Aquatic primary production in a high-CO₂ world

Etienne Low-Décarie, Gregor F. Fussmann, and Graham Bell

McGill University, Department of Biology, Stewart Biology Building, 1205 Avenue Docteur-Penfield, Montreal, QC, H3A 1B1, Canada

Here, we provide a review of the direct effect of increasing CO₂ on aquatic primary producers through its function as a source of carbon, focusing our analysis on the interpretation of this increase as an increase in the availability of a resource. This provides an interesting context to evaluate ecological and evolutionary theories relating to nutrient availability and leads us to: the assessment of theories about limitation of productivity and the integration of CO₂ into the co-limitation paradigm; the prediction of community composition and of change in communities from known changes in the environment; and evaluation of the potential for evolutionary adaptation in conditions that increase growth.

The neglected nutrient

Human activity is altering global biogeochemical cycles and might have ushered in a new geological era, the Anthropocene [1]. One of the fastest global changes caused by human activity is the continuing increase in CO₂ levels in the atmosphere: atmospheric CO₂ concentrations have now reached over 400 ppm [2], the highest for millions of years [3,4]. Public interest and research programs have largely been concerned with the incidental effects of this increase in atmospheric CO₂, notably climate change. However, the unique property of CO₂ in the biosphere is its conversion to biomass through photosynthesis. The relatively limited research interest in CO₂ as a key nutrient is related to its high global availability relative to other resources, especially phosphorus. The atmosphere provides an essentially unlimited supply of both nitrogen and carbon (as CO₂) to all living organisms, whereas phosphorus is almost exclusively provided by the slow weathering of mineral reservoirs [5]. The biological availability of nitrogen may be strongly limited by the energetic cost of fixing atmospheric supplies. When the biological fixation rates of both carbon and nitrogen are sufficient, phosphorus is expected to be the main biotic limiting resource globally for aquatic ecosystems over sufficiently large time scales [6].

The limited role assigned to CO₂ in the limitation of productivity is based on the assumption that only a single nutrient can control productivity at any given time. In addition to varying between systems, the availability of CO₂ in aquatic systems will likely increase with rising atmospheric CO₂ concentrations (Box 1), potentially altering the conditions of life for aquatic primary producers (Box 5). Furthermore, over the past decades, human activity has greatly increased the availability of nitrogen [7], phosphorus [8], and many micronutrients [9] in aquatic ecosystems, thus potentially increasing the role of CO₂. In this review, we reconsider the paradigm that only a single nutrient limits the productivity of aquatic systems, and challenge the disregard of CO₂ as a potentially important limiting resource. We suggest that CO₂ can function as a rate-limiting resource rather than a yield-limiting resource, and that it can interact with other resources in the co-limitation of productivity. We argue that the ecological responses observed as the result of CO₂ supplementation show that it can act as a limiting resource for phytoplankton. We assess the evidence for changes in phytoplankton community composition resulting from increasing atmospheric CO₂ and suggest that these changes are consistent with predictions based on the principle that the organisms that use a resource least efficiently are those that benefit most from an increase in its supply. Finally, we review the evidence for evolutionary change in response to increasing CO₂ levels, and suggest

Glossary

Carbon concentration mechanism (CCMs): ensemble of physiological systems that contribute to the accumulation of CO₂ around Rubisco. In phytoplankton, this can involve active transport of HCO₃⁻, CO₂ (Box 5), and/or H⁺ [103].
Chlorophytes: eukaryotic algae, also known as green algae, that are members of a clade of Chlorophyta [104].
Chrysophytes: eukaryotic algae, also known as golden algae, that lack an active CCM and produce siliceous cysts and scales that can be studied in the fossil record.
Diatoms: eukaryotic algae of the class Bacillariophyceae that produce cells enclosed in a silica frustule.
Free air carbon enrichment (FACE) experiments: experiments in which concentrations of CO₂ are increased locally without the use of chambers. CO₂ is pumped directly into the air and local concentrations are controlled through feedback with a sensor. These experiments allow the study of the response of a whole system to CO₂ enrichment under natural conditions, including airflow and mixing.
Redfield ratio: the average atomic ratio of carbon, nitrogen, and phosphorus [106:16:1] found in phytoplankton. This ratio can be considered as the optimal ratio for phytoplankton growth and deviations from it suggest nutrient limitation.
Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco): a key enzyme for the fixation of atmospheric CO₂ during photosynthesis and for the oxygenation of the resulting compounds during photorespiration.
Box 1. Increasing atmospheric CO$_2$ and carbon availability in aquatic ecosystems

Several biotic and abiotic factors regulate inorganic carbon concentration in aquatic ecosystems. Thorough reviews of carbon chemistry in aquatic systems and its relation to acidity have been provided elsewhere (for freshwater, see [87,88]; and for saltwater, see [89,90]). In many aquatic systems, dissolved inorganic carbon (DIC) is mostly present as bicarbonate, with <1% of DIC found as free CO$_2$. However, most phytoplankton can actively take up bicarbonate through their CCM and can facilitate the conversion of bicarbonate to free CO$_2$ within or outside the cell with the enzyme carbonic anhydrase (CA) [91].

Aquatic ecosystems can be either CO$_2$ sources (saturated and releasing CO$_2$ to the atmosphere) or sinks (taking up CO$_2$ from the atmosphere). Marine systems were historically near equilibrium with the atmosphere, but are now net sinks of CO$_2$ as they re-equilibrate with the increasing atmospheric concentrations [92]. The presence of large amounts of organic matter from terrestrial systems causes freshwater systems to be dominated by heterotrophic processes, and these systems act as net sources of CO$_2$ to the atmosphere ([93–95], but see [96,97]). Outgassing of CO$_2$ from freshwater systems is comparable to both total global net productivity and the total emissions from burning of fossil fuel [98].

The rate of gas exchange between water and air is directly proportional to the concentration gradient of the gas across the phase boundary [99]. Thus, assuming the ratio of photosynthetic and respiration rates remains constant under elevated CO$_2$, increasing atmospheric CO$_2$ will lead to increases in CO$_2$ and DIC concentrations and decrease pH in aquatic systems, including supersaturated freshwater systems. However, increasing CO$_2$ can affect rates of photosynthesis and respiration, potentially leading to complex feedbacks between DIC and its production and consumption (e.g., the priming effect [58]). In addition, other global changes may alter CO$_2$ concentrations in aquatic systems. Rising temperatures can increase the mineralization of dissolved organic matter [100], which could increase the amount of dissolved CO$_2$ and thermal stratification, which could alter the range and distribution of CO$_2$ concentrations within the water column [101]. The complex interplay of processes in the water and the atmosphere suggests that experiments that emulate the free air carbon enrichment (FACE) experiments performed in terrestrial systems [102] would be required to determine the exact changes in water chemistry that will be caused by increasing atmospheric CO$_2$ concentrations. Such experiments may reveal unforeseen tipping points in the response of aquatic ecosystems to increasing atmospheric CO$_2$.

that specific adaptation to elevated CO$_2$ and other environmental changes that increase growth is unlikely to evolve.

CO$_2$ in limiting nutrient paradigms

**Liebig’s law and CO$_2$ as a limiting resource**

Phosphorus is the main limiting resource for phytoplankton growth over geological time, because both nitrogen and carbon, which can limit growth on shorter time scales in some systems [10], are provided in abundance by the atmosphere and phosphorus is only made naturally available from the weathering of rock.

In freshwater, chlorophyll concentration is tightly correlated with phosphorus concentration both in space, across lakes, and in time, within lakes across seasons [6]. Whole-lake experiments first showed that supplementation with phosphorus and nitrogen increased algal yield [11] and induced short-term carbon limitation [12]; subsequently, it was shown that phosphorus addition was the crucial factor [13]. The identification of phosphorus as the main limiting resource in freshwater systems is widely credited with the successful limitation of the spread of eutrophication in many lakes and river estuaries [14].

In the oceans, the Redfield ratio (see **Glossary**) characterizes a fixed stoichiometric ratio of carbon and nitrogen relative to phosphorus [15]. Despite the variation in these stoichiometric ratios that has now been documented [16,17], the Redfield ratio remains a central principle for understanding biogeochemical cycles and nutrient limitation (although alternatives are being proposed; e.g., [18]). The prevailing paradigm for saltwater is nitrogen limitation due to lower rates of nitrogen uptake and assimilation than in freshwater systems [19]. Phosphorus might limit the net primary production of oceans on geological timescales [20,21], but few experiments have shown that phosphorus supplementation increases yield, whereas several experiments have shown that the addition of silicon, nitrogen, or iron causes increases in productivity [22]. This highlights the importance of time scale when trying to identify experimentally the processes that determine nutrient limitation in oceans [23].

The disregard for the potential role of resources other than phosphorus, including CO$_2$, is based on Liebig’s law of the minimum [24], which states that only one resource can limit productivity at any one time. Liebig’s law of the minimum remains the main principle of models investigating growth and competition for resources (e.g., [25,26], but see ‘Co-limitation by several resources’) and is an active topic of investigation in terrestrial systems [27,28]. The increasing availability of phosphorus [8] and nitrogen [29] in many ecosystems might reduce the limitation of productivity by these resources, thereby making it more likely that CO$_2$ limits productivity. Furthermore, Liebig’s law of the minimum was intended to guide the provision of nutrients to agricultural monocultures, and such a simple theory might be misleading when it is applied to diverse phytoplankton communities [30].

There is ample evidence that CO$_2$ can be a limiting resource, at least locally or on short temporal scales. CO$_2$ can limit productivity of eutrophic lakes in instances where photosynthetic demand exceeds diffusive influx from the atmosphere [12]. CO$_2$ supersaturation in lakes increases primary productivity up to tenfold when compared with the same system in equilibrium with the atmosphere, even in lakes where phosphorus limitation is expected [31]. In oceans, the experimental results are less clear, but CO$_2$ concentrations below current levels do reduce productivity [32] and higher CO$_2$ concentration, manipulated using acidification, increased productivity even at nutrient-poor sites [33]. Increased CO$_2$ greatly increases the productivity of benthic algae in marine systems [34]. Furthermore, most marine and freshwater phytoplankton have inducible carbon concentration mechanisms (CCMs) that serve to increase the concentration of CO$_2$ at the site of photosynthesis [35]. Although the effectiveness of CCMs varies across taxonomic groups (Figure 1), the evolution of such a mechanism across groups suggests a selective advantage to having a CCM. CO$_2$ availability can be limiting even when carbon is plentifully available in other forms, as is the case in aquatic systems with high pH.
Rate-limiting and yield-limiting resources. The concept of a single limiting resource can be reconciled with the ability of CO₂ to limit productivity. The solution is to integrate the concept of time scale [36] by distinguishing between rate-limiting resources and yield-limiting resources (Figure 2, [37,38] and implications for nutrient limitation measurements [39]). Rate-limiting resources are defined as resources whose concentration affects the speed of biomass accretion [growth rate (r)], whereas yield-limiting resources are resources whose total amount limits the potential maximum of biomass present in a system [carrying capacity (K)]. Rate-limiting resources have a low uptake rate compared with the uptake rate that would maximize growth. This can be caused by physiological limitations, such as the low affinity of transport systems, or by a low rate of supply to the local environment from a reservoir, such as the atmosphere in the case of CO₂. Resources directly involved in the uptake and storage of energy, such as CO₂ (Box 5), are likely to be rate-limiting resources. Yield-limiting resources become limiting when they are depleted from the environment because the provision of these resources from reservoirs is negligible on ecological time scales. Phosphorus is a yield-limiting resource. Dynamic systems with short boom-bust cycles, such as diel or seasonal cycles, might seldom have the time to reach the potential maximum biomass allowed by the availability of the yield-limiting resource. In these systems, realized yield might be controlled by the rate-limiting resource. Early models of phosphorus and CO₂ limitation of growth, which qualitatively match results from whole-lake experiments, describe CO₂ as a rate-limiting resource that can be important on short time scales, whereas phosphorus limits maximum yield and is important on larger time scales [40,41].

Co-limitation by several resources. Although different resources can limit growth rate and yield, a single resource can be the main limiting resource at any given time. However, there is growing evidence that neither growth rate nor maximum yield is always limited by a single resource [42]. A review of lake experiments indicated that the simultaneous addition of both nitrogen and phosphorus had a larger effect than the addition of either resource separately [43,44]. Synergistic responses to phosphorus and nitrogen addition have since been shown to be widespread in all major biomes [42,45]. The theory of a single limiting resource (Liebig’s law of the minimum) can still explain cases of synergistic responses, provided that one of the two added nutrients has an effect when added...
individually (Figure 3). This has been termed ‘serial co-limitation’ (for a visual explanation of serial co-limitation, see [46]) because only a single nutrient is limiting at any given time. As traditional drivers of eutrophication become more abundant, the potential for serial co-limitation involving CO2 grows. However, other types of synergic response to nutrient addition represent true deviations from Liebig’s law of the minimum (Figure 3 and Box 2).

Although co-limitation involving nitrogen and phosphorus appears to be widespread, the prevalence of co-limitation involving nutrient pairs that include CO2 is unknown (Box 5). Few studies that have investigated the response of phytoplankton to increasing CO2 have integrated the availability of another resource as a treatment. Most of these (eight out of nine experiments) showed responses that are in line with a synergistic response to CO2 and the addition of the other nutrient; three experiments showed a pronounced increase with the addition of both resources compared with the addition of the secondary resource alone (nitrogen, phosphorus, and vitamin B12; Figure 4). Independent co-limitation has been found for CO2 and phosphorus in a laboratory study of a phytoplankton species at low levels of both resources [47,48].

**Species-specific limitation**

One of the mechanisms for community-level co-limitation is provided by differences in the nutrient requirements of species within the community [49]. Major taxonomic groups of phytoplankton differ in both their ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) specificity factor (the preference of the Rubisco enzyme for CO2 rather than O2 as substrate, which controls the ratio of carboxylation and oxygenation activity of the enzyme) and in the ability of their CCM to increase internal carbon concentrations ([50]; Figure 1). Cyanobacteria are extremely efficient at raising their internal CO2 concentration
Box 2. Co-limitation: cases of true departure from Liebig’s law

Three types of true deviation from Liebig’s law of the minimum are widespread across all biomes for nitrogen and phosphorus [42] (Figure 3, main text): (i) low nutrient levels with several nutrients whose concentration is lower than the minimum at which they can be taken up by the cell (Figure 3B, main text). In dense algal blooms, both phosphorus and CO$_2$ can be drawn down to levels below the uptake capacity of aquatic primary producers; (ii) substitutable or aiding nutrients (reviewed in [105,106]; Figure 3C, main text). Substitutable resources are nutrients that can have the same biological role. For example, cadmium or cobalt can act as substitutes for zinc [107,108]. Aiding resources are those that enable the uptake or use of another resource, as has been found for copper and its function in the uptake of iron [109]. It can be postulated that CO$_2$ is the ultimate aiding resource and is co-limiting with all nutrients that enter the cell through active transport. Active transport is dependent on the energy produced through photosynthesis, which itself is dependent on CO$_2$ concentration and thus the uptake of resources requiring active transport might be dependent on CO$_2$ availability. Conversely, zinc, and its substituents cadib and cadmium, can act as aiding nutrients in the uptake of carbon as zinc is required for the functioning of carbonic anhydrase (CA) that is necessary to make use of the high availability of bicarbonate [110]; and (iii) different resources limiting growth of some species or genotypes belonging to the community (Figure 3F, main text, [48]). The productivity of each species conforms to Liebig’s law, but the productivity of the community does not. Although CO$_2$ concentrations might not limit overall community productivity, they might limit the productivity of certain types of organism (major taxa, species, or genotypes) within the community. This mechanism implies differences between types within a community and will lead to changes in community composition with increasing CO$_2$. This mechanism also highlights the inadequacy of applying Liebig’s law to diverse communities.

The effect of CO$_2$ on community dynamics

Differences between species or groups of species in their carbon economy are expected to lead to changes in community composition as atmospheric CO$_2$ concentration increases. The general principle that governs changes in community composition is simple: the group of phytoplankton that is currently most limited in its growth by CO$_2$ availability would stand the most to gain from an increase in CO$_2$ concentration and, thus, would be expected to increase in frequency in the community as CO$_2$ concentrations increase (Box 3). However, the response of the composition of phytoplankton communities to increasing CO$_2$ concentration is still uncertain and might differ between marine and freshwater systems.

Experiments in the sea have largely been designed to estimate parameters important in modeling global nutrient cycles (compiled and reviewed by [55]). In one mesocosm experiment, the frequency of fucoxanthin-containing phytoplankton (including diatoms and prymnesiophytes) was found to decrease with increasing CO$_2$ [56]. By contrast, two similar mesocosm experiments of the Pelagic Ecosystem CO$_2$ Enrichment (PeECE) program failed to show any detectable effect on community composition [57,58]. In the third experiment of the PeECE series, the response of the community to elevated CO$_2$ was not constant through time: once other nutrients in the mesocosms had been depleted, there was a linear increase in the frequency of chlorophytes with increasing CO$_2$ concentration [59,60]. The expansion of chlorophytes came at the expense of coccolithophores. These shifts in community composition following an artificially induced algal bloom are consistent with predictions from the physiology of major taxonomic groups (Figure 1). Cell size can also affect the response to increasing CO$_2$ [61]. Elevated CO$_2$ increases the relative abundance of larger species within diatom communities [32] and decreases the relative abundance of picophytoplankton [62].

In freshwater systems, community composition appears to be more closely linked with CO$_2$ availability. Phytoplankton blooms can reduce CO$_2$ concentrations in freshwater far below atmospheric concentrations and this might be one of the mechanisms that maintain a high frequency
of cyanobacteria during blooms of freshwater phytoplankton [63]. As in marine systems, the effect of CO$_2$ concentration on community composition in freshwater systems can be attributed in part to a pH effect [64]. However, studies using laboratory cultures buffered against pH changes showed changes in community composition that were consistent with predictions from the physiology of major taxonomic groups: chlorophytes usually increased under elevated CO$_2$ at the expense of cyanobacteria [65]. Change in phytoplankton community composition in freshwater systems might even be used to infer changes in CO$_2$ concentration. The abundance of species of diatoms appears to be strongly and differentially determined by CO$_2$ concentrations even when differences in pH are taken into account, to the extent that diatom community composition is a reliable predictor of geographic variations in CO$_2$ concentration across lakes [66]. Throughout the paleolimnological record, chrysophytes, which do not have CCMs, were most abundant during the middle Eocene, a period of elevated atmospheric CO$_2$ concentrations, and have increased in abundance over the recent past with increasing CO$_2$ [67].

In both marine and freshwater environments, the effect of increasing CO$_2$ on community composition can also act indirectly through its effect on pH [68]. Coccolithophores, which are calcifying phytoplankton, are poor at concentrating and utilizing CO$_2$ and, thus, would be expected to benefit from increased CO$_2$ availability (Figure 1). However, the decrease in pH resulting from an increase in CO$_2$ causes a decrease in the ability of coccolithophores to calcify and an associated decrease in their growth rate. Hence, it might be feasible to predict how the composition of phytoplankton communities will respond to increasing atmospheric CO$_2$ (Box 5). These predictions can rest on the simple principle that the types of phytoplankton least efficient at taking up and utilizing CO$_2$, whether it be large phytoplankton or chlorophytes, will increase in frequency with higher CO$_2$ concentrations, provided that these types are not disproportionately harmed by a decrease in pH.

**Evolution and adaptation to elevated CO$_2$**

The possibility of changes in the frequency of species within a community in response to increasing CO$_2$ leads naturally to the possibility of changes in the frequency of genotypes within a species and, hence, to the possibility of evolutionary change in response to increasing CO$_2$. However, most examples of evolutionary change have concerned adaptation to stressful environments where growth is reduced (e.g., [69]). Few studies have investigated the direct effect of elevated CO$_2$ under constant pH in aquatic systems (for a review of the evolutionary response of phytoplankton to ocean acidification, see [70]) or the evolutionary consequence of any other environmental change that results in increased growth rate (Boxes 4 and 5). Three evolutionary scenarios can be postulated to arise as a direct response to elevated CO$_2$.

The first scenario is that organisms might adapt specifically to elevated CO$_2$. Such adaptation could arise from the sorting of existing variation within a species or through the spread of novel mutations. The fact that there can be as much variation in response to CO$_2$ enrichment between ecotypes of the same species as there is between major taxonomic groups, indicates that variation on which selection can act to elicit adaptation is already present in some cases [71].
The second scenario is that organisms might accumulate mutations that are not detrimental under elevated CO\textsubscript{2} but would be costly under current ambient conditions (so-called ‘conditionally deleterious mutations’). The potential for such mutations is illustrated by the numerous mutagenesis experiments that led to the creation of genotypes that are capable of growth under elevated CO\textsubscript{2} but which have depressed fitness under ambient CO\textsubscript{2} conditions (e.g., [72,73]). Alternatively, the physiological mechanisms underlying the direct response to elevated CO\textsubscript{2} might necessarily reduce growth at current ambient CO\textsubscript{2} (functional interference or ‘antagonistic pleiotropy’). Both mutational degradation and functional interference lead to a negative indirect response to elevated CO\textsubscript{2} when evolved lines are exposed to current ambient concentrations.

The third scenario is that there might be no specific evolutionary change, direct or indirect. In addition to their ecological importance in aquatic ecosystems, microalgae including phytoplankton are good model organisms to study potential adaptation to elevated nutrients because large populations can be grown for hundreds of generations in small volumes within brief periods of time. After culture at ambient and elevated CO\textsubscript{2} concentrations for 1000 generations, no specific adaptation was detected in selection lines of *Chlamydomonas reinhardtii*. However, some selection lines grew poorly in ambient CO\textsubscript{2}, suggesting the accumulation of conditionally deleterious mutations in the CCM [74,75]. Similar patterns were found in microalgae naturally exposed to elevated CO\textsubscript{2} concentrations [76]. Efforts to extend these results to other species and taxonomic groups failed to elicit any specific evolutionary response to elevated CO\textsubscript{2}, either direct or indirect, even after over 750 generations of exposure [77]. Finally, even when the consequences of evolution were tested in the more ecologically relevant context of a community, long-term selection under elevated CO\textsubscript{2} and warming failed to cause detectable evolutionary changes [78].

The experiments that were conducted to detect evolutionary response to elevated CO\textsubscript{2} were performed in such a way as to maximize the probability that a response would occur. For example, long-term selection of a single species in isolation is expected to be more likely to cause adaptation to elevated CO\textsubscript{2} than is selection in the wild in complex communities (reviewed in [79] and shown specifically for the evolution of phytoplankton to elevated CO\textsubscript{2} [80]). Hence, the failure to observe specific adaptation in the laboratory suggests that it is unlikely to evolve in the field, at least in the short term of a few thousands of generations.

Specific adaptation to elevated CO\textsubscript{2} might also be obstructed in natural environments because CO\textsubscript{2} availability is variable in most habitats, and CO\textsubscript{2} concentrations can also be variable through time. Freshwater phytoplankton can face diel cycles of 100-fold differences in CO\textsubscript{2} availability [81], coastal habitats can face daily variations of 2.5-fold [82], and even the open sea experiences a similar level of variability over seasons [83]. Given that low CO\textsubscript{2} conditions are stressful, periods of low CO\textsubscript{2} concentration will maintain selection for organisms capable of growth at these low levels.

Traits allowing adaptation to low levels of CO\textsubscript{2} tend to be plastic and, thus, incur little cost at elevated CO\textsubscript{2}. Cyanobacteria can alter their CCM activity as a function of carbon availability [84] and chlorophytes can also switch off the CCM and reduce RubisCO content under elevated CO\textsubscript{2} [85]. Thus, the capacity to grow under low CO\textsubscript{2} concentrations might come with little or no trade-off for growth in high CO\textsubscript{2} conditions. This lack of trade-off reduces the potential for evolutionary change specific to elevated CO\textsubscript{2}.

At present, there are few examples of adaptation in response to environmental changes that increase growth, and few experiments have explored the response of organisms to such changes (Box 4). Adaptation in the context of elevated CO\textsubscript{2} concentrations might be more likely to occur through its effect of decreasing pH rather than through its direct effect as a carbon resource. Coccolithophores, the only phytoplankton group for which a decreased growth rate under elevated CO\textsubscript{2} has been reported, have been found to adapt to the acidic conditions of elevated CO\textsubscript{2} [86]. After long-term exposure to elevated CO\textsubscript{2}, adapted lines of the coccolithophores were able to regain their calcification and growth rates.

**Concluding remarks**

Predicting how phytoplankton will respond to global change, including rising CO\textsubscript{2} and increased availability of other nutrients, is essential to the accuracy of biogeochemical models and their estimates of atmospheric CO\textsubscript{2}, climate change, and even the productivity of fisheries. To provide accurate predictions, the current dogma of single-nutrient limitation should be reviewed in light of the possibility that nutrients can limit different aspects of productivity and that several nutrients can act in concert to control productivity. The effect of CO\textsubscript{2} on community composition needs to be investigated more thoroughly. Integrating current knowledge about phytoplankton physiology might provide a framework capable of predicting community composition changes in lakes and oceans. This framework is based on the expectation that the types of phytoplankton that are currently most limited by the availability of CO\textsubscript{2} will increase in frequency in the community. Accurate prediction might also require information about how CO\textsubscript{2} concentrations affect other members of the aquatic community, including macrophytes, bacteria,
and zooplankton. However, the difficulty of specific adaptation to elevated CO₂ implies that models are unlikely to require the inclusion of evolutionary change to make reliable predictions.

In this review, we have elucidated mechanisms by which the inexorable increase in the global supply of a major nutrient could drive changes in the productivity and composition of the phytoplankton communities of freshwater and marine ecosystems. Given that phytoplankton generate half of all primary production [20], it is important that we gain a clearer understanding of what these changes are likely to be and how they will come about.

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Appendix A. Supplementary data
Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.tree.2014.02.006.

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