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Ecological Stoichiometry

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Introduction

Ecological stoichiometry (ES) is the study of the balance of energy and multiple chemical elements in ecological interactions. Although much of the foundation of this field lies in studies of lakes (and especially of lake plankton), the application of ES has greatly expanded in 21st century, with extensions to streams, soils, grasslands, forests, and other ecosystems. This article provides a guide to recent introductory articles and reviews of the ES approach, to some of the foundational papers that preceded the formal definition of ES, and to a cross-section of papers dealing with biochemical, evolutionary, and ecological (especially biogeochemical) applications of ES. The field remains highly dynamic: a topic search on “ecolog stoichiometry” in ISI Web of Science yields more than 6,100 citations per year (in 2013; compared to less than five hundred in 1993). Thus, this annotated bibliography can only touch on the tip of this growing iceberg.

Introductory Works and Syntheses

The common framework provided by the study of multiple chemical elements pointed the way toward integration of diverse fields within ecology (physiological ecology, community ecology, biogeochemistry) and of ecology with other realms of biology, such as evolutionary biology. The possibility of direct elemental (P) limitation of consumer growth due to its “dilution” in the C-rich biomass that is generated when photoautotrophs (algae, plants) are nutrient-limited was inferred by workers studying freshwater zooplankton and reported in early papers such as Urabe and Watanabe 1992 and Sterner and Hessen 1994. The impacts of such stoichiometric imbalance on nutrient recycling were analyzed mathematically and compared to existing data (Sterner 1990). Soon thereafter, researchers began to hypothesize about the biochemical and evolutionary drivers that are responsible for the C:N:P ratios that characterize biomass of both consumers and producers, suggesting an important role of growth rate–related allocation to P-rich ribosomal RNA in the “growth rate hypothesis” that is developed in Elser, et al. 1996. Sterner and Elser 2002 is a foundational work that brought together a large number of disparate research threads in ecology and stimulated considerable new research, including an expansion of stoichiometric thinking into new realms (“biological stoichiometry”), such as biochemical allocation, life history evolution, and even cancer dynamics.

Elser, J. J., D. R. Dobberfuhl, N. A. MacKay, and J. H. Schampel. 1996. Organism size, life history, and N:P stoichiometry: Toward a unified view of cellular and ecosystem processes. *BioScience* 46:674–684.

This synthetic paper extends stoichiometric thinking downwards toward cellular and biochemical levels and sketches several hypotheses about observed variation in C:N:P ratios in biota, including the “Growth Rate Hypothesis” (GRH) connecting C:N:P ratios to growth rate and RNA allocation.

Sterner, R. W. 1990. The ratio of nitrogen to phosphorus resupplied by herbivores: Zooplankton and the algal competitive arena. *American Naturalist* 136:209–229.

Mathematical modeling of the mass balances of N and P into a strictly homeostatic consumer was used to predict a non-linear

relationship between the N:P of recycled nutrients and the N:P of ingested food as well as dependence on body N:P of the consumer.

Sterner, R. W., and D. O. Hessen. 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. *Annual Review of Ecology, Evolution and Systematics* 25:1–29.

An early synthesis of extant and emerging data highlighting the potential importance of stoichiometric imbalance between autotrophs and herbivores, integrating physiological to ecosystem level dimensions.

Sterner, R. W., and J. J. Elser. 2002. *Ecological stoichiometry: The biology of elements from molecules to the biosphere*. Princeton, NJ: Princeton Univ. Press.

This is considered the definitive textbook of the field. Written for graduate students and advanced undergraduates, the book develops and builds stoichiometric reasoning from cellular and biochemical levels through organismal physiology to trophic ecology and ecosystem nutrient cycling.

Urabe, J., and Y. Watanabe. 1992. Possibility of N or P limitation for planktonic cladocerans: An experimental test. *Limnology and Oceanography* 37:244–251.

This important paper introduces the concept of “Threshold Elemental Ratio” (TER) that delineates the breakpoint between C-limited and nutrient-limited growth for a consumer and provides estimates of TER for C:N and C:P for two species of freshwater zooplankton.

Review Papers

The rapid growth of the ES literature since the 1990s when seminal papers were published has stimulated the production of a variety of review papers and meta-analyses that bring together diverse empirical findings and theoretical advances testing and extending stoichiometric principles. These reviews include a consideration of the extension of ES to studies of stream and lake benthos in Cross, et al. 2005 and to terrestrial ecosystems in a comparative context in Sardans, et al. 2012. Hall 2009 not only reviews a broad range of studies in relation to core ES concepts but also includes an ambitious attempt to further generalize the approach into what he calls a “resource ratio theory for consumers,” explicitly extending the autotroph-based theory developed in Tilman, et al. 1982 (cited under Historical Perspectives) to higher trophic levels. The most recent review of ES developments in the aquatic realm is provided in Hessen, et al. 2013) and includes a meta-analysis of experimental tests of the Growth Rate Hypothesis.

Cross, W., J. Benstead, P. Frost, and S. Thomas. 2005. Ecological stoichiometry in freshwater benthic systems: Recent progress and perspectives. *Freshwater Biology* 50:1895–1912.

This review assembles published information about ecological stoichiometry in primary producers and primary consumers in both lake and stream benthos and develops various lines of reasoning about how ES differs in benthic vs. pelagic ecosystems.

Hall, S. R. 2009. Stoichiometrically explicit food webs: Feedbacks between resource supply, elemental constraints, and species diversity. *Annual Review of Ecology, Evolution, and Systematics* 40:503–528.

This comprehensive synthesis extends stoichiometric thinking via systematic development of a stoichiometric niche concept for consumers. Hall shows how applying this concept helps explain species coexistence among consumers and stabilizes intraguild predation. Finally, some key questions are answered concerning how the utility of stoichiometric theory can be extended and about its ultimate limitations.

Hessen, D. O., J. J. Elser, R. W. Sterner, and J. Urabe. 2013. Ecological stoichiometry: An elementary approach using basic principles. *Limnology and Oceanography* 58:2219–2236.

Four of the early developers of ecological stoichiometry approaches in freshwater plankton review a decade of ES work in aquatic ecosystems. In addition to the meta-analysis of studies related to the Growth Rate Hypothesis, the article surveys studies of stoichiometric homeostasis in autotrophs and consumers and summarizes work-testing mechanisms of stoichiometric homeostasis.

Sardans, J., A. Rivas-Ubach, and J. Penuelas. 2012. The elemental stoichiometry of aquatic and terrestrial ecosystems and its relationships with organismic lifestyle and ecosystem structure and function: A review and perspectives. *Biogeochemistry* 111:1–39.

This is an extremely wide-ranging review of existing data on C:N:P ratios in biomass in diverse habitats (marine, freshwater, and terrestrial) that also points to some useful future research avenues, including assessment of other trophic levels than just autotrophs and herbivores, studies of key elements beyond C, N, and P (e.g., K), and application of new techniques, such as metabolomics.

Historical Perspectives

While ecological stoichiometry developed rapidly beginning in the 1990s due to empirical and theoretical developments in freshwater plankton ecology, its intellectual roots are considerably deeper. Perhaps its tap root extends to Liebig's Law of the Minimum (Playfair 2016), which laid out principles for elemental limitation of plant production in the 19th century. Although this work is best known for its argument for single nutrient limitation (“the minimum”) of production, the work also contains a surprising integration of information about the elemental composition of soil, plant, and animal biomass and consideration of the role of animals and microbes in nutrient cycling. Another seminal work in ES with greater breadth than generally appreciated is Lotka 1925, in which Lotka establishes not only the basis of his eponymous (with V. Volterra) population dynamics equations but also a broad vision of the constraints imposed and feedbacks generated by the elemental composition of life. However, it would be nearly seventy years until the Lotka-Volterra equations were later put into a strictly stoichiometric framework as seen in Andersen 1993 and more recently in Loladze, et al. 2000. However, the foundational study that attracted the attention of generations of oceanographers (and beyond) to the fundamental importance of the stoichiometry of organisms is Redfield 1958. The stoichiometric framework itself built also on early progress in connecting growth to the cellular content of limiting nutrient element in what became known as the “Droop equation” and laid out in Droop 1974. This approach was later formalized into what became known as “resource ratio” competition theory (Tilman, et al. 1982) in a major advance in understanding and predicting patterns of coexistence and species dominance among algae and plants as a function of the supplies of multiple limiting nutrients. Another visionary and underappreciated work is Reiners 1986, which puts forth a wide-ranging set of constraints and causative pathways connecting geochemistry, biotic elemental demands, and global biosphere functioning.

Andersen, T. 1993. Grazers as sources and sinks for nutrients. PhD diss., Biologisk Institutt, Oslo.

This visionary book (Andersen's PhD dissertation) lays out key frameworks for emerging stoichiometric theory in freshwaters, including a way forward for easily incorporating the effects of high C:P ratios on herbivore growth.

Droop, M. R. 1974. The nutrient status of algal cells in continuous culture. *Journal of the Marine Biological Association of the United Kingdom* 54:825–855.

Droop (rhymes with “soap”) integrates Michaelis-Menten uptake kinetics with chemostat theory to formulate and test the “Droop equation,” which postulates a hyperbolic relationship between growth rate and internal content (“quota”) of the limiting nutrient; this is a formulation that is central to most stoichiometric models.

Loladze, I., Y. Kuang, and J. J. Elser. 2000. Stoichiometry in producer-grazer systems: Linking energy flow with element cycling. *Bulletin of Mathematical Biology* 62:1137–1162.

Building on the work of Andersen 1993, this paper presents formal mathematical and dynamical analysis of a “stoichiometrically explicit” version of the Lotka-Volterra equations, highlighting rich dynamics, bistability, and phenomena such as the “paradox of energy enrichment.”

Lotka, Alfred J. 1925. *Principles of Physical Biology*. New York: Dover.

Lotka is best known for his contribution to formal theory of population biology, but in this book he delineates a broad vision for biological systems, including biogeochemical cycling and organismal stoichiometric composition in constraining dynamics and feedbacks.

Playfair, Lyon P., ed. 2016. *Organic chemistry in its applications to agriculture and physiology*. By Justus Liebig. Cambridge, UK: Cambridge Univ. Press.

“Borrowing” heavily from the work of Carl Sprengel, this wide-ranging treatise introduces the eponymous “Law of the Minimum” as well as vitalism-plagued chapters about manure, “eremacausis” (decomposition), and the elemental composition (stoichiometry) of plant tissues. Originally published in 1840.

Redfield, A. C. 1958. The biological control of chemical factors in the environment. *American Scientist* 46:205–211.

This truly seminal work integrates observations of elemental composition of plankton made more than two decades earlier by Redfield and colleagues. Features data on deep-water N:P ratios in dissolved pools to paint a visionary model for the biogeochemical functioning of the global oceans. Rarely has such a grand vision been achieved based on so limited a data foundation.

Reiners, W. A. 1986. Complementary models for ecosystems. *American Naturalist* 127:59–73.

Here Reiners presents elemental composition and material constraints as a complementary perspective on ecological and evolutionary dynamics, supplementing dominant bioenergetics considerations that permeate ecology. His novel epistemological approach involves an argument based on axioms and theorems to build a formal model of how stoichiometry shapes a broad range of patterns in biogeochemistry, community ecology, and macroevolution.

Tilman, D., S. S. Kilham, and P. Kilham. 1982. Phytoplankton community ecology: The role of limiting nutrients. *Annual Review of Ecology, Evolution and Systematics* 13:349–372.

This treatise lays out a general theory of multiple resource competition using information from phytoplankton ecology, building especially on the Monod function and the modification by Droop 1974. This “resource ratio” approach underpins much modern work on resource competition and “trait-based” approaches, not only for phytoplankton but also for terrestrial plants.

Biochemical, Cellular, and Evolutionary Determinants of Organismal Stoichiometry

Elser, et al. 1996 (cited under Introductory Works and Syntheses) distinguishes proximate (biochemical and physiological) and ultimate (evolutionary) causes of variation in the stoichiometry of organisms. Here we provide an overview of some important contributions in these areas.

Biochemical and Physiological Determinants

A deep analysis of the elemental connections among biochemical, physiological, and ecological dynamics can be seen in Dynamic Energy Budget theory (DEB) as described in Kooijman 2005. Droop 1974 and Reiners 1986 (see Historical Perspectives) categorized organismal internal elements into two pools, protoplasm (cells content), and structural material (e.g., plant cell walls and bones). But where Reiners assumed constant stoichiometry for the protoplasmic component common to all life forms, in contrast to structural materials (which he saw as variable among organisms) Droop saw both components as highly variable. Elser, et al. 1996 (cited under Introductory Works and Syntheses) traces differences in protoplasm stoichiometry back to pools of major biochemicals, mainly proteins and nucleic acids. Organisms can show divergent stoichiometries already at the protoplasmic level by varying their proportions of different biochemical and organelles, thus creating a link between their elemental composition and life-history traits that depend on organelle investments (Klausmeier, et al. 2004). Allen and Gillooly 2009 showed how this approach based on organelles facilitates efforts connecting ecological stoichiometry and metabolic ecology theories that both focus on the fluxes of elements and of energy through organisms. Agren 2008 applies this idea to plants, using a simple model that tracks only N-protein and P-ribosomal rates of production, as well as highlighting another source of variation in stoichiometry, the storage of elements in vacuoles, inclusions, or specialized cells. Frost, et al. 2008 highlights another, often-neglected source of stoichiometric variation: the impact and contributions of infectious pathogens. In comparison with cellular components, the role of structural material in stoichiometry has been understudied. A bold hypothesis in Moen, et al. 1999 captured some attention. Based on a stoichiometrically explicit metabolic budget, this paper advances the hypothesis that the cost of producing P-rich antlers by the Irish elk might have precipitated its extinction when climate change induced a shift of vegetation toward tundra. Studies of fish stoichiometry also highlight the importance of bones in affecting P demands in vertebrates, as shown in Hendrixson, et al. 2007 for freshwater fish. More studies are certainly needed to understand the stoichiometric influences of structural material in comparison with intracellular components.

Agren, G. I. 2008. Stoichiometry and nutrition of plant growth in natural communities. *Annual Review of Ecology, Evolution and Systematics* 39:153–170.

Probably the best place to start on the stoichiometry of both aquatic and terrestrial plants. It also tackles both limiting and non-limiting elements, N and P, but also less-studied elements such as K, Ca, and S. It also provides a simple physiological model of N and P plant content variation but misses an effort to link it explicitly with the more widely used Droop model.

Allen, A. P., and J. F. Gillooly. 2009. Towards an integration of ecological stoichiometry and the metabolic theory of ecology to better understand nutrient cycling. *Ecology Letters* 12:369–384.

The most advanced attempt thus far to connect the theories of ecological stoichiometry and metabolic ecology into one framework. Hence, this is also a good introduction to both approaches.

Frost, P. C., D. Ebert, and V. H. Smith. 2008. Bacterial infection changes the elemental composition of *Daphnia magna*. *Journal of Animal Ecology* 77:1265–1272.

A convincing demonstration of the effects of infectious agents on the stoichiometry of their hosts.

Hendrixson, H. A., R. W. Sterner, and A. D. Kay. 2007. Elemental stoichiometry of freshwater fishes in relation to phylogeny, allometry and ecology. *Journal of Fish Biology* 70:121–140.

A thorough examination of differences in C, N, and P body contents among fishes from the same region, carefully accounting for all possible factors explaining the observed differences in stoichiometry.

Klausmeier, C. A., E. Litchman, T. Daufresne, and S. A. Levin. 2004. Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. *Nature* 429:171–174.

Assuming a link between the elemental composition of organisms and their investment in various organelles, the authors come here with a predictive model of the optimal stoichiometry of phytoplankton species under various growth conditions. Although still in need of refinement, this elegant model is a cornerstone for future phytoplankton eco-evolutionary models.

Kooijman, S. A. L. M. 2005. *Dynamic energy and mass budgets in biological systems*. 2d ed. Cambridge, UK: Cambridge Univ. Press.

This deeply synthetic work formalizes a comprehensive approach to cellular growth and metabolism based on a concept of “synthesizing units” and “reserves,” linking levels of organization from molecules to ecosystems.

Moen, R. A., J. Pastor, and Y. Cohen. 1999. Antler growth and extinction of Irish elk. *Evolutionary Ecology Research* 1:235–249.

The hypothesis of Irish elk extinction caused by high P demands for their antlers raised some controversy when advanced by the authors; nevertheless, it offers a striking example of how a basic dietary elemental need could have dramatic evolutionary impacts.

Evolutionary Pressures Shaping Organismal Stoichiometry

Selection pressures arising from elemental limitation are likely to affect cell physiology in the direction of a reduced use of the limiting element in order to optimize the growth rate of the selected organism (Hessen, et al. 2010). This is the hypothesis underlying research in the evolutionary adaptation of the stoichiometry of organisms. Elser, et al. 2000 contains an early assessment of evolutionary pressures shaping the stoichiometry of organisms, documenting a link between P content, growth rate and variation in the length of the intergenic spacer region of the rDNA as well as in rDNA copy number. Baudouin-Cornu, et al. 2001 reports an analysis of selection on element allocation down to the level of protein composition, considering how selection might shape the use of amino acids that differ in C, N, and S contents in the proteomes of *E. coli* and *S. cerevisiae*. Bragg and Hyder 2004 extended this to prokaryotic genomes and proteomes, linking their N content to elemental limitation while Acquisti, et al. 2009 did the same work in the case of plant genome N content and N limitation. However, Gunther, et al. 2013 provides a serious warning against hasty conclusions and advocates for a careful consideration of potential spurious correlations. Hessen, et al. 2010 predicts that genome size is negatively related to P limitation. Taking this line of thinking into deep macroevolutionary time scales, Quigg, et al. 2003 links elemental composition of current taxa to major past macroevolutionary events and geological-time environmental conditions. Kay, et al. 2005 pulls many of these studies together in a good overview of the different potential ways evolution can affect the stoichiometry of organisms.

Acquisti, C., J. J. Elser, and S. Kumar. 2009. Ecological nitrogen limitation shapes the DNA composition of plant genomes. *Molecular Biology and Evolution* 26:953–956.

The N content of the genome and proteome of domesticated plants is shown to be larger than of undomesticated species. Although the difference in N content is convincing, its attribution to differences in N limitation between species is not demonstrated in the study.

Baudouin-Cornu, P., Y. Surdin-Kerjan, P. Marliere, and D. Thomas. 2001. Molecular evolution of protein atomic composition. *Science* 293:297–300.

Signatures of elemental limitation in the protein composition of *Escherichia coli* and *Saccharomyces cerevisiae* is shown. Sulfur- and carbon-assimilatory enzymes tend to be depleted in sulfur and carbon respectively. A result that seems generalizable, since it was later found also for other organisms and other elements.

Bragg, J. G., and C. L. Hyder. 2004. Nitrogen versus carbon use in prokaryotic genomes and proteomes. *Proceedings of*

the Royal Society B-Biological Sciences 271:S374–S377.

Bragg and Hyder discuss a body of evidence suggesting that N and C relative use is correlated between the genome and proteome of prokaryotic organisms, a correlation mediated by genomic GC content.

Elser, J. J., R. W. Sterner, and E. Gorokhova, et al. 2000. Biological stoichiometry from genes to ecosystems. *Ecology Letters* 3:540–550.

The first and best developed stoichiometric hypothesis that links features at the level of the genomic structure to the cycling of elements in ecosystems. The chain of causality is well developed, although the growth-rate hypothesis it articulates has since seen its generality questioned.

Gunther, T., C. Lampei, and K. J. Schmid. 2013. Mutational bias and gene conversion affect the intraspecific nitrogen stoichiometry of the *Arabidopsis thaliana* transcriptome. *Molecular Biology and Evolution* 30:561–568.

By looking at microevolution within one plant species, *Arabidopsis thaliana*, this study contradicts the hypothesis of a decrease in transcriptome N content caused by N limitation. It suggests instead that a mutational bias from GC to AT base pairs leads to a correlative decrease in genomic N content.

Hessen, D. O., P. D. Jeyasingh, M. Neiman, and L. J. Weider. 2010. Genome streamlining and the elemental costs of growth. *Trends in Ecology and Evolution* 25:75–80.

Another way to associate genome structure and elemental limitation. Under P limitation, a reduction in genome size allows for a reallocation of P from DNA to RNA. The latter can then be used to maintain growth rate under P limitation.

Kay, A. D., I. W. Ashton, E. Gorokhova, A. J. Kerkhoff, A. Liess, and E. Litchman. 2005. Toward a stoichiometric framework for evolutionary biology. *Oikos* 109:6–17.

A product of the first “Woodstoich” workshop in 2004, this is a thorough review of the various ways stoichiometry and evolution are linked. Although the paper predates some of the major findings in this field, it is interesting if only because it discusses most of those later findings as hypotheses.

Quigg, A., Z. V. Finkel, and A. J. Irwin, et al. 2003. The evolutionary inheritance of elemental stoichiometry in marine phytoplankton. *Nature* 425:291–294.

A methodical study of the important and diverse group of pelagic photoautotrophs. It suggests interesting links between differences in phylogeny, plastid origin, stoichiometric composition, and past geological conditions in the ocean.

Causes of Stoichiometric Imbalances at the Level of Ecosystems

Stoichiometric imbalances result from mismatches between the composition of organisms and their resources. However, ultimately the relative amounts of different elements available are controlled by processes at the level of the ecosystems (Schade, et al. 2005).

Schade, J. D., J. F. Espeleta, C. A. Klausmeier, M. E. McGroddy, S. A. Thomas, and L. X. Zhang. 2005. A conceptual framework for ecosystem stoichiometry: Balancing resource supply and demand. *Oikos* 109:40–51.

Another product of the 2004 “Woodstoich” workshop, this paper presents a coherent framework that tracks the effects of

imbalances in resource supplies within and between ecosystems, using a resource-ratio based graphical approach as a unifying tool. It is also the first conceptualization of stoichiometry at the landscape level.

Unbalanced Supplies of Resources

Historically, phosphorus loading has been the first and most studied cause of imbalance in aquatic systems because of its wide-ranging effects on impacted ecosystems. The main contribution of stoichiometric approaches to the issue was to point to a link between total N:P ratios in water and dominance by cyanobacteria (Smith 1983). Later studies paint a more complex picture of the factors controlling cyanobacteria blooms but with stoichiometry still playing a central role (Schindler 2006). As mitigation measures progressively reduced point-source phosphorus loading in some situations, attention shifted toward another major anthropogenic alteration of resource supplies: nitrogen deposition. Increased atmospheric nitrogen deposition not only brings a shift in phytoplankton limitation toward P but can also affect higher trophic levels through stoichiometric imbalances as seen in Lepori and Keck 2012. The case of carbon, another essential element, is more complicated since its supply in ecosystems is intimately linked to the activity of autotrophs and to light availability. Urabe and Sterner 1996 follows the consequences of an imbalance in the light to nutrient supply from the alteration of C-to-nutrient ratios of autotrophs to growth limitation of herbivores. Theoretical explorations allude to effects of light:nutrient imbalances that are more profound than expected and affect the dynamics, stability, and persistence of autotroph-herbivore interactions, although experimental studies suggest that other factors (species diversity, microbes, perturbations, etc.) can complicate the picture, as reported in Jager, et al. 2008. Increases in CO₂ concentrations can potentially show similar effects to those of increased irradiance, as Bezemer and Jones 1998 shows in the case of terrestrial plant-herbivore interactions. Effects of CO₂ enrichment are especially interesting in the context of the current global change. Peñuelas, et al. 2012 looks at a wide panoply of impacts due to the stoichiometric consequences of various global change perturbations. Finally, Loladze 2014 reminds us that humans are mainly plant consumers and thus likely to suffer negative consequences from increases in plant carbon content and elevated C:element ratios.

Bezemer, T. M., and T. H. Jones. 1998. Plant-insect herbivore interactions in elevated atmospheric CO₂: Quantitative analyses and guild effects. *Oikos* 82:212–222.

A meta-analysis approach showing consistent effects of increases in atmospheric CO₂ concentrations on plant chemistry and herbivore growth.

Jager, C. G., S. Diehl, C. Matauschek, C. A. Klausmeier, and H. Stibor. 2008. Transient dynamics of pelagic producer grazer systems in a gradient of nutrients and mixing depths. *Ecology* 89:1272–1286.

A thorough coupled theoretical-experimental investigation of the light-nutrient hypothesis, in the context of different lake depths. The study is laudable as one of the few models in ecological stoichiometry that consider transient dynamics, an approach much more relevant to field experimental studies.

Lepori, F., and F. Keck. 2012. Effects of atmospheric nitrogen deposition on remote freshwater Ecosystems. *Ambio* 41:235–246.

One of the recent reviews on the topic of atmospheric nitrogen deposition, with an emphasis on remote ecosystems. Those are the most likely to feel the effects of atmospheric deposition, since they are isolated from other types of nitrogen enrichment.

Loladze, I. 2014. Hidden shift of the ionome of plants exposed to elevated CO₂ depletes minerals at the base of human nutrition. *eLife* 3.

An exciting application of the stoichiometric approach to an issue that is paramount to humankind's future, the nutritional quality of plant food under the threat of increased atmospheric CO₂.

Peñuelas, J., J. Sardans, A. Rivas-Ubach, and I. A. Janssens. 2012. The human-induced imbalance between C, N and P in Earth's life system. *Global Change Biology* 18:3–6.

This synthetic article considers the physiological basis on which the C:N:P stoichiometry of plant production is impacted by various global change processes, such as pCO₂, rising temperature, drought, N deposition, and species invasion.

Schindler, D. W. 2006. Recent advances in the understanding and management of eutrophication. *Limnology and Oceanography* 51:356–363.

A thorough review of the field of eutrophication in limnology, this article contains a critique of the appealing but incomplete hypothesis of an unequivocal link between N:P ratios in lakes and algal blooms. It paints a more complex picture where organisms, food web structure, and climate are also important players.

Smith, V. H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. *Science* 221:669–671.

This high-impact article was the first to propose the hypothesis of a link between cyanobacterial dominance and low TN:TP ratios in lakes on a solid worldwide set of data. This seminal paper won the 2014 John Martin Award of the Association for the Sciences of Limnology and Oceanography.

Urabe, J., and R. W. Sterner. 1996. Regulation of herbivore growth by the balance of light and nutrients. *Proceedings of the National Academy of Sciences of the United States of America* 93:8465–8469.

An early formulation and test of the light:nutrient hypothesis. The hypothesis is based on the observation that the balance of light intensity and nutrient supplies establishes the severity of nutrient limitation and thus leads to more carbon-rich, nutrient-poor primary producers. Consequences for consumers then follow this increase in carbon content at the base of the food web.

Other Abiotic Factors

Ubiquitous factors, such as temperature, affect biotic and abiotic rates, inorganic pools, and organisms alike, thus altering stoichiometric patterns even among similar ecosystems. The pattern of increased leaf N and P contents with latitude found in Lovelock, et al. 2007 is a more general pattern, valid for most terrestrial plants according to Reich and Oleksyn 2004. They advance a general mechanism, greater investment in fast growth rate and rRNA as an adaptation to shorter growing season. But in the case of plants, the pattern of increased P and N can also result from the confounding effect of changes in the underlying geology of soils with latitude (Lovelock, et al. 2007). Woods, et al. 2003 presents a meta-analysis of physiological studies in poikilothermic organisms when they are tested directly for a temperature effect on body nutrient contents, finding broad support that biomass is more nutrient (N, P) rich when organisms are acclimated to low temperature.

Lovelock, C. E., I. C. Feller, M. C. Ball, J. Ellis, and B. Sorrell. 2007. Testing the growth rate vs. geochemical hypothesis for latitudinal variation in plant nutrients. *Ecology Letters* 10:1154–1163.

A carefully controlled experimental test of the latitudinal increase in plant N and P contents, aimed at disentangling temperature and geology as drivers of the pattern.

Reich, P. B., and J. Oleksyn. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the United States of America* 101:11001–11006.

One of the broadest data sets published on foliar nutrient contents, confirming the suspected pattern of an increase in N and P leaf

content with latitude and a concomitant decline in N:P ratio.

Woods, H. A., W. Makino, J. B. Cotner, S. E. Hobbie, J. F. Harrison, K. Acharya, and J. J. Elser. 2003. Temperature and the chemical composition of poikilothermic organisms. *Functional Ecology* 17:237–245.

The largest comparative study of temperature effects on heterotroph stoichiometry. It also proposes convincing mechanisms to explain the pattern: increased biochemical allocations to nutrient-rich biomachinery at lower temperature to increase metabolic and biosynthetic rates.

Biotic Factors

As posited in Schade, et al. 2005 (cited under Causes of Stoichiometric Imbalances at the Level of Ecosystems), changes in the elemental supplies in ecosystems may not be imposed by external forcing but may result from the organisms themselves. N₂ fixation compensates for low N supplies while denitrification gets rid of any excess of N, thus resulting in a long term P control on total plant biomass in ecosystems (Arrigo 2005 and see Redfield 1958). A striking example in Small, et al. 2013 shows how modest nitrification rates in Lake Superior still lead to a five-thousand-fold increase in the NO₃:PO₄ ratio above the Redfield ratio. Organisms can also affect the level of resources in their ecosystem by altering the chemical properties of the organic matter that is recycled. Daufresne and Hedin 2005 reports modeling results that illustrate how plants can modify the net supply of resources in ecosystems, and change the competition outcome, simply by changing the loss potential of the detritus they produce. In soils, the stoichiometry of microbial decomposers plays a critical role, controlling whether nutrients are released or added to the decomposed organic matter, as well as the efficiency of the decomposition process (Manzoni, et al. 2010).

Arrigo, K. R. 2005. Marine microorganisms and global nutrient cycles. *Nature* 437:349–355.

An insightful rendering of the current state-of-the-art knowledge of the microbial control of the cycling of nitrogen and phosphorus in the ocean.

Daufresne, T., and L. O. Hedin. 2005. Plant coexistence depends on ecosystem nutrient cycles: Extension of the resource-ratio theory. *Proceedings of the National Academy of Sciences of the United States of America* 102:9212–9217.

A slight twist on the resource ratio model for plant competition, this paper suggests that plants can potentially exert some control on the competitive arena for nutrients by changing the types of detritus that are lost from the ecosystem.

Manzoni, S., J. A. Trofymow, R. B. Jackson, and A. Porporato. 2010. Stoichiometric controls on carbon, nitrogen, and phosphorus dynamics in decomposing litter. *Ecological Monographs* 80:89–106.

A rather simple stoichiometric model for microbial-controlled decomposition that proves predictive in a wide set of conditions, from tropical to polar regions.

Small, G. E., G. S. Bullerjahn, and R. W. Sterner, et al. 2013. Rates and controls of nitrification in a large oligotrophic lake. *Limnology and Oceanography* 58:276–286.

Measurement of nitrification rates brought a plausible explanation to the astounding accumulation of nitrate (and imbalanced N:P stoichiometry) observed in Lake Superior, highlighting the major role played by, or rather by the absence of, bacteria processing ammonium.

Consequences of Stoichiometric Imbalances

Stoichiometric imbalances between resources and their consumers have obvious effects on the latter. These effects can further propagate through the food web, affecting trophic levels higher in the food chains or changing the outcome of competition within trophic levels through feedback effects on the resources.

Direct Effects on Consumers

The first and foremost effect of elemental deficiency in a resource is a decrease in the growth rate of its consumer, together with collateral effects on other life-history traits as shown, for example, in Urabe and Sterner 2001. The hypothesis of a direct limitation of growth by elements was criticized, however, and a role for other limiting factors, such as unsaturated fatty acids, emphasized in Brett 1993. The controversy has been solved by showing that different limiting factors are not mutually exclusive and can affect the same consumer population at different points in time or through different life-history traits (Becker and Boersma 2010). Experiments in Plath and Boersma 2001 extended the range of resource elemental contents used in tests to show that both low and high contents of a given element can decrease the growth of a consumer. A fundamental concept in ascertaining whether a given consumer is likely to suffer from element deficiency is the threshold elemental ratio (TER), the food C:nutrient ratio above which the consumer growth is limited by the nutrient element (Anderson and Hessen 2005). The TER concept assumes clear boundaries between growth limitation by one or the other element (see also Introductory Works and Syntheses). This is reasonable for consumers with fixed stoichiometric composition but not necessarily for organisms that can store elements, such as some microorganisms (Egli 1991). Effects at the organismal scale imply effects on lower levels, such as on the transcription of the genes involved in the metabolism of elements (explored by Jeyasingh and Weider 2007). On a higher level, effects on individual consumers should result in effects at the population level and stoichiometrically explicit models indeed contain rich dynamics not seen in single-currency models (Nakazawa 2011 and Elser, et al. 2012)

Anderson, T. R., and D. O. Hessen. 2005. Threshold elemental ratios for carbon versus phosphorus limitation in *Daphnia*. *Freshwater Biology* 50:2063–2075.

A fundamental paper to read before utilizing the TER concept, since it includes maintenance considerations and thus demonstrates that the TER depends on both the quality and quantity of food.

Becker, C., and M. Boersma. 2010. Limiting levels of eicosapentaenoic acid: What do we really know? *Limnology and Oceanography* 55:459–462.

Revisits the biomolecule vs. elemental limitation controversy, more than fifteen years after it started. Although not the definitive answer, most 21st-century studies now work on a synthesis between the different potential limiting resources.

Brett, M. T. 1993. Possibility of N or P limitation for planktonic cladocerans: An experimental test and nutrient element limitation of zooplankton production—a comment. *Limnology and Oceanography* 38:1333–1337.

Early claims of negative effects of elemental limitation on the growth of primary consumers met many objections, most of them summarized in this comment paper.

Egli, T. 1991. On multiple-nutrient-limited growth of microorganisms, with special reference to dual limitation by carbon and nitrogen substrates. *Antonie Van Leeuwenhoek* 60:225–234.

An elegant and unambiguous multiple-element work that predates the development of formal stoichiometric theory but clearly shows the links between elements in resources, growth rate, storage, and stoichiometry in heterotrophic microorganisms.

Elser, J. J., I. Loladze, A. L. Peace, and Y. Kuang. 2012. Lotka re-loaded: Modeling trophic interactions under stoichiometric constraints. *Ecological Modelling* 245:3–11.

An overview of how the classical Lotka-Volterra approach to population dynamics is synthesized with key dimensions of the stoichiometric approach. This is important, since it opens the way to introducing stoichiometric considerations into the fields of theoretical population dynamics and food web models.

Jeyasingh, P. D., and L. J. Weider. 2007. Fundamental links between genes and elements: The evolutionary implications of ecological stoichiometry. *Molecular Ecology* 16:4649–4661.

A synthesis of sources in the literature that identifies the genes involved in the response of organisms to variation in the supply of P. It provides clues to those interested in the physiological and genetic responses of organisms to elemental limitation.

Nakazawa, T. 2011. The ontogenetic stoichiometric bottleneck stabilizes herbivore-autotroph dynamics. *Ecological Research* 26:209–216.

One of the few theoretical works that explicitly considers structured populations in a stoichiometric context. This is crucial, as most populations are structured in some way.

Plath, K., and M. Boersma. 2001. Mineral limitation of zooplankton: Stoichiometric constraints and optimal foraging. *Ecology* 82:1260–1269.

One of the first studies to explore the effect of high food P-content on the growth of *Daphnia* and uses a range wide enough to contain food with a large excess of P. This allowed observation of a negative effect of very P-rich food on growth that was as large as that for P-depleted food.

Urabe, J., and R. W. Sterner. 2001. Contrasting effects of different types of resource depletion on life-history traits in *Daphnia*. *Functional Ecology* 15:165–174.

Experiments on elemental limitation of growth rate are numerous, but studies that measure multiple life-history traits are more rare. This is one of those studies, providing the data necessary to reach a deeper understanding of population level effects of elemental limitation.

Effects on Competition

Resource-ratio competition theory is probably the earliest stoichiometry-based theoretical approach, predating even the formal definition of stoichiometric theory. The book *Resource Competition and Community Structure* (Tilman 1982) clearly shows how the elemental composition of autotroph species competing for essential resources determines the outcome of competition in simple controlled settings, together with the relative supply of the resources (also see Historical Perspectives). Total community diversity in more natural conditions seems also to be controlled by the balance of resource supplies (Braakhekke and Hooftman 1999). Huisman and Weissing 1999 also uses the resource-ratio framework to bring forward one possible mechanism (“coexistence in chaos”) for the “paradox of the plankton.” The resource ratio approach can also be extended to the case of heterotrophic consumers without too much pain (Danger, et al. 2008 and Iwabuchi and Urabe 2012). For *Daphnia* at least, trade-offs between, e.g., maximum growth rate and sensitivity to P-deficiency, seem to be operating (Seidendorf, et al. 2007) and can influence the outcome of competition (Jeyasingh, et al. 2009).

Braakhekke, W. G., and D. A. P. Hooftman. 1999. The resource balance hypothesis of plant species diversity in grassland.

Journal of Vegetation Science 10:187–200.

A detailed article that combines theory and experiment and advances the “Resource Balance Hypothesis.” This hypothesis posits that maximum plant diversity in natural communities is found when the stoichiometry of resource supplies in an ecosystem meets the optimum stoichiometry of the plant species present.

Danger, M., T. Daufresne, F. Lucas, S. Pissard, and G. Lacroix. 2008. Does Liebig’s law of the minimum scale up from species to communities? *Oikos* 117:1741–1751.

Bacterial communities are notoriously diverse. Modeling competition between multiple species for two resources, P and organic C, this work predicts co-limitation over a wider range of relative resource supplies for microbial communities than for single species.

Huisman, J., and F. J. Weissing. 1999. Biodiversity of plankton by species oscillations and chaos. *Nature* 402:407–410.

A striking paper showing how a simple model of plant competition for more than two resources can lead to chaotic trajectories and to the coexistence of more species than limiting resources, without the help of any external perturbation.

Iwabuchi, T., and J. Urabe. 2012. Competitive outcomes between herbivorous consumers can be predicted from their stoichiometric demands. *Ecosphere* 3:7.

A successful theory-experiment extension of the resource-ratio theory of Tilman 1982 to the case of *Daphnia*, this paper describes a simple graphical method to account for the effect of food stoichiometry on competition.

Jeyasingh, P. D., L. J. Weider, and R. W. Sterner. 2009. Genetically-based trade-offs in response to stoichiometric food quality influence competition in a keystone aquatic herbivore. *Ecology Letters* 12:1229–1237.

An example of an experimental evolution study showing how a genetic trade-off in resource use governs competition between clones of *Daphnia*.

Seidendorf, B., M. Boersma, and K. Schwenk. 2007. Evolutionary stoichiometry: The role of food quality for clonal differentiation and hybrid maintenance in a *Daphnia* species complex. *Limnology and Oceanography* 52:385–394.

Using interspecific hybridization, this article reveals a key trade-off between growth under high P and sensitivity to P deficiency, which potentially allows prediction of the competitive outcome between various species and clones of *Daphnia*.

Tilman, D. 1982. *Resource competition and community structure*. Princeton, NJ: Princeton Univ. Press.

A must-read book for all those interested in resource-consumer dynamics, resource competition, and plant community structure. Many of the more recent stoichiometric models are extensions of resource-ratio theory.

Effects on Trophic Interactions

Effects of stoichiometric imbalances are not restricted to direct impacts on consumers but can spill out, either along the food chain as shown in Boersma, et al. 2008 or indirectly through changes in the availability of resources for other consumers. An indirect effect of elemental limitation, detected a long time ago, is on microbial decomposers that coexist with primary producers. Bratbak and Thingstad 1985 shows how P limitation of phytoplankton cells leads in turn to P limitation of bacteria, due to phytoplankton excretion of excess C. The same team further focused on bacteria, developing models for different scenarios of bacterial growth regulation by their resources or their predators (Thingstad and Lignell 1997). In the terrestrial realm, stoichiometry and resource

exchanges are also crucial to understand plant-mycorrhiza interactions (Johnson 2010). Hall 2009 presents the most complete and mostly up-to-date recount of modeling to link food web ecology and ecological stoichiometry (cited under Review Papers). On the empirical level, few studies exist on the stoichiometry of whole food webs, but notable exceptions are Cross, et al. 2003 on detritus-based stream food webs and Mulder and Elser 2009 on grassland soil food webs. Unjustly ignored to a large extent in food web ecology, host-pathogen interactions are also affected by stoichiometry (Frost, et al. 2008).

Boersma, M., N. Aberle, F. M. Hantsche, K. L. Schoo, K. H. Wiltshire, and A. M. Malzahn. 2008. Nutritional limitation travels up the food chain. *International Review of Hydrobiology* 93:479–488.

Challenging the paradigm of energy limitation in secondary consumers and higher up in the food chain, the article discusses examples of P limitation in predators and advocates for a focus on nutrient limitation at all levels of food webs and not only primary consumers, at least in aquatic ecosystems.

Bratbak, G., and T. F. Thingstad. 1985. Phytoplankton-bacteria interactions: An apparent paradox? Analysis of a model system with both competition and commensalism. *Marine Ecology Progress Series* 25:23–30.

A coupled model-experiment study testing the earlier-formulated hypothesis of competition between algae and bacteria for elements, which is caused by the increased excretion of organic carbon by element-limited algae.

Cross, W. F., J. P. Benstead, A. D. Rosemond, and J. B. Wallace. 2003. Consumer-resource stoichiometry in detritus-based streams. *Ecology Letters* 6:721–732.

An application of stoichiometric theory to streams, which differs from most others by its coverage of nearly the whole food web rather than focusing on a few basal interactions.

Frost, P. C., D. Ebert, and V. H. Smith. 2008. Responses of a bacterial pathogen to phosphorus limitation of its aquatic invertebrate host. *Ecology* 89:313–318.

Pathogens get all their elements from their hosts, making them sensitive to the stoichiometry of the latter. This fact should have made them the obvious target of stoichiometric studies, such as in this article.

Hall, S. R. 2009. Stoichiometrically explicit food webs: Feedbacks between resource supply, elemental constraints, and species diversity. *Annual Review of Ecology, Evolution and Systematics* 40:503–528.

As the title indicates, an authoritative review of the current state of the field of stoichiometrically explicit food web studies.

Johnson, N. C. 2010. Resource stoichiometry elucidates the structure and function of arbuscular mycorrhizas across scales. *New Phytologist* 185:631–647.

Although stoichiometric by nature, plant-mycorrhizae interactions have largely been ignored in stoichiometric studies but not by this article. This is one of the first studies to tackle the various facets of these interactions using a fully explicit stoichiometric framework.

Mulder, C., and J. J. Elser. 2009. Soil acidity, ecological stoichiometry and allometric scaling in grassland food webs. *Global Change Biology* 15:2730–2738.

Soils are lagging behind most ecosystems in the number of stoichiometric studies done on them, but this paper redresses the balance. It shows a link between soil stoichiometry and size spectra of soil organisms in the Netherlands.

Thingstad, T. F., and R. Lignell. 1997. Theoretical models for the control of bacterial growth rate, abundance, diversity and carbon demand. *Aquatic Microbial Ecology* 13:19–27.

An essential paper that manages to condense the complexity of bacterial interactions with their resources and predators in a small number of simple models that can be used as modules in more complete food web models.

Stoichiometry and Nutrient Recycling in Ecosystems

Ecological stoichiometry is about conservation of matter and homeostasis constraints. What is not accumulated by organisms into their biomass according its elemental composition is thus rejected as waste back into their environment, potentially affecting the relative supplies of unbound elements in their ecosystem, the rates of losses and gains of these elements, and their availability for other organisms.

Consumer-Driven Nutrient Recycling

Consumer-driven nutrient recycling (CNR) is historically the first stoichiometric mechanism considered in the literature and involves the differential recycling of elements by homeostatic consumers (Sterner 1990, cited under Introductory Works and Syntheses). The approach analyzes how consumers affect the relative availability of the elements limiting the growth of primary producers by disproportionately recycling the elements that are in excess in their food (Sterner, et al. 1992). Vanni 2002 is a good overview and synthesis of CNR in freshwater systems: it highlights that the large stoichiometric effects of consumers on element availability are not always through their recycling of elements within ecosystems but also sometimes through their translocation of elements in and out of ecosystems. The experimental work of Paterson, et al. 2002 is a nice example of primary consumers affecting algal growth through their stoichiometry. Another caveat to classical CNR approaches is described in Daufresne and Loreau 2001, which is a theoretical work highlighting the importance of the mortality effect of grazing on producer limitation. Cherif and Loreau 2009 demonstrates that placing the plant-herbivore interaction within a food web context can lead to predictions that diverge from the simple consumer-driven nutrient recycling hypothesis, mainly through other indirect trophic interactions.

Cherif, M., and M. Loreau. 2009. When microbes and consumers determine the limiting nutrient of autotrophs: A theoretical analysis. *Proceedings of the Royal Society B-Biological Sciences* 276:487–497.

A tri-trophic model that includes microbial decomposers beside herbivores and plants, this article shows how indirect effects of herbivores, mediated by decomposers, can obscure their effect on nutrient availability as posited by the consumer-driven nutrient recycling.

Daufresne, T., and M. Loreau. 2001. Plant-herbivore interactions and ecological stoichiometry: When do herbivores determine plant nutrient limitation? *Ecology Letters* 4:196–206.

Modeling consumer-driven nutrient recycling in its entirety, this work paints a more complicated picture than in the incomplete, classical model of Sterner, et al. 1992. Indeed, stoichiometric alterations in the physiology of plants due to grazing can, under some conditions, counteract the effects of the consumer-driven nutrient recycling on the growth of plants.

Paterson, M. J., D. L. Findlay, A. G. Salki, L. L. Hendzel, and R. H. Hesslein. 2002. The effects of *Daphnia* on nutrient stoichiometry and filamentous cyanobacteria: A mesocosm experiment in a eutrophic lake. *Freshwater Biology* 47:1217–1233.

There are surprisingly few examples in the literature documenting the whole process of the consumer-driven nutrient recycling from producer ingestion down to changes in producer nutrient limitation. This study is one of the few, confirming the hypothesis but with a twist, since *Daphnia*-enhanced P sedimentation also plays a role.

Sterner, R. W., J. J. Elser, and D. O. Hessen. 1992. Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems. *Biogeochemistry* 17:49–67.

A foundational article that fleshed out the consumer-driven nutrient recycling hypothesis, although the expression itself was coined later in the “Stoichiometry of Consumer-driven Nutrient Recycling: Theory, Observations, and Consequences” (in *Ecology* 80 [1999], pp. 735–751). The article also presents the first empirical evidence for the biogeochemical effects of a mismatch between phytoplankton and zooplankton stoichiometries in natural settings.

Vanni, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 33:341–370.

Reviewing the importance of freshwater animals in the recycling of nutrients, Vanni introduces the important insight that consumers’ impacts are also imposed through their effects on imports and exports of nutrients in and out of ecosystems.

Role of the Detritus Pathway

Consumer-driven nutrient recycling approaches concentrate on those recycled nutrients that are directly available for primary production. However, most recycled elements, whether from primary producers or consumers, come in the form of organic matter that requires decomposition before being available for re-use by living organisms. Cebrian 1999 shows that autotroph stoichiometry is a crucial determinant of the fate of organic matter at the level of ecosystems (consumed by herbivores vs. accumulated as detritus). Kaspari, et al. 2008 goes into further detail, showing how different nutrients affect different parts of detritus production and processing in tropical forests. Cleveland and Liptzin 2007 provides a synthetic analysis that shows that the stoichiometry of microbial decomposers, as well as that of soil organic matter, are also crucial players, with both showing an astounding convergence toward unique C:N:P ratios. Even soil enzymatic activities converge toward a uniform scaling of C:N:P across ecosystems, according to Sinsabaugh and Shah 2012.

Cebrian, J. 1999. Patterns in the fate of production in plant communities. *American Naturalist* 154:449–468.

An impressive compilation of published flows of carbon at the level of ecosystems and biomes, suggesting that plant stoichiometry, itself connected to plant turnover rates, is the ultimate factor controlling herbivory rates, detritus production, and decomposition rates.

Cleveland, C. C., and D. Liptzin. 2007. C:N:P stoichiometry in soil: Is there a “Redfield ratio” for the microbial biomass? *Biogeochemistry* 85:235–252.

A compilation of soil data showing a remarkable consistency in the C:N:P ratios of soil organic pools and soil microbial biomass, an earthy equivalent to the oceanic “Redfield ratio.”

Kaspari, M., M. N. Garcia, K. E. Harms, M. Santana, S. J. Wright, and J. B. Yavitt. 2008. Multiple nutrients limit litterfall and decomposition in a tropical forest. *Ecology Letters* 11:35–43.

An analytical approach to plant stoichiometry effects on detritus production and decomposition in tropical forests and one of the few that venture off the beaten tracks of C, N, and P to consider other nutrients such as K, Ca, and Fe.

Sinsabaugh, R. L., and J. J. F. Shah. 2012. Ecoenzymatic stoichiometry and ecological theory. *Annual Review of Ecology, Evolution and Systematics* 43:313–343.

An extension of the soil “Redfield ratio” concept to the ratio of activities for the enzymes involved in the solubilization of soil organic

matter compounds before their uptake by microorganisms.

Future Directions

Stoichiometry's many forays into the various fields of biology (see previous sections) show the benefits gained from using a stoichiometric lens in the study of many biological phenomena. However, a more systematic integration of stoichiometry into the various established biological fields is still needed. Such attempts at theory integration have increased in the early 21st century. Aalto, et al. 2015, for example, summarizes and contextualizes previous host-parasite stoichiometric studies into a predictive framework. In Declerck, et al. 2015 the stoichiometry of resources is introduced as a selective force on organisms, using the developing framework of eco-evolutionary dynamics. Attempts at integrating stoichiometry with landscape ecology in Sitters, et al. 2015 and biogeochemical thermodynamics in Helton, et al. 2015 are also worth mentioning. Efforts in methodology integration in order to address cross-disciplinary questions are also a way forward, as exemplified in Roy, et al. 2015. It is only through such integrative efforts that stoichiometry will usefully contribute to answering the global environmental challenges that already affect society. Carnicer, et al. 2015 offers an informed perspective on the effects of stoichiometric alterations to biogeochemical cycles on biodiversity and ecosystem losses. In a more local perspective, Cease, et al. 2015 provides interesting first considerations on how different urban lifestyles modify environmental stoichiometry.

Aalto, S. L., E. Decaestecker, and K. Pulkkinen. 2015. A three-way perspective of stoichiometric changes on host-parasite interactions. *Trends in Parasitology* 31:333–340.

Host-parasite stoichiometric studies previous to this review lacked coherence, mostly because they investigated different systems within different contexts. Here, the authors provide a comprehensive and predictive framework that should make stoichiometry an unavoidable aspect to consider in future host-parasite studies.

Carnicer, J., J. Sardans, C. Stefanescu, A. Ubach, M. Bartrons, D. Asensio, and J. Penuelas. 2015. Global biodiversity, stoichiometry and ecosystem function responses to human-induced C-N-P imbalances. *Journal of Plant Physiology* 172:82–91.

This comprehensive paper integrates a broad array of studies to highlight the role of stoichiometric traits in understanding the impacts of multidimensional global change perturbations on plant biodiversity.

Cease, A. J., K. A. Capps, K. K. Gates, M. L. McCrackin, and D. A. Nidzgorski. 2015. Consumer-driven nutrient dynamics in urban environments: The stoichiometry of human diets and waste management. *Oikos* 124:931–948.

A product of the 2014 “Woodstoich” workshop, this paper cleverly integrates diverse data sets involving human diets in different regions and contexts, wastewater infrastructure, and projected sustainability scenarios and calls for future socio-ecological systems analyses to take a stoichiometric perspective.

Declerck, S. A. J., A. R. Malo, S. Diehl, D. Waasdorp, K. D. Lemmen, K. Proios, and S. Papakostas. 2015. Rapid adaptation of herbivore consumers to nutrient limitation: Eco-evolutionary feedbacks to population demography and resource control. *Ecology Letters* 18:553–562.

A straightforward but yet unprecedented experimental test of the selective pressure of P deficiency on rotifers, showing a simple, striking eco-evolutionary response of the latter. Still a far stretch from a theory of the stoichiometry of microevolution, this work, however, paves the way to similar simple, reproducible experiments that will generate the patterns on which to build the theory.

Helton, A. M., M. Ardon, and E. S. Bernhardt. 2015. Thermodynamic constraints on the utility of ecological stoichiometry

for explaining global biogeochemical patterns. *Ecology Letters* 18:1049–1056.

This analysis of large data sets of nitrogen and DOC availabilities in various aquatic systems calls for an integration between stoichiometry and thermodynamics, matter, and energy. This is unavoidable if one's aim is to push to its limits the potential of chemical principles to explain ecology.

Roy, Chowdhury P., D. Frisch, D. Becker, J. A. Lopez, L. J. Weider, J. K. Colbourne, and P. D. Jeyasingh. 2015. Differential transcriptomic responses of ancient and modern *Daphnia* genotypes to phosphorus supply. *Molecular Ecology* 24:123–135.

Combining resurrection ecology, transcriptomics, and classical competition experiments to highlight historical anthropogenic effects on *Daphnia* evolution, the authors here offer a brilliant demonstration of the power of integrative approaches in unraveling multilevel processes.

Sitters, J., C. L. Atkinson, N. Guelzow, P. Kelly, and L. L. Sullivan. 2015. Spatial stoichiometry: Cross-ecosystem material flows and their impact on recipient ecosystems and organisms. *Oikos* 124:920–930.

Another “Woodstoich” product in 2014, this paper takes a spatially explicit approach to stoichiometric analysis of coupled and uncoupled element flows and highlights literature gaps and needs for new research in the relatively unexplored landscape of landscape stoichiometry.

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