

Ecosystem Patterns and Processes

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Introduction

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Introduction

Ecosystems are complex entities composed of diverse organisms expressing a myriad of life histories, body sizes, and metabolic pathways embedded in a dynamic physical and chemical environment. A suite of internal processes create an intricate web of relationships that control the flow of energy and materials within and between ecosystems. Contributing to the complex nature of ecosystems is the breath of spatial and temporal scales over which ecosystems operate. Ecosystems occupy spatial scales from meters to hundreds of kilometers and temporal scales from days to centuries owing to contrasting organismal life spans. For instance, consider boreal forests. There, organism life histories range from a few days (i.e., bacteria in the soil) to centuries (i.e., trees) generating a plethora of timescales over which ecosystem function can be addressed. However, the most characteristic aspect of ecosystem research is that it explicitly incorporates the chemical and physical environment, often requiring multidisciplinary approaches to characterize patterns and identify controlling mechanisms.

Ecosystem studies are largely organized around two complementary themes, energy flow and elemental cycling. Because ecological stoichiometry examines the nature, control, and implications of elemental balances in ecological processes, it also provides an appropriate framework for linking elemental cycles in nature. Elements required for life, such as carbon (C), nitrogen (N), phosphorus (P), calcium (Ca), and trace metals, are conserved as they move between organisms and their environment. That is, elements cannot be destroyed and are instead used, released back into the environment, reused again by organisms, and so forth, cycle after cycle. Continuous elemental flow between the environment and organisms with specific elemental compositions creates important ecological constraints, the implications of which represent one aspect of ecological stoichiometry.

Ecological stoichiometry offers insight into ecosystem dynamics because it readily applies to the composite nature of ecosystems. Stoichiometric constraints affecting

primary producers and higher trophic levels have consequences for the relative cycling rates of elements. This condition has an important implication; if we understand the stoichiometric interactions between organisms, we should be able to predict and understand stoichiometric outcomes at the ecosystem level. However, elemental cycling is not simply the sum of assimilative growth, trophic transfer and mineralization (conversion of organic compounds to inorganic forms). Rather, a suite of other biogeochemical processes also influence the availability and cycling of elements. In this chapter, we discuss the consequences of relative nutrient availability for ecosystem processes and review research that has used a stoichiometric approach to investigate the coupling of nutrient cycles in nature.

Nutrient Limitation of Ecosystem Production

Nutrient limitation is a fundamental concept in ecological research and, at its core, is a question of ecological stoichiometry. Primary production is usually stimulated by nutrient addition. Increased production following fertilization has been identified by some as one of the most repeatable and predictable features of nature and one humans rely upon for their food supply. Modern research into nutrient limitation can be traced to Justus Liebig, who developed the “law of the minimum” to explain why crop yield was most often stimulated by a single element, though that element may change from one system to the next. Simply put, the law of the minimum states that the nutrient present in the lowest amount relative to organism demand will limit growth and production. Liebig’s law rests on an implicit assumption that an organism’s elemental composition is relatively constrained and that its production will reduce elemental pools until one element becomes rare enough to limit production.

As a modern research topic, nutrient limitation spans levels of organization from individuals to ecosystems. At the ecosystem scale, investigations of nutrient limitation tend to focus on primary rather than secondary

production because it represents the interface between the physical and chemical environment and the resident biological community. Rates of material flow across this boundary and the factors that influence those rates are fundamental topics in ecosystem science. From a stoichiometric perspective, limitation status is a product of relative nutrient supply and demand for those elements by biota capable of 'using' inorganic nutrient forms (e.g., plants, bacteria, and fungi). At the scale of an organism, relative nutrient requirements are controlled by growth rate, specific physiological processes, and plasticity therein. At the ecosystem scale, nutrient demand is also influenced by trophic structure (e.g., relative abundance of primary producers), nonassimilative biological processes (e.g., denitrification) and various physical and chemical processes (e.g., precipitation, weathering, leaching). Nevertheless, we frequently speak of biological production in forests, grasslands, lakes, and streams as nitrogen or phosphorus limited because nutrient imbalances between inorganic pools and organism stoichiometry are pronounced or experimental manipulations have indicated that the system responded in some way to nutrient addition.

In terrestrial ecosystems, N limitation is most common though P-limitation has been observed. Global scale patterns in soil nutrient availability suggest that N limitation is most pronounced in recently glaciated temperate areas with P-poor soils dominating tropical regions. More current research indicates that foliar chemistry tracks this pattern with lower C:N and higher N:P ratios typical of leaf tissue from tropical versus temperate ecosystems. A frequent explanation for N limitation is the rarity of N in mineral substances relative to P and the difficulty of transforming dinitrogen gas to forms available to plants and microorganisms (biologically mediated N-fixation). A secondary explanation of N limitation in terrestrial ecosystems relates to the relative mobility of dissolved forms of N and P. Phosphorus mobility in soils is poor due to sorption kinetics of dissolved P-forms. Therefore, as P cycles from organic compartments to inorganic forms (via mineralization), there is a tendency for it to remain in the local environment. Nitrogen is mineralized from organic material as ammonium (NH_4^+), which like dissolved P has poor mobility in soils. However, microbial activity rapidly converts ammonium to a much more mobile form, nitrate (NO_3^-), via nitrification, which can be rapidly leached from soils. In addition, loss of N in dissolved organic forms (e.g., humic and fulvic acids) has been shown to be an important avenue of N loss. The development of P-poor soils and the potential for P-limitation become pronounced as landscapes and associated ecosystems age. Research on geological chronosequences in Hawaii and New Zealand indicates that terrestrial ecosystems move toward P-limitation with age due to the establishment of N-fixing organisms, accumulation of organic N in soils, and long-term losses of P via

weathering and subsequent leaching. Tropical ecosystems have also been shown to tend toward P-limitation for similar reasons (i.e., highly weathered soils and abundant N-fixation). In the modern era, a human-induced change in the abundance of biologically available N is also likely to push terrestrial systems away from N limitation (potentially toward P-limitation) even in relatively undisturbed ecosystems (via atmospheric deposition).

In aquatic habitats, the prevailing contention has historically been that phosphorus tends to limit gross primary production in freshwater ecosystems, whereas nitrogen tends to limit production in marine environments. However, recent reviews indicate that this conclusion is an oversimplification and the nature of nitrogen and phosphorus limitation of gross primary production in aquatic ecosystems appears more complicated than previously thought. Unlike the terrestrial case presented above, anthropogenic nutrient enrichment of lakes indicates greater relative additions of P versus N. In contrast, human impacts on stream and river ecosystems tend to increase nitrogen availability relative to phosphorus. Recent reviews also suggest gross primary production in marine offshore ecosystems is often limited by phosphorus or micronutrients, whereas gross primary production in coastal marine ecosystems tends to be N limited. An unfortunate stoichiometric outcome of human activity has arisen from elevated N in rivers alleviating primary producer limitation in coastal waters. Excess production in many estuaries has led to extensive 'dead zones' created by anaerobic conditions that develop as excess production is mineralized.

Efficiency in Elemental Use

In the previous section, we discussed the stoichiometric patterns in nutrient limitation. However, there is considerable variation in published relationships between biomass accrual and nutrient supply such that the relationship between nutrient availability and production is often not linear. We now turn our attention to examining how primary producers differentially accumulate biomass under nutrient-limiting conditions. The nutrient use efficiency (NUE) concept describes the amount of producer biomass generated per unit of nutrient taken up by organisms. Where conclusions about limitation are categorical, NUE is a continuous variable that reflects the relative influence of nutrient availability on net production.

NUE is normally expressed as the ratio of producer growth to the amount of nutrients assimilated by the organism. More explicitly, NUE is the ecosystem-scale expression of the ratio between individual photosynthetic nutrient use efficiencies (PNUE; flux of nutrient relative to carbon fixation) and individual growth rates (μ) such that $\text{NUE} = \text{PNUE}/\mu$. Relationships between net

photosynthesis and organism N content demonstrate that PNUE can vary by an order of magnitude (25–200). Combined with variation in organism growth rates, it is not surprising that NUE varies considerably among ecosystems.

In stoichiometric terminology, variation in NUE indicates that ecosystems are nonhomeostatic, or plastic, with respect to nutrient use. Why should biomass production become less efficient with increased nutrient availability? A frequent explanation is that strong selective pressures for greater efficiency at low-nutrient concentrations drive the observed pattern. However, there is no obvious explanation for why efficiency would be reduced under high nutrient conditions from either a competition or natural selection perspective. The likely explanation relates to the multiplicity of factors that can limit primary production. For example, under conditions of rapid biomass accumulation, light limitation of producer growth through self-shading increases, leading to smaller producer growth per unit of nutrient absorbed (i.e., reduced producer NUE) if resident organisms are plastic in their elemental composition. Another explanation presented in the literature relates to trophic structure and the strength of top-down control of primary producer biomass. When top-down control of primary producers is strong, as in systems with an even number of trophic levels, rapid consumption maintains primary producers in a state of rapid growth with consequent increased nutrient content (as described elsewhere in this encyclopedia).

Nutrient use efficiency has largely been a primary producer concept though there is no conceptual barrier to its application to heterotrophic organisms. In part, this may stem from the historical perspective that higher trophic level organisms are strongly homeostatic in their elemental composition (and thus have constant NUE). However, by now it should be apparent that heterotrophic stoichiometry is not fixed. This observation has recently led to a carbon-based corollary of NUE. Carbon use efficiency (CUE) has been defined as secondary production divided by net primary production. Many people will recognize this as the stoichiometric repackaging of trophic transfer efficiency (based on C rather than energy). In lakes, CUE has been demonstrated to vary by more than two orders of magnitude (0.002–0.4%). We are unaware of similar data from terrestrial systems. Stoichiometric theory predicts that consumers will use nutrients more efficiently when C:nutrient ratios are high. Consumers tend to use carbon inefficiently under these conditions because they will need to release excess carbon as they accrue biomass. All else being equal, it follows that CUE and NUE should be inversely related, a prediction that has yet to be assessed as far as we are aware.

Up to this point, we have focused our discussion on ecosystems where nutrients enter biotic pools through

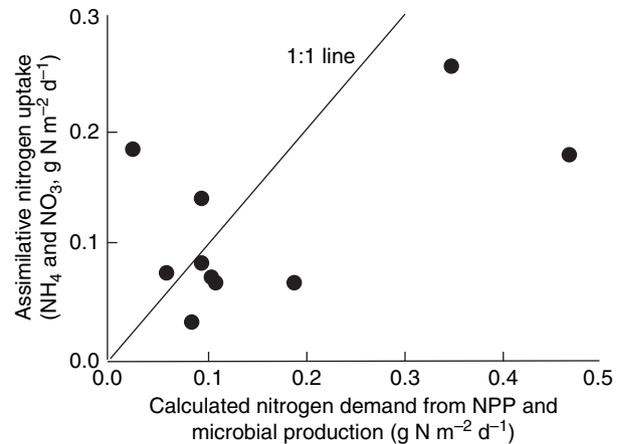


Figure 1 The relationship between measured assimilative nitrogen uptake and calculated nitrogen demand for biomass production. The line indicates where equal values would fall. Adapted from Webster JR, Mulholland PJ, Tank JL, *et al.* (2003) Factors affecting ammonium uptake in streams: An interbiome perspective. *Freshwater Biology* 48: 1329–1352.

autotrophic production. However, heterotrophic microbial production is also an important avenue through which nutrients must flow in most, if not all, ecosystems. For example, in headwater streams heterotrophic production often exceeds photoautotrophy. As a result, nutrient assimilation through microbial heterotrophs has received considerable attention. Lotic ecosystem ecologists have a rich history of measuring ecosystem-scale metabolic rates (respiration and gross primary productivity) and nutrient uptake. Recently, stoichiometric relationships have been combined with metabolic measurements to predict nutrient demand. In the Lotic Intersite Nitrogen experiment (LINX), algal and bacterial C:N ratios and carbon use efficiencies (though not expressed as such) were combined with estimates of heterotrophic respiration and gross primary production to predict nitrogen uptake in several stream ecosystems. Using whole-stream ^{15}N - NH_4 experiments and an oxygen mass balance approach for measuring ecosystem metabolism, these researchers found that predicted and measured rates of N uptake were similar and straddled the 1:1 line, though considerable variation existed (Figure 1). Given the number of assumptions in this analysis, the observed variance was not surprising and they concluded that continued application and improvement of this approach holds promise for illuminating links between carbon and nutrients as they move from inorganic to biotic pools.

Primary Producers and Consumers

Material flow in ecosystems incorporates more than the fluxes between inorganic nutrient pools and organisms capable of accessing these pools. In addition, material fluxes

between organisms, like those discussed in previous entries, coalesce with important ecosystem-scale consequences. One stoichiometric characteristic that is consistently important across scales of biological organization is the contrast between first-order consumers (i.e., organisms that obtain all or part of their energy requirements from consuming primary producer biomass or detritus) and the primary producers they feed upon. As discussed in prior sections, primary producers tend to have higher carbon content and lower N and P content than their consumers. The extent of elemental differences between primary producers and first-order consumers depends on the ecosystem considered. In freshwater and marine pelagic systems where primary production is dominated by algae and cyanobacteria, differences between producers and first-order consumers in body nitrogen and phosphorus concentrations are smaller than the differences observed in benthic and terrestrial ecosystems dominated by vascular plants.

Despite this heterogeneity, the trend for higher body nitrogen and phosphorus concentrations in first-order consumers relative to their diet is consistent across ecosystems. In this article, we are less interested in the causes for these differences (e.g., differences in nutrient homeostasis) than in their implications. The first implication is that the potential exists for first-order consumers to be nutrient rather than carbon (C) limited if food C:nutrient ratios provide carbon in excess of the consumer's energy requirements. In this situation, we expect an increase in the N or P concentrations in the producer tissue to cause higher growth rates in the consumer. This hypothesis has been validated with many experimental manipulations including microbial, invertebrate, and vertebrate first-order consumers. The second implication is that nutrient limitation of first-order consumer growth should be greater in terrestrial than in aquatic ecosystems, since C:nutrient imbalances are greatest where vascular plants dominate primary production.

Given these two implications, what kind of patterns of matter flow in ecosystems can we expect? One expectation is that as we move from ecosystems composed of primary producers with poorer nutrient quality (lower body nitrogen and phosphorus concentrations) to those with greater N and P content, we should observe higher rates of herbivory (i.e., intake of producer biomass by herbivores) and first-order detritivory (i.e., intake of producer detritus by detritivores) and resulting decomposition (Figure 2). That should be the case whether we compare aquatic ecosystems only, terrestrial ecosystems only, or we include both types of ecosystems in the comparison. In addition, because aquatic first-order consumers should have faster growth rates than their terrestrial counterparts, we should also observe higher rates of herbivory and first-order detritivory in aquatic than in terrestrial ecosystems. The hypothesized higher herbivory and first-order detritivory rates in ecosystems

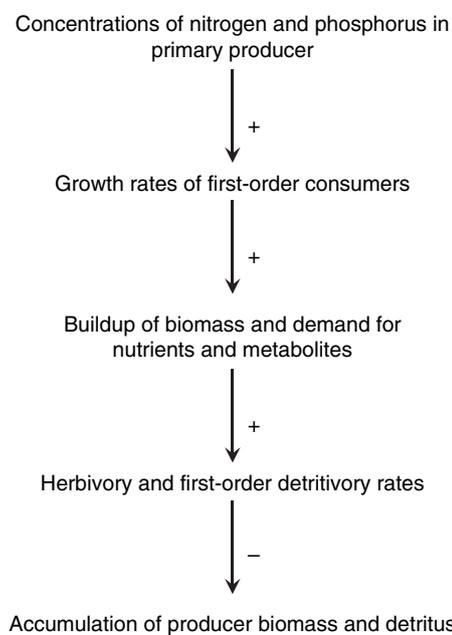


Figure 2 Dependence of growth rates of first-order consumers on nitrogen and phosphorus concentrations in the diet and expected patterns of herbivory, first-order detritivory, and accumulation of producer biomass and detritus across ecosystems.

composed of richer primary producers suggests another important trend; because losses of producer biomass and detritus would be larger for richer producers than for poorer producers due to promoted herbivory and decomposition, we could also expect smaller pools of producer biomass and detritus in ecosystems composed of richer producers.

Herbivory

Humans have known for sometime that herbivores prefer more nutritional plants and that soil fertilization, by increasing plant nutritional value, usually leads to increased foraging by herbivores. However, only recently has it been demonstrated that a strong empirical association between herbivory rates, expressed as the percentage of gross primary production consumed by herbivores, and food N and P concentrations spans a broad range of ecosystem types (Figure 3). This association holds whether only aquatic ecosystems are compared, only terrestrial ecosystems are compared, or both types of ecosystems are included in the comparison. In general, aquatic ecosystems have a larger percentage of gross primary production consumed by herbivores than do terrestrial ecosystems (Table 1), supporting the expected stoichiometrically derived pattern of higher herbivory rates in ecosystems composed of richer producers (algae vs. vascular plants). The strength of the relationship is surprising in view of the many other factors that can also affect herbivory, such as

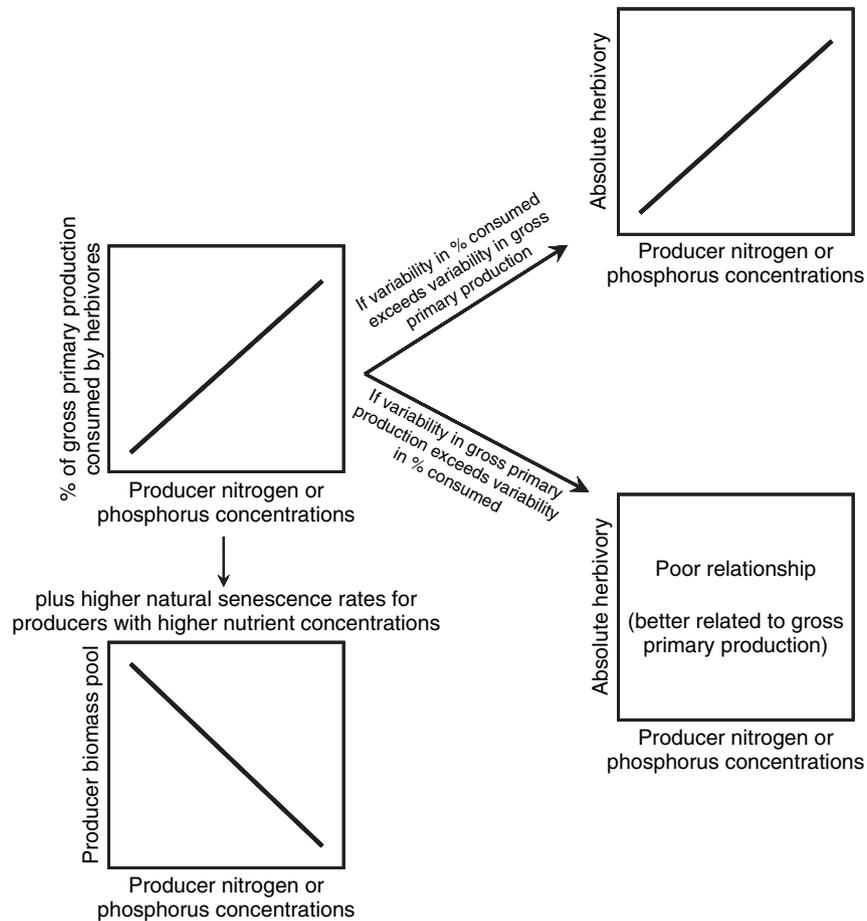


Figure 3 Patterns of herbivory, and implications on the size of the producer biomass pool, observed across a broad range of ecosystems.

Table 1 Overall differences in producer nutrient concentrations and matter flow and storage between aquatic and terrestrial ecosystems. Differences are expressed in relative terms

	<i>Aquatic ecosystems</i>	<i>Terrestrial ecosystems</i>
Nitrogen and phosphorus concentrations in producer biomass/detritus	High	Low
Herbivory rates (% of gross primary production consumed)	High	Low
Pool of producer biomass	Low	High
First-order detritivory rates (% of producer detritus mass lost per day)	High	Low
Pool of producer detritus	Low	High

herbivore type and size, feeding specificity, migratory behavior, and intensity of predation on herbivores.

The relationship described above suggests important consequences for trophic functioning and elemental cycling. By removing a larger percentage of gross primary production, aquatic herbivores should exert greater control of producer biomass than their terrestrial counterparts. On this basis, it can also be expected that ecosystems with highly nutritional producers will tend to have relatively small pools of producer biomass compared to ecosystems with similar values of gross primary production but of poorer nutritional quality. Finally,

herbivores in nutritionally rich ecosystems have a greater impact on elemental recycling in ecosystems with richer producers since a larger fraction of producer biomass passes through herbivores before being recycled back into inorganic nutrient pools.

In contrast, when herbivory is expressed as an absolute flux (i.e., quantity of producer biomass consumed per unit area per unit time), consumption rates do not increase with primary producer N and P content when examined over a broad range of ecosystems (Figure 3). In part, this relationship results from the poor relationship between gross primary production and N and P concentrations

when analyzed over a broad range of ecosystems. This may seem counterintuitive until one considers the suite of environmental factors known to influence gross primary production (e.g., temperature, humidity, and soil redox conditions among others). Differences in the relationship between relative (percentage) and absolute herbivory rates and ambient food quality are also an artifact of broad variation in primary production rates. Primary production rates can vary by several orders of magnitude. Therefore, even modest relative consumption rates (percentage of production consumed) like those expected under low-nutrient content can result in large absolute values of herbivory. That is, the relationship between primary production and absolute herbivory rates trumps the relationship between food N and P content and relative herbivory rates. Interestingly, relative herbivore production (i.e., ratio of herbivore biomass produced per unit of producer biomass ingested) does not appear to vary systematically among ecosystems.

First-Order Detritivory

First-order detritivory is the consumption of primary producer detritus. First-order detritivores include microbial decomposers (i.e., bacteria and fungi) and detritivorous invertebrate (and very rarely vertebrate) organisms that feed upon primary producer detritus and attached microbial decomposers. The ingestion of producer detritus by

microbial decomposers and invertebrates is difficult to measure and thus, direct values of first-order detritivory are rare in the literature. Alternatively, first-order detritivory is often estimated as the temporal rate of loss of producer detritus mass incubated in containers or mesh bags (i.e., ‘detritus incubation’ method), which can be measured much more easily. This method has received criticisms, mainly because some of the producer detritus mass lost in mesh bags is not consumed by the first-order detritivores enclosed in the bags but instead is flushed out of the bags. However, rates derived in this manner are suspected to hold for comparisons across ecosystems because natural variation in first-order detritivory is expected to exceed the methodological error.

For many decades it has been clear to researchers that richer producer detritus (i.e., producer detritus with higher concentrations of nitrogen and phosphorus) decays faster than poorer detritus, which indicates that richer producer detritus is subject to higher rates of consumption by detritivores. Nevertheless, comparisons between producer detritus decay rates and nitrogen and phosphorus concentrations in the detritus encompassing a broad range of ecosystems have not been done until recently. The comparisons have shown that faster decay rates, expressed as the percentage of detritus mass lost per day, are associated with higher nitrogen and phosphorus concentrations in the detritus, albeit not strongly, across ecosystems (**Figure 4**). The unexplained variance in this

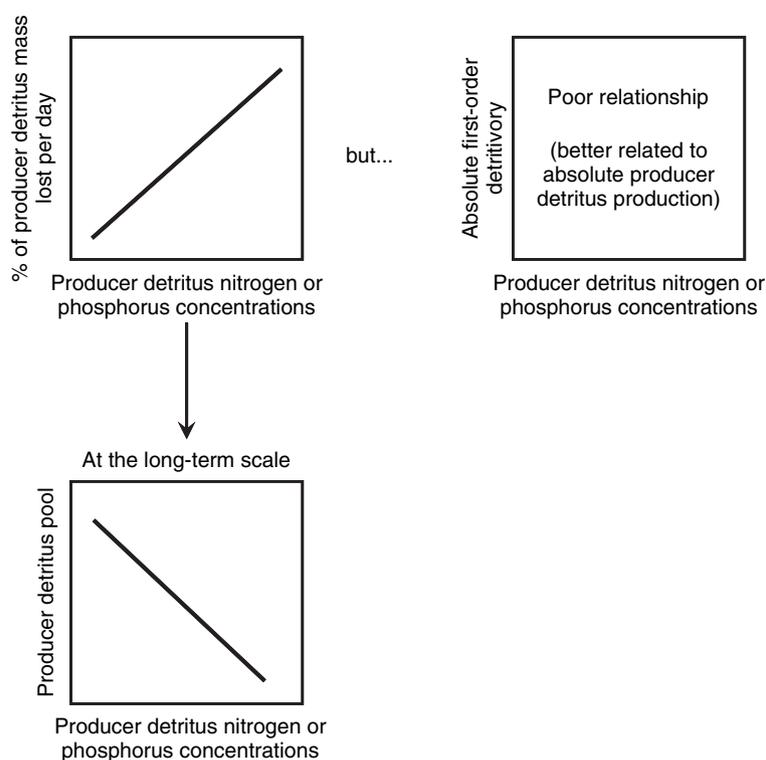


Figure 4 Patterns of first-order detritivory and implications on the size of the producer detrital pool, observed across a broad range of ecosystems.

relationship is not surprising given the many environmental factors that can affect detritus decay rates, such as temperature, humidity, redox conditions, type and size of the detritivore population, and predation intensity on the detritivore population. These broad comparisons demonstrate that detritus in aquatic ecosystems tends to have a higher percentage of mass lost per day than do detrital pools in terrestrial ecosystems (Table 1).

As with herbivory, when rates of producer detritus decay are expressed in absolute terms (i.e., quantity of producer detritus mass lost per square meter per year), decay rates and nitrogen and phosphorus concentrations in the detritus are often unrelated across a broad range of ecosystems (Figure 4). The reasons are twofold: first, absolute producer detritus production (i.e., quantity of producer detritus generated per square meter per year) is unrelated to the nitrogen and phosphorus concentrations in the detritus across a broad range of ecosystems; second, absolute producer detritus production varies more broadly than does the percentage consumed by detritivores. Thus, absolute rates of producer detritus decay, which result from the product between absolute producer detritus production and the percentage consumed by detritivores, will often be more closely associated with absolute producer detritus production than with the percentage consumed when a broad range of ecosystems are compared and, by extension, will often be unrelated to the nitrogen and phosphorus concentrations in the producer detritus. This logic is identical to that presented above for herbivory since it is the lack of a relationship between nutrient content and primary production driving the differences between relative and absolute consumption rates (as herbivory or detritivory).

Pools of Producer Biomass and Detritus

The tendency toward larger percentages of gross primary production consumed by herbivores with higher producer nitrogen and phosphorus concentrations suggests that, all else being equal, ecosystems composed of nutrient-rich primary producers will have lower producer biomass and accumulate primary detritus (derived from primary producer tissue) more slowly than systems dominated by nutrient-poor producers. This expectation will hold if gross primary production varies to a lesser extent than does the percentage consumed by herbivores across the ecosystems compared. If, in contrast, gross primary production varies to a greater extent than does the percentage consumed by herbivores across the ecosystems compared, then the quantity of matter available for storage as producer biomass will be more closely associated with rates of gross primary production than with the percentage consumed by herbivores. Unfortunately, too few comparisons across ecosystems have been done to conclude with rigor whether these expectations hold. However, one

recent comparison including a broad range of aquatic and terrestrial ecosystems demonstrated that ecosystems with nutrient-rich producers tended to have smaller pools of producer biomass (Figure 3). Interestingly, in the ecosystems compared in this study gross primary production varied more broadly than did the percentage of production consumed by herbivores. This observation is a direct contradiction to the arguments presented above which predict that biomass pools should track primary production rates rather than patterns in producer nutrient content.

Evolutionary constraints may provide an answer to this apparent contradiction. Primary producers with higher nitrogen and phosphorus content tend to grow faster, have shorter life spans, and higher natural mortality rates (i.e., senescence) than their low-nutrient counterparts. Thus, when a broad range of ecosystems are compared, nutrient-rich producers have both larger proportions of their biomass consumed by herbivores and higher natural mortality rates (Figure 3). Both mechanisms lead to smaller pools of producer biomass under high-nutrient conditions across a broad range of aquatic and terrestrial ecosystems despite large differences in gross primary production. Indeed, recent modeling advances have confirmed this prediction.

The moderate tendency toward higher percentages of producer detritus mass lost per day with higher nitrogen and phosphorus concentrations in the detritus observed when a broad range of ecosystems are compared suggests that, if the differences in absolute producer detritus production do not exceed the differences in the percentage consumed by detritivores, ecosystems with richer producer detritus should also tend, at least moderately, to have smaller pools of producer detritus. The rationale is analogous to the case of producer biomass pools discussed above. The observation that aquatic ecosystems, which tend to have richer primary detritus and higher percentages of producer detritus production consumed by detritivores, generally have smaller pools of producer detritus when compared to terrestrial ecosystems is consistent with this hypothesis (Table 1).

Large-Scale Implications of Ecological Stoichiometry

In this and other entries, ecological stoichiometry has been presented as a theoretical and empirical approach for linking organism biochemical properties to larger-scale ecological patterns and processes. A logical framework for ecological stoichiometry (though the term was not used) was initially formalized by W. A. Reiners in the mid-1980s. Up to that time, ecosystem science had been largely organized around energetics. Reiners offered his framework as a complementary view of ecosystems in which the flow of matter, rather than energy, was the organizing feature.

Using a limited number of logical steps, Reiners combined biochemical and ecological axioms (true statements) to derive a series of theorems that describe how biological processes control biogeochemical cycling from local to global scales (Figure 5). One of Reiners' principal axioms

(axiom 2) was that protoplasmic life is consistent across organisms. We now know that this axiom is not strictly true and that cellular stoichiometry can vary, with important ecological implications. Interestingly, this shortcoming has not diminished the utility of this logical sequence because

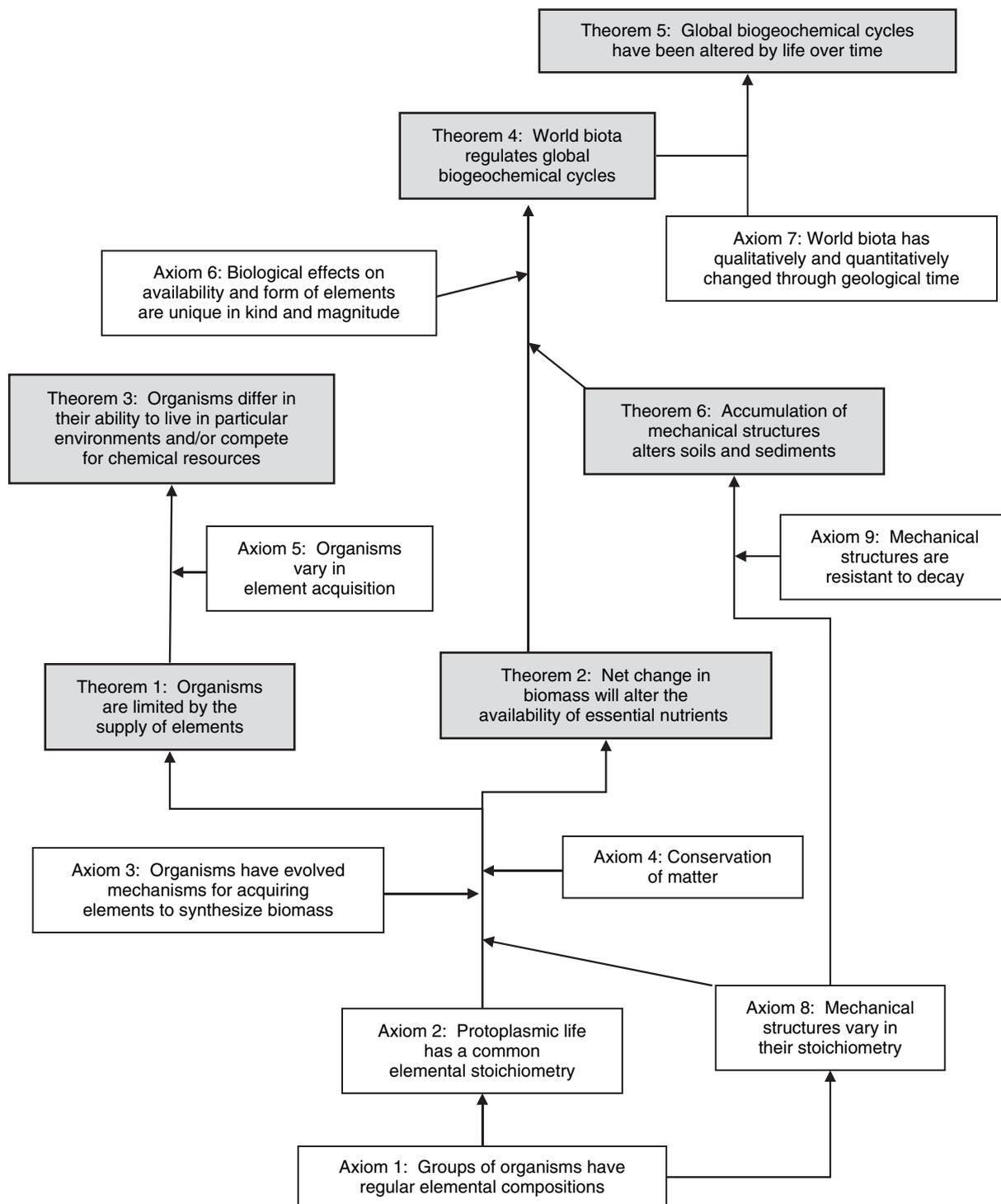


Figure 5 A logic flowchart of stoichiometric theory illustrating how a small number of axioms from biochemistry (clear boxes) lead to theorems describing global biogeochemical cycles (shaded boxes). Adapted from Reiners WA (1986) Complementary models for ecosystems. *American Naturalist* 127: 59–73.

it still remains useful for understanding how stoichiometric variation at basal levels of biological organization can cascade to have ecosystem and even global scale implications.

Prior to Reiners' theoretical work, A. C. Redfield found a surprising congruence in C:N:P ratios in plankton from widespread regions of the world's oceans. In this seminal work, Redfield determined that ocean seston had a consistent C:N:P stoichiometry equal to 106:16:1. The 'Redfield ratio', as it has become known, is perhaps the most famous result in ecological stoichiometry and many have come to revere it as a rare ecological constant, analogous to better-known constants in chemistry and physics. Perhaps more surprising, and more interesting in the context of this entry, seston C:N:P mirrors the ratio of these elements in dissolved pools. Redfield interpreted the equivalence between N:P ratios in seston and dissolved pools as evidence that N and P had balanced flow into and out of biotic pools. Furthermore, regressions of ocean N and P concentrations pass through the origin, indicating that these elements are depleted from ocean water simultaneously. Given the myriad of geological and meteorological factors that could influence nutrient availability in the world's ocean, there is no *a priori* expectation for this equivalence. Redfield's explanation for this finding was that the biota controlled the relative availability of these elements in the ocean. He went on to suggest that P, rather than N availability limited ocean production because biological processes (e.g., N-fixation) are capable of adjusting N availability to match P constraints. Contemporary support for Redfield's contention is found in recently published models of N-fixation in the open ocean. In addition, extensive datasets on N-fixation in lakes clearly indicates that overall N:P ratio constrains when and where N-fixation is active (restricted to conditions where molar N:P < 20). Interestingly, similar mechanisms have been invoked to explain the development of P-limitation in terrestrial soils as they age (as discussed earlier in this article). Redfield's findings have proved important beyond the realm of oceanography because they suggest that biotic processes control element cycles at global scales, a world view that Reiners and others would further develop.

Global scale coupling of C, N, and P cycles involve a highly complex set of interactions between Earth's subsystems (biosphere, atmosphere, and geosphere). Feedbacks among these systems operate over a suite of spatial and temporal scales and include interactions between terrestrial, freshwater, and ocean ecosystems that remain poorly understood. However, this complexity has not hindered researchers from exploring the role of biological processes in structuring biogeochemical cycles and their evolution through geological time. Perhaps the best example of such work relates to maintenance of global atmospheric oxygen concentration. Oxygen has remained between 15% and 35% of the atmosphere for

the last several hundred million years. Under current biogeochemical conditions, atmospheric oxygen turns over every 4000 years. Combined, these observations suggest that a dynamic system of feedbacks may exist to stabilize oxygen content. Biotic activity is a principle driver of modern oxygen cycling. The production and breakdown of organic matter produces and consumes equal amounts of oxygen and as a result does not perturb the existing oxygen levels. However, biomass standing stock has not been constant through time. In addition, slow cycling of oxygen through nonbiotic processes such as carbonate precipitation, oxidation of uplifted iron, photolysis of water, and oxidation of ammonium also influence long-term patterns in oxygen concentration. Combined, it is not obvious why these processes should combine to create stability in the atmospheric pool. One mechanism for the maintenance of this stability is variation in the efficiency of P burial in the world's oceans. A thorough discussion of this mechanism is beyond the scope of this text. Suffice it to say that the crucial feature of this mechanism is the positive relationship between oxygen content and the efficiency of P burial via precipitation with iron hydroxides. Efficient P burial ultimately leads to reduced delivery to the photic zone, reduced autotrophic activity, and consequent oxygen production. Other examples of biologically driven feedback mechanism have been identified by several authors. Feedbacks, and their role in autoregulation of Earth system properties, require constraints and ecological stoichiometry suggests that the elemental composition of core biomolecules and the processes that create them provide these constraints.

Given the pervasiveness of human activity and its impact on element abundances, efforts to understand the complexity associated with biological and physical controls on biogeochemical cycling are of paramount importance if society is to forecast ecological conditions and design strategies for responsible stewardship. Though a vigorous debate continues over the relative importance of biological and geological processes in controlling global scale elemental cycles, it is nevertheless critical to continue to explore the stoichiometric underpinnings of biological processes and their consequences for ecosystem and biosphere structure and function.

See also: Biogeochemical Models; Denitrification; Detritus; Ecological Efficiency; Ecological Stoichiometry: Overview; Ecosystems; Evolution of Oceans; Evolutionary and Biochemical Aspects; Excretion; Freshwater Lakes; Grazing Models; Grazing; Growth Constraints: Michaelis–Menten Equation and Liebig's Law; Homeostasis; Lake Models; Microbial Models; Organismal Ecophysiology; Population and Community Interactions; Temperate Forest; Trace Elements.

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Ecosystem Services

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Introduction

Defining Ecosystem Services

Examples of Ecosystem Services

Capturing the Value of Ecosystem Services

Conclusions

Further Reading

Introduction

The world's ecosystems yield a flow of essential services that sustain and fulfill human life, from seafood and timber production to soil renewal and personal inspiration. Although many societies have developed the technological capacity to engineer replacements for some services, such as water purification and flood control, no society can fully replace the range and scale of benefits that ecosystems supply. Thus, ecosystems are capital assets, worthy of at least the level of attention and investment given to other forms of capital. Yet, relative to physical, financial, human, and social capital, ecosystem capital is poorly understood, scarcely monitored, and, in many cases, undergoing rapid degradation and depletion.

Recognition of ecosystem services dates back at least to Plato. This recognition of human dependence on ecosystems, in the past and today, is often triggered by their disruption and loss. Direct enjoyment of services, such as the extraction of timber, fish, and freshwater, can reduce the quantity and quality produced. The provision of ecosystem services can also be affected indirectly and inadvertently. Deforestation, for instance, has exposed the critical role of forests in the hydrological cycle – mitigating flooding and reducing erosion. Release of toxic substances has uncovered the nature and value of physical and chemical processes, governed in part by microorganisms that disperse and break down hazardous materials. Thinning of the stratospheric ozone layer has

sharpened awareness of the value of its service in screening out harmful ultraviolet radiation.

Defining Ecosystem Services

Simply put, ecosystem services are the conditions and processes through which ecosystems, and the biodiversity that makes them up, sustain and fulfill human life. Ecosystem services are tightly interrelated, making their classification somewhat arbitrary. The Millennium Ecosystem Assessment (MA) – the formal international effort to elevate awareness and understanding of societal dependence on ecosystems – has suggested four categories.

First, 'provisioning services' provide goods such as food, freshwater, timber, and fiber for direct human use; these are a familiar part of the economy. Second, and much less widely appreciated, 'regulating services' maintain a world in which it is biophysically possible for people to live, providing such benefits as water purification, pollination of crops, flood control, and climate stabilization. Third, 'cultural services' make the world a place in which people want to live; they include recreation as well as esthetic, intellectual, and spiritual inspiration. Fourth, 'supporting services' create the backdrop for the conditions and processes on which society depends more directly. All of these services are provided by complex chemical, physical, and biological cycles, powered by the sun, and operate at scales ranging from