The evolution of biological stoichiometry under global change

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Anthropogenic influences are simultaneously perturbing multiple biochemical cycles, as well as climate, in the biosphere (Falkowski et al. 2000). To address such effects, an explicitly multi-variate approach is needed. Furthermore, to understand the full gamut of ramifications of such changes for the functioning of ecosystems and for biodiversity in the long- and short-term, a perspective that connects fluxes of chemical elements to underlying physiological and genomic mechanisms and to evolutionary processes is needed. One such perspective is offered by biological stoichiometry, the study of the balance of energy and multiple chemical elements in living systems (Elser and Hamilton 2007), a perspective that has emerged from a more focused application of stoichiometric thinking to ecological interactions (Sterner and Elser 2002).

In August 2009 the second “Woodstoich” workshop was held at the Kawatabi Experimental Farm, Japan (Tohoku University Kawatabi Seminar Center), five years after the first Woodstoich workshop held in Finse, Norway (Hessen and Elser 2005) and forty-years after the Woodstock concert revolutionized western culture. In keeping with the 1st Woodstoich, a team of four postdoctoral researchers was chosen as a scientific steering committee; the team then chose 20 workshop participants from among more than 80 applicants. Participants formed four working groups to take on novel analyses and syntheses of questions related to biological stoichiometry: the strength of stoichiometric homeostasis across diverse taxa, the allometric scaling of key stoichiometric parameters, the role of stoichiometry in influencing sexual selection, and the impact of stoichiometric mechanisms in invasion ecology. Groups worked on conceptual, theoretical and meta-analytical analyses in the months leading up the workshop and then finalized their papers during the first days of the meeting. Manuscripts were sent for pre-arranged 24-h peer review and each manuscript received three external anonymous reviews. Authors were then able to begin preparing their responses and revisions before the end of the 5-d event, after which additional reviews and revisions were completed. Thus, the papers you can read on the following pages reflect the most up-to-date thinking of some of the best young minds working in ecology, evolution, behavior, and functional biology.

Regulation of elemental composition

What Walter Bradford Cannon called “homeostasis” (Cannon 1932) is an old but still crucial issue in current biology for understanding how organisms regulate and maintain appropriately their identities and integrities in the face of changes in internal and external environments (Kitano 2002). For ecology, understanding implications of physiological homeostasis is becoming much more important than ever, considering the fact that increased anthropogenic activities for the past couple of hundred years have dramatically changed the biogeochemical cycling at rates that our ecosystems have never experienced (Falkowski et al. 2000). Thus, recent environmental issues such as eutrophication, acidification, carbon dioxide increase, and climate warming involve inevitably changes in supply rates and ratios of energy and various biologically important elements to organisms. Whether or not organisms can maintain themselves against putative changes in environmental conditions, therefore, depends at least on their ability to regulate internal conditions despite changes in ratios and ratios of energy and elemental supplies.

Early theories of ecological stoichiometry assumed that, while autotrophic species change their relative elemental contents depending on rates and ratios of energy and nutrient supplies, heterotrophic species are strictly homeostatic in the relative elemental contents of their bodies (Hessen 1992, Urabe and Watanabe 1992). Although this assumption of strict homeostasis for heterotrophs has been shown to be not strictly true in a qualitative sense (DeMott 2003), little is known quantitatively about the strength of stoichiometric homeostasis in heterotrophic and autotrophic organisms. Using meta-analyses for data in recent literature, Persson et al. (2010) show that, although the degree of stoichiometric homeostasis in heterotrophic species was generally stronger...
than that in autotrophic species, it widely varied both within and among taxonomic groups they examined. At the same time, they cautioned that the present knowledge on the strength of stoichiometric homeostasis both for autotrophs and heterotrophs relies on very limited observations for a very narrow taxonomic range of organisms. The findings of Persson and colleagues will be serve as a firm basis for stimulating further observations and for developing improved theories of community organization and nutrient cycling under changing environmental conditions.

**Ecological efficiencies and scaling**

Beyond biological stoichiometry, other approaches have also recently made progress in establishing the general rules that functionally link multiple levels of biological integration. One of these is the metabolic theory of ecology, the study of how size-scaling affects metabolic properties of living systems from cells to ecosystems (West et al. 1997). Consistent with a call emerging from the first Woodstoich (Moe et al. 2005), a number of recent efforts have attempted to forge a synthesis of biological stoichiometry and the metabolic theory of ecology (Kerkhoff et al. 2005, Jeyasasingh 2007, Allen and Gillooly 2009).

The paper by Doi et al. (2010) moves this effort substantively forward by focusing on the potential size-dependence of the threshold elemental ratio (TER), a key concept of ecological stoichiometry (Hessen 1992, Urabe and Watanabe 1992, Sterner and Elser 2002). The TER is the nutrient:C ratio of a food below which the consumer’s growth rate will be limited by the food’s nutrient content. Thus, the TER is closely related to how tolerant a consumer can be of poor quality food and may modulate the effects of stoichiometric food quality on species composition of consumer guilds as well as on trophic efficiency in food webs. The TER depends on three things: the consumer’s nutrient:C ratio, its maximum growth efficiency (GGE_N or GGE_P) for the nutrient, and its maximum growth efficiency for carbon (GGE_C). All three are likely to depend on size but it is not clear if these scaling relations differ and thus modulate the overall size-dependence of the TER with important implications for size-structure in food webs (Mulder and Elser 2009). Doi and colleagues conducted a meta-analysis of more than 800 studies reporting various aspects of the TER for species across 18 orders of magnitude in body size. In contrast with predictions of metabolic theory, they document strong size-dependence of element growth efficiencies. Furthermore they show that GGE_N and GGE_P are highly correlated and thus N-based food quality sensitivity (i.e. TER for N:C) will likely be mostly determined by the consumer’s N:C ratio. Meanwhile the scaling patterns for GGE_P and GGE_C suggest that the P:C TER should decrease with increasing body size (i.e. larger consumers should be less sensitive to food P-content) but their initial analysis of a limited TER data set did not directly support that prediction. Regardless, these efforts are a significant step in the direction of integrating biological stoichiometry with metabolic scaling, providing tools that can help predict how diverse biota might respond to future anthropogenic disruptions that accompany global change.

**Sex and nutrients**

Alongside biological stoichiometry and the metabolic theory of ecology, a third broad framework that aims to bring about greater integration of diverse fields of biology is the geometric framework for nutritional ecology (Kearney and Porter 2006, Simpson et al. 2009). These approaches share foundations and goals, and yet in some respects are very different (Raubenheimer et al. 2009). Biological stoichiometry, with its focus on elements and body composition, abstracts biological systems to a greater extent than does the geometric framework, which focuses on nutrients and more explicitly incorporates the notion of biological fitness. Biological stoichiometry therefore has its centre of gravity at the higher levels of populations, communities and ecosystems, whereas the geometric framework is centered at the level of functional traits, organisms and populations.

The paper of Morehouse et al. (2010), on the relationship between sexual reproduction and resources, explore the complementarity between the geometric framework and biological stoichiometry. Morehouse and colleagues review a broad literature illustrating the ubiquitous implications of nutrition for the divergent roles of the sexes, from anisogamy to sexually selected traits and mate choice. This highlights the need for a unified view of the relationship between sexual reproduction and nutrition, which spans levels of organization from physiology to ecology. Morehouse et al. present a visual scheme illustrating this, and emphasize that this integration calls for a nutritionally explicit approach that distinguishes the separate and interactive roles of specific nutrient currencies. They demonstrate how geometric analysis of macro-nutrition can approach this from the functional viewpoint, and how biological stoichiometry may be used to explore the ecological implications. Morehouse et al. conclude by presenting a simple mathematical model that explores how sex-specific nutrient requirements can impact on population dynamics.

**Stoichiometry and biological invasion**

Irrespective of what framework one uses to structure ecological research, be it stoichiometry, metabolic theory, or nutritional ecology, an overarching theme is better understanding the determinants of biodiversity, or why species show the patterns in distribution and abundance they do. No process is perhaps more central to the dynamics of biodiversity than biotic exchange. Our circulating air and water masses have transported species from one habitat to another for billions of years, sometimes to no particular consequence, such as when cattle egrets arrived in the Americas (Crosby 1972), or sometimes leading to radical change, such as aboriginals in Australia (Bowman 1998). Where would we be if newly volcanic islands, like the Galapagos or Hawaiian archipelagoes, were never invaded or if the Isthmus of Panama did not form and trigger massive reorganization of American mammalian fauna (Lessa and Farina 1996)?

In the modern world, however, the dominant force behind biotic exchange is human transport, bringing with it unprecedented rates of exchange. Invasion is therefore not a perverse or enigmatic phenomenon, but a well-known and
important ecological process that is simply out of whack, occurring at unprecedented rates that exacerbate biodiversity loss, adversely alter ecosystem functioning and the services they provide, and incurring enormous economic costs (Anthony 2007, Theoharides and Dukes 2007).

Unfortunately, invasion biology is a mess and attempts to develop general frameworks for the ecology of invasive species, beginning with Elton (1958), have been an important part of our discipline’s attempt to better understand the phenomenon. There are many hypotheses, some tested empirically while others remain as theory, but we are a long way off from any comprehensive theory of invasive species (Cronk and Fuller 1995, Richardson et al. 2000). More than likely, in fact, there is probably no one-size-fits-all theory of invasive species and different frameworks will provide different insights (Puth and Post 2005, Fridley et al. 2007, Theoharides and Dukes 2007). González et al. (2010) provide three hypotheses derived from the ecological stoichiometric framework. Using a combination of meta-analyses of current literature and theoretical arguments, they examine how several mechanisms invoked in the complex, confusing, and sometimes contradictory literature on biological invasions, can be better understood through a stoichiometric framework. They do not presume to provide a comprehensive theory of invasive species, but suggest some overlooked mechanisms that could very well improve our ability to predict why some exotic species become dominant and wreak the ecological havoc, and incur enormous economic costs.

The future of biological stoichiometry

As with any scientific approach, the future of biological stoichiometry lies with its success in application by new practitioners — will this way of studying living systems offer sufficient insight on ongoing dynamics, including those imposed by global change, to merit further investigation, modification, and application? If so, then it may continue to evolve and contribute to the establishment of fundamental connections among the multiple levels of biological organization that are now responding to perturbations of climate, nutrient supply, and community structure. If not, then new generations of models will be needed and these will be generated by new generations of ecologists and evolutionary biologists. As at Woodstock, it is difficult to predict which of these new performers will leave a lasting legacy but the papers that follow offer a glimpse of such future possibilities.

References


Elton, C. S. 1958. The ecology of invasions by animals and plants. – Methuen.


