 2017), which is a dimensionless parameter that relates fractional change in P:C or N:C with a fractional change in a particular environmental driver, while the other drivers are kept constant. The five environmental drivers are: (1) phosphate, (2) nitrate, (3) irradiance, (4) temperature, and (5) iron. These are the top drivers of open-ocean phytoplankton group (Boyd et al., 2010). Although CO_2 is another potentially important driver, we did not consider the effects of CO_2 on elemental ratios as a previous meta-analysis studies showed that no generalization can be made with respect to the direction of trends in P:C or N:C ratios as a function of CO_2 concentration (Kim et al., 2018; Liu et al., 2010). We systematically screened peer-reviewed publications on monoculture laboratory experiment studies, which isolate the effect of a specific driver from other confounding drivers. We compute effect size for each driver-stoichiometry pair from independent studies and subsequently determine the grand mean across all studies to quantify the effectiveness of each driver on P:C and N:C ratios. Further, we compare grand mean effect size for different major phytoplankton groups for detecting any systematic variability between phytoplankton groups.

2 Materials and Methods

2.1 Bibliographic search and screening

We selected experimental studies that assessed the effects of nutrients (dissolved inorganic phosphorus, dissolved inorganic nitrogen, iron), irradiance, and temperature on P:C and N:C ratios of marine phytoplankton. In order to compute stoichiometric sensitivity factors (section 2.2), we selected experiments conducted over at least three different levels of the driver of interest while other driver values are kept constant. Firstly, we conducted a literature search using Web of Science (last accessed in February 2019) with the following sequence of key terms: (TS=(phytoplankton OR algae OR microalgae OR diatom OR coccolithophore* OR cyanobacteri* OR diazotroph*) AND TS=(stoichiometr* OR "chemical composition" OR "element* composition" OR "nutritional quality" OR "nutrient composition" OR "nutrient content" OR "nutrient ratio*" OR C:N OR C:P OR N:P OR P:C OR N:C OR "cellular stoichiometr*" OR C:N:P OR "element* ratio*" OR "food qualit*" OR "nutrient concentration" OR “carbon budget”) AND TS = (phosph* OR "phosph* limit*" OR nitr* OR "nitr* limit*" OR iron OR "iron limit*" OR nutrient OR "nutrient limit*" OR "nutrient supply" OR "nutrient availabilit*" OR "supply ratio*" OR eutrophication OR fertili* OR enrichment OR temperature OR warming OR light OR irradiance OR "light limit*") AND TS = (marine or sea or ocean OR seawater OR aquatic)). This search yielded 4899 hits. We also closely inspected all the primary studies mentioned in the 8 recent review papers including meta-analyses studies on elemental stoichiometry of phytoplankton in aquatic environment (Flynn et al., 2010; Geider and La Roche, 2002; Hillebrand et al., 2013; Moreno and Martiny, 2018; Persson et al., 2010; Thrane et al., 2016; Villar-Argaiz et al., 2018; Yvon-Durocher et al., 2015). The list is also augmented with data from additional four studies that did not appear in the literature search or in the review papers but were cited in the original studies. Subsequent selection processes based on abstracts, graphs, tables, and full text, and removal of duplicates led to a total of 64 papers (Fig. 1). The N:C and P:C ratios were extracted with use of GraphClick (Arizona Software, 2010) to read off values from graphs when necessary. In cases where N:P and only one of either P:C or N:C is provided, the remaining ratio is determined by either multiplying or dividing by N:P. Similarly, elemental ratios are computed from the measurements of phytoplankton POC, PON, and POP when the ratios are not explicitly given in the original studies. When more than two factors were manipulated in the same studies, multiple experimental units are extracted. Here, experimental unit refers to a controlled experiment of stoichiometry of a phytoplankton species under some growth conditions (e.g., nutrients, temperature, irradiance) with a minimum of three levels of independent variable. The only exception was when the additional driver was CO_2, and in this case we utilized responses to each driver at the ambient or control CO_2 level. We only considered experimental monoculture studies of marine phytoplankton species to isolate the effects of specific environmental driver from other confounding drivers that cannot be controlled in the field. When the species habitat was not noted in the original study, AlgaeBase (www.algaebase.org) was used to determine whether the species is marine or freshwater species. Our final dataset consists of 81 experimental units of P:C and 165 experimental units of N:C from 64 studies encompassing 7 taxonomic phyla (Bacillariophyta, Chlorophyta, Cryptophyta, Cyanobacteria, Haptophyta, Miozoa, and Ochrophyta) (Table 1).

2.2 Stoichiometry sensitivity factor as effect size

The effect size in this study is the stoichiometry sensitivity factor s_Y^X (Tanioka and Matsumoto, 2017), which relates a fractional change in a stoichiometry (response variable X) to a fractional change in environmental driver (variable Y):

$$s_Y^X = \frac{\partial X/X}{\partial Y/Y} = \frac{\partial \ln X}{\partial \ln Y} \qquad (1)$$

where the partial differentials indicate that other factors are kept constant. For convenience, we use the term "s-factor" in the rest of this paper when describing s_Y^X in a generic sense. In essence, the magnitude of s-factor is a measure of how sensitive X (P:C or N:C) is to a change in stressor level Y, and the sign

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indicates whether X changes in the same direction as Y (positive sign) or in the opposite direction to Y (negative sign). The s-factor allows for different kinds of response: a linear response of X with respect to Y ($s_Y^X = 1$), a near hyperbolic response that saturates at high X ($0 < s_Y^X < 1$), an exponential growth ($1 < s_Y^X$), a decay ($0 > s_Y^X$), and the null response ($s_Y^X = 0$). Importantly, an advantage of using s_Y^X as effect size is that its magnitude is a direct measure of the strength of interaction over range of stressor values as opposed to measures such as Hedge's *d* and log response ratio which only compares the effect of stressor on two end point values (control and treatment). Further, ability of s_Y^X to describe nonlinear behavior often displayed in biological and chemical systems is more realistic than a simple linear regression.

2.3 Meta-analysis

Stoichiometry s-factor and its standard error for each individual experiment unit are obtained by carrying out linear regression on the log-transformed X and Y. When using temperature as the environmental driver, we converted degrees Celsius into absolute temperature scale Kelvin. In analyzing iron manipulation experiments, we computed stoichiometry s-factor with respect to change in biologically available free dissolved inorganic iron concentration (Fe'). We estimated Fe' from total dissolved iron concertation, temperature, irradiance, and pH (Sunda and Huntsman, 2003) when iron availability in the original research is provided in terms of total dissolved iron concentration instead of Fe'. For calculating s-factors for PO_4 ($s_{PO_4}^{P:C}$ and $s_{PO_4}^{N:C}$), we only selected experiments where NO_3 concentrations are kept constant. The same was true for calculating dependency on NO_3 ($s_{NO_3}^{P:C}$ and $s_{NO_3}^{N:C}$). We defined s-factors separately ($s_{NP}^{P:C}$ and $s_{NP}^{N:C}$) for studies where both PO_4 and NO_3 are manipulated simultaneously to adjust the N:P supply ratio.

We summarized s-factors by a random-effects model meta-analysis to determine the weighted mean s-factor using the *metafor* R package (Viechtbauer, 2010). For each environmental driver-stoichiometry pair, we conducted an overall meta-analysis across all the studies (where $n \geq 5$) as well as meta-analysis within 3 plankton functional types (PFT) as a categorical moderator. To calculate the PFT averaged s-factors, we fitted separate random-effects model within each level of PFT. A Wald-type test (Viechtbauer, 2010) was used to test whether mean s-factors for PFTs are statistically different from each

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other. PFTs classified in our study are: (1) diatoms (Bacillariophyta); (2) eukaryotes excluding diatoms; and (3) cyanobacteria. This classification is chosen in order to give a relatively balanced distribution of studies and power across moderator categories. Similar classification of PFTs are commonly employed in the global ocean biochemical models (e.g., Dunne et al., 2013; Ilyina et al., 2013; Moore et al., 2004). All the statistical analyses were performed with R v3.5.2 (R Core Team, 2018) and the codes of the functions used to run all the analyses are available in the Zenodo data repository (https://doi.org/10.5281/zenodo.3515471).

3 Results

We present s-factors for each of the five environmental factors and discuss whether the s-factors obtained are: (1) consistent or mixed across studies and across PFTs; (2) positive or negative; and (3) significantly different from 0. The summary of s-factors for each driver-stoichiometry pair is provided in Table 2.

3.2.1 Effects of Phosphate

The response of P:C ratio to changes in phosphate was consistent, positive, and significant across studies (Fig. 2a) where increase in PO_4 lead to higher P:C. Diatoms have the largest stoichiometric flexibility ($s^{P:C}_{PO_4} = 0.75 \pm 0.08$, $n = 2$, $p < 0.0001$) followed by eukaryotes ($s^{P:C}_{PO_4} = 0.39 \pm 0.06$, $n = 3$, $p < 0.0001$) and cyanobacteria ($s^{P:C}_{PO_4} = 0.29 \pm 0.04$, $n = 3$, $p < 0.0001$). The overall mean $s^{P:C}_{PO_4}$ across all the studies is 0.43 ± 0.09 ($n = 8$, $p < 0.0001$), which means that on average P:C ratio of phytoplankton changes by 0.43% for every 1% change in PO_4 concentration. On the other hand, the effect of phosphate on N:C was weak and not significant overall ($s^{N:C}_{PO_4} = 0.02 \pm 0.02$, $n = 8$, $p = 0.4$) where the magnitudes of s-factors are less than 0.10 in all but one experimental unit.

3.2.2 Effects of Nitrate

The response of N:C to changes in NO_3 was similar to the response of P:C to PO_4 changes and was consistent, positive, and significant. An increase in NO_3 lead to higher N:C ratios with the statistically significant overall mean s-factor of 0.20 ± 0.03 ($n = 13$, $p < 0.0001$) (Fig. 2b). This result indicates that

NO_3 is one of the primary drivers of N:C. Again, diatoms are the most sensitive PFT with the highest s-factor ($s_{NO_3}^{N:C}$ = 0.22 ± 0.04, n = 8, p < 0.0001), followed by eukaryotes ($s_{NO_3}^{N:C}$ = 0.17 ± 0.04, n = 4, p < 0.0001). The s-factor for cyanobacteria is negative ($s_{NO_3}^{N:C}$ = -0.12 ± 0.18) but the sample size is minimal (n = 1). There were not enough observations in total (n < 5) to conduct meta-analysis on the effects of nitrate on P:C but our analysis shows that s-factors are positive for both diatoms and eukaryotes.

3.2.3 Effects of Nitrate:Phosphate supply ratio

An increase in NO_3:PO_4 supply ratio increases P limitation and decreases N limitation. As anticipated from the two previous subsections, increase in NO_3:PO_4 resulted in lower P:C and increased N:C with negative mean $s_{NP}^{P:C}$ of -0.30 ± 0.04 (n =17, p < 0.0001) and positive mean $s_{NP}^{N:C}$ of 0.09 ± 0.03 (n = 21, p = 0.0002) (Fig. 2c). Diatoms have the largest mean s-factor out of the 3 PFTs in terms of the magnitude with $s_{NP}^{P:C}$ and $s_{NP}^{N:C}$ of -0.41 ± 0.08 (n = 4, p < 0.0001) and 0.12 ± 0.02 (n = 5, p < 0.0001) respectively. Overall, the magnitudes of $s_{NP}^{P:C}$ consistently exceed those of $s_{NP}^{N:C}$ which suggests that P:C is more plastic than N:C with respect to changes in N:P supply ratio.

3.2.4 Effects of Irradiance

The response of P:C to changes in irradiance was not consistent or statistically significant overall (Fig. 3). The mean $s_I^{P:C}$ across all studies and across each PFT are not statistically different from 0, reflecting the weak and mixed responses. N:C ratio meanwhile showed weak but consistent responses where increase in irradiance lead to lower N:C, giving negative $s_I^{N:C}$ overall ($s_I^{N:C}$ = -0.05 ± 0.01, n = 59, p < 0.0001). Mean $s_I^{N:C}$ for all the PFTs are similar in magnitude and are not statistically different from each other (p > 0.05).

3.2.5 Effects of Temperature

The response of P:C to temperature changes was variable across different species and PFTs (Fig. 4). Diatoms display mixed responses, and the mean s-factor is negative overall but not significant. Eukaryotes also show mixed responses but the overall mean is positive because of the large s-factor associated with

Rhodomonas sp (Bi et al., 2017). In contrast to diatoms and eukaryotes, cyanobacteria have consistently negative s-factors for all 12 experimental units but one. As a result, mean s-factor for cyanobacteria is statistically significant with a negative sign ($s_T^{P:C}$ = -7.8 ± 3.3, n = 12, p = 0.02). The mean s-factor across all the studies is negative ($s_T^{P:C}$ = -2.0 ± 2.0) but not statistically significant (n = 34, p = 0.3).

The effect of temperature on N:C was also variable across different species and PFTs (Fig. 4). Although mean s-factors across all studies and for all PFTs are positive, none are statistically significant. Compared to $s_T^{P:C}$, the magnitude as well as the standard error of $s_T^{N:C}$ are smaller which suggest that change in N:C with respect to temperature is less pronounced compared to P:C.

3.2.6 Effects of Iron

Iron availability increased P:C and s-factors for diatoms and cyanobacteria are positive ($s_{Fe}^{P:C}$ = 0.09 ± 0.05 and $s_{Fe}^{P:C}$ = 0.19 ± 0.07, respectively) (Figure 5). Yet, the insufficient of sample size precluded us from carrying meta-analysis on overall effects of iron on P:C. The effect of iron on N:C was generally weak and s-factors the magnitude of $s_{Fe}^{N:C}$ does not exceed 0.05. For cyanobacteria however, $s_{Fe}^{N:C}$ is consistently negative and the overall s-factor is significant ($s_{Fe}^{N:C}$ = -0.03±0.01, n = 3, p < 0.0001).

4 Discussion

4.1 Basic framework

One of the fundamental tenets of the chemical oceanography is the Redfield Ratio, which implies that phytoplankton cells at balanced growth achieve a constant cellular P:N:C ratio at the well-known molar ratio of 1:16:106 (Redfield et al., 1963). Balanced growth is achieved for nutrient-replete algal cells growing under steady state conditions where the balance between uptake of elements and assimilation into cellular functional pool is achieved (Berman-Frank and Dubinsky, 1999; Klausmeier et al., 2004). Under such conditions, the growth rate of all cellular constituents averaged over one generation is the same, whether it is the carbon-specific, nitrogen (protein)-specific, or phosphorus (DNA)-specific growth rates (Falkowski and Raven, 2007). In the real ocean however, the ideal condition required for balanced growth is rarely achieved as the phytoplankton growth is usually limited by one or more factors (Moore et al., 2013; Moore and Doney, 2007). For example, the deficiency of essential nutrients limits the formation of building blocks of new cells (e.g., N for proteins, P for nucleic acids and ATP), light limitation slows carbon assimilation (i.e. making of carbohydrates and reductase), and low temperature slows down the essential cellular transport and enzymatic reactions for growth (Madigan et al., 2017). Similarly, excess supply above cellular requirement can lead to reduction in growth rate via nutrient toxicity; photoinhibition from excess irradiance; protein denaturation, collapse of cytoplasmic membrane, and thermal lysis from excess warming although such cases in the marine environment are rarer compared to those in freshwater environment. The steady state assumption is also not always justified due to short-term and long-term changes in physical conditions of ocean. A good example of such change is phytoplankton bloom in the spring where the transient changes in surface temperature, irradiance and nutrient supply rate alter the growth rate and elemental stoichiometry of phytoplankton (Polimene et al., 2015; Talarmin et al., 2016). Growth limitations and transient changes in the environmental conditions are likely to be the two fundamental drivers for the divergence of measured P:N:C of phytoplankton from Redfield P:N:C observed in nature (Geider and La Roche, 2002; Martiny et al., 2013b; Moreno and Martiny, 2018).

The degrees to which phytoplankton P:N:C ratios are affected by stresses depend both on the cellular stress response mechanisms and the magnitude of the environmental change as well as temporal variability of environmental drivers. Most types of stress responses can be divided into a stress-specific, primary response and a general secondary response (Brembu et al., 2017). The stress-specific responses are strong, robust and consistently observed across photosynthetic organisms, while secondary responses are variable amongst different organisms. Primary and secondary responses are closely related to acclimation (plasticity response) and adaptation (evolutionary response) respectively. In essence, acclimation refers to environmentally induced trait change of an organism in the absence of any genetic change, while adaptation involves genetic changes driven by natural selection (Collins et al., 2020). Since primary responses do not involve genetic adjustment or natural selection, the responses are fast and often commonly shared amongst different marine phytoplankton. For example, changing the nutrient uptake affinity of a lineage within a generation in response to changing nutrient supply is a commonly seen trait across all phytoplankton groups. On the other hand, secondary response depends both on the environmental condition and genotype (Brembu et al., 2017). The secondary responses take longer time (usually up to few hundred generations) and there is typically no single, unique response even when referring to a single species or functional group and a specific environmental driver (Collins et al., 2020).

By adopting this framework, we are able to use the s-factor as a proxy to understand the relative importance of primary responses over secondary responses in altering the P:C and N:C ratios. For example, if the sign of a s-factor is consistent across all the studies for a particular environmental driver-stoichiometry pair, we may deduce that change in elemental ratio is due to a primary response. On the other hand, we can infer that the change in the ratio is due to a secondary response if there are no consistent responses across all species and groups. If the P:C and N:C ratios are not significantly affected (i.e. s-factors are close to 0), we would infer that such environmental driver does not perturb the balance between carbon assimilation and growth. In the subsections below, we discuss for each environmental driver whether there are any underlying patterns present amongst different studies and speculate on cellular mechanisms responsible for producing such patterns (see Fig. 6 for schematic illustration).

4.2 Macronutrients (Phosphate and Nitrate)

Overall, we observe consistent trend across all studies where P:C and N:C increases with increase in the supply of phosphate and nitrate respectively (Fig. 2). Since the direction of change between and X:C and the supply of element X are positively related, $s_{\mathrm{PO_4}}^{\mathrm{P:C}}$ and $s_{\mathrm{NO_3}}^{\mathrm{N:C}}$ are both positive. Observations of phosphate/nitrate against particulate organic matter P:C and N:C indeed broadly follow this general trend (Galbraith and Martiny, 2015; Tanioka and Matsumoto, 2017). Similarly, we observed consistent stoichiometric responses for changes in N:P supply ratio where increase in N:P lead to lower P:C and higher N:C. This makes intuitive sense because higher N:P supply ratio would increase availability of N with respect to availability of P. Positive correlation between X:C with respect to availability of element X across all the species and studies suggest that this is a primary plasticity response and effectively decouples intracellular reserves of element X and carbon from the ambient availability of X.

Phytoplankton can temporally store excess nutrient intracellularly until the rate of carbon assimilation catches up to achieve steady-state balanced growth. Excess phosphorus for example can be stored mainly as polyphosphate (Dyhrman, 2016) and excess nitrate can be stored primarily as protein and free amino acids (Liefer et al., 2019; Sterner and Elser, 2002). Phytoplankton can consume these internal stores of nutrients (e.g., polyphosphates under P limitation) while maintaining the level of carbon fixation, when the uptake of the nutrients does not meet its demand for growth (Cembella et al., 1984). In addition, phytoplankton can reduce their ribosomes and RNA content under P limitation as RNA typically accounts for 50% of non-storage phosphorus (Hessen et al., 2017; Lin et al., 2016) which would conserve phosphorus for other uses in cell resulting in lower P:C ratios. Similarly, cells can reduce synthesis of N-rich protein content under N limitation resulting in lower N:C ratio (Grosse et al., 2017; Liefer et al., 2019). These transient processes controlling the intracellular content of P or N (but not C content as much) likely result in positive correlation between P:C and N:C with macronutrient concentrations.

Although $s_{PO_4}^{P:C}$ and $s_{NO_3}^{N:C}$ are consistently positive across all the studies, they are noticeably higher for diatoms than for other phytoplankton groups (Fig. 2a, b). There are several hypotheses for explaining this trend. One of the most plausible hypotheses is related to the size and storage capacity difference amongst phytoplankton groups (Edwards et al., 2012; Lomas et al., 2014). Since diatoms are generally larger and possess more storage capacity, they are capable of greater luxury uptake and accumulation of internal P and N reserves when the nutrient is in excess (Garcia et al., 2018b). On the other hand when nutrients are scarce, large cell size of diatoms allow them to increase their carbon content considerably by accumulating excess carbon as polysaccharides and lipids (Liefer et al., 2019; Lin et al., 2016). Another plausible hypothesis concerns variability in acclimation/adaptation strategy at the genetic level (Dyhrman, 2016). Recent studies suggests that different phytoplankton groups exhibit different levels of transcriptional responsiveness and have dissimilar strategies for nitrate (Lampe et al., 2019) and phosphate (Martiny et al., 2019b) uses. In particular, diatoms have superior abilities to uptake and store nutrients by being able to quickly regulate their gene expression patterns required for nutrient uptake compared to other phytoplankton groups (Cáceres et al., 2019; Lampe et al., 2018, 2019). These hypotheses provide plausible explanation for why diatoms have elevated stoichiometry sensitivity to nutrients compared to other phytoplankton groups.

A previous meta-analysis study showed that cellular N:P ratio of phytoplankton is significantly positively correlated with N:P supply ratio of nutrients (Persson et al., 2010), providing a picture that essentially “algae are what they eat”. As cellular N:P is effectively a ratio between cellular N:C and P:C, our analysis is consistent with this picture because the mean plasticity of P:C is greater than that of N:C (i.e. the magnitude of $s_{\mathrm{NP}}^{\mathrm{P:C}}$ is significantly greater than that of $s_{\mathrm{NP}}^{\mathrm{N:C}}$ with the opposite sign; Fig. 2c). We would expect $s_{\mathrm{NP}}^{\mathrm{P:C}}$ and $s_{\mathrm{NP}}^{\mathrm{N:C}}$ to be more equal in magnitude if cellular N:P ratio was more homeostatic. Cellular N content generally covaries with cellular protein contents (Leonardos and Geider, 2004; Liang et al., 2019), while cellular P content covaries with macromolecular pools of RNA, DNA, and phospholipids (Liefer et al., 2019). Large stoichiometry sensitivity of P:C over N:C suggest N-uptake and protein synthesis change does not keep pace completely with P-uptake and synthesis of P-rich molecules. This pattern of larger stoichiometric flexibility of P:C over N:C with respect to nutrient availability has also been observed globally in the marine environment (Galbraith and Martiny, 2015) consistent with our meta-analysis result.

4.3 Irradiance

Light availability affects photoacclimation of phytoplankton and subsequently the cellular allocation of volume between N-rich light-harvesting apparatus, P-rich biosynthetic apparatus, and C-rich energy storage reserves (Falkowski and LaRoche, 1991; Moreno and Martiny, 2018). At a fixed growth rate, high irradiance should downregulate production of N-rich light harvesting proteins and pigments in order to minimize the risk of photooxidative stress. Excess carbon is stored as C-rich storage compounds such as lipids and polysaccharides (Berman-Frank and Dubinsky, 1999). As a result, N:C is expected to decrease under high light. In contrast, under low light condition, macromolecular composition should favor N-rich light harvesting apparatus over C-rich storage reserves, thus elevating N:C. This line of reasoning would predict negative s-factors for the effect of irradiance on N:C, which is borne out in our meta-analysis (Fig. 3).

The magnitude of $s_{\mathrm{I}}^{\mathrm{N:C}}$ is consistently less than 0.1 and the responses are weak across all PFTs. This result agrees with a previous study which compiled experimental data prior to 1997 (MacIntyre et al., 2002). It is possible however that s-factors obtained in our meta-analysis are underestimated as there are several methodological factors that may mute the effect of irradiance on N:C ratio of phytoplankton. Firstly, not all studies were carried under nutrient (nitrate) limited condition, hence the downregulation of N-rich light harvesting apparatus was not needed to maintain growth. Secondly, the growth rate was not controlled in all the studies. Ideally, chemostat/turbidostat experiments are most suited for isolating the effect of environmental driver as it allows direct manipulation of growth rate. This is because any change in cellular nutrient:C ratio can be attributed to a specific environmental driver rather than to changes in specific growth rate (Hessen et al., 2002). However, for practical and economic reasons, batch and semi-continuous culture are more commonly used (La Roche et al., 2010). Thirdly, we did not consider the effect of light regimes (i.e. the length of light and dark hours) and diel changes on N:C. Longer light period leads to a more stable N:C over the course of the day as the amount of carbon fixed remains relatively constant, while experiments with longer dark hours leads to larger diel change in N:C (Lopez et al., 2016; Mohr et al., 2010; Ng and Liu, 2015; Talmy et al., 2014). We speculate that the lack of diel changes may have muted the underlying photoacclimation responses. Despite these experimental limitations, consistency in the s-factors across all studies indicates irradiance measured by photon flux density is one of the key determinants for N:C. This is consistent with the global observation (Martiny et al., 2013a) and model studies (Arteaga et al., 2014; Talmy et al., 2014, 2016) where N:C of phytoplankton is higher in the light-limited polar/subpolar regions than in the light-replete low latitudes.

In contrast to the total cellular C and N quota, P quota should only be affected by change in irradiance if P is the main limiting nutrient (Moreno and Martiny, 2018). Under P limitation, P:C is expected to decrease at increased light level because the total supply of inorganic phosphorus will not be able to keep up with the increase in photosynthetic carbon fixation, leading to decoupled uptake of C and P (Hessen et al., 2002, 2008). Conversely, P:C is expected to increase at lower irradiance because carbon fixation decreases while phosphorus uptake remains constant (Urabe and Sterner, 1996). We did not observe such P:C responses, as only 1 out of the 17 experiments units used in our meta-analysis was clearly P-limited. We speculate that other experimental conditions such as temperature, growth phase, and nutrition status muted the effects of irradiance on P:C leading to an overall statistically insignificant s-factor.

4.4 Temperature

For microorganisms, temperature is arguably the most important environmental factor affecting growth and survival (Madigan et al., 2017). Temperature controls the kinetic responses such as enzyme activity, cell division, and nutrient uptake which all are thought to occur at higher rates with elevated temperatures (Hessen et al., 2017). Also, temperature can alter macromolecular composition, rate of protein synthesis, and storage of elements (Moreno and Martiny, 2018). Phytoplankton are able to efficiently grow over a range of temperatures around the optimal growth temperature but their growth at substantially different temperatures can lead to photodamage (Huner et al., 2008), inhibition of protein synthesis (Li et al., 2019), or the decline in photosynthetic efficiency (Falk et al., 2006). As a result, a growth curve of phytoplankton is unimodal (Boyd et al., 2013; Zhu et al., 2017) with increasing growth rate from the minimum temperature to the optimum temperature and decreasing growth rate towards the maximum temperature (Madigan et al., 2017).

Broadly, there are two kinds of species, a thermal specialist whose growth rate rapidly drops off as temperature exceeds the optimal temperature, and a thermal generalist whose growth rate remains constant over a wide range of temperatures (Collins et al., 2020). Since the P:C and growth rate are intricately linked (Sterner and Elser, 2002), our meta-analysis suggests that cyanobacteria are thermal specialists because an increase in temperature significantly decreased P:C across all studies (Fig. 4). Although the underling mechanism for explaining lower P:C at higher temperature is not fully understood, there are three hypotheses (Paul et al., 2015): (1) increase in metabolic stimulation of inorganic carbon uptake over phosphorus uptake; (2) increase in nutrient use efficiency which enables greater carbon fixation for given nutrient availability; and (3) “translation compensation theory,” which predicts that less P-rich ribosomes are required for protein synthesis and growth as the translation process becomes kinetically more efficient (McKew et al., 2015; Toseland et al., 2013; Woods et al., 2003; Xu et al., 2014; Zhu et al., 2017). In this meta-analysis, the decrease in P:C in cyanobacteria at elevated temperatures (Fig. 4) is possibly attributable to a combination of these three hypotheses (Fu et al., 2014; Jiang et al., 2018; Martiny et al., 2016), as they are likely not mutually exclusive.

For non-cyanobacteria phytoplankton, their stoichiometric response to changes in temperature was mixed even among closely related phytoplankton lineages (Fig. 4). This suggests the importance of species-specific adaptive/evolutionary response to warming (Schaum et al., 2018; Taucher et al., 2015). Another important factor to consider is the interactive effect of temperature with other environmental drivers. Multiple studies suggest that the effect of temperature on growth and metabolic rates are masked out by nutrient and/or light limitations (Marañón et al., 2018a, 2018b; Qu et al., 2019; Roleda et al., 2013). These factors may explain why, for example, the coccolithophore *Emiliania huxleyi* grown under different supply ratios of inorganic N:P responded differently at different temperatures (Bi et al., 2018). At a low N:P supply ratio (i.e. under N limited condition), P:C decreased with warming, but the trend reversed and the magnitude of s-factor is smaller under P limited condition. We also cannot rule out the possibility that mixed responses may be an artifact of the experimental methods because the majority of the experiments were carried under batch method where the growth rates are not controlled. This makes it inherently difficult to tease apart the influence of temperature and growth rate on elemental stoichiometry.

A previous meta-analysis (Yvon-Durocher et al., 2015) and this work both support the idea that P:C is more flexible than N:C with respect to change in temperature, which suggest that intracellular P content is more sensitive to change in temperature than intracellular N content. The two studies differ in that our study did not reveal a clear, overall signal of the temperature effect on P:C except for cyanobacteria (Fig. 4), whereas the previous study found a statistically significant, overall negative linear relation between temperature and P:C (Yvon-Durocher et al., 2015). An important consideration in this regard is that the previous meta-analysis used studies up to 1996, while the data we included in our meta-analysis were substantially supplemented with data reported after 1996.

4.5 Iron

Iron is used in key biochemical processes such as electron transport, respiration, protein synthesis, and N fixation (Marchetti and Maldonado, 2016; Twining and Baines, 2013). Many of the iron-dependent processes are required for harvesting energy and biochemical intermediates. As energy acquisition is equivalent to light acquisition in phototrophs, it makes sense that s-factors for iron are similar in the signs and magnitudes to those of light. Although the effect of iron on N:C is weak, similar in magnitude to that of light, the mean s-factor for cyanobacteria is statistically significant where an increase in iron leads to decrease in N:C. This suggests that an increase in the carbon assimilation via photosynthesis and/or a reduction in the formation of nitrogen rich compounds such as porphyrin and phycobiliprotein that are essential for light harvesting (Falkowski and Raven, 2007; Twining and Baines, 2013). The iron s-factors for diatoms on the other hand are mixed across the studies and the overall mean value is not significant. This suggests that change in Fe availability affects cellular C and N proportionally for diatoms (Greene et al., 1991; van Oijen et al., 2004; Roche et al., 1993; Takeda, 1998). These contrasting results between cyanobacteria and diatoms may be due to differences in growth conditions. For example, temperature, phosphorus, and/or irradiance can moderate how iron affects phytoplankton physiology (Boyd, 2019; Bucciarelli et al., 2010; Mills et al., 2004; Strzepek et al., 2019). In addition, iron requirement is generally higher in nitrogen-fixing cyanobacteria than in non-nitrogen-fixing species (Sunda and Huntsman, 1995). There was not enough data on P:C to carry out meta-analysis. Yet a number of laboratory studies, which were excluded from this meta-analysis due to the lack of requisite data (at least 3 per experiment), have shown that N:C and P:C may decrease (Berman-Frank et al., 2001; De La Rocha et al., 2000; Muggli and Harrison, 1996; Price, 2005; Sugie and Yoshimura, 2013) or increase (Doucette and Harrison, 1991; Maldonado and Price, 1996; Sakshaug and Holm-Hansen, 1977) significantly with increasing Fe-limitation. In future, more studies are needed to provide a more coherent picture on how iron would affect P:C and N:C.

4.6 Implications for global biogeochemical cycles

We can give a first-order estimate of how much the elemental stoichiometry of marine phytoplankton may change in the future given a typical projection of the change in the key environmental drivers and the estimates of the s-factors (Table 3; Fig. 6). Global climate models generally predict a decline in macronutrients and increase in temperature and irradiance as a result of surface warming, increased vertical stratification and reduced mixed layer depth (Bopp et al., 2013; Boyd et al., 2015). Iron concentration in surface is expected to increase as stratification would reduce biological production and leave more iron underutilized at the surface, assuming the same iron input (Boyd et al., 2015). With large projected declines in macronutrients (-28.0% for phosphate, -18.7% for nitrate), we estimate that P:C and N:C for diatoms would decrease by 21.0% and 4.1% respectively in the 2100s (Table 3). This translates to increase in C:P and C:N by ~30 units (molar) and ~0.3 units (molar) assuming the modified Redfield C:N:P of 117:16:1 as the present-day value (Anderson and Sarmiento, 1994). In the case of cyanobacteria, further increase in C:P is expected due to temperature increase. The total C:P change ranges from +10%

to +33% across all the PFTs, with diatoms having the largest % increase, followed by cyanobacteria and eukaryotes. For C:N, we estimate an overall increase by 1~5% with the largest % change in diatoms closely followed by eukaryotes. In summary, this simple calculation highlights potentially a large shift for C:P, whose change is predominantly driven by phosphate.

In the real ocean, none of the environmental changes discussed will likely occur in isolation. For example, irradiance, temperature, and nutrient availability are often linked because the change in light availability will affect sea surface temperature, which in turn will alter vertical stratification in the water column and nutrient upwelling. Indeed, a meta-analysis on the pair-wise effects of environmental drivers on elemental stoichiometry of phytoplankton has shown that interactions of two environmental stressors can impose predominantly non-additive effects to C:N:P of phytoplankton, and that the effect of multiple environmental stressors is more than simply the sum of its parts (Villar-Argaiz et al., 2018). In addition, a recent multi-driver study carried for eight different drivers has shown that only a few dominant drivers can explain most of the evolutionary changes in population growth rates (Brennan et al., 2017). We are not aware of a similar multi-driver study conducted specifically for phytoplankton stoichiometry, but our results demonstrate that the macronutrients are the dominant controls on C:N:P, and thus we believe we have captured the first order behavior of C:N:P.

Similarly, the link between C:N:P of individual phytoplankton cells and of the larger ecosystem community including heterotrophs is complex, and it is not possible to simply assume that C:N:P ratios of organic matter collected in the ocean reflects the stoichiometry of uptake and production by phytoplankton. In addition to the individual phytoplankton stoichiometry, the bulk organic matter stoichiometry reflects the phytoplankton community composition (Bonachela et al., 2016; Weber and Deutsch, 2010) as well as the stoichiometry of organic matter accumulation and remineralization, which can be decoupled from the organic matter production ratio (Schulz et al., 2008). For example, the observed N:C ratio of biogenic sinking organic matter is close to the Redfield ratio even at very low nutrient conditions (Copin-Montegut and Copin-Montegut, 1983; Martiny et al., 2013a), which would predict low phytoplankton N:C. This apparent decoupling between phytoplankton N:C and bulk organic matter N:C may reflect the fact that heterotrophic bacteria and grazers that process organic matter derived from phytoplankton are more protein-rich (higher N:C) and homeostatic than phytoplankton (Sterner and Elser, 2002). In addition, processes such as viral shunt (Jover et al., 2014) and preferential remineralization of phytoplankton macromolecules (Frigstad et al., 2011; Grabowski et al., 2019; Kreus et al., 2015) can also decouple phytoplankton C:N:P from the bulk organic matter C:N:P.

There are some limitations and weaknesses in the current suite of ocean biogeochemistry models in predicting spatial and temporal distribution of essential biogeochemical elements such as nitrogen, phosphorus, and oxygen. For example phosphate concentrations are systematically overestimated in the surface (Martiny et al., 2019a) and the global distribution of nitrogen fixation, denitrification, and oxygen minimum zones exhibit substantial variability between models (Fu et al., 2018). Recent global biogeochemical models are therefore starting to incorporate a more realistic representation of plankton physiology, which includes flexible phytoplankton C:N:P (e.g., Buchanan et al., 2018). Modeling studies with flexible phytoplankton stoichiometry have demonstrated that proliferation of C-rich phytoplankton under future climate scenario has the potential to buffer expected future decline in carbon export and net primary productivity caused by increased stratification (Kwiatkowski et al., 2018; Tanioka and Matsumoto, 2017). This buffering effect cannot be simulated by biogeochemical models with fixed phytoplankton C:N:P.

Many of the global models with flexible C:N:P currently employ simple linear models where elemental stoichiometries are expressed as a function of single macronutrient (phosphate or nitrate). Our meta-analysis showed that temperature and light dependencies are also important for determining C:N:P. One way to combine the dependencies of multiple environmental drivers (e.g., P, N, Irradiance, and Temperature) in a single equation is the power-law formulation (Tanioka and Matsumoto, 2017):

$$[\mathrm{X{:}C}] = [\mathrm{X{:}C}]_0 \left(\frac{[\mathrm{PO_4}]}{[\mathrm{PO_4}]_0}\right)^{s_{\mathrm{PO_4}}^{\mathrm{X:C}}} \left(\frac{[\mathrm{NO_3}]}{[\mathrm{NO_3}]_0}\right)^{s_{\mathrm{NO_3}}^{\mathrm{X:C}}} \left(\frac{\mathrm{I}}{\mathrm{I_0}}\right)^{s_{\mathrm{I}}^{\mathrm{X:C}}} \left(\frac{\mathrm{T}}{\mathrm{T_0}}\right)^{s_{\mathrm{T}}^{\mathrm{X:C}}} \qquad (\mathrm{X = P\ or\ N}) \qquad (2)$$

where subscript “0” indicates reference values. The s-factors obtained from this meta-analysis are the exponents of Equation (2) for different PFTs. Within the context of the power law formulation, our results would indicate, for example, that diatoms would have the largest plasticity in P:C and N:C compared to other PFTs. Under future warming, diatoms’ high s-factors may thus play an important role in buffering the expected future decline in carbon export and net primary productivity (Kemp and Villareal, 2013).

5. Conclusions

Our meta-analysis represents an important bottom-up approach in predicting on how elemental stoichiometry of phytoplankton may evolve under the climate change. We conclude that macronutrient availability is the most significant and shared environmental driver of P:C and N:C. Changes in P:C and N:C by macronutrients are driven by primary/plasticity responses commonly shared across phytoplankton. In addition, light availability is a key driver for modulating N:C ratio. Our analysis shows that diatoms have the higher stoichiometric plasticity compared to other plankton groups. Diatoms' large stoichiometric flexibility and high intrinsic growth rate can explain their unexpectedly high diversity (Malviya et al., 2016) and large contribution to carbon export globally even in oligotrophic regions (Agusti et al., 2015; Nelson and Brzezinski, 1997). The effects of other environmental drivers (temperature and iron) on P:C and N:C were either mixed amongst species and/or weak suggesting that these drivers elicit secondary responses. Future laboratory-based studies focused on exploring the effects of temperature and iron will be useful in filling the gaps to gain more mechanistic views on how these drivers affect different plankton species. In addition, a further investigation on how multiple environmental drivers would interactively alter the elemental composition of phytoplankton would be needed for a complete understanding.

Data availability: All the data and codes used in the meta-analysis are available in Zenodo data repository (https://doi.org/10.5281/zenodo.3515471).

Author contributions: TT and KM designed the study. TT carried out the literature review, data selection, analysis, and created figures. Both TT and KM wrote the manuscript.

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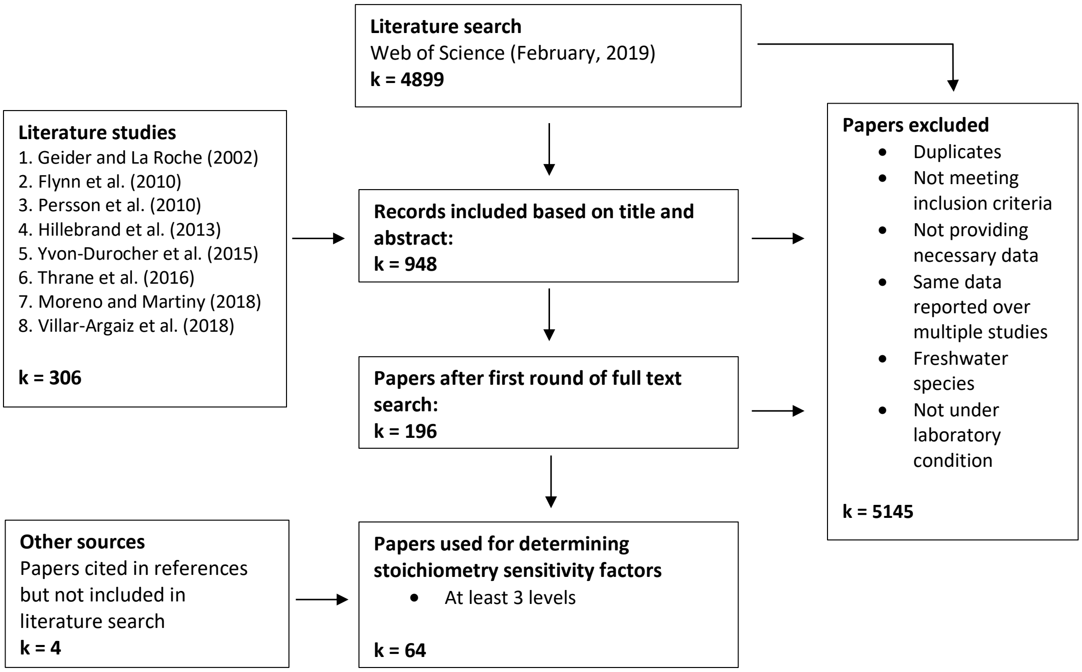
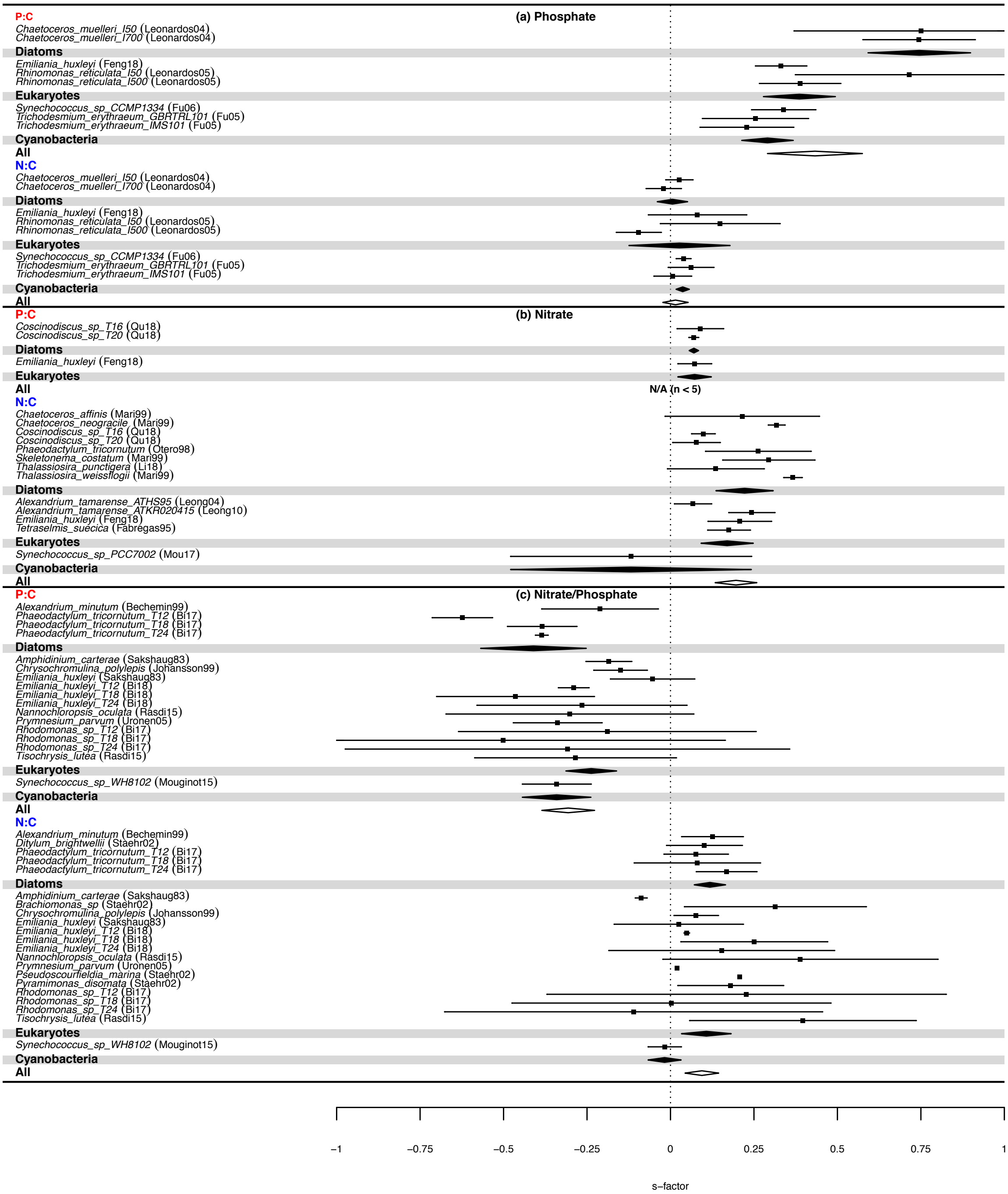


Figure 1: Flow chart showing (1) the preliminary selection criteria and (2) the refined selection criteria used for determining s-factors. Numbers (k values) correspond to the number of studies. See Supplementary Table 1 for a list of studies included in the meta-analysis.



120 **Figure 2: S-factors for P:C and N:C with respect to changes in (a) Phosphate, (b) Nitrate, and (c) Nitrate/Phosphate for individual experimental units and different phytoplankton functional types (PFTs). Mean values for PFT are indicated by filled diamond. Mean across all PFTs are indicated by open diamonds. Error bars represent the 95% confidence intervals. "N/A" signifies that the total experimental units were less than five for a given driver-stoichiometry pair in order to carry out a meta-analysis.**

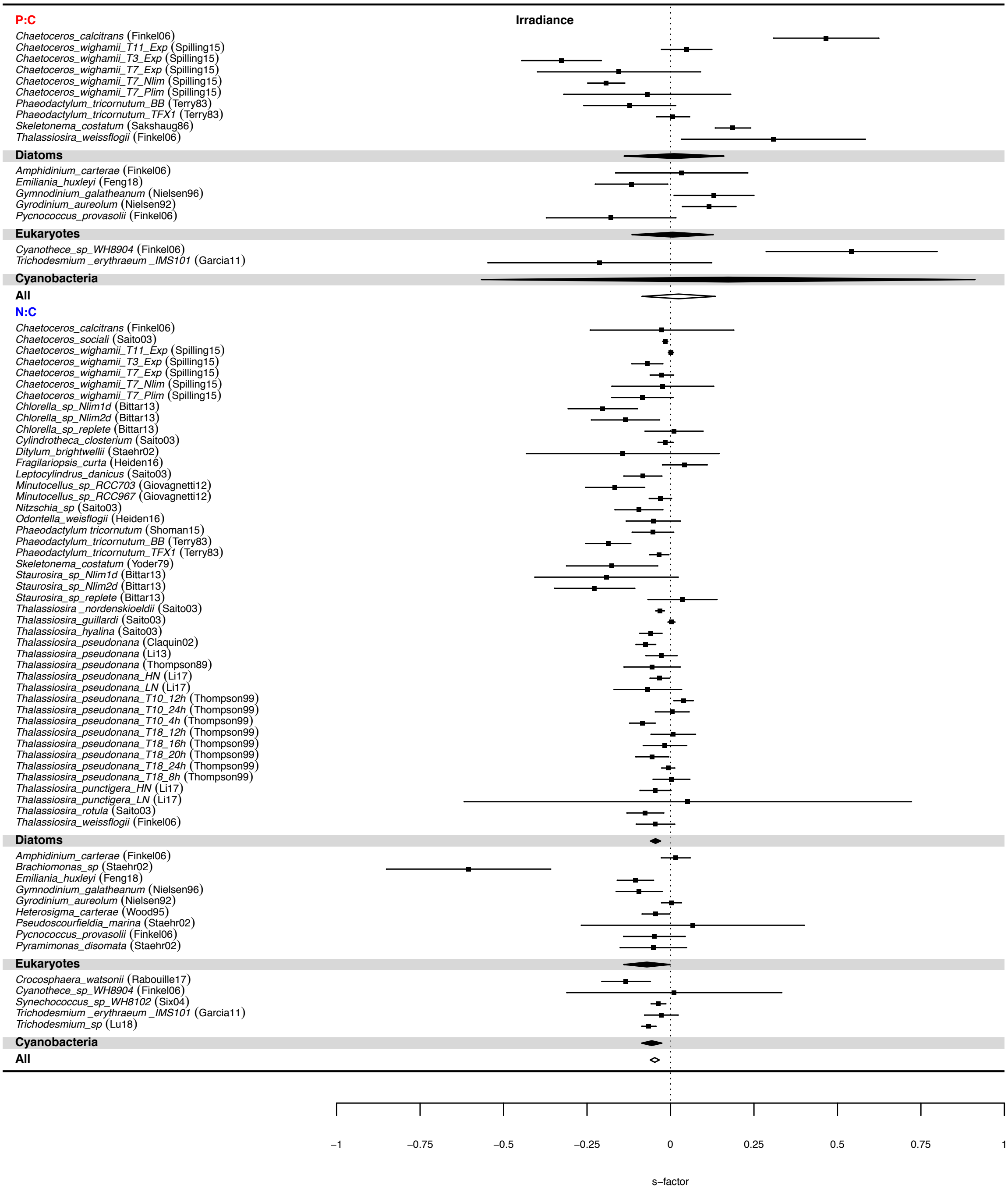


Figure 3: S-factors for P:C and N:C with respect to changes in irradiance for individual experimental units and different PFTs. Legend and error bars are as Figure 2.

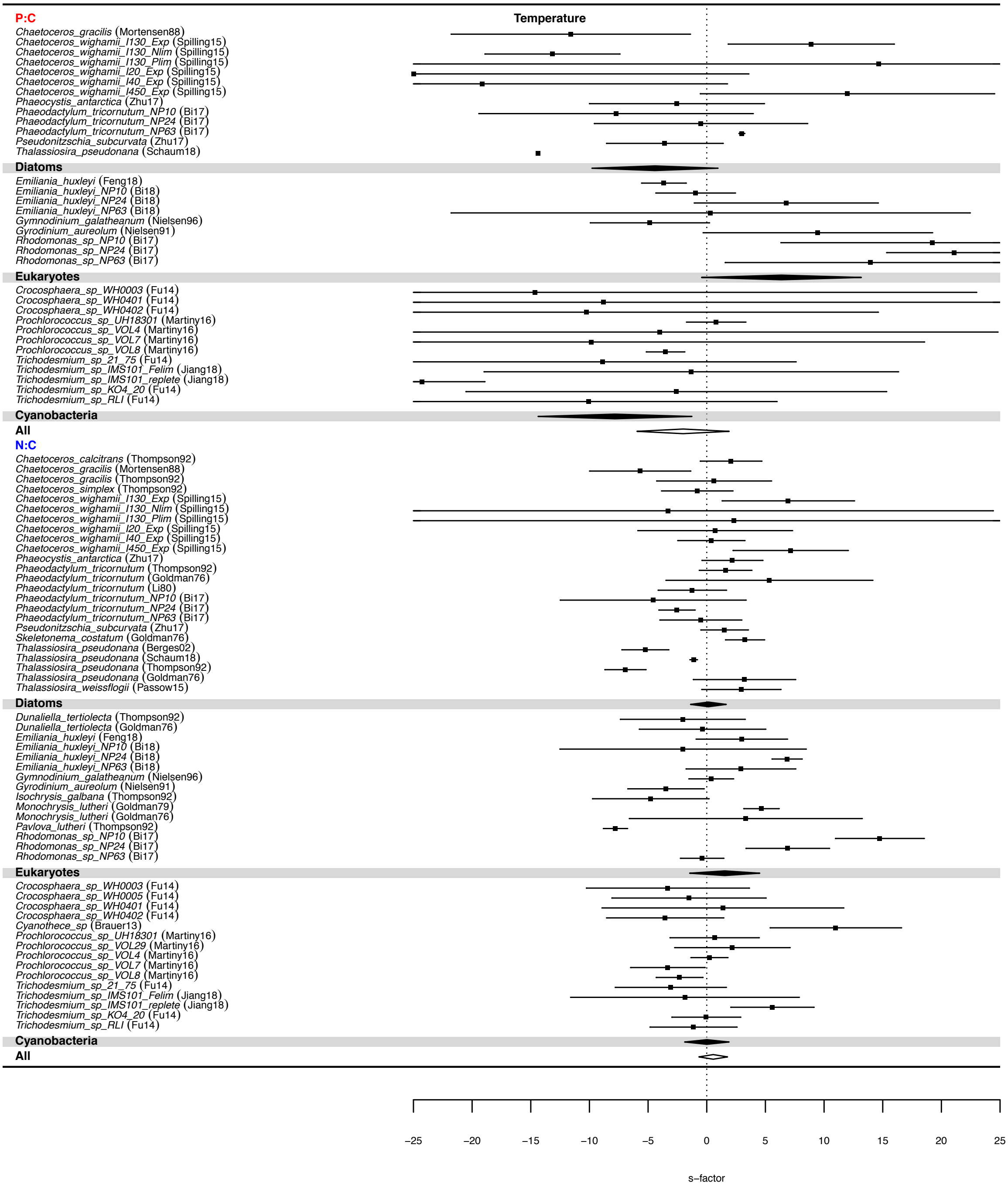


Figure 4: S-factors for P:C and N:C with respect to changes in temperature for individual experimental units and different PFTs. Legend and error bars are as Figure 2.

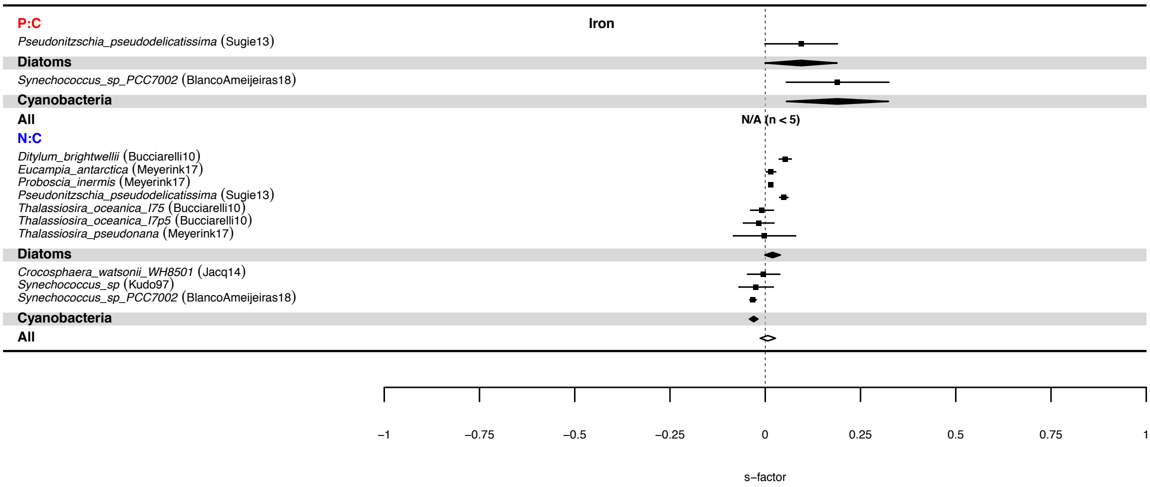


Figure 5: S-factors for P:C and N:C with respect to changes in iron for individual experimental units and different PFTs. Legend and error bars are as Figure 2.

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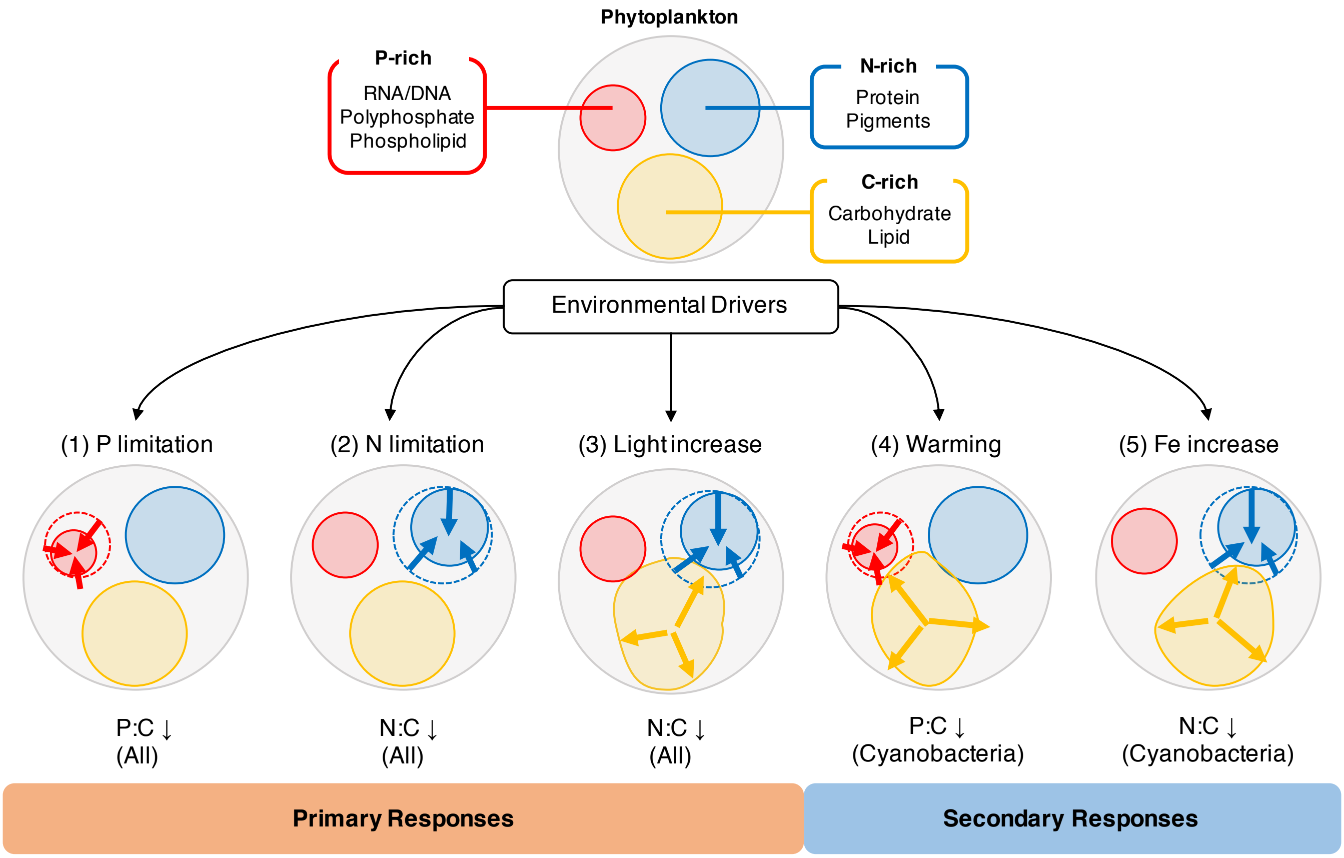

150 **Figure 6: Illustration of how the five environmental drivers under a typical future climate scenario affect the cellular allocation of volume between P-rich (red), N-rich (blue), and C-rich (orange) pools. Primary responses ((1) ~ (3)) are responses displayed in all the PFTs, while secondary responses ((4) and (5)) are displayed only in certain PFTs. In (3) ~ (5), changes in allocation of cellular volume between carbon and other pools could happen separately or simultaneously.**

Driver	P:C				N:C			
	Diatoms	Eukaryotes	Cyanobacteria	Total	Diatoms	Eukaryotes	Cyanobacteria	Total
P	2	3	3	8	2	3	3	8
N	2	1	0	3	8	4	1	13
NO_3/PO_4	4	12	1	17	5	15	1	21
I	10	5	2	17	45	9	5	59
T	13	9	12	32	24	15	15	54
Fe	1	0	1	2	7	0	3	10
Total	32	30	19	81	91	46	28	165

Table 1: Breakdown of the number of experimental units for environmental driver-stoichiometry pairs for P:C and N:C.

Driver	$s^{P:C}$				$s^{N:C}$			
	Diatoms	Eukaryotes	Cyanobacteria	Overall	Diatoms	Eukaryotes	Cyanobacteria	Overall
P	**0.75±0.08^{b}**	**0.39±0.06^{a}**	**0.29±0.08^{a}**	**0.43 ± 0.09**	0.01±0.02^{a}	0.03±0.08^{a}	**0.04±0.01^{a}**	0.02±0.02
N	**0.07±0.01^{a}**	**0.07±0.03^{a}**	N/A	N/A (n < 5)	**0.22±0.04^{a}**	**0.17±0.04^{a}**	-0.12±0.18^{a}	**0.20±0.03**
NO_3/PO_4	**-0.41±0.08^{a}**	**-0.24±0.04^{a}**	**-0.34±0.08^{a}**	**-0.30±0.04**	**0.12±0.02^{b}**	**0.11±0.04^{ab}**	-0.02±0.03^{a}	**0.09±0.03**
I	0.01±0.08^{a}	0.01±0.06^{a}	0.17±0.38^{a}	0.03±0.06	**-0.05±0.01^{a}**	**-0.07±0.04^{a}**	**-0.06±0.02^{a}**	**-0.05±0.01**
T	-4.4±2.7^{a}	6.4±3.5^{b}	**-7.8±3.3^{a}**	-2.0±2.0	0.14±0.78^{a}	1.53±1.52^{a}	0.01±0.97^{a}	0.55±0.62
Fe	0.09±0.05^{a}	N/A	**0.19±0.07^{a}**	N/A (n < 5)	0.02±0.01^{b}	N/A	**-0.03±0.01^{a}**	0.01±0.01

Table 2: Summary of s-factors for P:C and N:C. Values represent the means ± SE. Numbers in bold are statistically significant ($p < 0.05$) for a given driver. Different letters indicate significant differences between PFTs ($p < 0.05$). Overall s-factor across all studies are not calculated if the total experimental units were less than 5.

Driver	Δ (C:P) (molar)			Δ (C:N) (molar)		
	Diatoms	Eukaryotes	Cyanobacteria	Diatoms	Eukaryotes	Cyanobacteria
P↓ (-28%)	+27~35	+12~17	+21~38	/	/	+0.06~0.1
N↓ (-18.7%)	+1.3~1.7	+0.9~1.7	/	+0.3~0.4	+0.2~0.3	/
I↑ (+0.7%)	/	/	/	< +0.01	< +0.01	< +0.01
T↑ (+0.9%)	/	/	+14~36	/	/	/
Fe↑ (+6.5%)	/	/	-6 ~ -2.5	/	/	/
Combined Effects (% change)	+30~39 (+26~33%)	+15~21 (+13~18%)	+32~78 (+10~24%)	+0.3~0.4 (+4~5%)	+0.2~0.3 (+3~4%)	+0.08~0.1 (+1%)

Table 3: Projected change in C:P (molar) and C:N (molar) between 1981-2000 and 2081-2100 given model-based projected changes in environmental drivers from Boyd et al. (2015). Changes in C:N and C:P are calculated separately for each driver with s-factors from Table 2 combined with reference C:N:P of 117:16:1 for diatoms and eukaryotes; and C:N:P of 329:45:1 for cyanobacteria, both of which are consistent with the values used by Boyd et al. (2015). Ranges are derived from propagating standard error for the s-factors. We used Equation (2) in the main text for estimating the combined effect of multiple drivers.