

A conceptual framework for ecosystem stoichiometry: balancing resource supply and demand

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The development of ecological stoichiometry has centered on organisms and their interactions, with less emphasis on the meaning or value of a comprehensive ecosystem stoichiometry at larger scales. Here we develop a conceptual framework that relates internal processes and exogenous factors in spatially- and temporally-linked ecosystems. This framework emerges from a functional view of ecosystem stoichiometry rooted in understanding the causes and consequences of relative stoichiometric balance, defined as the balance between ratios of resource supply and demand. We begin by modifying a graphical model based on resource ratio competition theory that relates resource supply and demand to ecosystem processes. This approach identified mechanisms, or stoichiometric schemes, through which ecosystems respond to variable resource supply. We expand this view by considering the effects of exogenous factors other than resource supply that comprise a stoichiometric template that influences stoichiometric balance within ecosystems. We then describe a number of examples of patterns in organismal stoichiometry in several types of ecosystems that illustrate stoichiometric schemes and factors that impinge directly on stoichiometric patterns. Next, we conduct an initial analysis of the stoichiometric effects of spatial linkages between ecosystems, and how those relate to boundary dynamics and hot spot development. We conclude by outlining research directions that will significantly advance our understanding of stoichiometric constraints on ecosystem structure and function.

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Ecological stoichiometry theory provides an integrative framework that links biogeochemical patterns at a global scale to physiological constraints that operate at cellular and organismal levels (Sternner and Elser 2002). This body of theory is well-suited for the analysis of ecosystems, which are complex entities that span multiple spatial and temporal scales and involve both living

and non-living components. The conceptual development of ecological stoichiometry has centered mainly on organisms; their response to resource stoichiometry, their interactions with each other, and their influence on the coupling of multiple biogeochemical cycles. In the process, we have learned much about stoichiometry as it relates to specific ecosystem processes, but have little

conceptual clarity as to the meaning or value of a comprehensive ecosystem stoichiometry. Our overarching goal is to begin the development of a conceptual model describing potential interactions between internal processes and exogenous factors in spatially- and temporally-linked ecosystems that impinge directly on stoichiometric patterns.

We define whole ecosystem stoichiometry to be the ratio of elements summed across all biotic and abiotic compartments, which Golley and Richardson (1977) referred to as the “chemical structure of an ecosystem”. An operational definition of whole ecosystem stoichiometry requires an explicit definition of spatial and temporal scale (Levin 1992). Spatial and temporal scales, in turn, define which elements are ‘in play’ ecologically. Whole ecosystem stoichiometry is hard to measure because difficulties arise in determining ecosystem boundaries; both in terms of spatial location, and which compartments are considered to be part of the system (i.e. air, rocks, depth of soil or water column to include). Furthermore, a significant proportion of elemental content is contained in compartments that change very slowly and are therefore largely unavailable (i.e. wood in long-lived trees, occluded P in soil, N₂ gas in air or water). Because of the difficulties in defining system boundaries, this traditional definition of whole ecosystem stoichiometry is of little utility in developing a general conceptual framework to guide our understanding of stoichiometric processes at the ecosystem level.

Here we develop a more functional conceptualization of ecosystem stoichiometry, one rooted in understanding the causes and consequences of relative stoichiometric balance, defined as the match between ratios of elemental supply and demand. Stoichiometric balance can be applied to specific consumer–resource interactions or to the sum of processes occurring within an ecosystem. A major unanswered question in ecological stoichiometry is do ecosystems tend to become more stoichiometrically balanced over time, or more precisely, under what conditions do ecosystems tend towards stoichiometric balance? In this paper, we develop a conceptual framework to guide research into the answer to this question based on this functional view of ecosystem stoichiometry.

Recent and more classical work has identified large scale patterns in organismal stoichiometry in several types of ecosystems, which allow us to infer internal and exogenous ecosystem processes that influence relative stoichiometric balance. We briefly highlight this body of literature and use it to illustrate ecosystem responses to a suite of environmental factors that determine whether ecosystems become more stoichiometrically balanced. In addition, recent developments in landscape ecology point to the need for explicit attention to causes and consequences of spatial linkages between ecosystems,

and we expand our conceptual framework to include these types of interactions.

Stoichiometric balance: a conceptual framework

Theoretical arguments suggest that organisms tend towards stoichiometric balance with their resource supply (Redfield 1958, Chapin 1980, Reynolds and Pacala 1993, van den Berg et al. 2003, Sterner et al. 2004), resulting in co-limitation by multiple key resources. At the ecosystem level, there is empirical evidence for co-limitation, most often by N and P, in aquatic (Elser et al. 1990) and terrestrial (Gusewell et al. 2003) ecosystems. To understand how such ecosystem-level co-limitation can arise, we use Tilman’s (1982) graphical model of growth and resource competition as a framework to understand the causes and consequences of stoichiometric balance and imbalance in ecosystems (Fig. 1A). We then expand this framework beyond a simple focus on resource supply to generate a conceptual model that includes other exogenous factors (Fig. 2) and is designed to further our understanding of the causes of imbalances in ecosystems. Tilman (1982) originally developed this model for interactions between two species, and here we expand its application to whole ecosystems.

Ecosystems respond to shifts in resource supply in multiple ways. These responses can affect any of the three different components of the model in Fig. 1: the shape and location of the zero net growth isocline (ZNGI), the slope of the consumption vector, and the location of the resource supply point (Fig. 1B,C; these terms are defined in Fig. 1A). In Fig. 1B, the right angle in each species’ ZNGI is now rounded off. This represents the action of a suite of mechanisms leading to co-limitation at a range of resource ratios, rather than one fixed resource ratio. These mechanisms include changes in resource-acquisition via changes in physiology, morphology, or behavior (see Appendix A for model details). This is similar to the concept of ‘mixed limitation’ developed by Thingstad (1987). Additionally, in Fig. 1C, ZNGIs for several individual species are distributed along a tradeoff curve in their competitive ability for R1 and R2 (Tilman 1982). Given a continuous range of species along this tradeoff curve, a species whose elemental stoichiometry closely matches the supply ratio will displace all others. When supply ratio changes, interspecific competition tends to maintain stoichiometric balance. This balance can also be maintained by reducing the loss of a scarce nutrient through differential recycling (Hedin et al. 1995, Daufresne and Hedin pers. comm.), which lessens the demand for that nutrient from external supplies and changes the stoichiometric ratio of demand. This leads to a change in the

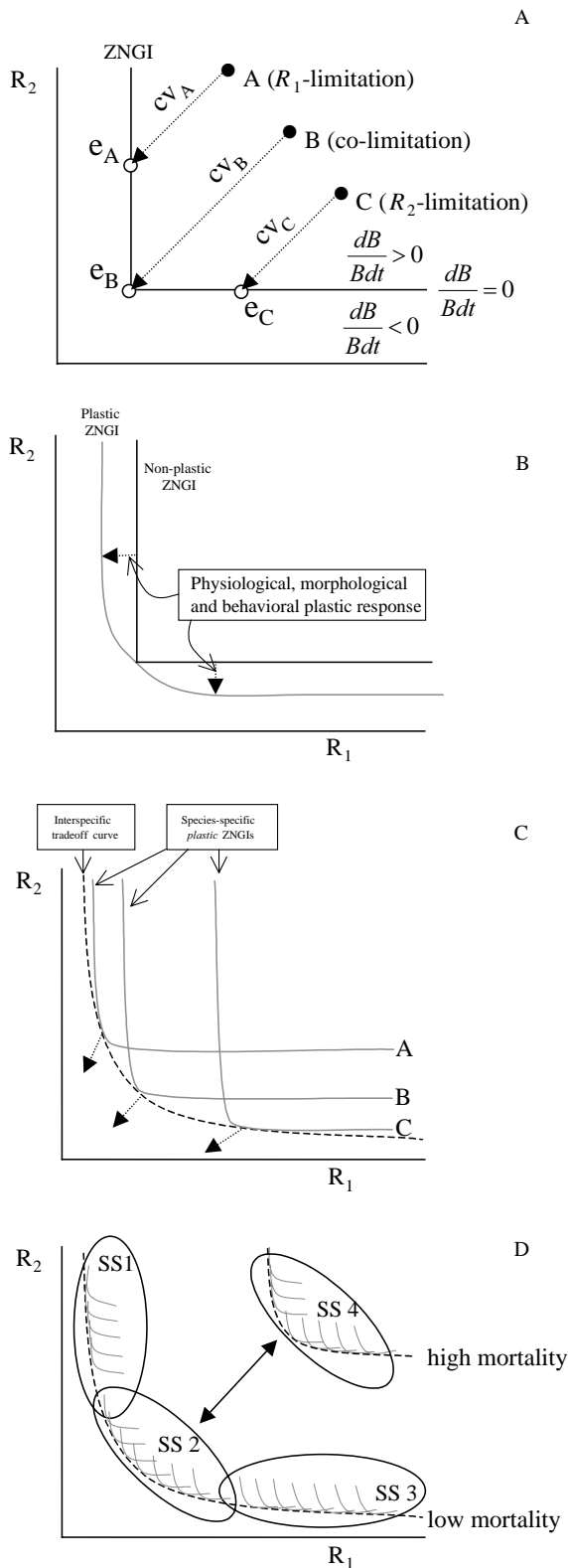


Fig. 1 (Continued)

A slope of the net consumption vector, representing uptake minus recycling (Daufresne and Hedin pers. comm.). Finally, the location of the resource supply point is altered when novel processes arise that bring previously unavailable sources of the scarce nutrient into play, either via the arrival of new species or facultative responses of resident species. Examples include nitrogen-fixation (Redfield 1958) and degradation of organic phosphorus pools (Linquist et al. 1997). These species- or community- level responses combine to influence stoichiometric balance at the ecosystem level. The specific ways in which an ecosystem adjusts to resource supply define its stoichiometric scheme (Fig. 1D).

This last class of ecosystem responses, through changes in resource supply ratios, clearly implies that unavailable sources of nutrients are considered external to the system when we are considering the relative stoichiometric balance between supply and demand. These nutrient pools do not become part of the system until a process arises that brings them into the available pool. In fact, it may very well be that severe imbalances between supply and demand lead to the development of novel processes tapping a previously unavailable nutrient pool.

Stoichiometric balance may occur, but it may be dynamically unstable as found for plant-herbivore systems (Andersen 1997, Loladze et al. 2000), and competition between N-fixing and non-fixing plants (Schwinning and Parsons 1996, Jenerette and Wu 2004). Stability may be maintained over longer time periods, however, as these oscillating systems can be averaged (Sanders and Verhulst 1985), again emphasizing the importance of temporal scale. In addition, recent theoretical work suggests that stoichiometric mechan-

B

C

D

Fig. 1. Development of a graphical model of ecosystem stoichiometry, after Tilman (1982). Each axis represents the concentration of the available form of an essential resource. (A) The three basic components of this theory, considering a single species with fixed physiology. The zero net growth isocline (ZNGI) represents the set of available resource levels where net consumer growth ceases. The right-angle shape derives from Liebig's law of the minimum, that growth is limited by the nutrient in shortest supply relative to demand. The supply point (solid circles) represents the concentration of each nutrient entering the ecosystem. The consumption vector (dashed arrows labeled CV) represents the consumer's fixed stoichiometric ratio in which the consumers take up resources. The equilibrium resource levels (open circles) must lie on the ZNGI. Mass specific growth rate is represented by $\frac{dB}{Bdt}$ where B is algal density (Appendix A). The three supply points shown here represent an R1-limited, an R2-limited, and a co-limited single-species situation. (B) Physiological plasticity in resource acquisition replaces the right-angle non-plastic ZNGI (solid line) with a rounded-corner plastic ZNGI (dashed line, see Appendix A for model details). (C) Multiple species with different elemental stoichiometries have ZNGIs that lie along a dashed tradeoff curve. (D) Four stoichiometric schemes (SS) adapted to different stoichiometric templates: R1-limitation, co-limitation, and R2-limitation at low mortality rates (SS 1-3), and high growth/mortality rates (SS 4) at high R1 and R2 availability.

isms may lead to stable coexistence of grazers on a single plant resource (Hall 2004, Loladze et al. 2004).

An ecosystem's stoichiometric scheme will vary in space and time in response to environmental conditions in which the system resides. The model described above focuses solely on the influence of resource supply ratios and suggests that all ecosystems should tend towards stoichiometric balance at equilibrium. Other factors besides resource supply, however, complicate this model through their effects on life history traits of organisms that influence the stoichiometry of their resource requirements. For example, Woods et al. (2003) show that a broad range of organisms adapted to low temperatures exhibit higher N and P contents. They attribute this pattern to a higher N and P requirement to maintain high catalytic capacity for the maintenance of metabolic activity and growth rates. In addition, Elser et al. (2000) show higher P in *Daphnia pulex* in response to a shorter growing season. They hypothesize that a shorter growing season selects for higher growth rate, which is linked to body P content, and therefore P demand by *Daphnia* (see Sterner and Elser 2002 for a detailed description of link between P and growth rate).

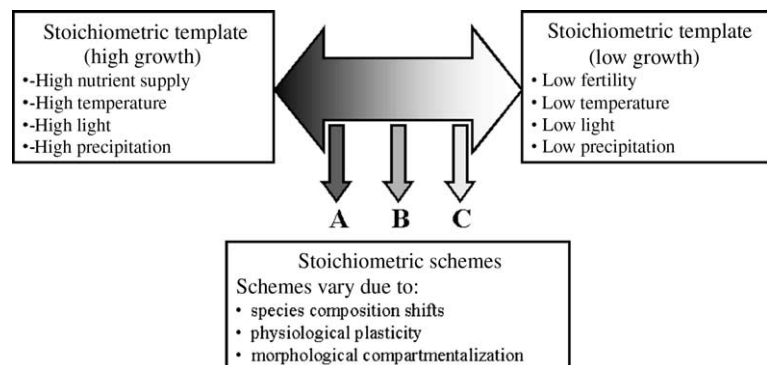
These examples demonstrate that stoichiometric traits can be driven by variables other than resource supply ratios. Indeed, the stoichiometric scheme of an ecosystem is likely to be the result of an array of responses to environmental conditions that directly impinge on stoichiometric traits. Similar to Southwood's physical habitat template (Southwood 1977), we refer to the suite of exogenous conditions, whether static or dynamic, which impact the elemental composition of an ecosystem as a stoichiometric template. Temperature and growing season length are two examples of factors that contribute to this template; others include local geologic substrate, precipitation, solar radiation, disturbance, and various external resource supplies, all of which vary at multiple spatial and temporal scales. Biological interactions may also be part of the stoichiometric template, with organ-

isms that perceive the environment at larger scales acting as ecosystem drivers, through positive or negative interactions with other species. When these factors oppose each other in their effects on either the stoichiometry of demand or supply, the stoichiometric template may cause, or maintain, stoichiometric imbalances. Identifying the key physical and chemical factors that define a stoichiometric template is an important research frontier, and will require a multitude of empirical and theoretical approaches. Below, we review what is known about global patterns in ecosystem stoichiometry, and discuss what we can infer from these patterns about organism and ecosystem responses to variation in resource supply.

Global patterns and controls on ecosystem stoichiometry

Regulation of the N:P ratio in the oceans provides one of the best known examples of stoichiometric balance in an ecosystem. Redfield observed that pelagic N:P stoichiometry of the ocean (15N:1P) closely matches the average N:P ratio in phytoplankton (16N:1P; Redfield 1958, Falkowski 2000, Falkowski and Davis 2004). Geological and biological processes interact to control the fluxes of P, while N-fixing phytoplankton control the influx of fixed N from the atmosphere. The abundance of N-fixing species is determined by competition between N-fixing and other phytoplankton: N-fixers are selected when the ocean is N-limited ($N:P < \text{Redfield ratio}$), but are out-competed when the ocean is P-limited ($N:P > \text{Redfield ratio}$) because N-fixers are poor competitors for P. This community dynamic drives marine pelagic N:P stoichiometry to match the N:P of the phytoplankton. In this model, in the absence of large P supplies, N-fixers would be excluded without loss of N through denitrification. Recent mathematical models (Tyrell 1999, Lenton and Watson 2000) have validated this verbal argument. In

Fig. 2. Stoichiometric templates (upper boxes) and stoichiometric schemes characterize how forcing and response variables relate to ecosystem stoichiometry as presented in the accompanying text. Stoichiometric templates refer to the magnitude of forcing variables characteristic of the scale above the ecosystem of interest and vary over a continuum ranging from conditions that favor high growth to those that favor low growth rates. A stoichiometric scheme represents the suite of stoichiometric traits that enable an ecosystem to operate on a specific stoichiometric template (vertical shaded arrows).



contrast to the oceans, lakes are more influenced by their surrounding watersheds, leading to greater variability in whole ecosystem stoichiometry (Elser and Hassett 1994, Sterner and Elser 2002). However, Smith (1983) noted the occurrence of N-fixers predominately in lakes with epilimnetic TN:TP ratios less than 29, in qualitative accordance with Redfield's mechanism of N:P regulation.

This argument can be seen graphically (Fig. 3). The ZNGI of the N-fixer is a vertical line because it has an exclusive external source of N; in a sense the resource supply point is different for N-fixers than for other phytoplankton, because N-fixers have access to a pool of N unavailable to their competitors. The ZNGIs intersect because of the assumption that the N-fixers are poorer P competitors than non-fixers. The N-fixers' consumption vector is parallel to the P-axis because they are assumed to not consume N from the pool represented by the N-axis; the other species' consumption vector corresponds to its N:P ratio. The supply point initially corresponds to the N:P ratio in the deep water that supplies nutrients through upwelling and mixing. The N:P of this supply point applies moves up over time (point A–D in Fig. 3) due to the net input of N to the ecosystem through N-fixation. The above arguments assume P limitation of N-fixers. Although P-limitation of N-fixation has been demonstrated (Sañudo-Wilhelmy et al. 2001), there is also evidence for light- (Hood et al. 2004) and iron-limitation (Berman-Frank et al. 2001, Kustka et al. 2003) as well as co-limitation (Mills et al. 2004). Limitation by resources other than P complicates the simple feedback system described above, but does not significantly alter the conclusion that biotic control over ocean N:P stoichiometry is substantial.

We can also apply this approach to terrestrial ecosystems, but there are some fundamental differences to keep in mind. First, in the surface ocean the ratio of nutrients from upwelling is determined largely by the ratio of nutrients in the organic matter that sinks down from the surface layer (Redfield 1958); thus creating a feedback

loop by which the stoichiometry of the living biota largely determine the stoichiometry of the supply point. In contrast, mineral nutrients in terrestrial ecosystems are derived from weathering and reflect the physical and chemical characteristics of the local parent material (Jenny 1941). The biota can modify the strength of the geochemical influence through differential recycling of essential mineral nutrients and in ecosystems on highly weathered soils recycling replaces weathering as the primary source of nutrients (Walker and Syers 1976, Tiessen and Stewart 1984, Lenton 2001). Additionally marine ecosystems are connected to one another through large scale mixing mechanisms such as upwelling and the 'conveyor belt' currents that transport water on the global scale. Terrestrial ecosystems have only small scale mixing mechanisms resulting in stronger local and regional signals. Finally, measurement of available nutrients and whole ecosystem stoichiometry are logistically simpler in pelagic marine ecosystems. Terrestrial ecosystems are composed of multiple compartments, which differ both in stoichiometric signatures (Table 1) and turnover times in both the biota and soil matrix.

Although the caveats above may affect the application of this graphical model to terrestrial ecosystems, there is evidence for general stoichiometric patterns in foliage across regional and global scales that suggests some similarities between aquatic and terrestrial ecosystems. Commonly, foliar nutrients have been used as an indicator of ecosystem nutrient status, even though the proportion of total ecosystem nutrients held in this pool can vary widely (Golley and Richardson 1977, Vitousek 1982). These analyses show strong evidence of a global scale pattern in nutrient availability in soils (Jenny 1941), with N-poor soils dominating recently glaciated temperate areas and P-poor, highly-weathered soils dominating tropical regions. Evidence has accumulated that vegetation responds to this variation in predictable ways. Increased soil N availability and decreased soil P availability are reflected in decreased C:N and

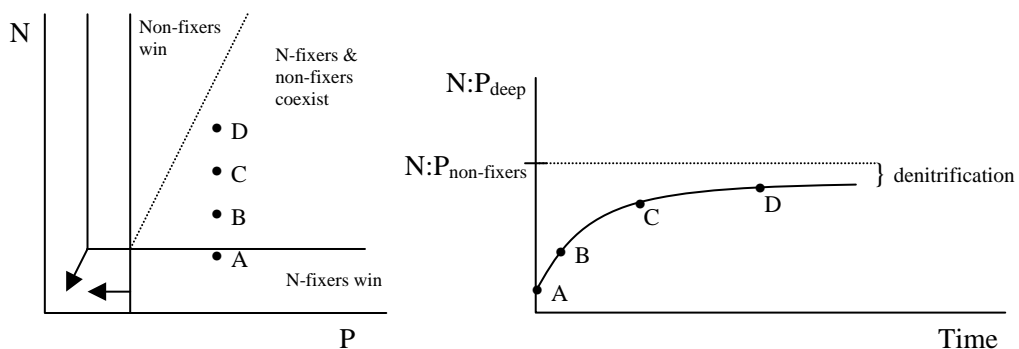


Fig. 3. Graphical model of the regulation of N:P in the ocean by competition between N-fixing and non-fixing phytoplankton. The non-fixers' ZNGI is a right-angle curve, the N-fixer's ZNGI is a vertical line because it has an exclusive N source. Over long time scales, the supply point moves from point A to D as N-fixers increase the N:P supply in deep water.

Table 1. C:N:P ratios for various plant tissue classes.

| Forest type | Leaves | Stem wood | Branches | Roots |
|---------------------------|------------|--------------|-----------|-------------|
| Temperate mixed hardwood* | 157:6.3:1 | 4700:9:1 | 783:6.5:1 | 522:3.9:1 |
| Temperate eucalypt* | 407:11.7:1 | 25620:12.6:1 | 4904:12:1 | 2475:10.8:1 |
| Tropical lowland** | 528:21.9:1 | 6064:38.5:1 | n/a | 1515:39.1:1 |

* data from Pastor and Bockheim 1984, Feller 1980, Johnson et al. 2001 and Silver et al. 2000.

** data for leaves and stems from Johnson et al. 2001 data for root pools from a similar forest reported in Silver et al. 2000.

increased N:P ratios in tropical as compared to temperate forest foliage (Table 1, Vitousek 1984, Reich and Oleksyn 2004, McGroddy et al. 2004).

Patterns in foliar stoichiometry respond to shifts in soil nutrient supply, both spatially (above), but also temporally over the course of soil development (Vitousek 1982). Both spatial and temporal shifts follow the tradeoff curve of our graphical model (Fig. 4). This process has been particularly well documented on chronosequences ranging from the Hawaiian Islands to Alaska (Crews et al. 1995, Wardle et al. 2004). Due to mineral weathering young soils are P- rich, and have yet to develop significant N pools. As soils develop, N pools increase due to biological activity (N-fixation) and P pools decrease due to losses from physical processes (Walker and Syers 1976, Crews et al. 1995).

The shifting stoichiometric templates along developmental or latitudinal gradients cause variations in stoichiometric schemes in terrestrial ecosystems, reflected in changes in foliar nutrients that correspond to changes in soil nutrients (Table 1, McGroddy et al. 2004). These large scale patterns contrast with the widely reported constancy in marine N:P and strongly suggest that terrestrial biota are less effective than their marine counterparts at shifting the ratio of resource supply to match a generalized physiological optimum and instead have adjusted their stoichiometric demands on the

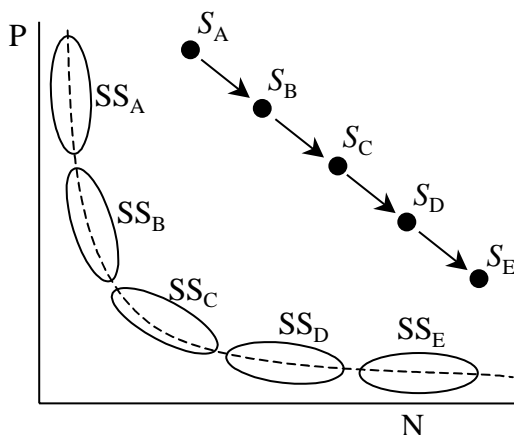


Fig. 4. (A) Graphical model of long-term ecosystem succession. As soils age, they shift from low-N, high-P to high-N, low-P, moving the supply point along the trajectory shown. This shifting stoichiometric template selects for a corresponding series of stoichiometric schemes.

regional scale to match local nutrient conditions. While the role of N fixation in N accumulation is similar in terrestrial and marine ecosystems, it seems that terrestrial N fixation does not result in the same striking similarity between N:P of nutrient pools and producer tissue. Why does the marine model described above not work in terrestrial ecosystems? The effects of factors such as P dynamics during soil development, light availability, trace metals, and climate have been discussed as potentially limiting the impacts of N fixation in terrestrial ecosystems (Vitousek and Howarth 1991, Cleveland et al. 1999, Hungate et al. 2004), but this remains a significant question for future research.

As mentioned previously, shifts in stoichiometric schemes are due in part to physiological plasticity, which results from shifts in allocation to acquisition of elements at the cellular, organ, and organismal levels (Chapin 1980, Vitousek 1982). These tradeoffs are associated with shifts in metabolic processes and in allocation to different organs. Under low nutrient availability, at both cellular and organismal levels, nutrient use efficiency (NUE, sensu Vitousek 1982) increases, resulting in higher C:nutrient in producer tissue. In terrestrial ecosystems, plants also shift allocation of resources among organs with different nutrient contents (Table 1) resulting in a shift in overall stoichiometry of the individual. Differential allocation to below-ground and aboveground organs in terrestrial plants is the best studied example of this process. Unfortunately there is little data currently available on stoichiometric responses of compartments other than foliage to shifts in nutrient availability. Currently, this limits our ability to predict specific effects of allocation shifts on regional and global scale stoichiometric patterns, and represents an important research frontier. Plasticity with respect to NUE or allocation allows persistence of an individual in an environment where the selection pressures vary due to variations in the nutrient supply point, and should result in stoichiometric balance in the ecosystem. The level of stoichiometric balance achieved, however, will be modified by other factors comprising the stoichiometric template.

In addition to differing with respect to stoichiometric signatures, different plant organs also have distinct turnover times (e.g. weeks to years for leaves and high order fine roots, decades to centuries for stem wood; Gill and Jackson 2000, Chambers et al. 2001, Pregitzer et al.

2002). Different growth strategies in plants in response to resource availability may lead to changes in temporal dynamics relevant to stoichiometric factors. Stoichiometric schemes that favor resource conservation (corresponding to SS 1–3 in Fig. 1D) often involve slow growth and greater allocation to structural compartments with long turnover times (Grime 1977) while schemes favoring high resource extraction (rapid growth, SS4 in Fig. 1D) are often the reverse. These schemes differ considerably in their effects on rates of nutrient cycling.

As described above and in Appendix A, physiological plasticity results in ZNGIs with rounded corners (Fig. 1b) and a wider range of ratios resulting in co-limitation. Physiological plasticity is only an effective response over a limited range of supply points. When this range is exceeded, the result is a shift in community composition to a species or community with a consumption vector that more closely matches the resource ratio of the new supply point, moving the equilibrium up or down on the tradeoff curve (Fig. 1c). Global patterns in C:N:P of foliage described above are certainly the result of a combination of these two types of response.

So far, our discussion has been rooted in theory heavily influenced by equilibrium-based views of nature. However, stoichiometric templates, including resource supply ratios and other exogenous factors described above, vary in space and time at multiple scales. This variation has potentially enormous effects on stoichiometric balances within ecosystems, including whether or not ecosystems approach equilibrium. Spatial and temporal heterogeneity in stoichiometric templates can promote coexistence of species exhibiting contrasting stoichiometric schemes (Tilman and Pacala 1993), and in turn, biodiversity can buffer the response of ecosystems

to external fluctuations (Lehman and Tilman 2000, Norberg et al. 2001). Alternatively, heterogeneity, particularly temporal fluctuations, may prevent ecosystems from reaching equilibrium, thereby maintaining stoichiometric imbalances in many ecosystems.

Ecosystem connectivity: a stoichiometric perspective

In our discussion of stoichiometric templates, we introduce the idea that multiple exogenous factors may interact to maintain stoichiometric imbalances in a single isolated ecosystem. Ecosystems are rarely isolated in space, however, and ecologists now recognize that local phenomena are rarely controlled by site-specific factors alone (Polis et al. 1997, Aber et al. 1998, Reiners and Driese 2001). Like other levels of biological organization, ecosystems interact through the exchange of energy, information, and material (Reiners and Driese 2003, Loreau and Holt 2004). This has led to conceptual advances in meta-population theory (Hanski 1999), landscape ecology (Pickett and Cadenasso 1995), and theory addressing subsidized food webs (Polis et al. 2004). We can use our graphical model as a starting point to explore ecosystem interactions, and the effects of ecosystem interactions on stoichiometric balance. Using this approach, the export from one ecosystem, a function of the equilibrium point, influences the resource supply ratio of the downstream ecosystem through the movement of unused resources via some vector of transport (i.e. movements of water, air, organisms, etc., Fig. 5).

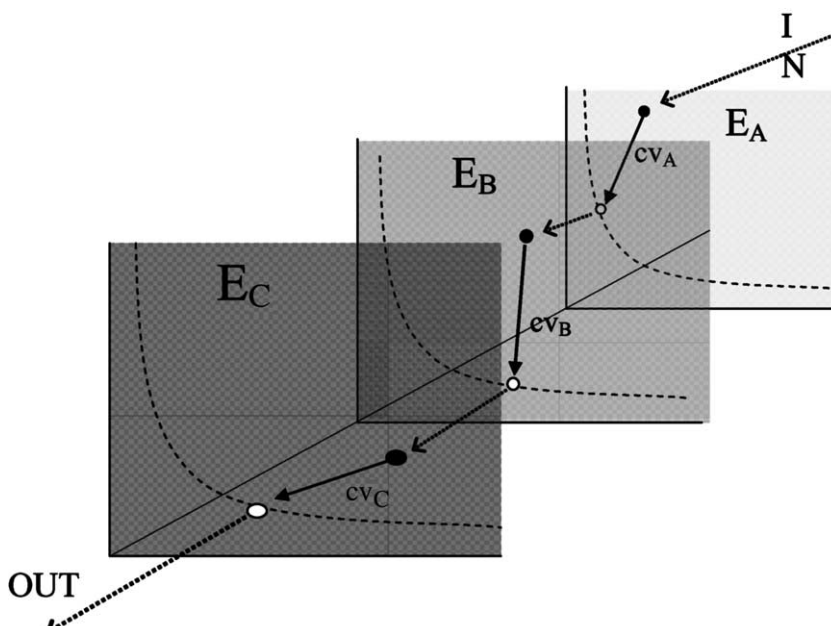


Fig. 5. A graphical model of spatially linked ecosystems ($E_A - E_C$). Nutrients flow from ecosystem E_A through ecosystem E_C , linking the resource equilibrium point of upstream ecosystems with the supply point of downstream ecosystems. Spatial variation in the non-resource-related stoichiometric templates can select for different stoichiometric schemes in each ecosystem.

Recent theoretical developments suggest that movement of organisms and materials from one ecosystem to another can significantly alter the supply ratio for the receiving ecosystem (Loreau et al. 2003). The impact of organism migration manifests itself both quantitatively through increases in resource or qualitatively through a shift in species composition. For instance, if herbivores from an ecosystem characterized by a stoichiometric scheme that favors low N:P ratios move into an ecosystem with a scheme driven by factors leading to high plant N:P, then migration creates a stoichiometric imbalance between herbivore needs and resources in the receiving ecosystem. The immigrant herbivore would recycle nutrients at high N:P ratio (Sterner 1990), further increasing the relative abundance of N in the ecosystem. One consequence of this sequence of events may be degradation of the receiving ecosystem as a suitable habitat for that herbivore such that the receiving ecosystem becomes a 'sink' habitat for that species. If either dispersal or the quality of the source patch is high, however, a population could be maintained (Holt 2004, Miller et al. 2004), resulting in new stoichiometric constraints in the receiving ecosystem and greater stoichiometric imbalances in the landscape. The immigration of herbivores from neighboring ecosystems becomes an important part of the stoichiometric template in the recipient ecosystem.

Boundaries regulate fluxes of materials and organisms between ecosystems and the stoichiometric effects of those exchanges (Fig. 6, Cadenasso et al. 2003). The extent to which the constraints discussed above develop depends on the influence of the boundary on the magnitude and form of exchange. Boundaries may increase, reduce or transform the flux of material and organisms, particularly their stoichiometric characteristics and effects. These effects are generally a function of differential boundary permeability, which in turn is a function of both structural features of the boundary (Cadenasso et al. 1997) and the degree and type of contrast between the ecosystems the boundary separates (Strayer et al. 2003). An example of the stoichiometric effects of an ecosystem boundary occurs at the interface between oxic and anoxic waters. In oxic waters, dissolved inorganic N is dominated by nitrate due to sufficient nitrification rates. When hydrologic flux across oxic-anoxic boundaries combines sufficient nitrate with labile organic carbon resources in the recipient ecosystem, nitrate is lost via high rates of denitrification at this interface (Schade et al. 2001). In contrast, P is unaffected as it moves across this boundary. Therefore, denitrification renders this boundary less permeable to N than it is to P, shifting N:P in the anoxic environment.

This example illustrates how boundaries become hot spots (sensu McClain et al. 2003) of biogeochemical activity in a landscape (Fig. 6). In general, biogeochem-

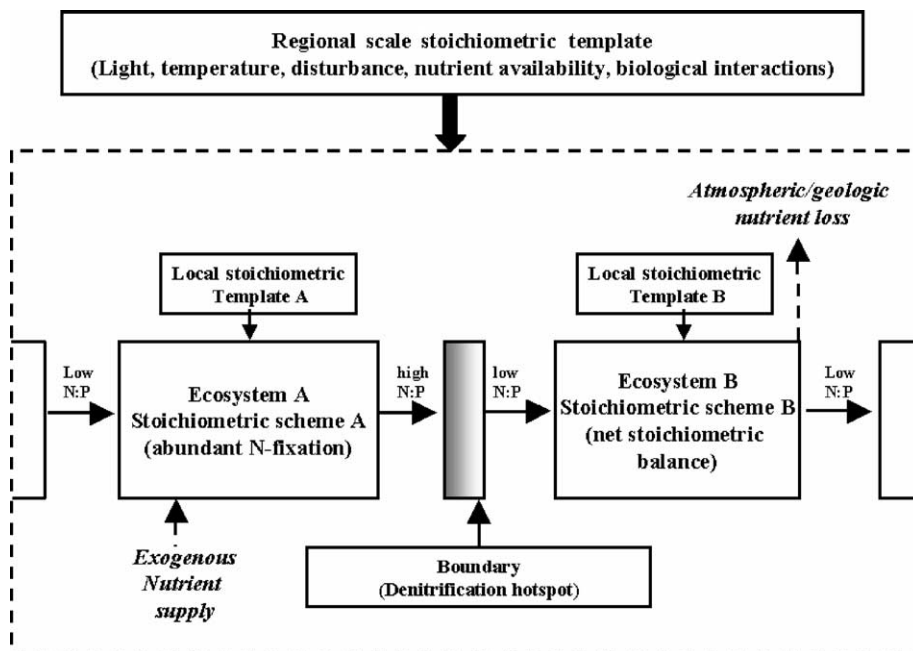


Fig. 6. Ecosystems interact through multiple propagating vectors including many that transport materials from one ecosystem to another (e.g. wind, water, animal movement, seed dispersal). Ecosystem interactions occur within the constraints imposed by broader ecological scale, i.e. the regional stoichiometric template. The local stoichiometric template combines with regional constraints to favor a specific stoichiometric scheme in each ecosystem. In this figure ecosystem interactions are unidirectional for sake of simplicity, as might be the case in interacting systems along a steep toposequence.

ical processes vary in rate and relative importance across the landscape and this heterogeneity is a consequence of material movement and mixing. Hot spots occur when and where resources mix to create optimal ratios that support high biogeochemical activity, either at boundaries or specific locations within ecosystems. They are important because the magnitude of their influence on larger scale phenomena is disproportionate to their spatial extent. Hot spot development is a product of stoichiometric interactions within and among ecosystems, and may produce heterogeneity in resource ratios of supply and/or demand, potentially creating stoichiometric imbalance in the ecosystem or landscape as a whole. Though McClain et al. (2003) focus on hydrological vectors of material flux, clearly the concept can be broadened to incorporate other vectors through which elements are propagated in space.

Often gradients of multiple resources drive the formation of hotspots, particularly when optimal ratios of resources occur along opposing gradients. In marine and lacustrine ecosystems, the main axis of variation is vertical. For example, Klausmeier and Litchman (2001) model the vertical distribution of phytoplankton in opposing gradients of light and nutrients. Deep chlorophyll maxima arise in poorly mixed water columns representing hot spots of biogeochemical activity where an optimal combination of light and nutrients generates peaks in productivity. Below this point, phytoplankton productivity is limited by light, above this point by nutrients.

In many landscapes, a prevailing transport direction links ecosystems along a central axis. Terrestrial and riverine ecosystems linked by fluvial transport are distributed along a topographic gradient, which facilitates assessments of stoichiometric imbalances through serially linked ecosystems. Shaver et al. (1990) found the N:P ratios of the import and export terms changed by ~30–250% along an arctic hydrologic flowpath linking discrete vegetation and soil patches. Similarly, Kling et al. (2000) observed substantial shifts in N:P ratios as water passed through a drainage characterized by alternating stream and lake sub-sections. These examples demonstrate the importance of the spatial arrangement, or configuration, of ecosystems in determining the effects of spatial linkages on stoichiometric templates.

Though our focus is on the consequences of ecosystem interactions through space, we recognize that this analysis could be extended to cover temporal dynamics. Understanding temporal linkages within an ecosystem will require knowledge of life history traits and successional dynamics that are absent in our discussion above. Though we are unable to develop the temporal component of ecosystem linkage here, we recognize that this topic is an important future research direction.

Challenges/future directions:

In the text above, we develop a series of simple models that help conceptualize stoichiometric interactions occurring within and among ecosystems at various scales. Developing these models helped us identify a set of mechanisms (i.e. stoichiometric schemes) through which ecosystems can alter their stoichiometry and move toward a stoichiometric balance with resource supply. This relative balance is modified through the effects of an array of exogenous factors (i.e. stoichiometric template). This framework permits broad scale comparisons of ecosystems from a stoichiometric viewpoint, and exposes a number of significant future research challenges.

One important challenge worth emphasizing here is the development of rigorous numerical approaches to assess the influence of configuration and ecosystem interactions in complex landscapes on ecosystem stoichiometry (Urban and Keitt 2001). Network theory is one approach that may prove useful in exploring the structure and strength of ecosystem connectedness. Successfully applied in the social sciences (Newman 2003), network theory has only recently been applied to ecological systems. For example, network models applied to lake food webs indicated that lake organisms were more highly connected than previously suspected (Dunne et al. 2002, Williams et al. 2002). Network theory may be able to identify whether specific motifs exist in landscapes (Rodríguez-Iturbe and Rinaldo 1997) and what their importance may be. In the context of this discussion, a motif represents a series of linked ecosystems with contrasting stoichiometric schemes that repeat in the network structure. Therefore, a network approach may provide a means of synthesizing and exploring the influence of spatial linkages between contrasting stoichiometric schemes across large-scale processes.

Though we have rooted our conceptual development in existing theoretical frameworks and in the published literature, many basic questions remain unanswered. A brief list of these includes:

- 1) which factors (physical, chemical and biological) define a stoichiometric template and how do multiple temporal and spatial scales change the importance of various factors?
- 2) do ecosystems in nature tend towards stoichiometric balance? If not, what prevents them from doing so?
- 3) how are the internal structure and functions of ecosystems affected by the stoichiometric composition of the influx of materials (flows of organic and inorganic nutrients including animal populations)?
- 4) how do stoichiometric imbalance, boundaries and ecosystem arrangements drive landscape scale patterns?

These questions comprise a set of research priorities that will significantly advance our understanding of stoichiometric constraints on ecosystem function and the influence of spatial heterogeneity, configuration and boundary dynamics. We are just beginning to merge ecological stoichiometry with ecosystem and landscape science. We believe that a successful integration will result in major advances in each of these disciplines. We hope that our conceptual development will serve as a stepping-stone toward this integration.

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Appendix A

Figure 1 corresponds to the following model for one plant with a fixed stoichiometry growing on two essential resources (here N and P).

$$\begin{aligned}\frac{dN}{dt} &= a(N_{in} - N) - Q_N \min\left(\frac{f_N(N)}{Q_N}, \frac{f_P(P)}{Q_P}\right) B \\ \frac{dP}{dt} &= a(P_{in} - P) - Q_P \min\left(\frac{f_N(N)}{Q_N}, \frac{f_P(P)}{Q_P}\right) B \\ \frac{dB}{dt} &= \min\left(\frac{f_N(N)}{Q_N}, \frac{f_P(P)}{Q_P}\right) B - mB\end{aligned}$$

where N (P) is available N (P), B is the plant population density, N_{in} (P_{in}) is N (P) concentration in input medium, a is flowthrough rate, Q_N (Q_P) is the N content per individual, f_N (f_P) is the N- (P -) uptake functional response, and m is the mortality rate. Growth is determined by the nutrient which is taken up in the

smallest amount relative to its demand. Uptake is typically modeled with a Michaelis-Menten functional response

$$f(R) = \frac{v_R R}{R + K_R}$$

for resource R , where v_R is the maximum uptake rate and K_R is the half-saturation constant. In order to maintain a fixed stoichiometry, uptake of the nonlimiting resource is coupled to uptake of the limiting resource.

Legovic and Cruzado (1997) and Klausmeier et al. (2004) developed a model of two essential resources that allows flexible stoichiometry. In this model, the supply point is (N_{in}, P_{in}) , the consumption vector is (Q_N, Q_P) , and the ZNGI is found by setting $dB/(Bdt) = 0$. Physiological plasticity in maximum uptake rates occurs when organisms can adjust v_N and v_P to achieve co-limitation. This does not change the consumption vector (which is determined by the organism's stoichiometry) but does result in a curved ZNGI (Vincent et al. 1996). Changes in nutrient content (Q) affect both the consumption vector and the ZNGI.