Reviews
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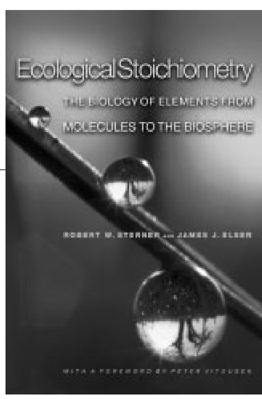
Is Biology Just Chemistry?

Different areas in biology are often criticized for being either too myopic and not asking questions about how their results fit into a larger framework or for being too broad and ignoring important details. A few research programs are now attempting to make general claims derived from simple, micro-level phenomena. This is great progress for biology, resolving some of the tensions between different approaches. A merging of these fields may lead to even greater advances. One of the most exciting of these new programs is ecological stoichiometry (ES), which has been spearheaded by Sterner and Elser. Their recent book provides an overview of this developing field. With clear exposition they explain how analysis at the level of molecules can have broad implications for many macro-level ecological phenomena. Moreover, they keep their theory closely tied to available data and to the design of new experiments, thereby bridging the gap between two dividing perspectives in biology. As such, *Ecological Stoichiometry* contains a much needed overview of this research program as well as a good example of future directions in biology.



ECOLOGICAL STOICHIOMETRY: THE BIOLOGY OF ELEMENTS FROM MOLECULES TO THE BIOSPHERE
by Robert W. Sterner and James J. Elser,
Princeton University Press,
Princeton, NJ, 2003
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Sterner and Elser use the first part of their book to develop the essential ideas behind ES. The foremost assumption is that an entire organism can be treated as a single, extremely large molecule. Humans, for example, are reducible to the formula:

$$H_{375,000,000}O_{132,000,000}C_{85,700,000}N_{6,430,000}Ca_{1,500,000}P_{1,020,000}S_{206,000}Na_{183,000}K_{177,000}Cl_{127,000}Mg_{40,000}Si_{38,600}Fe_{2,680}Zn_{2,110}Cu_{76}I_{14}Mn_{13}F_{13}Cr_{7}Se_{4}Mo_{3}Co_{1}. \quad (1)$$

This expresses the abundances of elements relative to a single cobalt (Co), which has a total abundance of about 1 mg in humans. Through interactions with abiotic pools and other organisms, e.g., eating and osmosis, chemicals are interchanged, and mass balance must hold. In the words of Sterner and Elser, "Organisms are chemical entities and are produced, maintained, and propagated by chemical reactions, albeit in the form of highly complex coupled networks, which are the product of evolution." Most organisms attempt to maintain elemental balance. Failure to do so often results in serious problems such as malnutrition or scurvy. As a result, most animals are homeostatic, meaning that their chemical formula changes very little with time in response to changes in the environmental abundances of elements. When the biological demands for one or more nutrients cannot be matched by the environmental supply, those nutrients are called "limiting nutrients," and it becomes difficult for organisms to maintain homeostasis. Organisms cope with this by using different strategies of storage and egestion, and which strategies are most advantageous depends on the ratios of elemental abundances in the environment, e.g., marine versus freshwater systems. Therefore, predicting which species will thrive is critically dependent on the environmental setting.

Sterner and Elser demonstrate that a great deal of information about ecological phenomena can be gleaned from these few ideas. For example, the chemical compositions of plants exhibit more plasticity than that of animals, which is a critical means by which ecosystems attempt to adapt to changing environmental conditions. Consequently, by studying the stoichiometry (chemical composition and requirements) of plants and proceeding to catalog the nearly unchanging chemical compositions of animals, significant progress can be made toward understanding which populations of organisms will grow and persist and which will diminish in size and possibly go extinct under different environmental conditions or conversely, toward understanding why organisms that have evolved in different environments use different life history strategies. Sterner and Elser convincingly show that this approach can be used to make numerous predictions with important implications at the organismal and ecological levels.

Early work in this direction was done experimentally by Redfield [1] and theoretically by Reiners [2]. Redfield discovered that the ratio of the abundances of carbon (C), nitrogen (N), and phosphorus (P) within oceans is matched by the organisms living in the ocean, e.g., plankton. Moreover, this ratio is virtually fixed across oceans; for every phosphorus there are 16 nitrogens and 106 carbons. This is an important result because it establishes the universality of certain stoichiometric rules and because it illustrates the balance and interplay between organisms and their environments. Because of the seminal nature of the "Redfield Ratio," most of the subsequent work in ES has focused on the ratio of elements. Because carbon is relatively constant in most organisms, ratios of C:N or C:P are good measures of the total abundance of N or P. Moreover, expressing equations in terms of ratios allows for easier connections between organisms and their environments. The total abundance of any given element within an environment is vastly larger than that in an individual organism. Thus, the relative abundances are the important quantities because they elucidate the match between organisms and their environments. Unfortunately, there are two negative aspects to always expressing abundances in terms of ratios. First, it is difficult to interpret statistical methods as applied to ratios. Second, and this is a problem with the convention but not the ratios themselves, placing carbon in the numerator of the ratio implies that increasing levels of phosphorus or nitrogen correspond to decreasing values for C:P or C:N. As a result, plots rise in the inverse direction that intuition would suggest, leading to much confusion for the uninitiated reader.

One of the major results discussed in the book and one of the major links between organisms and the chemical makeup of their environment is the Growth Rate Hypothesis (GRH). Using simple arguments Sterner and Elser derive an explicit formula that relates C:N to the mass-specific growth rate of individuals and the efficiency of nitrogen in sequestering carbon. This provides the most direct and explicit connection between the environmental abundance of elements, organismal biochemistry, and organismal development. Similar relations are derivable for other stoichiometric ratios. Empirical data provide good qualitative and quantitative support for the GRH. Most of the available data, including those obtained from experiments performed by Sterner and Elser, for testing this and other hypotheses are for zooplankton and insects. Because the data are limited to these taxonomic groups, one must question how general the results are, but I suspect that the relation and the qualitative features of the insect and zooplankton data will hold across many different levels within an ecosystem. The GRH is the first step toward developing a fully mechanistic model of ES that incorporates the dynamics of ecological phenomena.

Throughout the book Sterner and Elser excitedly bring attention to many important problems still to be solved in ES and point out that this research could be extended to understand and predict much more about ecological phenomena. This leads us to the questions that inspired the title of this review. One must wonder whether simply improving ES is enough to answer all these questions or whether other fields of research, including areas of biology and physics, must be incorporated to obtain a full theory of ecosystems and their relation to fundamental, mechanistic processes. Sterner and Elser concede that ES "does not and cannot explain everything of interest in the ecological and evolutionary worlds," but they spend too little time attempting to explain the mechanistic processes behind most of the phenomena they describe. Moreover, they are just beginning to pay attention to some other fields within biology from which ES would likely benefit. Of course, this is understandable because of limited time and energy on the part of the authors. As the book demonstrates, they have been quite busy! However, given the brevity of discussion of energetic and allometric theories, which respectively consider energy to be the primary variable in ecosystems [3–5] or relate physiological and ecological parameters to metabolic rate and thus to body size and temperature [6, 7], and food web ecology, which describes interactions between organisms belonging to different levels of a food chain within an ecosystem [8, 9], as well as several disparaging remarks about single-currency explanations, it seems this neglect may also be due to a lack of appreciation for these other disciplines. Sterner and Elser comment that, "Given the robustness of these relationships, thoughts should be directed toward understanding the broad and highly general patterns they produce. Single-currency frameworks, whether they be based on energy, carbon, nitrogen, or something else, do not and cannot capture these effects."

But typically, when a result is very robust and broad, it does point to a single, powerful underlying cause and not to many different causes that give rise to the same phenomenon by some accident. There are not multiple reasons why all objects in a vacuum fall to the Earth at 9.8 m/s^2. Moreover, when discussing Ågren's productivity equation and Droop's equation, they note that Ågren ". . .argues, the cell quota model of Droop is more descriptive and less mechanistic. To us [Sterner and Elser] this difference is somewhat philosophical." If science aspires to be more than a curve-fitting exercise for different equations (not to imply that the valuable Droop equation is mere curve fitting), understanding the mechanistic processes behind phenomena is essential and much more than a philosophical distinction.

Resources are used both as the construction material for organisms and as the power for doing the construction. The latter directly links stoichiometry and energetics, but even the former provides a link. Resources, regardless of their use by the organism, are not just fed to organisms in the field. Organisms must go out and acquire resources, and concurrently, they must avoid predators. The ability of organisms to do this is directly linked to their metabolic rates [10]. Sterner and Elser remark, "A focus on elements raises the question of how safe it is to ignore the biochemical arrangement of elements in organisms" and proceed to discuss the "architecture" of organisms and the utility of neglecting it. However, this completely avoids questions concerning the dynamics involved with transferring elements to locations throughout the body after ingestion. Once the resources are acquired, there are numerous chemical fluxes that serve to appropriately distribute elements within the body, and this is a complicated, dynamical process [11].

A feedback between energetics and stoichiometry exists at all levels of biological organization, but this does not mean that the two are alternative currencies. Considering each organism to be a giant molecule, reveals nothing about the dynamics or movement of organisms, molecules, or anything else. Considering the dynamics and movement of organisms and blood, without considering which resources must be obtained, which resources are limiting, and where these limiting resources are located, also misses an essential piece of the puzzle. Furthermore, knowledge of necessary resources and the energetics of how organisms move to obtain and process them does not address the fact that organisms may only be able to extract the resources from a small subset of the forms in which it occurs, due to issues of digestion, tooth or beak structure, or terrestrial versus aquatic abilities. Food webs should be extremely useful in answering these sorts of questions. By integrating these three approaches, a more complete and synthetic theory of ecological phenomena will be forged. Kooijman [12] has already begun work in this direction. Elser et al. [13] is a thoughtful essay that includes some ideas for relating ES and allometry, and Gillooly et al. [14] use an analysis that combines ES and energetics. Sterner and Elser devote parts of Chapters 7 and 8 to issues concerning food webs, and although their treatment raises many salient issues, it is mostly descriptive, and their analyses focus just on single links within food webs.

Combining ES, allometric and energetic theories, and food web ecology would be a tremendous advance in the understanding of ecological phenomena and should be a future direction pursued by all of these groups. Before this synthesis can occur, each of these areas must be understood separately. Sterner and Elser have completed a major portion of the exploration of ES. When discussing questions similar to the one raised in the title of this article, Sterner and Elser rightly respond, "What do you mean by just?" Their book is seminal and presents a clear, well-reasoned overview of ES, thereby providing the biological community with an essential piece to the puzzle of integrating micro- and macro-level biology.

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Biochemistry or biological chemistry, is the study of chemical processes within and relating to living organisms. A sub-discipline of both chemistry and biology, biochemistry may be divided into three fields: structural biology, enzymology and metabolism. Over the last decades of the 20th century, biochemistry has become successful at explaining living processes through these three disciplines. Almost all areas of the life sciences are being uncovered and developed through biochemical methodology and 2) Chemistry, physics, biology are sciences. Can you give the names of some other sciences? Geography, astronomy, geology are sciences.Â 8) What modern technologies do you know? Computers, the Internet, smart devices, robots, 3-D printers - these are just a few examples. 9) What in your opinion are the most important sciences nowadays? I think physics is the most important science because knowledge of physics helps us to understand the world that is getting more technological every single day. Biology is very important, too. It combines elements from both biology and chemistry. Biochemistry became a separate discipline in the early 20th Century.Â Biochemistry is the study of the chemical reactions that take place inside organisms. It combines elements from both biology and chemistry. Biochemistry became a separate discipline in the early 20th Century. Biochemists study relatively large molecules like proteins, lipids, and carbohydrates, which are important in metabolism and other cellular activities; they also study molecules like enzymes and DNA. Biochemistry, study of the chemical substances and processes that occur in plants, animals, and microorganisms and of the changes they undergo during development and life. It deals with the chemistry of life, and as such it draws on the techniques of analytical, organic, and physical chemistry. Biology incorporates both. This lesson is about some basic chemistry because when you know that, you will understand biology better. Let's start with the scientific definition of matter. Matter is anything that has mass and occupies space, meaning that all living things are matter. A whole field of science called biochemistry is devoted to studying the chemical parts of and processes in organisms. You, however, just need to know about some basic forms of matter that are part of every living thing: atoms, isotopes, ions, and chemical bonds. Let's start with the atom. Structure of an A