Ecological stoichiometry and its implications for aquatic ecosystem sustainability
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Aquatic ecosystems are increasingly stressed not only by increased nutrient loads (eutrophication) but also by changing forms and proportions of nutrients. Nutrient enrichment, composition and stoichiometry interact with aquatic food web dynamics in complex ways. Both algal species composition and emergent properties within species change with changing nutrient composition, in turn affecting food webs at all levels. Consumers further regulate – and may even accelerate – discrepancies in nutrient stoichiometry by various feedbacks, release, and recycling pathways. Stoichiometric regulation of aquatic ecosystem structure also occurs at the sediment interface via altered biogeochemical processes and benthic food webs when nutrient composition changes. Thus, multiple feedbacks serve to alter food web structure when nutrient loads are altered. Such feedbacks may also lead to conditions conducive to invasive species and altered stable states as illustrated for the San Francisco Bay Delta and the Rhine River.

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Introduction
Much has been written about the eutrophication of lakes, estuaries and coasts ([1[••],2,3] and references therein). Anthropogenic activities have significantly altered nutrient loads and their composition, in turn profoundly affecting ecosystem health [4]. For example, well-documented effects of increased nutrient loads and eutrophication include loss of biodiversity, increased harmful algal blooms, and development of dead zones [5,6]. Beyond eutrophication, changes in nutrient loads are impacting ecosystem dynamics in complex ways. Changes in nutrient form (chemical state, oxidized vs reduced, organic vs inorganic, dissolved vs particulate) and the proportion of different elements (C, N, P, Si, etc.) have both proximal

and ultimate effects on ecosystems (*sensu* [7]). The stoichiometry (proportions) of nutrients, especially nitrogen (N) and phosphorus (P), in many aquatic systems is changing as a result of both increasing nutrient loads (often dominated by N) on the one hand, and management efforts focused on single nutrient control (often P) on the other. At the primary producer level, many of these effects are well understood, framed largely in the concepts of Leibig's law of the minimum and Redfield stoichiometry (reviewed by [8[•],9,10[•]]). At the proximal scale, here defined as the scale of growth of primary producers, nutrient form and concentration affect the cell physiological processes of uptake, assimilation, and those, in turn, regulate the internal concentrations that regulate growth (e.g. [11]). At the ultimate scale, the total load and balance of nutrient elements have effects that propagate through the food web, with the potential of transforming ecosystems to new stable states. The regulation of food web structure by nutrient stoichiometry is further controlled by the various and complex feedbacks, release, and recycling pathways that that are all fundamentally constrained by nutrient load, form or stoichiometry. Just as different elemental ratios may affect the composition of the primary producers, different nutrient requirements of higher trophic levels will have an impact on their ability to thrive as community composition changes at the base. The latter is the emphasis of this brief communication.

Stoichiometry, biotic feedbacks, and biogeochemistry
An ecological stoichiometric approach is based on the transfer of elements through the food web, not just the flow of carbon (C) [12[••]]. Generally, homeostatic mechanisms keep the acquisition of materials and energy in balance with the cellular growth demands of primary producers and the general consistency of Redfield stoichiometry in phytoplankton is corroborative (e.g. [10[•]]). Ecological stoichiometry recognizes that at the base of the food web, the elemental composition of the primary producers is affected by nutrient composition whether nutrients are limiting or not. While the total nutrient load of the nutrient considered to be limiting for phytoplankton production may control overall biomass, the composition, both in form of nutrients and the proportion of different nutrient elements affects the composition of the primary producers. When nutrient loads change in amount, form or proportion, cellular adjustments in acquisition efficiency lead to altered emergent properties such as the proportions of ribosomes, enzyme activities, gene regulation, cellular pigmentation complement, and

cellular elemental composition [12••]. These properties have implications for competition and species success, leading, eventually, to changes in species dominants and biodiversity. In addition, properties such as lipid composition, toxin production, cell membrane thickness, and other chemical constituents, which are also, at least partly, functions of cellular elemental availability, can alter the quality of food for consumers, in some cases turning 'good' food to 'bad' [13,14]. Production of toxins in algae, for example, often occurs when nutrient stoichiometry is not in classic ('Redfield') stoichiometric proportions [14,15]. Toxic species can be harmful to higher trophic levels, disrupting normal ecosystem function. The dominance of such algae can result in a failure of normal predator-prey interactions, which in turn enhances the transfer of nutrients that sustain such species at the expense of competing algal species [16–18].

While primary producers may be flexible to some degree in their elemental composition [19••,20], heterotrophs are typically far less flexible [10•,12••,21••]. The nutritional quality of the food at the base of the food web affects all aspects of the abilities of consumers to meet their nutritional and reproductive demands. Nutrient stoichiometry and food quality can have differential effects on consumers depending on their life stage, for example, larval or adult [22–25]. Larvae would be expected to have higher P demands, for example, than adults, owing to their higher growth rates [22]. Heterotrophs typically maintain a more strict stoichiometry than phytoplankton through their various excretion and release mechanisms [12••,26], and the relationship between their biomass elemental requirements and the proportion of those elements in their food determines the extent to which they are a sink or a source of N, P or C [12••,27]. In general, as one moves up the food web, stoichiometric constraints on grazers increase, as does the organismal requirement for P, owing to fixed stoichiometry in body tissue, especially bone [12••]. Heterotrophs thus can exert significant control on the N and P available for primary producers [12••,28].

The biota thus modify the environment through nutrient uptake and regeneration which differs from species to species based on their elemental requirements and the nutrient substrates available to them as dissolved nutrients or as food. In addition to the biotic feedbacks and regulatory controls whereby individual organisms maintain their stoichiometry under mass balance constraints, at the ecosystem level, growth of different species also modifies the physical and chemical environment through alterations in physical habitat (e.g. turbidity, flow), light, oxygen, pH, as well as substrate availability. These factors can alter the pathways by which nutrients are released from the sediment, or the rates by which they are transformed in the sediment or water column by such processes as nitrification, denitrification, anammox, or dissimilatory nitrate reduction to ammonium (DNRA).

In eutrophic systems, increased algal productivity may lead to depressed water column oxygen which may result in increased recycling of N and P by changes in redox potential, or pH [29••,30,31]. These fluxes can positively reinforce an ecosystems' degradation trajectory, as suggested to be the case for the Chesapeake Bay [31]. By contrast, in systems with a reduced nutrient load, lower algal abundance in the water column, higher light, and higher redox potential may help to reinforce higher rates of nitrification and denitrification, leading to nutrient removal and potentially eutrophication reversal [31]. Biogeochemical pathways together with homeostatic control serve to provide the mechanism(s) whereby nutrient dynamics support trophodynamic structure. Positive reinforcing feedbacks of biogeochemistry and homeostasis shift ecosystems to new stable states; such shifts can be gradual or abrupt and communities may not return to their original state once the disturbance (in this case, altered nutrient loads) is removed.

Altered ecological stoichiometry and associated ecological feedback mechanisms may also help to explain the potential for a system to support the growth of organisms previously not found in an area, that is, biological invasions. While changes in climate, land-use and other factors have long been recognized to be related to a system's susceptibility for invasive species to thrive, so too is the possibility that altered nutrient loads may make an environment more suitable for species with different nutritional requirements [29••]. Such a suggestion does not negate the importance of external vectors bringing invaders to a new area, but nutritional loads, and the associated ecological feedbacks that may alter habitat, adds a mechanism to explain why some shifts occur when they do, and when and why particular species are successful in new environments [29••].

Examples from comparative systems

Two estuarine examples illustrate the important feedbacks between changes in nutrient loads and their stoichiometry, biogeochemistry, food web structure and potential for biological invasions. The San Francisco Bay Delta, a heavily modified and anthropogenically impacted estuarine system, has had major changes in nutrient loads over the past several decades ([29••,32] and references therein). In particular, increases over time in the N:P ratio of the major nutrient loads have been attributed, at least partly, to increases in wastewater N and removal of P from laundry detergents [29••]. Coincident with, and related to, these changes are declines in water column algal biomass (as chlorophyll *a*), a shift in the dominant zooplankton species from the calanoid *Eurytemora affinis*, to the invasive cyclopoid *Limnoithona tetraspina*, as well as invasions of the Asiatic clam, *Corbula amurensis*, the macrophyte, *Egeria dense*, and various species of centrarchid fish [29••]. *Egeria dense* is thought to do particularly well under increasing water column N:P

Figure 1

Current Opinion in Environmental Sustainability
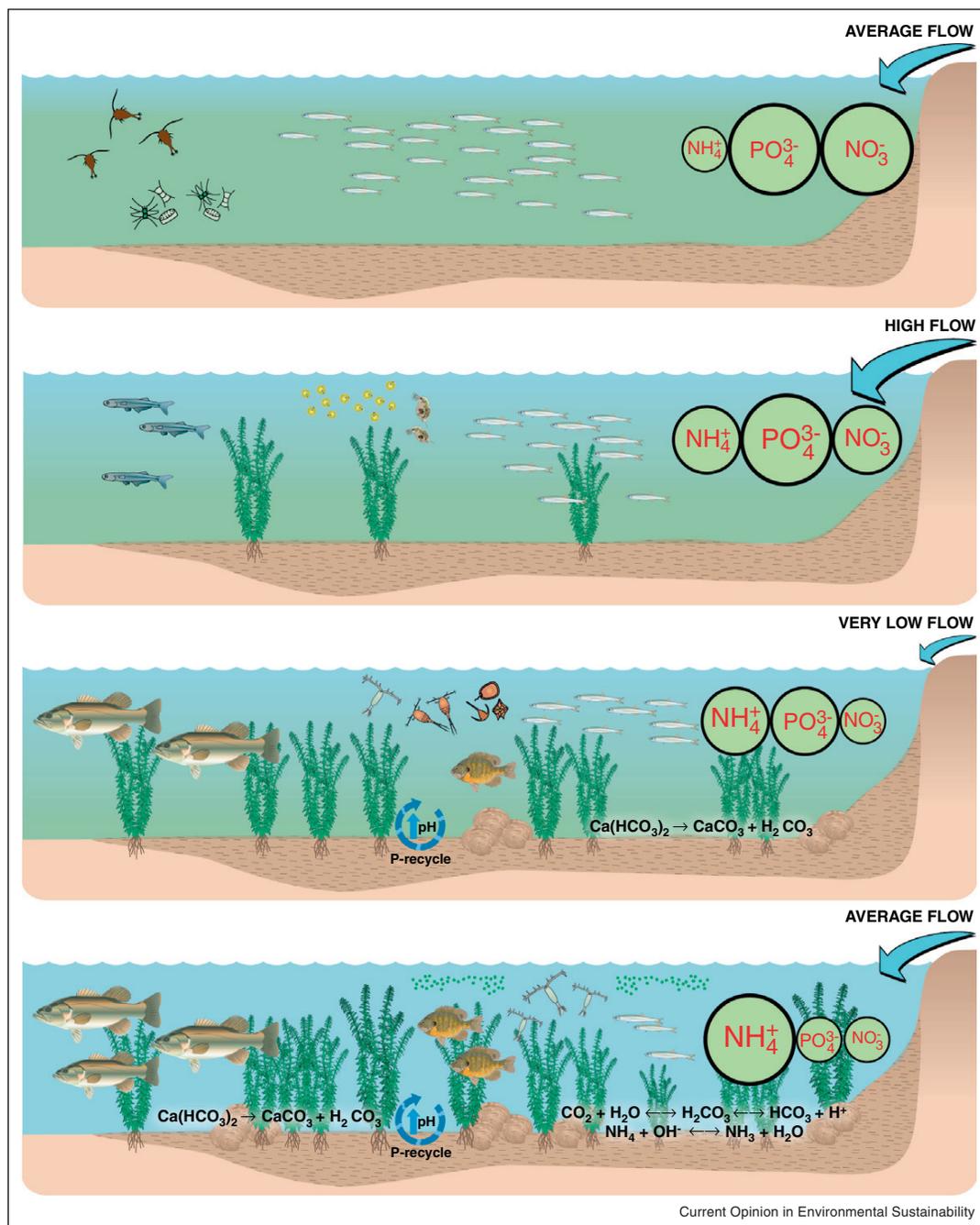
Conceptual depiction of the change over time in major nutrients, flow, dominant biogeochemical processes, and the food web of the San Francisco Bay Delta illustrating how multiple feedbacks serve to alter food web structure when nutrient loads are altered. The first panel represents the period from 1975 to ∼1982, when flow was low, and diatoms were the dominant phytoplankton, and the calanoid copepod *Eurytemora* was the dominant copepod, and pelagic planktivorous fish were common. The second panel represents the period from ∼1982 to 1986 when flow was high, and NH_4^+ was increasing. During this period the food web began to change. Under very low flow conditions, depicted by the third panel, and representing ∼1987–1995, the NH_4^+ load was high but PO_4^{3-} began to decrease. The food web also began to change significantly, with changes in the dominant phytoplankton and zooplankton, increasing abundance of macrophytes, increased importance of sediment nutrient processes, and increase in piscivores. Finally, post 1995, NH_4^+ loads remain high, while PO_4^{3-} loads have decreased. Sediment biogeochemical processes are of increasing importance in nutrient processing, macrophyte production is important and piscivorous fish have increased. Reproduced from Glibert *et al.* [29••] with permission of the publisher.

loads because it can access P through the sediments, and can tolerate high N, especially in the form of NH_4^+, in the water column. It also serves as an 'ecological engineer', decreasing nutrients through uptake, reducing turbidity by trapping sediments, and providing refuge for zooplankton and habitat for fish such as largemouth bass [33]. More importantly from a chemical perspective, it is able to use bicarbonate effectively though a well-developed carbon-concentrating mechanism (e.g. [34]). The consequence is that it does not become C-limited even under periods of high productivity, in turn elevating pH on a diel basis in the surrounding water as it grows, in some cases substantially. Once pH is elevated, the fundamental physical–chemical relationships related to P adsorption–desorption in the sediment change, as does N biogeochemistry [35,36]. Moreover, under increased pH conditions, the biogeochemistry of calcification is altered, increasing the potential for calcification and the growth of calcifying organisms. The change in the abundance of the clam *C. amurensis* from the time of its introduction in the mid-1980s to 2005 has been shown to be highly and positively correlated to the increase in total N:total P ($r^2 = 0.46$; $n = 20$; $p < 0.01$; all data log transformed), and the average annual abundance of this species has also been found to be highly and positively correlated with mean annual average pH in the estuary ($r^2 = 0.64$; $n = 19$; $p < 0.01$; species abundance data log transformed) [29••]. Thus, over time nutrient loading changes, biogeochemical changes and foodweb changes were intertwined (Figure 1).

The River Rhine presents a parallel example [37,38]. From 1977 to 2005, total P loads declined over 6-fold owing to reductions in wastewater loading from municipal and industrial facilities and the total N:total P ratio increased 3-fold, in turn resulting in an 8-fold decline in water column chlorophyll *a* [38]. Cumulative non-indigenous species increased from ∼20 to >50 during these years, a rate of accumulation higher than seen in any year of record, dating back to 1825 [37]. Most of these species were molluscs (22% of total) and crustacea (51% of total); among the molluscs, the most abundant were the clam *Corbicula fluminea* and the mussel *Dreissena polymorpha* (zebra mussel) [37]. The annual rate of change in number of animal non-indigenous species and the rate of change in the ratio of total N:total P in the water column over this ∼30-year time period are highly and positively correlated ($r^2 > 0.40$; $n = 28$; $p < 0.05$). In addition, invasive macrophytes, including *E. dense*, are increasingly common in the Rhine [39], as they are in the San Francisco Bay Delta.

While there are many vectors that may deliver non-indigenous species to new areas, there is no question that altered biogeochemical composition of the water column, and the associated shifts in primary production can set in motion a cascade of changes that facilitate the success of new species. Thus, both the Rhine and the Bay Delta had similar types of ecosystem changes following changes in N:P stoichiometry: significant declines in chlorophyll *a*, invasions of *E. dense*, bivalve clams, and changes in crustacea. These examples illustrate that when P is reduced relative to N, and when the system production becomes more benthic in nature, new dominants may emerge. In the case of filter-feeding molluscs, they, in turn, may help to maintain the new water quality condition by enhanced filtration of the water column.

Conclusions and implications

Nutrient stoichiometric control of ecosystem structure and sustainability must be viewed within the context of other factors in the environment, including the multiple stressors that now impact systems, as well as the scale (spatial, temporal and organismal; proximate or ultimate) on which the system is being examined. Trophodynamics and biogeochemical processes are fundamentally coupled, but are also fundamentally constrained by the availability and composition of elements relative to the needs of the organisms. Ecological stoichiometry affects ecosystems by setting elemental constraints on the growth of organisms, with several important implications for the health and sustainability of aquatic systems. Stoichiometric imbalances may accelerate transformations of nutrients or may alter the processes by which nutrients are cycled in the ecosystem, further altering nutrient availability or form for primary producers [28,40]. Food *quality* is linked to food web outcome via feedback effects and nutrient biogeochemistry, key processes determining biodiversity. Models of ecosystem function based on classic nutrient or growth kinetic relationships, or flow of single elements (i.e. C), are ill-suited to capture the complexities of stoichiometric effects on ecosystems [41]. Although far more complex than single currency models, multiple currency models and ecological stoichiometric concepts should be among the considerations that should go into a new generation of ecosystem models [11,29••,42•,43].

Ecological stoichiometry should be incorporated into our thinking, management, and modeling of the dynamics of nutrient-impacted systems. Imbalances in stoichiometry may have impacts on ecosystems even at nutrient loads normally taken to be saturating or supersaturating. The effect of stoichiometric constraints has implications, for example, on bioenergetics and all aspects of fish nutrition, both from a basic ecological perspective as well as applied, including aquaculture [21••,44]. Moreover, ecological stoichiometry bears significantly on the debate of whether aquatic ecosystem restoration efforts should focus on P removal, N removal, or both (e.g. [45,46,47••] and references therein). Single nutrient removal strategies drive ecosystems into states of stoichiometric imbalance [29••]. Imbalances in stoichiometry may destabilize the dynamics of consumers, shifting systems to new conditions. Single

nutrient removal strategies may have unintended consequences for aquatic ecosystems.

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