

system stability a major challenge for ecological research (McCann 2000). This challenge is unlikely to be met by the ecological theory if it confines itself to theoretically unjustified, axiomatic assumptions, like the assumption of $R \propto M^0$ within the metabolic approach of Brown et al. (2004), which, as we have argued, is empirically unsupported.

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A ONE-RESOURCE "STOICHIOMETRY"?

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The approach of Brown et al. (2004) might succeed or fail on two levels. On one level, it can be used as a purely statistical, predictive tool. Examples given by Brown and colleagues leave no doubt that temperature and body size "explain" (in the statistical sense) a great deal. We do need good predictive models for many reasons, one of them for incorporating more ecology and thus improving models of global change. The second, more difficult, level has to do with the reasons *why* those statistical predictor variables work the way they do, and *why* they are good predictors in the first place. The processes that Brown et al. propose—fractal scaling of distribution networks and thermodynamic kinetics of "metabolism"—may truly be the mechanistic basis for the observed patterns, but that, of

course, is less certain than is the existence of good statistical correlations.

Brown et al. view the "big three" variables to be temperature, body size, and stoichiometry. Temperature turns out to be approachable using decades-old formulations of Arrhenius, Boltzmann, and others. It is a shock that these models, which have been shown to work for "simple" biological functions such as oxygen consumption or even bacterial growth (Johnson et al. 1974), also do a splendid job with the more complex variables of standing stock and even diversity (which are not even rates). The critical and surprising result here is that so much ecological temperature dependence is described by the Arrhenius-Boltzmann equation, with near-constant activation energy. What that success itself means is a fascinating question, perhaps related to just what is "metabolism." In spite of their complexity, do one or a small number of core metabolic pathways regulate organism growth, so that

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those kinetics dominate the signals at these higher levels of observation? Body size relationships also have had a long history of study, and a family of power laws has been explored very thoroughly; this literature has been reenergized by the fractal distribution theory.

Given the success of models with just these two variables (e.g., Brown et al. 2004: Figs. 1–8), why might the third—stoichiometry—even be needed? At least in the statistical sense, not much is left to explain. But here the mechanistic sense must be considered. Rate limitation of growth (and therefore metabolism, as defined by Brown et al.) usually involves scarcity of some material(s) or resource(s). Therefore, although it *might be* that models without explicit mention of material resources can be good statistical tools (level one), to understand how these systems work and why they have the structure they do, we must explicitly include the rate-limiting steps and processes (level two). The fractal scaling of distribution networks might relate to movement of many kinds of materials, but it is very hard to reconcile a temperature–kinetic control of one step of metabolism with the fact that ecologists know that, in nature, organisms face multiple limiting constraints. Either many key biochemical steps have nearly identical temperature dependence, or the Boltzmann–temperature interpretation collides with current understandings about the multiplicity of limiting factors in nature.

What is the best way to incorporate material limitations with temperature and body size models into broad-scale, macroecology models? Or, stated more generally, what does a combination of metabolic control theory (see Fell 1997) and ecology look like? Brown et al. (2004) suggest one possibility. They incorporate a single term, linear with organism nutrient content, and generate a comprehensive model including stoichiometry (see also Brown et al. 2004: Fig. 9). Is this then the cardinal equation of macroecology,

$$X = M^{-3/4} e^{-E/kT} R + \text{error}$$

where M , E , k , and T are as in Brown et al. (2004), and X stands for some ecological parameter of interest, and R stands for “resource”? Might such an equation really “explain” (in both senses, statistical and mechanistic) so much?

We can ask if a single linear term in R is enough to do the job. If we correct for M and T , or let them be subsumed into the error term, and just explore how X varies with R , we now are simply asking how some parameter of interest varies with the amount of a limiting resource. Stoichiometrically, if there is but one potentially limiting reagent and all else remains equal, product yield will indeed be a simple linear function of the limiting reagent’s amount. However, when more than one reagent may limit a reaction, the expectation is more complicated. Over broad ranges of productivity and, hence, resource abundance, many ecological phenomena are nonlinear with productivity. Over broad

ranges, biomass often increases with the limiting nutrient via a saturating, not linear, function (Stern and Elser 2002). Work with even- and odd-link trophic models (Oksanen et al. 1981, DeAngelis 1992) suggests that responses to nutrient enrichment are dependent on trophic structure. Diversity may increase, decrease, or have some hump shape with respect to productivity (Rosenzweig 1995). There are many other examples of nonlinear resource effects, and these cast considerable doubt as to whether there is a Boltzmann-equivalent term with a single functional form when dealing with limiting substances.

Resources are a more heterogeneous lot than is temperature. They range from light and chemical energy to water and a handful of nutrient elements. In some contexts, space itself, or hiding or nesting sites are limiting. Often, more than one of these resources plays some role in controlling rates at any one time, and sometimes having a lot of one resource means that you can do with less of another. Also, do we mean resources *within* or *external* to the organism? Finally, in many contexts, these substances exist in a plethora of forms and the simple act of determining what pool of resources is involved provides some real limitation to universality of these measures.

Brown et al. (2004) sidestep all of this complexity when they assert: “Far from being distinct ecological currencies, as some authors have implied (Reiners 1986, Stern and Elser 2002), the currencies of energy and materials are inextricably linked by the chemical equations of metabolism.” First, a clarification: what is ecological stoichiometry about, if it is not about these inextricable linkages? Elser and I agree that resources are linked! The critical point is the nature of the linkage. The context in which the statement of Brown et al. is true is under fixed stoichiometric coefficients. With fixed stoichiometric coefficients (i.e., constant nutrient ratios), knowing one substance tells you everything about all substances, because they are all simple proportions of one another. At a sufficiently broad scale, such an assumption might be fine, in that the chemistries of different living systems are more alike than they are different: they all are based on C, N, P, etc., and all living things need proteins, phospholipid membranes, nucleic acids, etc. At some highly approximate level, living things do have a uniform stoichiometry. However, I say “might” because even with fixed coefficients, strategies for winning in a world of scarce “resource one” might not work for other resources. One need only think of the different strategies that plants need for obtaining light compared to soil resources. In lakes, systems under strong N limitation often become dominated by large, inedible species of cyanobacteria, whereas P or Fe limitation produces systems of very different structure and dominance by very much smaller cells; other trophic-level effects follow from these. Community and ecosystem structure and function are strongly controlled by the identity of the

limiting resources. The saturating functions of biomass and productivity alluded to in the previous paragraph are probably caused by shifts in the identity of limiting substances when one of them becomes very abundant. Lessons can be learned from dynamic consumer–resource models. A larger number of potentially limiting substances opens up opportunities for coexistence (Tilman 1982), a theoretical prediction recently elegantly shown empirically by Interlandi and Kilham (2001). When the number of resources increases from one to only three, entirely new, complex dynamics are possible (Huisman and Weissing 2001). For another example, several of my co-workers and I have done work at a variety of time and space scales on light gradients where the fixed stoichiometry of a simple, single-species population of herbivores creates positive relationships between primary and secondary productivity in one range of the experiment, but negative relationships in the other range (Urabe and Sterner 1996, Sterner et al. 1998, Urabe et al. 2002). At low light levels, both primary and secondary production are energy limited, whereas at high light levels, herbivores switch to material (phosphorus, we believe) limitation. These kinds of shifts—*driven by* element linkage, not *in spite of* element linkage, as a casual reading of Brown et al. might imply—are a signal that the identity of resources does matter a great deal; it will not generally work to boil them all down to a single, univariate measure. I hypothesize that for most “X,” it does matter whether the limiting resource is light, or nitrogen, or iron, or some combination of all of these.

Furthermore, for many important ecological questions, assumptions of fixed stoichiometry simply break down. Plants have different composition than animals, for example, and even within species, differing growth rates are associated with different chemical contents (Elser et al. 2003). Organisms do link the rates of uptake and use of separate resources, but in an adaptive, flexible way that responds to shifting stoichiometric ratios. Note, for example, the very different fluxes of C, N, and P in metabolic networks under different limiting factors in the study of Dauner et al. (2001). To what extent does the set of all possible resources contain redundant information, so that the set can be collapsed to a univariate measure? The claim by Brown et al. (2004) that one can overlook the multiplicity of limiting resources because they are all linked together, and are all linked to a single universal currency of energy is an echo of a previous era in ecology, where bioenergetics was the hoped-for organizing concept (Slobodkin 1972, Morowitz 1992, Hairston and Hairston 1993). It was not, and we are beyond that.

Incorporation of materials into broad-scale macroecology models need not be distastefully complex, or so idiosyncratic as to resist all generality. I think that there is quite a bit more work to do and that ultimately, even at broad scale, we will almost always need a multivariate, not a univariate, perspective on resources.

Biology has evolved fascinating responses to the optimization problems that the shifting availability of these resources creates.

Again, so that this message is not lost: I'm a fan of the Brown et al. (2004) approach. Macroecology has produced a set of amazing, inspiring, and, I believe, also extremely useful microbes-to-monsters plots. But much of the important work ahead of us in ecology is at finer spatial and temporal scale. I also believe it to be the case that the utility of macroecology models will be proportional to the scale of interest. Tools are most useful when applied to the right job.

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COMMENTARY ON BROWN ET AL.'S "TOWARD A METABOLIC THEORY OF ECOLOGY"

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What Brown has called "a metabolic theory of ecology" is powerful and exciting in scope, accomplishments, and promise, . . . and controversial in some of its details. Let me confess that I am a spectator on the sidelines of the field, rather than an active player. Indeed, I am uncomfortable about commenting because most of my information comes from personal friendships with players on both sides of the controversial part, and from privileged information in manuscripts that journal editors send me from a misinformed sense of my expertise. Accordingly, I shall take the easy path that commentary offers, and make this a public statement of tentative thoughts rather than making any attempt at a scholarly piece. In particular, I shall cite a small selection of papers deliberately construed to support my points, rather than giving the literature the review that it deserves. I hope that friends will remain friends, and that editors will revise their impression of my wisdom.

It is hard to say enough about the excitement and interpretive potential of a theory that unites the explanation of patterns of scaling from intracellular physiology to community dynamics, and that allows measurements throughout those scales to give useful approximations of numbers needed to address global issues and to pose interesting evolutionary questions. Fortunately, the canonical proponents have done an excellent job of advertisement, mostly in the pages of *Science* and *Nature*, . . . and they have responded to those of their critics who have also reached the same venues. I cheerfully endorse most of what I have read there. But there are still some important points that leave me uneasy, along with students and colleagues at home and abroad.

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The first point is the empirical question of whether the primary scaling factor is $\frac{2}{3}$ or $\frac{3}{4}$, when for example, Fig. 1B of Brown et al. (2004), a log–log plot of normalized temperature-corrected metabolic rate against body mass, has a best-fit value of 0.71, . . . exactly midway between $\frac{2}{3}$ and $\frac{3}{4}$. This same point is made more carefully and more forcefully by Dodds et al. (2001). The variety of contexts in which scaling factors are modulo $\frac{1}{4}$ rather than modulo $\frac{1}{3}$ is encouraging (Brown et al. 2004 and references therein), but it would be worthwhile to review this literature to separate definitive tests from instances in which the $\frac{3}{4}$ scaling of metabolism with size entered as an assumption at the outset.

There is also the semi-theoretical question of whether there need be an "either–or" choice. The naïve version of the theoretical argument for exactly $\frac{2}{3}$ assumes that the fundamental organizing geometry of organisms is Euclidean and spherical; resources are acquired by surfaces and used by volumes, but the distribution of these resources can complicate the analysis. The original argument for exactly $\frac{3}{4}$ assumes that the fundamental geometry of organisms is fractal (West et al. 1997). In the $\frac{3}{4}$ theory, resources are also acquired by surfaces, but the theory explicitly and exactly optimizes a fractal network for distribution of these resources. Here I go into hazy analogical thinking, but it strikes me that different modalities of distribution and different shapes of organisms could favor the applicability of different balances of the theories . . . and a scaling rule with power $\frac{3}{4}$, $\frac{2}{3}$, or something in between.

The third point is the paradox that the $\frac{1}{4}$ -power scaling rule works so well over a range of sizes and shapes of organisms whose explicit resource-distributing networks are variously fractal, tree-like but not fractal, and not even tree-like. This strongly suggests that the fractal assumption that lies at the heart of the devel-