Elements of ecology and evolution

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Ecological stoichiometry (ES) is the study of the balance of energy and multiple chemical elements in ecological interactions (Sterner and Elser 2002). This field has many roots, but most proximally it has emerged from studies of trophic interactions in freshwater plankton and focused primarily on the ratio of carbon to phosphorus (C:P) in the freshwater cladoceran Daphnia and that of their phytoplankton food. Two important findings emerged from these seminal studies some 15 years ago: first, the observation that release of key nutrients like nitrogen (N) and P depended, in a predictable manner, on C:N:P ratios in the zooplankton consumer relative to that in its phytoplankton food with effects on phytoplankton nutrient limitation (Elser et al. 1988, Sterner et al. 1992) and, second, the discovery that of direct elemental limitation, N or P, of consumer growth due to high C:nutrient ratio in its food (Hessen 1992, Urabe and Watanabe 1992, Sterner 1993). These two observations can be considered two sides of the same stoichiometric coin and we now appreciate that consumers (and especially herbivores and detritivores) frequently have to dispose of excess C from their diets, causing reduced efficiency of growth at the organismal level and reduced trophic transfer efficiency at the ecosystem level. The validity of these principles has been experimentally verified in an increasing number of studies. From this small pelagic, freshwater realm, the concept of ecological stoichiometry has expanded to other organisms, other ecosystems, from genes and cells to ecosystems and global regulation of elemental cycles. These developments, at least up until 2001, are reviewed by Sterner and Elser (2002). In this collection of papers the authors demonstrate the very newest applications and horizons for stoichiometric theory and investigation, pointing towards ways that ES might be more fully elaborated at different levels of organization and used to understand new questions and problems.

Some words on the process leading up to this collection of papers is in order, since they have evolved in quite an unusual way: in the academic year 2003–2004 the Center for Advanced Study at the Norwegian Academy of Sciences and Letters hosted an international research group on ecological stoichiometry. During this year, various senior scientists working in ES met in Oslo to develop new theoretical studies, analyze data sets, and otherwise discuss the current and future status of the field. That senior scientists might find occasion for introspection is not unusual; even less unusual is that they might emerge with recommendations about possible future directions for the field. Unsurprisingly, very often these future directions happen to be the ones that they are best suited to address. However, most up-and-coming scientists are often frustrated by such machinations, as they also have ideas about the current state-of-the-art and where future priorities should lie. So, as a final outcome of this year, adding to the list of conventional papers that were produced, it was decided to arrange a workshop for a group of young scientists to develop and produce multi-authored papers addressing the present and future of ES. The desire was to create an opportunity for young scientists to instigate some kind
of a cultural revolution within the field by providing them with a forum for their views about what the field of ES has accomplished and how it might progress. There was also a strong desire to create a new means of scientific collaboration in this arena and to take a quantum leap beyond the normal pace at which scientific ideas are developed and communicated, a goal that is especially important in fields that are developing rapidly and for young scientists seeking to establish their credentials.

In the spirit of this and in recognition of the timing of the workshop, it was decided to call the event “Woodstock 2004” (the workshop took place from 12–17 August, while the original Woodstock festival occurred in 1969 from 15–17 August). The first step was to select a steering committee consisting of five postdoctoral scientists actively working in ES, each to take the lead of five groups: evolution; physiological mechanisms; population-community dynamics; large scale (ecosystems, regions, biosphere); and applications to environmental problems. The steering committee then oversaw a process by which participants were selected from among the many applications to attend that were submitted. As a result of this process, a diverse group was assembled, with representation of scientists working on most habitats of study, types of ecology and evolution, and modes of analysis and coming from four continents and fifteen countries. Next, a web forum for the selected participants was established and participants were assigned to the different groups according to their backgrounds and interests. Discussions then began intensively in June 2004 as the groups sought to focus their ideas, develop a paper outline, and, eventually, produce a first draft. Thus, all groups arrived at the meeting site (the Alpine Research Station at Finse, Norway) on 12 August 2004 with a rough draft in hand. On the third day of the workshop, each of the completed manuscripts was e-mailed to 3–4 independent reviewers who had previously agreed to return their assessments within 24 h. It is to the tremendous credit of the reviewers that fourteen substantive reviews were received in that time window. Thus, decision letters were prepared within two days of manuscript submittal and the authors could begin their revisions. Revised versions were received within 3 weeks of the decision letters, allowing recommendations for acceptance to be forwarded to Oikos’ senior editor less than one month after the start of the workshop.

The five papers in this set cover nearly the full gamut of biology, from cellular metabolism to the global biosphere. In the first paper, Kay and co-authors sketch an agenda by which stoichiometric thinking might further illuminate our understanding of evolutionary change by better identifying some of the functional tradeoffs involved in resource acquisition and use. Departing from past emphases on connections among P-limitation, rDNA-genes, and ribosomes, the authors cover evolutionary implications of nutrient imbalance at various levels of complexity. The mechanistic underpinnings of evolutionary tradeoffs are illuminated by Frost and colleagues, who provide an integrated treatment of the handling of energy and nutrients by autotrophic and heterotrophic organisms in a nutrient-imbalanced world. In the third paper, Moe and colleagues build to the levels of population dynamics and community structure, noting that stoichiometric theory is relatively well incorporated into population ecology theory but considerably under-developed for various aspects of community ecology. Beyond the level of species interactions, nutrient use and processing by organisms manifests at the ecosystem level in predictable ways and indeed stoichiometric studies are perhaps best developed at the ecosystem scale (Sterner and Elser 2002). In paper four, Schade and co-authors expand stoichiometric analysis of ecosystems by presenting a more spatially explicit approach to consider how the transactions of multiple elements play out in the context of landscape hot spots and hydrologic connections. Finally, the sign of the maturity of any research field is its ultimate application to particular problems of interest to society. Along these lines, Ptcanik and colleagues discuss how stoichiometric analysis might help us in understanding and perhaps ameliorating important environmental impacts, such as the effects of agricultural practice on nutrient exports from watersheds and the effects of such exports on downstream ecosystems. In these papers you will find, we believe, novel insights about how energy and matter together shape ecological and evolutionary processes at various levels. We also hope you will find at least a small piece of the original spirit of Woodstock, in which the unfettered energy of young people became focused in a single moment of time and left an lasting legacy.

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References