CAN FUNCTION AT THE ORGANISMAL LEVEL EXPLAIN ECOLOGICAL PATTERNS?

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Introduction

Brown et al. (2004) propose that "first principles of chemistry, physics, and biology" can be used to link the function of individual organisms to ecological processes. By arguing that metabolic rate controls ecological processes at all levels of organization, from the individual to the biosphere, they propose that a metabolic theory of ecology can be a powerful unifying principle. Because the scope of their vision is so broad, and because the models on which these ideas are based are controversial, the papers by Brown, West, and their collaborators (cited in Brown et al. 2004) have stimulated lively intellectual debate within and between disciplines, and have spawned new research in a number of different fields. By stirring the pot with their broad-reaching ideas, Brown and his colleagues are making a significant contribution to the advancement of both physiology and ecology, whether or not their theories turn out to be correct or general in their applicability.

Mechanistic vs. Phenomenological Models

Mathematical models in ecology and organismal biology can be mechanistic or phenomenological. The strengths and limitations of these two approaches have been debated (reviewed by Schoener 1986, Koehl 1989). Mechanistic models assume that particular processes determine the behavior of a system, and build a quantitative description of how the system works based on these underlying mechanisms. An example of such an approach is the modeling cited by Brown et al. (2004) of how materials are distributed within organisms by branching transport systems. This mechanistic approach shows how uptake and transport rates of resources within an organism can limit its metabolic rate, and predicts that whole-organism basal metabolic rate should scale as body mass raised to the ¾ power. In contrast, other models are phenomenological descriptions of a system. For example, the regression equations describing the data in Figs. 1–5 in Brown et al. (2004) provide quantitative expressions of how the systems being plotted behave, showing *that* processes

occur at particular rates, rather than *how* those rates are produced. Although phenomenological models provide an effective way of organizing observations to reveal patterns and of making predictions about the performance of systems for which we have data, mechanistic models can be powerful tools for developing our understanding of how a system works.

Studying Organism-Level Function to Understand Ecological Processes

Brown et al. (2004) argue that metabolic theory can help to explain the patterns observed in many ecological processes. This approach is part of a long, although sometimes ignored, tradition of studying how processes operating at the level of individual organisms can determine the properties of populations, communities, and ecosystems (reviewed in Koehl 1989). The philosophical underpinnings of using such a reductionist approach in ecology were discussed by Schoener (1986). To put the metabolic theory of Brown et al. (2004) in perspective, we will mention a few examples of earlier attempts to use basic laws of physics and chemistry to explain defined aspects of organismal-level function and the ecological consequences of those functions.

Theories of heat and mass transport have been coupled with analyses of physical aspects of the environment to reveal constraints on distributions and interactions of organisms. This approach has been used to explain ecological phenomena ranging from predator–prey interactions (Porter et al. 1975) to reproductive strategies (Kingsolver 1983). More recently, this biophysical approach has been used to explore some of the ecological consequences of global climate change (e.g., Grant and Porter 1992, Helmuth et al. 2002). A different reductionist approach, focusing on the function of heat-shock proteins, is also being used to explore how thermal tolerance relates to biogeographic patterns of species distributions (e.g., Tomanek and Somero 1999).

Foraging ecology provides some other examples of using basic principles of chemistry and physics to relate the function of organisms to ecological processes. Chemical reactor theory has been used to understand the kinetics of digestion by guts of different designs, and the functional insights emerging from such analyses have been used to explain ecological patterns in

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foraging strategies (e.g., Penry and Jumars 1987). Similarly, basic rules of aerodynamics have been used to explain the mechanical and energetic constrains on foraging by flying animals, providing functional explanations of ecological patterns, such as the absence of folivory among flying animals (Dudley and Vermeij 1992), or the different foraging strategies used by hummingbirds living at low vs. high altitudes (Feinsinger et al. 1979).

Basic principles of fluid and solid mechanics have also been used to analyze the susceptibility of benthic and intertidal marine organisms to physical disturbance (e.g., Denny 1999, Koehl 1999), an important process in structuring many communities. A scaling rule that emerged from the physics was hypothesized to explain the observation that organisms on wave-swept shores are small, but subsequent research showed that this physical constraint is usually not what limits the size of those organisms (Denny 1999). However, investigation of the hypothesis led to many discoveries about the mechanical design of marine organisms, the spatial and temporal patterns of physical stresses in wave-swept habitats, and the interplay of mechanical design and life history strategy in variable environments (reviewed in Denny 1999, Koehl 1999).

The metabolic theory of ecology of Brown et al. (2004) is much more ambitious than any of the examples just cited. Earlier applications of organismal functional biology to address ecological problems have focused on specific processes, such as foraging or disturbance. In contrast, Brown et al. (2004) point out the applicability of the metabolic theory to a wide range of ecological issues, from life history to population interactions and ecosystem processes. Therefore, as organismal biologists and ecologists debate and test the assumptions and predictions of the metabolic theory, its impact no doubt will be far greater than that of the earlier, more narrowly focused links between basic chemistry and physics with ecology.

The Model Has Stimulated New Synthesis and Research in Organismal Biology

An earlier attempt to provide a mechanistic explanation for the scaling of metabolic rate with body size, the elastic similarity model of McMahon (1973), was controversial and spawned a flurry of research activity and new discoveries about the biomechanics of skeletal design in animals and plants, and of locomotion. The controversies swirling around the models proposed by Brown and collaborators seem to be having a similar effect on the field of physiology. For example, debate about one of the underlying assumptions of the model, that the terminal branches of a biological transport network (such as capillaries, or mitochondria) are invariant in size, has led to re-examination of experimental data about the morphology and performance of cardiovascular systems (Dawson 2001) and about mito-

chondrial structure and function (Porter 2001) in animals of different sizes.

Physiologists studying metabolic pathways have objected to the idea that a single process, transport of materials through hierarchical, fractal-like networks, limits metabolic rate (e.g., Darveau et al. 2002). Although the alternative model proposed by Darveau et al. (2003) is seriously flawed (e.g., Banavar et al. 2003), we should not ignore the body of experimental work showing that a variety of interrelated physiological and biochemical processes all contribute to limiting the rates of ATP synthesis and use in cells. These processes, some of which are important in controlling the overall metabolic rate of an animal when it is at rest while others play a larger control role when the animal is active, scale differently with body size.

Another assumption of the metabolic theory of Brown et al. (2004) is that natural selection has acted to minimize energy expenditure within a biological transport system. This assumption flies in the face of long-standing arguments that complex physiological or morphological systems that perform a variety of different functions that affect fitness, and that evolve in changing environments, are not likely to show optimization of a single criterion (reviewed in Dudley and Gans 1991). Nonetheless, optimization models have proven to be powerful tools in guiding empirical research (reviewed in, e.g., Koehl 1989), and the models of Brown and colleagues are clearly serving as a catalyst for interesting new discussions and experiments in physiology.

If the Model Is Phenomenological, Will It Still Be Useful to Ecologists?

Even if the mechanisms responsible for the size dependence of metabolic rate that have been hypothesized by Brown et al. (2004) turn out to be inconsistent with future experimental evidence, the allometric equations produced by their model may still prove to be useful descriptions of how the rates of various ecologically important processes vary with body size and temperature. However, several cautionary notes should be mentioned about their central theme that metabolic rate varies with body mass raised to the ¾ power. Whether an exponent of ¾ can be statistically distinguished from one of ⅔, given the scatter in the data, has been examined by a number of investigators (e.g., Dodds et al. 2001). Furthermore, although the universal model describing the metabolic rate data spanning 20 orders of magnitude in body mass (from tiny microbes to large mammals) has an exponent of ¾, the exponents for specific clades of organisms within the composite data set can be higher or lower (e.g., Riisgård 1998, Dawson 2001, Dodds et al. 2001). Perhaps more worrying is the observation, for a variety of invertebrates, that the metabolic rates of young, rapidly growing individuals scale with body mass raised to higher exponents than do those of slowly growing older stages and adults

(Riisgård 1998). Because of ontogenetic changes and species differences in temperature sensitivity, Rombough (2003) also cautions against using models that are based on comparisons across different life stages and types of organisms to make predictions about responses of particular species.

Brown et al. (2004) are the first to point out that variation of the data not explained by their metabolic theory provides clues to factors other than body size and temperature that can affect metabolic and ecological processes, and they list some ecological patterns that probably do not have a metabolic explanation. Nonetheless, the simple expression that they have developed to predict the combined effect of size and temperature on whole-organism metabolic or production rate (Brown et al. 2004: Eq. 4) is a useful way of summarizing observations spanning a vast range of organism size, thereby providing a powerful tool for making predictions about various ways in which the metabolism of individual organisms might determine important ecological processes. Whether or not all of the aspects of the metabolic theory of Brown et al. (2004) turn out to be right, this theory will make significant contributions to our understanding of how organisms and ecosystems work because it is focusing attention on the importance of metabolism to ecological processes, is inspiring so much new research, and is serving as a catalyst for communication between organismal biologists and ecologists.

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