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METABOLIC ECOLOGY: LINKING INDIVIDUALS TO ECOSYSTEMS

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INTRODUCTION

Metabolism sustains life and controls the growth, reproduction, and longevity of living entities. As Brown et al. (2003, 2004) show, the ''fire of life'' is central to our understanding of patterns and dynamics at all levels of biological organization. However simple, it took 70 years to substantiate this statement; from Kleiber's (1932) conclusion that the mass of the organism raised to the ¾ power was the best predictor of metabolism to the model of West et al. (1997, 1999) that explains this relationship as a consequence of fundamental attributes of biological networks. This work paved the way to the Metabolic Theory of Ecology (MTE) outlined by Brown et al. (2004). We think that the theory outlined by Brown and co-workers represents a breakthrough that endows ecological sciences with a fresh perspective and a quantitative theory to tackle ecological complexity, from individuals to ecosystems. However, as with any new theory in science, it can be improved and refined.

THEORETICAL UNDERPINNINGS OF THE METABOLIC THEORY

The ultimate success of the emerging metabolic theory of ecology (Brown et al. 2003, 2004) depends to a large extent on whether it is truly a mechanistic theory based on first principles, or whether, like so many other theories in ecology, it is fundamentally phenomenological.

The theory is based on what we call a *general metabolic equation* (GME):

$$P = F(M, T, R) \tag{1}$$

where P is the rate of some metabolic process, which is some function F of body mass (M), temperature (T), and the concentration of the materials (R) needed to fuel and maintain metabolism. Following Gillooly et al. (2001) and Brown et al. (2003), who argue that the effects of M and T are multiplicative, and assuming that the effects of concentration of materials is also multiplicative, Eq. 1 becomes

$$P = B_0 M^{3/4} \exp(-E/kT) f(R) \tag{2}$$

where B_0 is a constant, E is the ''activation energy of metabolism,'' k is Boltzmann's constant, and f is a heretofore unspecified function. In the strictest sense, Eq. 2 is not a mechanistic equation; rather, it is statistical mechanical. By this we mean that the functions used in the equation emerge from the properties of the ensemble of molecules that comprise the physical unit that is generating metabolic energy (typically, an organism).

The statistical mechanics of the body size effect has a strong theoretical justification (West et al. 1997, 1999). However, the effect of temperature on metabolic rate as modeled by Gillooly et al. (2001) uses the exponential form given in Eq. 2 with relatively little theoretical justification. In statistical mechanics, the term $\exp(-E/kT)$, often referred to as the ''Boltzmann factor,'' is proportional to the fraction of molecules of a gas that attain an energy state of E (Schrodinger 1941, Pauling 1970) at an absolute temperature T. To react, the molecules must possess ''activation energy,'' that is, they must collide with one another with sufficient energy to change their state (Pauling 1970). Temperature increases the proportion of molecules that attain sufficient energy to react. Hence, the Boltzmann factor can be used to describe the rate of the reaction. This heuristic approach for using the Boltzmann factor in describing metabolism would be extremely difficult to derive in a mechanistic fashion, considering the very large number of different biochemical reactions that comprise metabolism. We should therefore consider the Boltzmann formulation used by Gillooly et al. (2001) as an approximation of a much more complicated functional relationship between metabolism and temperature.

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The concentration of resources (R, or stoichiometry) is the third component of the GME. However, its relationship to metabolism lacks an analytical expression, which prevents the MTE from making explicit how it interacts with T and M in affecting individual or population attributes. At first glance, it is not entirely clear how to include stoichiometric effects in the GME (the function f in Eq. 2). However, it is reasonable to expect that f should have a multiplicative effect on metabolism, and because organisms often show a ''functional response'' in reaction to changes in the abundance of a limiting resource, f could be modeled as a Michaelis-Menten function (Real 1978, Maurer 1990). If the ingestion rate is proportional to the metabolic rate, then one would expect that metabolic processes, such as biomass production, would show a similar sort of saturating response and that the Michaelis-Menten equation could be used. There is, in fact, experimental evidence that such responses do occur (Giebelhausen and Lampert 2001).

Interestingly, each term in the GME relates to processes whose primary mechanistic effects occur on different spatial and temporal scales. Temperature has its primary effect at the molecular scale, by influencing the rate of molecular movements through the parts of the metabolic machinery that depend on passive diffusion. Body size affects metabolism at a larger scale via constraints derived from fractal-like distribution networks. Finally, stoichiometric effects occur at the scale of the whole organism in interaction with its environment. This feature of the GME bequeaths the MTE with a desirable property: cross-scale integration.

We think that the MTE still requires refinement and further articulation. However, there is sufficient evidence to suggest that the MTE may provide a fundamental theoretical link between what we know about physical systems and what we know about ecological systems.

THE MTE AND THE STRUCTURE OF LOCAL ECOLOGICAL SYSTEMS

The MTE rests heavily on individual-level phenomena, which by aggregation allow one to make predictions upon whole-system patterns, processes, and rates. It is striking how strong the fit between predicted and observed patterns usually is, considering that most data on individuals and species populations come from different places around the world, with different biogeographic histories, disturbance regimes, and productivities. It might seem striking that a theory that is, for the most part, free of ecological context (Marquet 2002) can be so powerful. However, this is to some extent expected, given that the theory focuses on ''bulk properties'' of ecological systems that are less affected by local ecological idiosyncrasies. The MTE is a theory about central tendencies in ecological phenomena that predicts how the average individual, population, and ecosystem should behave and be structured. Although many would say that the interesting biology is in the scatter and that such a thing as an average ecological system does not exist, but just different realizations of the average system, it is important to recognize that unless we have a mechanistic theory that provides us with an expected baseline, we are not able to identify any deviation worth explaining in the first place. In this sense, both approaches are interesting and complementary.

We have no doubt that the MTE can provide many insights on fundamental ecological questions at local, regional, and global scales. In particular, at a local scale: (1) it provides an explanation of why, in a local community, population density should scale as $M^{-3/4}$ within trophic levels and as M^{-1} across them, a pattern that has been empirically observed in aquatic ecosystems (e.g., Marquet et al. 1990); and (2) it predicts that population energy use should be independent of body mass within trophic levels, but should decrease at higher trophic levels. Further, the amount of energy that moves from one level to the next should be affected by the characteristic metabolic scaling of the species in each trophic level. However, there are other important patterns within local communities, such as species abundance and species size distributions, to which the MTE could be applied, and that, in principle, it should be able to explain, since they affect and are affected by energy fluxes.

A close examination of the MTE shows that several predictions can be made regarding the effects of resource supply upon equilibrium abundance and how abundance should vary across resource and temperature gradients for metabolically different organisms. In particular, Eq. 9 of Brown et al. (2004) states that the equilibrium number of individuals or carrying capacity (K) in a local community should vary as $K \propto RM^{-3/4}e^{E/kT}$. Further, because metabolic rate (P) is $P \propto M^{3/4}e^{-E/kT}$ (Brown et al. 2004: Eq. 4), we can express carrying capacity as

$$K \propto \frac{R}{P}. \qquad (3)$$

Eq. 3 implies that, given a fixed amount of resources R, organisms with lower metabolic demands will achieve higher equilibrium population numbers or carrying capacities. For any given temperature, mass-corrected metabolism is higher in some groups than others (see Brown et al. 2004: Fig. 1a); thus, everything else being equal, carrying capacities should follow the inverse pattern, decreasing from plants to endotherms. In other words, there should be a negative relationship between the intercept of the mass-corrected relationship between metabolic rate and temperature and the total abundance of metabolically different organisms in a given community. This relationship would be even stronger if we were to consider trophic structure and the fact that energy or resources become more limiting farther up in a food chain. Because organisms with

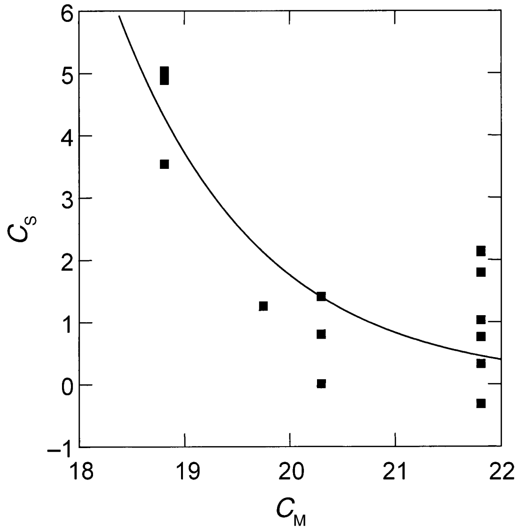

FIG. 1. Relationship between area-corrected number of species expressed as the intercept of the species–area curve (C_S), and mass- and temperature-corrected metabolic rate expressed as the intercept of the mass-corrected metabolic rate vs. temperature (C_M). Data are for the Channel Islands, Sea of Cortes, and West Indies, and include plants, reptiles, land snails, birds, and mammals. Within each system, we only use islands for which data on all groups were available. The solid line corresponds to the best-fit exponential equation $C_S = \exp(15.6 - 0.75C_M)$.

lower metabolic demands are more likely to sustain higher population numbers, they will, on average, support more populations of different species above the minimum size required for persistence. Thus, higher species richness should be expected for groups with lower metabolic needs. This argument, similar to the one traditionally used to explain the effect of energy availability on species diversity (e.g., Wright 1983, Currie 1991), predicts that in a local community, species diversity in any given metabolic group should be inversely correlated with metabolic demands. Our analysis shows (Fig. 1) that there is indeed a negative relationship ($F_{1,12} = 67.07$, $P < 0.001$, $r^2 = 0.84$) between the area-corrected number of species (represented by the intercept of the species–area relationship C_S) and the temperature- and mass-corrected metabolic rate (represented by the intercept of the mass-corrected metabolic rate vs. temperature, C_M) for metabolically different groups of organisms in islands. That this relationship exists indicates the heuristic value and predictive power of the MTE. It is especially significant because many other factors besides metabolism affect the number of species on islands. In addition, resource supply rate is not the same for all species groups because of their trophic position, yet the pattern seems to be robust to this.

The main point that we want to make with this analysis is that the MTE can provide fruitful insights and testable predictions to advance our understanding of the structure of local ecological systems. However, further development and testing of this approach will require the collection of more and better data on the richness, density, biomass, and metabolic activity of species within local ecosystems. We need standardized data on biodiversity, which will allow for rigorous tests of the MTEs predictions at a local scale. This might be a daunting task, but to advance in our understanding, we need comprehensive and complete analyses of ecological systems. The 13 years and millions of dollars invested in sequencing the human genome can help to save lives, but to characterize ecological systems in terms of their total species composition, abundance, and function, or the ''econome,'' can help to save the human enterprise on earth.

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