

## ENERGY PARTITIONING BETWEEN DIFFERENT-SIZED ORGANISMS AND ECOSYSTEM STABILITY

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### INTRODUCTION

The metabolic approach to ecology presented by Brown et al. (2004) stems from the seminal work of West et al. (1997). They hypothesized that material transport within living beings is organized such as to minimize the scaling of total hydrodynamic resistance through vascular networks. Based on this assumption, the organismal metabolic power  $P$  was theoretically predicted to scale with body mass  $M$  as  $P \propto M^{3/4}$ . By additionally assuming that organismal metabolic processes accelerate with temperature in the same manner as individual biochemical reactions, a temperature correction factor was added to this scaling:

$$P \propto M^{3/4} e^{-E/kT}. \quad (1)$$

At the organismal level, these results were criticized on both theoretical and empirical grounds (e.g., Dodds et al. 2001, Chen and Li 2003, Makarieva et al. 2003, 2004a). In particular, Makarieva et al. (2004a) showed how the application of the metabolic approach to the ontogenetic growth problem (West et al. 2001) resulted in violation of the energy conservation law. In this short commentary, however, we will focus on the potential of the metabolic approach to explain patterns in population and ecosystem dynamics.

### LINKING INDIVIDUAL AND ECOSYSTEM ENERGETICS: THE LOGIC

The relationship linking individual to population energetics is:

$$NP = R \quad (2)$$

where  $N$  (number of individuals per square meter) is the population density of individuals of a given body size,  $P$  is the rate of individual energy use (Watts per individual), and  $R$  (Watts per square meter) is the area-specific rate at which the population consumes energy resources from the environment. Eq. 2 is obvious and essentially identical to Eq. 9 of Brown et al. (2004), if the latter is related to unit area and Eq. 1 is taken into account.

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A variable of critical importance in both ecology and organismal biology is body size. A successful biological theory is expected to be able to predict the dependence of individual metabolic power on body size on the basis of some fundamental assumptions pertaining to organismal morphology and biochemistry. For example, the assumptions that underlie Eq. 1 can be classified as being of this kind.

Similarly, an ecological theory will be able to successfully predict the scaling of population energy use,  $R$ , with body size only if it identifies and takes into account some fundamental principles of an ecological community's organization. As long as the basic principles of the metabolic approach are restricted to the organismal level, none of them is relevant to the ecosystem-level question of whether larger organisms should claim larger, smaller, or equal shares of an ecosystem's productivity than smaller organisms. The metabolic approach stretches to the ecosystem scale by making a simplifying assumption that if  $R$  is independent of body size, then the scaling of population density  $N$  with body size will be determined by the scaling of individual metabolic power.

However, it is unclear whether there is a dependence of  $R$  on body size. If there is such a dependence, what are the fundamental causes and consequences? Although the metabolic approach refrains from answering this question, a growing body of evidence suggests that the scaling of  $R$  with body size varies predictably with the degree of ecosystem stability, thus providing clues to this central problem of modern ecology (McCann 2000).

### ENERGETIC DOMINANCE OF SMALLER ORGANISMS IN STABLE ECOSYSTEMS

There is some evidence showing that the smaller organisms claim larger shares of an ecosystem's productivity in relatively stable ecosystems. For example, Sprules and Munawar (1986) studied the scaling of phytoplankton population density  $N \propto M^\beta$  in 67 sites forming a stability gradient: from self-sustainable, oligotrophic ecosystems of open ocean and large lakes to highly unstable, "flushing" eutrophic ecosystems of shallow lakes and coastal zones that receive major discharges of nutrients and contaminants. They found that the scaling exponent consistently increases from

$\beta \approx -1.16$  in stable ecosystems to  $\beta \approx -0.76$  in unstable ones. These results indicate that in stable ecosystems smaller organisms consume a larger proportion of the ecosystem's energy flux than larger ones, whereas in unstable ecosystems the energy partitioning among different-sized organisms becomes more equitable. Biddanda et al. (2001) confirmed the emerging pattern and showed that in the most stable aquatic ecosystems, bacteria (the smallest organisms) fully control the energy use, accounting for 91–98% of total ecosystem's respiration. In highly eutrophic waters, the share of bacterial respiration decreases to 9%, indicating the growing role of larger heterotrophs in less stable ecosystems.

In an extensive survey of phytoplankton (6339 seawater samples), Li (2002) grouped the phytoplankton community into three size classes; the difference in cell mass between the smallest and the largest classes is about three orders of magnitude ( $M_{\text{small}}/M_{\text{large}} \sim 10^{-3}$ ). The pattern characterized by Li (2002) was that the ratio between population densities of the smallest and the largest cells grows with increasing degrees of the ecosystem's stability, the latter being estimated by the degree of eutrophy and intensity of water mixing (Li 2002: Figs. 2a and 3a, respectively). In stable ecosystems, the smallest cells outnumber the largest ones by about four orders of magnitude,  $N_{\text{small}}/N_{\text{large}} \sim 10^4$ . This allows the estimation of the scaling exponent  $\beta$  as  $\beta \sim \log_{10}(N_{\text{small}}/N_{\text{large}})/\log_{10}(M_{\text{small}}/M_{\text{large}}) \sim -4/3$ . Again, we are faced with energetic dominance of the smallest organisms in stable ecosystems. In unstable ecosystems, the difference between  $N_{\text{small}}$  and  $N_{\text{large}}$  is about one order of magnitude only, producing an approximate slope of  $\beta \sim -1/3$ .

When the differences in the degree of stability of studied ecosystems are ignored and all phytoplankton data are pooled in one plot (Li 2002: Fig. 2b), one obtains  $\beta = -0.78$ . The ecological meaningfulness of this result (interpreted by Brown et al. [2004] as supportive of their approach) is questionable. Depending on the degree to which stable and unstable ecosystems are represented in the cumulative data set, the scaling exponent can vary within broad margins, being more a function of data assortment procedure than reflecting properties of real ecosystems.

Turning to terrestrial ecosystems, Damuth (1993) reported 39 values of scaling exponent  $\beta$  for a total of 557 mammalian species grouped according to habitat types, which he classified into closed (forests, woods) and open (savannahs, grasslands). Thus defined, open ecosystems appear to be more unstable both in terms of biomass fluctuations (e.g., Van de Koppel and Prins 1998) and environmental degradation processes like soil erosion (Lal 1990). The 39 scaling exponents listed by Damuth (1993) vary from  $-1.4$  to  $+0.42$ , with a mean of  $-0.71$ . However, if one analyzes the scaling exponents separately in closed vs. open ecosystems, it is observed that the closed (more stable) ecosystems

are, on average, characterized by a significantly more negative scaling exponent  $\beta$  than are open (less stable) ecosystems, ( $-0.88 \pm 0.31$  vs.  $-0.50 \pm 0.40$ , mean  $\pm 1$  SD;  $P < 0.01$ ), consistent with the results for aquatic ecosystems.

#### PERSPECTIVES FOR THEORETICAL RESEARCH OF THE ALLOMETRIC $R$ — $M$ SCALING

These analyses suggest that the potential of the  $R$ — $M$  scaling as an informative indicator of ecosystem stability is tangible and calls for a serious scrutiny (Makarieva et al. 2004b). There are straightforward arguments justifying the direct relevance of the energy use patterns to ecosystem stability and opening the way for theoretical research (Gorshkov et al. 2000). In accordance with the statistical law of large numbers, several small organisms consume the same energy flux in a more balanced manner than does one large organism, thus lowering the risk of both underexploitation or overexploitation of the available resources and reducing fluctuations of a community's biomass and nutrient-cycling processes. This is like dividing your money among several investments; return will be stabilized and loss minimized. Ecosystems where energy use is dominated by smaller organisms (but not for terrestrial plants, as we will discuss) are therefore expected to be more stable than ecosystems where large organisms consume considerable portions of a community's energy flux.

The large apparent size of many plants (e.g., trees) is due to a large amount of metabolically inactive tissues (wood) that do not participate in energy conversion processes (Makarieva et al. 2003). Instead, the photosynthetic power in terrestrial plants is exerted by units of relatively small size: leaves and needles. In contrast to rigidly correlated organs within an animal body, different photosynthesizing units of the same plant are correlated only very weakly. This allows plants to make use of the law of large numbers and to stabilize the flux of primary productivity, in the same manner as numerous small heterotrophs are able to stabilize the flux of decomposition. Our prediction is therefore that, similar to the way in which the smallest phytoplankton (unicellular photosynthesizing units) dominate energy flux in stable aquatic ecosystems (Li 2002), the major flux of solar energy in stable terrestrial ecosystems should also be claimed by plants having the smallest photosynthesizing units. For example, stable late-successional stages in boreal forests are dominated by conifers that have much smaller photosynthesizing units (needles) than grasses and deciduous trees of early-successional stages (Whittaker 1975). We believe that studying the nature and size of photosynthesizing units (rather than the currently emphasized apparent plant size) will yield important insights into how terrestrial ecosystems are organized.

The increasing anthropogenic pressure imposed on natural life-support systems makes the problem of eco-

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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