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THE VALUE OF NULL THEORIES IN ECOLOGY

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Reactions to the metabolic theory of ecology (MTE) proposed by Brown et al. (2004, this issue) are likely to fall into the following categories.

Enthusiastic support.—MTE persuasively demonstrates how a few simple, well-founded physical principles concerning energy and temperature can explain an impressive fraction of the natural variability in organism-level productivity, developmental rates, mortality, and other life history traits, and in ecosystem-level carbon turnover, population density, and resource partitioning. This is particularly impressive, given that the theory assumes nothing about many of the concepts that most ecologists had probably thought to be essential input to any comprehensive theory, such as reproductive strategies, succession, stability, food webs, spatial distribution of individuals and species, stochastic and cyclic temporal variability, the influence of disturbance regimes, and organism behavior (including its role in determining effective environmental temperature). MTE will be a major component of a parsimonious theory of nearly everything in ecology. Here at last is an agenda for ecology.

Limited admiration.—MTE explains parsimoniously a very limited subset of ecosystem traits, but it cannot hope to say anything useful about most of the things that we care about in ecology, such as reproductive strategies, succession, stability, food webs, spatial distribution of individuals and species, stochastic and cyclic temporal variability, the influence of disturbance regimes, and organism behavior. A parsimonious theory of nearly everything in ecology is, at best, far in the future. In the meantime, there are also critical questions in applied ecology. What will ecosystems look like under global warming? What sustains and what threatens ecosystem services? How can ecosystems be restored and managed? How can we best design reserves? We do not have the luxury of waiting indefinitely for some future comprehensive theory of ecology to answer these practical questions; unfortunately, MTE will not help us here.

Skeptical dismissal.—The unexplained variances in MTE are large and all those ignored aspects of ecology (listed in *Limited admiration*) would have to be ingredients in any theory that would convincingly explain even just the limited things that MTE purports to explain. One needs to consider nearly everything to explain anything in ecology; parsimony and ecology are immiscible.

In some fields of science, responses to proposed new radical advances are more tightly bounded than this. Nearly all physicists accept the goal of a ‘‘theory of everything’’ (TOE), and they may well achieve that goal if ‘‘everything’’ is understood to mean all of the physical phenomena that occur at subatomic and cosmological scales. Less clear, however, is whether any such theory could also encompass emergent physical phenomena at intermediate scales, where we live.

Brown et al. (2004), making the case for *Enthusiastic support*, suggest that MTE, in combination with population genetics and evolution, can indeed provide the basis for an ecological TOE. Although the successes of the physics-based MTE are unlikely to dispel skepticism about the possibility of a physics-based TOE for biological phenomena, could MTE plus evolution and genetics conceivably do the trick, as Brown et al. suggest? More generally, what would an ecological TOE look like? Is it possible in ecology, and if so, how would we get there from here?

An ecological TOE would provide, at the very least, an accurate and predictive understanding, across all ecologically interesting spatial and temporal scales, of the distribution and abundance of organisms in interaction with each other and their environment. Unlike physics, however, ecology has to deal with contingency. A theory that beautifully describes the distribution and abundance of organisms at the spatial scale of a meadow and the temporal scale of an NSF grant would also have to scale up spatially to deal with the geologic contingency of continent edges and temporally to encompass global warming. Because of that, most ecologists would probably answer our rhetorical question ‘‘Is a TOE possible?’’ with a resounding ‘‘no.’’ I tend to agree, although hesitantly, because I think we can go farther than we have—by embracing, rather than dismissing, approaches such as MTE.

Progress in science comes from the interplay of enlarging possibilities (envisioning options for how nature might work) and narrowing those options (empirical testing). Clearly stated null hypotheses and null models help to accomplish the latter because their failures permit us to identify situations in which a non-null alternative is needed. Failure is what drives science forward.

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MTE also will surely fail if pushed too far. The unexplained variances in the figures in Brown et al. (2004) are undoubtedly just a preview of what will arise as the theory attempts to widen its domain of applicability. A recently proposed ‘‘neutral theory’’ of ecology (Hubbell 2001) is probably also ‘‘wrong,’’ and, indeed, instances of its failure to accurately describe patterns in nature have been suggested (Condit et al. 2002, Clark and McLachlan 2003). If ecology were physics, this might be considered sufficient evidence to dismiss such theories entirely, but given the parsimony of both of these theories, that would not promote progress in ecology.

Theories are of most interest when the ratio of the number of predictions that they make to the number of assumptions and adjustable parameters in the theory is large. The MT of Brown et al. (2004) and Hubbell’s neutral theory are examples of theories based on very few assumptions and very few adjustable parameters, yet they are potentially capable of predicting a wide range of phenomena.

Suppose that the interrelationships among many types of phenomena are reasonably well predicted by a theory, yet each phenomenon is, separately, better predicted by some ad hoc explanation or cobbled-together model than by that theory. If those successful explanations or models each require a different set of assumptions or parameters for each comparison, then it may be premature to reject the theory. In other words, the insight afforded by the theory into the interconnections among phenomena previously thought to be disconnected ought to trump slightly better fits afforded by ad hoc explanations.

As a natural extension of the idea of null hypotheses and null models, I suggest that the notion of a ‘‘null theory’’ is of value in ecology. By a null theory, I mean a set of relatively few and clearly stated assumptions that can be used to make a comprehensive set of falsifiable predictions about a wide variety of issues in ecology. In contrast to null models, which address specific ecological questions, null theories attempt to provide a single coherent set of answers to many questions. Without a null theory, those questions might have been considered independent of one another; a null theory would unify them under one framework. Each of those questions might be addressed with a null model, but in typical applications of null models, a unique null model is tailored to each question. Thus, there are many ways to create models of what nature might be like if it were random. For example, random models for the species–area relationship could involve random assignments of individuals, random assignments of species, or random shuffling of census quadrats. If a common set of assumptions about randomness were used to create an array of null models that together addressed a comprehensive collection of questions, then the array of models would fit our notion of a null theory; indeed, it might be called a random null theory. But surely there is no reason to restrict null theories to those that are random.

A decade ago, a null metabolic theory of ecology could have been constructed around the body-mass-to-the-two-thirds-power scaling law, because that is a null expectation based on surface : volume ratios. All of the equations that Brown et al. (2004) discuss could have been written then, with ⅔ replacing ¾, and an equally comprehensive theory developed. Although such a theory was never constructed, falsification of the two-thirds-power metabolic rule paved the way for what Brown et al. have accomplished.

Just as it is the failures of null hypotheses and null models that most enlarge our understanding, so it is the mismatches between collections of data and null theories that make null theories useful. We should expect null theories to ‘‘fail,’’ just as we expect null hypotheses and null models to fail under many circumstances. However, by examining the instances in which a null theory fails to describe all of the data, and in particular looking carefully at the patterns in the discrepancies, we can establish more firmly the existence of mechanisms in nature that explicitly violate the simple assumptions underlying the theory, and thereby learn a great deal about how nature works. Whether the outcome of this is an improvement of the null theory or the development of a whole new theoretical construct may be less important than is the added insight into the mechanisms at work in ecology.

Eventually, the patterns of success and failure of null theories may suggest the outlines of an ecological theory of nearly everything. Such a theory, rising from the ashes of null theories, might even be considered just another null theory—it won’t really matter what we call it. The important thing is that it be falsifiable, and that it parsimoniously predict many more phenomena than it has parameters to adjust. It would be exciting if its base were broader than physics.

MTE is certainly parsimonious and its predictions match observations in nature to a remarkable degree over many orders of magnitude of variation in biological parameter space. At the same time, it appears so far to be able to address only a modest fraction of questions of concern to ecologists. It is a fine example of a null theory in that (1) it ties together multiple phenomena within one set of extremely simple assumptions, and (2) departures from its predictions can inform us about other factors besides metabolism and temperature that are at work in ecology. In the search for a TOE, or at least a more comprehensive null theory of ecology—one that would improve, and expand the scope of, MTE—Brown et al. should look forward to MTE’s failures with enthusiasm.

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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):

$$P = F(M, T, R) \qquad (1)$$

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

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

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

$$K \propto \frac{R}{P}. \tag{3}$$

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

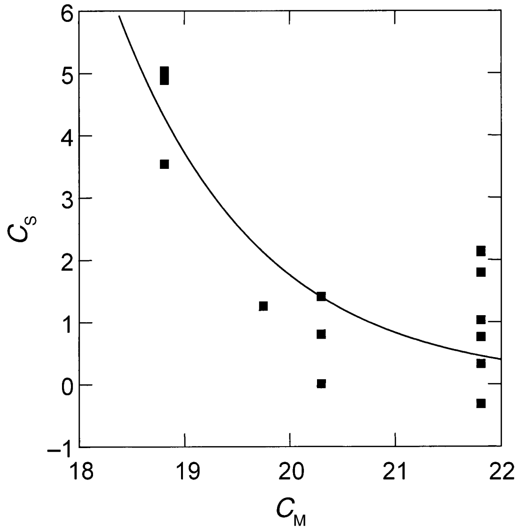

FIG. 1. Relationship between area-corrected number of species expressed as the intercept of the species–area curve (C_S), and mass- and temperature-corrected metabolic rate expressed as the intercept of the mass-corrected metabolic rate vs. temperature (C_M). Data are for the Channel Islands, Sea of 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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DOES METABOLIC THEORY APPLY TO COMMUNITY ECOLOGY? IT'S A MATTER OF SCALE

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When the seven of us read and discussed Brown et al. (2004), there were moments of insight, of enthusiastic consensus, and of strongly divergent opinion. We agreed that the empirical relations and scaling theory of Brown et al. (2004) hold great appeal because of their power to abstract and simplify some of the complexity of nature. The earth harbors several million species, each having unique aspects to its morphology, physiology, and life history. A fundamental goal of science is to simplify and explain such complexity. Brown et al. (2004) do just this. They have documented robust patterns relating the body size and temperature of species to their basal metabolic rate; plotted on log–log scales, these empirical functions are well fit by straight lines. Moreover, they have used these scaling relations to make numerous predictions about other patterns and processes, thus greatly extending an approach that already had been shown to have considerable power (e.g., Huxley 1932, McMahon and Bonner 1983, Peters 1983, May 1986).

One question that generated considerable debate among us was whether metabolic scaling theory represents a fundamental mechanism that has shaped life on earth, or whether it is a description of correlated patterns of as yet poorly known causes. Brown et al. (2004) hypothesize that scaling relations have a fundamental basis that comes from the universality of metabolic activation energy and of the fractal branching networks that determine resource distribution within individual organisms. This elegant hypothesis intrigued us. It brought to the forefront questions raised when we spent a semester last year reading many of the papers upon which Brown et al. (2004) is based. Are slopes really multiples of ¼, or is this just the best small-whole-number ratio approximation? How might mechanical constraints, which may scale differently with body size (e.g., McMahon and Bonner 1983), contribute to these patterns? Larger organisms must, after all, have a higher proportion of their mass in woody stems or bones or other support tissues that have low metabolic costs but high costs for their construction. Might growth rate (McMahon and Bonner 1983) be the controlling variable, rather than metabolic rate? Or might body size and metabolism be easily measured surrogates of the actual traits that determine species interactions and abundances? After all, within the framework of community ecology, it is traits such as competitive ability, dispersal, and predator defenses, and not metabolism and body size, that directly determine which species win or lose, which persist and speciate, or which go extinct.

Of the various predictions that Brown et al. (2004) derived, perhaps the most surprising to community ecologists may be that within a trophic level, species of vastly different body sizes should get equal shares of their limiting resources. Simply put, all of the herbivorous arthropods within a 10-fold range of body sizes should consume roughly the same amount of food as all of the herbivorous mammals within a 10-fold range of body sizes. This suggests that, on average, species should be getting approximately equal-sized ''slices'' of the limiting resources for which they compete. Does this mean that there are limits to similarity that lead to relatively even packing of competing species along gradients? If so, what mechanisms could cause this, and how would community ecologists test this prediction in the field?

Another prediction made by Brown et al. (2004) is that higher temperatures in the tropics may lead to faster metabolism, shorter generation times, and thus faster rates of speciation, accounting for the latitudinal biodiversity gradient. This is an interesting alternative to other hypotheses for latitudinal diversity gradients, such as the hypothesis that diversity is lower toward the poles because of higher rates of extinction from a less stable climate and glaciation, or that there are fewer ways to survive and grow in progressively colder habitats because life is a water-based (not an ice-based) process. The metabolic approach may also offer insight into *r* vs. *K* selection. Brown et al. (2004) suggest that species selected for fast population growth rates would necessarily have higher metabolism, smaller body size, and higher temperature. *K*-selected species are not necessarily selected for slow population growth rates, but this may be a consequence of selection for predation resistance or resource use efficiency, which often are

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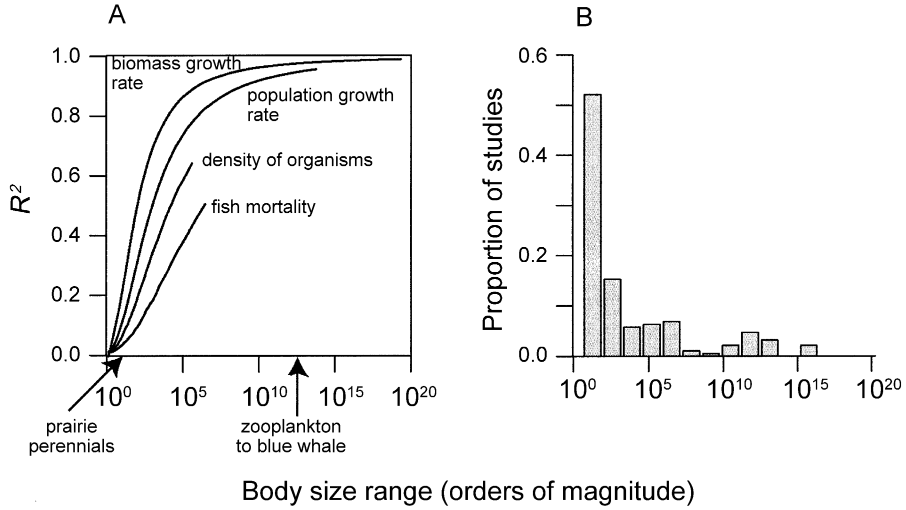

FIG. 1. (A) Predictive power of body size. We used the data in Brown et al. (2004) and simulations to explore the relationship between the range of organism sizes studied and the explanatory power of size. First, we calculated the unexplained variance around the regression lines in Figs. 2, 3, 5, and 6 of Brown et al. (2004) using the slope, number of sample points, and R^2 of relationships between size and organismal biomass growth rate, fish mortality, population growth rate, and population density. Next we calculated R^2 for simulated data sets of species covering narrower ranges in body size. To do this, we randomly sampled 100 ''species'' from a uniform distribution of body sizes between a specified size range. We next generated response variables for each species (i.e., predicted biomass growth rate, fish mortality, population growth rate, and population density) using observed slopes and intercepts and estimated variance. Finally, we used simple linear regressions to calculate the R^2 between organism size and the process of interest. We repeated this 200 times for each of 200 equally distributed size ranges (from 0 to the size range used in Brown et al. [2004]). Lines connect the mean R^2 values for each size range. (B) Size range of studied organisms, based on papers in the journal *Ecology*. We examined all recent papers in *Ecology* that referenced specific organisms or types of organisms (190 papers from issues 1–9, volume 84, 2003). We tabulated the organisms described in each paper, assigned them to size classes, and then determined the orders of magnitude size range (difference between the $\log_{10}$ estimated mass in grams of the largest and smallest organisms). The horizontal axis is organism size range; the vertical axis is the number of papers that studied species in that range.

enhanced by larger body size. These examples again suggest that the robustness of scaling relations may come not from their direct mechanistic relevance, but from the ability of a single variable, body size, to abstract a suite of correlated traits when making comparisons across broad scales. Whatever the underlying mechanisms might be, the predictions in Brown et al. (2004) demonstrate that scaling relations can be a powerful way to reduce dimensionality and to abstract some of the complexity of nature.

We had considerable debate, though, about the breadth of applicability of metabolic scaling theory. It is clear that scaling relationships hold best when examining patterns across a wide spectrum of body sizes (such as from microbes to megafauna) within an ecosystem, continent, or the globe (Fig. 1A). Because detailed, mechanistic treatments of the interactions among all species in an ecosystem are impossible, abstraction is essential. Metabolic theory may, for instance, allow better parameterization and understanding of ecosystem nutrient and energy fluxes caused by the large size range of species, such as from bacteria to sequoias, in ecosystems.

It is less clear, however, if metabolic scaling will prove useful in addressing many of the central questions of population and community ecology, such as population regulation and controls of coexistence, of species relative abundance patterns, and of diversity (e.g., Tilman 1999, Hubbell 2001, Sterner and Elser 2002, Chase and Leibold 2003). Much of community ecology pursues these questions by exploring the mechanisms of local interactions among often similar-sized species. An analysis of the relations reported by Brown et al. (2004) shows that the strength of the correlation between various ecological processes and body size diminishes as the range in body sizes decreases (Fig. 1A). The variation in species traits that seems so small when comparing bacteria to elephants looms large when comparing beech trees to oaks, or a prairie grass with a prairie forb.

The data presented in Brown et al. (2004) show that organisms of similar body size can have >20-fold differences in their traits. Moreover, these data show that body size explains only 2–20% of the observed variance in predicted responses when species fall within a 10-fold range in body sizes (Fig. 1A). Scaling relations thus have increasingly limited predictive ability in comparisons of organisms of more similar size. Such comparisons, however, are a central part of ecology; roughly half of a sample of papers recently published in *Ecology* focused on only one species or on several species that were within an order of magnitude in body mass (Fig. 1B).

Much of our recent work has focused on how the identity and number of grassland plant species interacting in a local neighborhood influences processes such as primary productivity. The species that we study are herbaceous perennials that differ by less than ¾ of an order of magnitude in adult body size. In our biodiversity experiment (Tilman et al. 2001), the number of plant species explained 37% of the variance in total biomass in 2002 (linear regression: $N = 168$, $P < 0.0001$). Species number and functional group composition explained 68% of this variance in total biomass (multiple regression: $F_{28, 139} = 10.4$, $P < 0.0001$). The scaling approach, which works so well across large scales of body size, predicts at most 12% of the variance in various ecological processes for the range of body sizes in our study (Fig. 1A). Thus, on our scale, plant functional traits and plant diversity are much more important than body size. Conversely, our work on the local neighborhood effects of diversity gives little, if any, insight into the potential relationship between diversity and productivity on geographic scales where species come from different species pools and where other factors, such as climate, soil, and plant traits, are correlated and change simultaneously.

An analogy and an insight into the power and limits of the scaling approach come from a consideration of another complex system with which we are familiar: computers and related digital devices. Like an organism, a silicon circuit has a metabolism, measured by how much electricity it consumes. The volume of information that a digital device can process, the airflow needed to cool it, its reliability and longevity, and other properties are all a function of its size and, thus, its metabolism. Such macroscopic properties of digital devices are essential for whole-system tasks like designing power supplies and writing warranties. The relationship of metabolic scaling to ecology is analogous; it gives significant insights into *macroscopic* ecological patterns and predicts other patterns and processes across large scales and whole systems. Many different functions, however, can be performed by digital devices with identical sizes and energy demands, just as many different ecological roles can be performed by organisms of similar size and temperature. It is these ecological roles, not metabolisms per se, that determine species coexistence and abundances and ecosystem functioning.

One of the mysteries of scaling theory is why it has such great explanatory power at large scales, but not at small scales. The vast diversity of alternative roles that can be filled by organisms of equal body size probably accounts for the ≥20-fold variation observed around the mean scaling trend. Perhaps when comparisons are made across larger body size ranges, the constraints of body size and its correlates increasingly predominate over the interspecific trade-offs in resource use, dispersal, and disease resistance that are the more proximate determinants of species interactions and abundance. If, as seems likely, scaling relations do have their basis in metabolic activation energy, fractal branching, and structural constraints, then these forces must be acting at a deeper level, such as by defining body size and metabolic constraints that shaped the form and functioning of life as single-celled organisms evolved into multicellular plants and animals.

In summary, Brown et al. (2004) have provided a new window through which we can ponder nature. The simplicity and potential generality of the view that they provide is welcome; ecology as a discipline cannot afford to wallow in special cases. Metabolic theory provides a unique and insightful macroscopic perspective, one that appears to have great utility for comparisons of organisms of vastly different sizes. The possible causes of these patterns, the applicability of the approach to studies of similar-sized organisms, and the potential synthesis of mechanistic and macro-ecological approaches are challenges that are likely to be pursued for years to come.

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USING THE METABOLIC THEORY OF ECOLOGY TO PREDICT GLOBAL PATTERNS OF ABUNDANCE

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Introduction

Studies of abundance (N)—the number of individuals of a taxon in a given area and time—have traditionally focused on the dynamics of local species populations over generations. The conceptual basis of this approach has been demographic (i.e., dN/dt = birth rate − death rate + migration rate). Brown and colleagues (2004) in introducing the Metabolic Theory of Ecology focus on a different question: how should abundance in entire communities at equilibrium vary as we move about in space and time? Their answer, the Metabolic Theory of Abundance (henceforth MTA), uses a mass balance approach (Odum 1971, Kaspari et al. 2000). It has the potential to guide work on this subject for years to come.

Brown and colleagues ask us to picture abundance not as the net arrival of mortal, reproductive units with legs, but as the number of co-occurring energy transformers. K is the equilibrial abundance of individual ectotherms limited by the same resources, of similar size, and that experience the same environment. This formulation of K may be strange to ecologists from the demographic school. But the body size, trophic habits, and abundance of higher taxa and functional groups have shown themselves worthy of study (e.g., Siemann et al. 1996).

In the MTA, K varies with resource availability, access to those resources, and the way the resources are divided up among individuals:

$$K \sim [R]M^{-3/4}e^{E/kT}. \tag{1}$$

$[R]$ is the resource supply rate. Brown and colleagues focus on energy, which places us on the familiar grounds of metrics like Net Primary Productivity (in grams of carbon per square meter per year). The MTA predicts that K should increase linearly with $[R]$, ceteris paribus, although no data are presented to support this prediction. The ability of living cells to do metabolic work, and hence to access available $[R]$, is a negative decelerating function of environmental temperature T (in Kelvin), E is the activation energy (~0.63 eV; 1 eV = 96.49 kJ/mol), and k is Boltzmann's factor. This prediction holds for trees, and more messily, for a collection of animal ectotherms (Allen et al. 2002). So far we have described the amount of energy captured by our taxon or trophic group. To find K, this energy must be divided up based on the individual's capacity to use it. Whole-organism metabolism rate scales to $M^{3/4}$, so K should be a negative decelerating function of M (Damuth 1981, Enquist et al. 1998). In sum, the MTA focuses on how available energy is harvested and respired. It is thus explicitly bottom-up (Power 1992); mortality from predation is assumed to be negligible or at least invariant with M, T, and $[R]$.

The MTA is a clear offspring of macroecology (Brown 1995), meant to be tested at broad spatial and taxonomic scales spanning a broad range of M, T, and $[R]$. It does what good theory should do. It builds from first principles, addresses the shape of long-standing patterns (Blackburn and Gaston 1997), predicts other non-intuitive patterns (Damuth 1981), and would even change the way we plot our data (e.g., by a priori correcting for mass and temperature). Finally, it pulls together $[R]$, T, and M, three factors that have often been treated in isolation. So what challenges and opportunities do we face as we gear up to test the MTA?

Testing the MTA—Quantifying Abundance

The MTA focuses on how energy is captured and partitioned by individuals. Because available energy $[R]$ attenuates each time carbon-rich molecules are harvested, excreted, and respired, Brown and colleagues (2004) are careful to specify that abundance ideally refers to all members of the same trophic group (an alternative focus on taxon abundance would come with the assumption that the proportion of $[R]$ harvested by that taxon is invariant across sites). It is thus not surprising that much of the early work in MTE (Enquist et al. 1998, Enquist and Niklas 2001) has mined global plant data sets. Plants occupy an unambiguous trophic group. Plants are also easy to count. But where are the data sets for *consumer* abundance across global gradients of $[R]$ and T?

Global abundance data sets should be a basic goal of ecology. Such data are scarce, however, because mobile organisms are hard to count and relative abundance estimators are hard to standardize across habitats (Southwood 1978). Luckily, terrestrial brown food webs (detritus, microbes, microbivores, and their pred-

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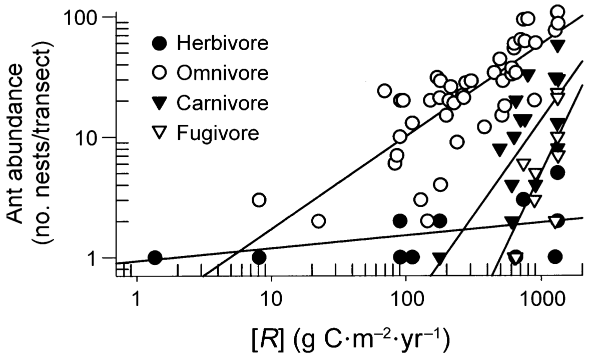

FIG. 1. Studies of 49 ant communities arrayed along the productivity gradient ([*R*] is the resource supply rate) show that trophic groups accumulate at different rates with net aboveground productivity (Kaspari 2001). Note the log–log scale.

ators) address many of these limitations (Copley 2000): they occur everywhere from the poles to the tropics; they can be quantified in 1-m^2 plots (Coleman and Crossley 1996); and the taxa (the microbivores in a patch of litter may include ciliates, rhizopods, nematodes, collembola, oribatids, millipedes, and ants) span a range of *M* (Moore et al. 1988). I am confident that the MTA will foster the collection of new abundance data in the same way that quantitative biodiversity theory (Rosenzweig 1995, Hubbell 2001, Allen et al. 2002) is promoting studies of species richness.

Ecological stoichiometry constitutes a second challenge to the MTA. Individuals regularly confront elemental deficits beyond carbon (Mertz 1987). For example, primary consumers from the green and brown food webs (herbivores and decomposer microbes, respectively) appear especially likely to face stoichiometric imbalances (Kaspari and Yanoviak 2001, Sterner and Elser 2002, Davidson et al. 2003). How can an energy-based theory deal with environmental deficits in elements like N, P, and Mb?

One solution is to quantify the energy costs of those activities required to meet elemental deficits. The herbivores that travel to find limiting sodium-rich plants (Belovsky 1978) or that compensate for defensive compounds in their food (Berenbaum and Zangerl 1994) are both doing so by catabolizing sugars. If so, the slope of the [*R*]–*K* curve should be an inverse function of the group's stoichiometric deficit. For example, soil ant abundance increases as NPP$^{3/4}$ (net primary production, as yet uncorrected for *M*; *personal observation*) across the New World (Kaspari et al. 2000). Different ant trophic groups, however, accumulate differently (Fig. 1; see Kaspari 2001). Herbivore abundance increases slowly with NPP, predators and fungivores more quickly. Omnivores have an intermediate slope. A working hypothesis is that ant herbivores have low [*R*]–*K* slopes because they must work harder than predators to meet their stoichiometric deficits.

TWO VARIATIONS ON A THEME OF METABOLISM AND ABUNDANCE

The MTA characterizes environments by their mean [*R*] and *T*. Both, however, become more seasonal moving from the equator toward the poles. The MTA may thus ignore a key reality of ectotherm life: metabolic costs and productivity vary seasonally. For example, in all but the most productive biomes (i.e., wet tropical rain forests), the same NPP can be squeezed into a few months or spread out over the year (contrast tundra with mediterranean shrubland). In a seasonally cold biome where NPP is concentrated in the summer months, ectotherms can eat when food is plentiful and respire less of that energy away when winter comes. In contrast, an ever-warm environment extracts year-long respiration costs. Somewhat counterintuitively then, environments with winters can provide a metabolic refuge and enhance *K* compared to aseasonal environments with the same mean [*R*] and *T* (Kaspari et al. 2000). Seasonality matters. This may be another reason for the observation of Allen et al. (2002) that *N*'s for ectotherms, but not endotherms, decline toward the warm tropics.

Finally, holding [*R*] and *T* constant, *K* is predicted to decrease as $M^{-3/4}$. But why should *M* vary from place to place? Intriguingly, two of the leading models for body size gradients have [*R*] and *T* as their independent variables. Where predation risk is high, the optimal body size should decrease with NPP (Kozlowski 1992). Ectotherm size at maturity has long been shown to decrease with *T* (Atkinson 1995). If community body size gradients are real, this suggests that where *M* is a function of *T* and [*R*], the MTA may be overparameterized!

PROSPECTS

The MTA challenges community ecologists to look beyond our traditional focus on species toward the properties of higher taxa and functional groups. It challenges us to pursue fundamental natural history—size, abundance, trophic relationships—for all taxa at a global scale. As ecologists, we obviously have some distance to go before we understand even the basic patterns of abundance. The MTA provides one interesting and quantitative road map for the journey ahead.

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AN ILLUSION OF MECHANISTIC UNDERSTANDING

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INTRODUCTION

James Brown and his colleagues (2004) are at the forefront of a recent resurgence of interest in explaining the ubiquitous relationships between the body size of organisms and everything that they do (West et al. 1997, 1999). Here, Brown et al. argue that their general allometric model for metabolism, expanded to include temperature effects and stoichiometric constraints, offers a mechanistic framework to unify ecological thinking. Body size, temperature, and stoichiometry have long been recognized to drive many aspects of biology and ecology; thus, in general terms, the approach is familiar and reasonable. The claim that a metabolic theory could link ecology as a whole is interesting and challenging, but surprisingly poorly justified by Brown et al. (2004). We discuss two main problems with their argument.

DO WE KNOW THE MECHANISM BEHIND ALLOMETRIC RELATIONSHIPS? DO WE NEED TO?

The claim of a mechanistic basis to the metabolic theory of ecology is premature. There is currently no agreement on the mechanism(s) that generates allometric relationships. The network model proposed by West et al. (1997, 1999) focuses on the metabolism of individuals and assumes optimal distribution of energy through a fractal network, but this approach has been strongly criticized (Dodds et al. 2001). Several other models, based on very different processes and assumptions, also have been proposed (life history optimization, Kozlowski and Weiner [1997]; internal metabolite transportation, Dreyer and Puzio [2001], Ban-

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avar et al. [2002]; resource partitioning, Kooijman [2000]; chemiosmosis and life history evolution, Demetrius [2003]; the multiplicity of biochemical pathways, Hochachka et al. [2003]), but have not yet been compared critically. We should not be lured by the illusion of mechanistic understanding.

Moreover, no single allometric exponent is generally accepted. We disagree with the dogmatic use of a ¾ exponent by J. Brown and colleagues, to the point of correcting body mass in their analyses by this exponent. A unique ¾ exponent for allometric relationships of metabolic rates is currently undefensible, both on theoretical and on empirical grounds. In contrast to West et al. (1999), most of the recent alternative models of metabolic rate allometry suggest a range of possible exponents. Allometric exponents are expected to vary with the mass dependence of survivorship (Kozlowski and Weiner 1997), thermal regulation (≥⅔ for endotherms, ≤1 for ectotherms; Kooijman [2000]), balance between metabolic supply and demand (although ¾ is an optimal value; Banavar et al. [2002]), level of activity (basal vs. maximum metabolic rate; Hochachka et al. [2003]), and variability in population size (⅔ for species with rapidly fluctuating population sizes, ¾ for species with stable population sizes; Demetrius [2003]). Deviations from a ¾ exponent also have been found empirically. Recent analyses of very large data sets for birds and mammals support a ⅔ exponent (Dodds et al. 2001, White and Seymour 2003). Similarly, the exponents for population density–body size relationships vary among communities, and the overall relationship has an exponent significantly steeper than −¾ (Cyr et al. 1997*a*, *b*). The energy equivalence rule and the suggestion that trophic transfers explain the steep slopes measured in pelagic systems were specifically tested with an extensive data set, and discounted by Cyr (2000). Despite more than a century of work on this topic, the jury is still out on the magnitude of the allometric exponents.

This lack of mechanistic understanding does not deter from the potential importance of a metabolic theory of ecology. The existence and the strength of allometric and of temperature relationships are well established. The question raised by Brown et al. is really whether these powerful relationships account for ecological interactions at all other scales of interest, from population to community to ecosystem ecology.

HOW DO WE CROSS SCALES WITH A METABOLIC THEORY OF ECOLOGY?

A second, more serious problem arises in extending this metabolic framework to scales of increasing complexity. The approach proposed by Brown et al. (2004) is largely justified by the existence of macroecological patterns. These general relationships are very useful in providing a broad context to interpret data, but are not meant to provide precise predictions under specific conditions. Unless these models are greatly refined (and this is not a trivial matter of adjusting coefficients), they will be of little use to population and community ecologists. Few population ecologists would be satisfied with values of $r_{\max}$ or K (sensu Brown et al. (2004), i.e., mean population density) that span several orders of magnitude. This is not to say that a metabolic approach cannot work.

A metabolic framework, if modeled at the right scale, can be powerful. More refined physiological models do exist, and have been applied successfully in population ecology (Kooijman 2000, Nisbet et al. 2000). These models assume that organisms have clear constraints on how they can partition resources. The energy and material available to them (i.e., assimilated from their food) are divided among metabolism (for maintenance of tissues and basic functions), somatic production, and reproduction, and the input of energy and material must match any change in biomass plus outputs. The dynamic energy and material budget models proposed by Kooijman (2000) and Nisbet and colleagues (2000) account for the effects of body size, temperature, and stoichiometry, and can be used to predict various aspects of population dynamics. These models offer a powerful framework to test theoretical issues in population ecology, but are much more complex than the models proposed by Brown et al. (2004) and require careful parameterization for individual species. There are no shortcuts, yet.

The extension of these physiological models to more natural conditions and to communities is less obvious. Careful tests of the dynamic budget models have shown that even simple aspects of more natural systems (e.g., low food availability, low food quality) can alter the dynamics of a population in very significant ways (e.g., Nelson et al. 2001). It is well recognized that population dynamics are context dependent, and will change depending on interactions with other species (competitors, predators) and with the environment (e.g., Chase et al. 2002). The dynamics of natural populations are unlikely to simply follow from constraints on the energy budget of individual organisms, but must take into account a suite of external factors. Increasing the complexity of models beyond a few variables is generally counterproductive, so a simple extension of these physiological models to natural populations or to communities may not be possible. A different modeling framework may be required.

Community ecology is replete with general patterns (e.g., species–abundance curves, species–area curves, diversity–productivity relationships, density–body size relationships, community size spectra, food web structure, predator–prey size ratios). The mechanisms generating these relationships are still uncertain, but there is no doubt that the availability of energy and material affects the biomass, productivity, and diversity of organisms in communities. However, measuring how much resource is really available to organisms is a difficult task, and there is no reason to believe that species of all sizes have equal access to resources (as suggested by the energy equivalence rule). Even apparently simple questions have baffled ecologists for decades. For example, how is energy divided among species in a community and how efficiently is it transferred through food webs? Models of energy and material transfer need to be tested on communities of organisms that actually live in the same environment. Global allometric relationships built from data collected in many different communities, such as those used by Brown et al., include too many other sources of variability (Cyr 2000) and are useless for this task. A metabolic framework that would integrate community ecology is promising, but remains to be tested in a convincing manner.

The approach proposed by Brown et al. (2004) is most easily justified for ecosystem ecology, and has indeed been applied successfully in this context. There are two reasons for this. First, the currencies of interest (energy, nutrients, and other chemical elements) are the same. Second, the error associated with predictions from general allometric models is not unrealistically large compared to errors associated with many ecosystem variables. Ecosystem ecologists commonly have to use low-precision measurements and estimates when dealing with large spatial and temporal scales. When more precise predictions are necessary, the use of more detailed models (e.g., Kooijman 2000) is possible. There are many good examples of the effectiveness of an allometric/metabolic approach in ecosystem ecology (e.g., Vanni 2002).

Ecologists have long recognized the strength of allometric relationships and the ubiquitous role that temperature plays in biology. By proposing a metabolic theory of ecology, Brown et al. challenge us to explore the implications of these well-known relationships at all scales. This approach has already shown promising results in theoretical population ecology and in ecosystem ecology, but the case remains to be made convincingly for populations under more natural settings and for communities. The mechanisms proposed by Brown et al. (2004) are interesting. However, the conceptual unification of ecology is more likely to depend on our ability to relate variables and processes across scales of increasing complexity than on a mechanistic interpretation of patterns.

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METABOLIC RATE OPENS A GRAND VISTA ON ECOLOGY

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INTRODUCTION

Wouldn't it be nice if ecologists could use a few simple parameters, such as the size of an organism and the temperature at which it operates, to predict individual mortality, population growth rate, species diversity, or ecosystem production? Boldly going where few ecologists tread, Jim Brown seeks a grand synthesis in ecology that transcends specific organisms and environments. For much of the past decade, he and his colleagues have worked to develop unifying ecological principles from basic physical and chemical constraints on organisms.

In this new paper, Brown et al. (2004) open a new vista on ecology by (1) nominating metabolic rate as the essential integrator of organismal biology, (2) providing a bold new synthesis of the effects of mass and temperature on metabolic rate, and (3) proposing a number of hypotheses about the influences of mass and temperature on aggregate ecological phenomena ranging from whole organisms to community structure to ecosystem processes. In this commentary, we address each of these contributions, emphasizing the second.

METABOLIC RATE AS THE INTEGRATOR AND ORGANIZER OF DISPARATE THEORY

Brown et al. (2004) begin by defining metabolism as the biological processing of energy and materials. Although it is difficult to measure field metabolic rates, much evidence suggests that basal metabolic rate is governed by resource uptake, chemical transformation, and the distribution of transformed resources throughout the body. Metabolic rate is therefore both a simple and valuable integrating concept and a key linkage between physical and chemical processes and the individual, community, and ecosystem. If we can measure it, metabolic rate gives us a holistic measure of individual performance unconfounded by issues of allocation to growth and reproduction.

A particularly novel component of this paper by Brown and colleagues is their deliberate challenge to the long-standing tradition of considering energy and materials as separate currencies for examining ecological questions (e.g., Reiners 1986). Instead, Brown et al. argue that energy and materials ''are inextricably linked by the chemical equations of metabolism'' (p. 1774). This alternative viewpoint will definitely provoke spirited discussions among ecosystem ecologists and may spark a careful reconsideration of the heretofore independent research on energy and materials.

THE COMBINED EFFECTS OF MASS AND TEMPERATURE ON METABOLISM

After making their argument for the primacy of metabolic rate, Brown et al. (2004) provide an equation for metabolic rate as a function of body size (as indexed by mass; West et al. [1997], Enquist et al. [1998]) and temperature (as summarized by the Bolzmann factor; Gillooly et al. [2001]). Their equation predicts individual metabolic rate (MR) from the average mass (M, in grams) and the average operating temperature (T, in Kelvin):

$$\mathrm{MR} = aM^{3/4}e^{-E/(kT)} \qquad (1)$$

where a is a scaling constant, E is the activation energy, and k is Boltzmann's constant.

We believe that Eq. 1 has the potential to revolutionize the field of ecology. However, we consider it to be a working hypothesis for two reasons. First, the equation needs to be more explicitly rooted in quantitative derivations from axiomatic properties of physical and chemical systems. Second, the fundamental hypotheses generated by this theory must face stronger and more appropriate empirical tests. We will detail each of these concerns.

Concerns about the derivation

Eq. 1 is the cornerstone of Brown et al. (2004), but a full derivation of the form of the equation has not yet been provided. The partial derivation provided by Gillooly et al. (2001) suggests that the equation rests on the following logical steps.

1) Whole-organism metabolic rate (MR) is defined as the sum of the rates of energy produced by individual biochemical reactions R_i:

$$\mathrm{MR} = \sum_i R_i. \qquad (2)$$

We believe that this link between MR and its mechanistic underpinnings requires explicit support from the biochemical literature, especially because the behavior of a chain of reactions is usually better described by the behavior of the limiting reaction than by the sum of the reactions in the chain (e.g., Voet and Voet 1995).

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2) Each individual reaction depends on the product of three components: the concentration of reactants (c_i), the fluxes of reactants (f_i), and the kinetic energy of the system (k_i):

$$R_i \propto c_i f_i k_i. \tag{3}$$

This unsupported assertion is logically necessary to allow the simple form of Eq. 1, but can kinetic energy really be isolated from the fluxes of reactants in a chain of reactions? We would appreciate references to confirm this claim.

3) To justify the independence of mass and temperature in Eq. 1, Gillooly et al. (2001:2249) state that the concentrations and fluxes ''contain the majority of the body mass dependence,'' (an apparent empirical result, not shown in the paper), such that their product scales with body mass as $M^{3/4}$ for each reaction:

$$R_i \propto (M^{3/4})k_i. \tag{4}$$

This substitution rests on the work of West et al. (West et al. 1997, Enquist et al. 1998), who predicted that whole-organism metabolism is constrained by the effective surface areas across which resources are exchanged with the environment. We would like to see the substitution of $M^{3/4}$ for ($c_i f_i$) for each reaction explained more carefully, because different reactions do have different mass dependencies (e.g., Hochachka et al. 2003) and the assumption of equal mass dependencies is what makes it possible to separate the mass and temperature effects on metabolic rate (see [5]).

4) Assuming that k_i ''contains the dominant temperature dependence'' (Gillooly et al. 2001:2249; an apparent empirical result not shown) and is therefore proportional to the Boltzmann factor for each reaction, we obtain:

$$R_i \propto (M^{3/4})(e^{-E_i/(kT)}). \tag{5}$$

5) Finally, by assuming that the activation energies E_i are identical for all reactions in the summation, Gillooly et al. (2001) factored out the mass and temperature terms to obtain:

$$\begin{aligned} \mathrm{MR} = \sum_i R_i &\propto \sum_i [(M^{3/4})(e^{-E/(kT)})] \\ &\propto (M^{3/4})(e^{-E/(kT)}). \end{aligned} \tag{6}$$

That activation energies differ among the component reactions of metabolism is supported by data provided in Gillooly et al. (2001) and Brown et al. (2004) indicating a range of E_i's for different organisms and properties.

Thus, we believe that the available literature does not yet provide the links to physical and chemical first principles to support the independence of mass and temperature effects on metabolic rate implied by Eq. 1.

Concerns about the empirical analyses

At some point in its development, new theory needs to be confronted with real-world measurements (Hilborn and Mangel 1997). We have some concerns about the data and statistical methods used by Brown et al. (2004). First, field metabolic rates (FMR) for whole organisms are difficult, if not impossible, to measure in most organisms, so most tests of the metabolic theory have used laboratory estimates of basal metabolic rates (BMR). This is justified by Brown et al. (2004) by the curious biological phenomenon in which the average FMR is some ''fairly constant multiple, typically about two to three, of the basal metabolic rate'' (p. 1773). The assumed proportionality of FMR and BMR permits inference to organisms in the field, but we see this assumption as an inferential chasm that only a strong theory of measurements (sensu Ford 2000) could bridge. Second, the analyses of Brown et al. use a single value of metabolic rate, mass, and operating temperature for each species, and we are told little about how the single values per species were derived (even in species with sexual dimorphism or indeterminate growth, for which choosing a single value is not a trivial issue). Is it really appropriate to use a mean or median to summarize the distribution of values exhibited by real organisms?

Third, the analyses in Brown et al. do not comply with current statistical standards for comparative studies, as they fail to correct for the complications introduced by errors-in-variables (Model II regression; Sokal and Rohlf 1995, McArdle 2003) and the lack of phylogenetic independence within taxa (Harvey and Pagel 1991). Moreover, lack-of-fit tests (Draper and Smith 1981) indicate that a line is not the best fit through the observed data, at least for the analyses depicted in Fig. 1 of Brown et al. (2004). In short, it is premature to draw conclusions about the similarity of mass and temperature effects estimated from data to the values predicted by metabolic theory, based on the analyses provided by Brown et al. (2004).

The exciting prospects raised by Eq. 1

Despite our concerns, we strongly believe that the synthesis by Brown et al. of mass and temperature effects on metabolism lays the groundwork for a valuable and unique filter for studying the complexity of natural systems. For example, Eq. 1 of Brown et al. (2004) provides a way to disentangle the confounding effects of mass and temperature and then to look for patterns in the residuals. Consider an example with the increased environmental temperatures expected under climate change. Eq. 1 predicts the effects of increased operating temperature on the metabolic rate of organisms of a given mass. Consequent predictions of ontogenetic growth rate, standing biomass, and biomass turnover guide us to both what variables to monitor and their interpretation. Strong deviations from predicted ontogenetic growth (e.g., Brown et al. 2004: Fig. 3) or biomass turnover (e.g., Brown et al. 2004: Fig. 9) would clearly indicate systems needing further investigation.

Alternatively, consider the genetically modified organisms (GMOs) with modifications to growth rates (e.g., Atlantic salmon; Hew et al. [1995], Abrahams and Sutterlin [1999]) and abiotic tolerances (e.g., many food crops; Sharma et al. [2002]) which are rapidly being incorporated into our environment. A metabolic theory of ecology could provide a baseline prediction for how GMOs with altered growth rate or temperature responses should be different from their parent populations. In fast-growing GMO salmon, for instance, metabolic rate should be elevated and the strengths of interactions with both competitors and prey should be predictable.

EXTENSIONS OF THE METABOLIC THEORY BEYOND INDIVIDUALS

The third major component of the Brown et al. (2004) paper extends the metabolic theory to population, community, and ecosystem metrics. Although space prevents us from making a full comment on this aspect of the paper, we would like to point out that in deriving the equations for these metrics, Brown and colleagues generally assume that the combined dynamics of multiple organisms are at steady state. For example, the equation to predict population-level survival and mortality rates from the average individual mass and operating temperature relies on a ‘‘population balance’’ in which organisms that die are replaced by new individuals (i.e., the net population growth rate is 0). This assumption allows Brown et al. to bypass the complexity of temporal dynamics within particular organisms or ecosystems, which matches the static, cross-system comparisons used in their paper. However, it is much less likely to apply when the focus is on the dynamics of specific real-world populations. We believe that the same physical and chemical principles will almost certainly constrain individuals whether or not they are at a population or community equilibrium, and we urge ecologists to work toward relaxing the equilibrium assumption in further extensions of the metabolic theory to higher level ecological processes.

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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 mitochondrial 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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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:

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

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, 2004*a*). In particular, Makarieva et al. (2004*a*) 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:

$$NP = R \tag{2}$$

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.

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

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$\beta \approx -1.16$ 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 ($M_{\mathrm{small}}/M_{\mathrm{large}} \sim 10^{-3}$). 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, $N_{\mathrm{small}}/N_{\mathrm{large}} \sim 10^4$. This allows the estimation of the scaling exponent β as $\beta \sim \log_{10}(N_{\mathrm{small}}/N_{\mathrm{large}})/\log_{10}(M_{\mathrm{small}}/M_{\mathrm{large}}) \sim -4/3$. Again, we are faced with energetic dominance of the smallest organisms in stable ecosystems. In unstable ecosystems, the difference between N_{small} and N_{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 β 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 β than are open (less stable) ecosystems, (-0.88 ± 0.31 vs. -0.50 ± 0.40, mean ± 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. 2004*b*). 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 ecosystem 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 explicity 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 constaints. Either many key biochemical steps have nearly identical temperature dependence, or the Bolzmann-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 (Sterner 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 heterogenous 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, Sterner 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.

The first point is the empirical question of whether the primary scaling factor is ⅔ or ¾, 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 ⅔ and ¾. 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 ¼ rather than modulo ⅓ 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 ¾ 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 ⅔ 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 ¾ assumes that the fundamental geometry of organisms is fractal (West et al. 1997). In the ¾ 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 ¾, ⅔, or something in between.

The third point is the paradox that the ¼-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-

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opment of the original version of the theory needs to be replaced by a more general network. Such an approach should explore explicitly how the cost and efficiency of that network change with departures from the optimized fractal structure. Starts in this direction have been made by the authors of the original theory in its biological context (West et al. 1999, 2001), and by others (Banavar et al. 1999, 2002, Dodds et al. 2001, Gutierrez 2002), some of whom derive scaling rules that vary between ¾ power and ⅔ power. Particular exponents can also arise from mechanisms of competitive space-filling at the community level (e.g., Kinzig et al. 1999), and it would be worthwhile to look for them anywhere where resources flow through an array of tiny consumers that remove a fraction of what they encounter (e.g., small leaves scattered through a big tree [Horn 1971]; to pick an example only because I know the author). It is too early to make a generalization from this variety of ideas, but perhaps the network of distribution need only be efficient and hierarchical, not just near-fractal, for exponents to be modulo ¼ (West et al. 1999), or very near it (others cited previously). Other modifications may come from biological variations in the dimensionality of the surface over which resources are acquired, and details of the metric of the volume over which they are distributed and used, . . . but I expect these to be small enough to contribute more to explaining residuals than to changing the average scaling of attributes to body size.

The initial assumption of size-independent metabolic units (West et al. 1997) has received little published criticism, perhaps because most biologists can cite so many examples from their own specialties. Accordingly, Brown et al.'s (2004) extension of the consequences of this assumption to organism, population, and ecosystem is novel, interesting, and powerful, independent of any arguable details.

Some would quibble about the possible role of multiple normalization factors in fitting varied organisms to a common line on a graph, but it doesn't bother me. As Brown et al. (2004) point out, the normalization factors are appropriate subjects for interpretation in terms of specific biological attributes. Indeed, one of the great strengths of this metabolic theory is that a demonstrated allometry allows the all-pervasive effect of body size to be accounted for, so that residuals from the allometry may call for detailed biological interpretation. Alternatively, the residuals may provide data from organisms of different sizes to test theoretical predictions about such biological details. Brown et al. (2004) also point out that even after normalization the residuals from some of their regressions span a 20-fold range (and I read some of their figures as providing a 50-fold range between extremes). That offers plenty of opportunity for structural idiosyncracies and biologically interesting details to ''fine-tune'' an average relationship that spans as much as 20 orders of magnitude in size. Brown et al. (2004) make this point over and over again in a wide range of contexts, from physiology to evolution and from cell to ecosystem.

Indeed this is what makes the whole enterprise of ''A Metabolic Theory of Ecology'' so exciting and worthwhile. Brown et al. (2004) have derived an extraordinary range of interpretation and prediction from ''first principles.'' The original framing of the first principles (West et al. 1997) engendered criticisms and subsequent modifications that made them less confining (West et al. 1999, 2001), and such improvements continue. The extensions of the original theory to the population and community levels have an internal biophysical consistency, and strong empirical support that still allows enough variation to demand biological explanation. Furthermore, the theory may help in the search for that explanation.

Robert MacArthur would have been very pleased with Brown et al. (2004). He was always interested in patterns at any scale from organism to community to biogeography, and from ecology to evolution. He had a particular interest in how body size affected those patterns. He was a theoretician and a naturalist, with a conceptual brilliance when he combined the two. Here is how he might have viewed the controversy over details:

> *Ecological patterns, about which we construct theories, are only interesting if they are repeated. They may be repeated in space or in time, and they may be repeated from species to species. A pattern which has all of these kinds of repetition is of special interest because of its generality, and yet these very general events are only seen by ecologists with rather blurred vision. The very sharp-sighted always find discrepancies and are able to say that there is no generality, only a spectrum of special cases. This diversity of outlook has proved useful in every science, but it is nowhere more marked than in ecology.*
> —MacArthur 1968:159.

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RESPONSE TO FORUM COMMENTARY ON ''TOWARD A METABOLIC THEORY OF ECOLOGY''

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We welcome the opportunity to respond to the commentaries in this Special Feature. We are well aware that this is not the last word. A full evaluation of the metabolic theory of ecology (MTE) will be rendered over time by the wider ecological community and will probably take years. Here we address some general and specific issues raised by the commentaries. The MTE is very much a work in progress—hence the ''toward'' in the title of Brown et al. (2004). To facilitate progress, we try to clarify some of the controversial or at least still unresolved issues, rather than simply defend our paper.

We begin with some general points that emerged from several commentaries.

Is the exponent ⅔ or ¾?—The values of the allometric exponents for whole-organism metabolic rate and other biological rates and times are ultimately empirical questions. These questions have intrigued biologists for about 70 years, ever since Kleiber (1932) measured the basal metabolic rates of mammals and birds spanning a wide range of body masses, and found that the slope of his log–log plot was almost exactly ¾. Extensive studies, culminating in several synthetic books on allometry in the 1980s, appeared to have resolved the issue. These books unanimously concluded that most allometric exponents were quarter powers rather than the third powers expected on the basis of Euclidean geometric scaling (McMahon and Bonner 1983, Peters 1983, Calder 1984, Schmidt-Nielsen 1984).

The issue was reopened recently, in particular when Dodds et al. (2001) and White and Seymour (2003) analyzed data on basal metabolic rates of mammals and birds and obtained exponents closer to ⅔ than ¾. Savage et al. (2004) have commented on these studies. We summarize only the two key points:

1) It is problematic to claim a definitive value based on analyses of existing data on mammalian and avian basal metabolic rates. The estimated exponent varies from ~0.65 to 0.85, depending on which measurements and taxa are included, and which statistical procedures are used.

2) Dodds et al. (2001) and White and Seymour (2003) compiled and analyzed data only on basal metabolic rates of mammals and birds. Savage et al. (2004) performed analyses of many additional data sets, including basal, field, and maximal whole-organism metabolic rates, and many other biological rates and times. The data included not just mammals and birds, but many other taxa from both terrestrial and aquatic environments. The variables ranged from cellular and molecular to whole-organism and population levels. The exponents varied, but showed distinct peaks and mean values at almost exactly ¾ for whole-organism basal and field metabolic rates, −¼ for mass-specific metabolic rates and many other biological rates (e.g., heart rates and population growth rates), and ¼ for biological times (e.g., blood circulation times and gestation periods).

Based on this evidence, Savage et al. (2004) concluded that there is little justification for reopening the argument that biological allometries in general have third-power exponents. Important additional evidence for the pervasiveness of quarter-power exponents comes from our recent research, which is based on new compilations and analyses of published data. For example, refer to Figs. 2, 5, and 8 in Brown et al. (2004), which plot data for rates of whole-organism biomass production, maximal population growth (r_{max}), and ecosystem carbon turnover across a wide range of body

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sizes, taxa, and environments. The exponents, 0.76, −0.23, and −0.22, respectively, are very close to the predicted values of ¾, −¼, and −¼, and the 95% confidence intervals do not include the Euclidean alternatives of ⅔, −⅓, and −⅓.

What is the mechanistic basis for quarter-power exponents?—The data on biological allometries are well described by power laws, implying that they are the result of self-similar or fractal-like processes. West et al. (1997, 1999*a*, *b*) developed general mechanistic models based on geometric and biophysical principles that explain the quarter-power exponents. These models address the general problem of distributing metabolic resources within an organism and, more specifically, describe the structure and function of mammal and plant vascular systems. The models of West et al. hypothesize that the quarter-power scaling exponents reflect the optimization of these transport networks due to natural selection. Although the organisms themselves are three-dimensional, an additional length variable is required to describe the branching networks, resulting in scaling exponents with 4, rather than the Euclidean 3, in the denominator. The structures and dynamics of resource distribution networks are hypothesized to be dominated by self-similar fractal-like branching, although it is likely that some networks may be ''virtual'' (e.g., within cells of prokaryotes) rather than ''hard wired'' (e.g., vascular systems of vertebrates and higher plants).

These models of West et al. have been criticized by several authors. Cyr and Walter (2004) cite most of the published critiques. West and collaborators are trying to respond to the most serious criticisms, but this takes considerable effort and introduces inevitable time lags (see Brown et al. 1997, Enquist et al. 1999, West et al. 2002; 2003*a*, *b*, *in press*, Allen et al. 2003, Brown et al. 2003, Gillooly et al. 2003). Several other responses are still in press or unpublished. We will not address the criticisms here, except to state that we have yet to see compelling theoretical or empirical evidence that would cause us to retract or substantially change the models of West et al. Like the content and implications of the broader MTE, the rigor and realism of the models for quarter-power scaling will be decided not by the participants in the immediate debates, but by the broader scientific community in the fullness of time.

What is a mechanism, and a mechanistic theory?—Several commentaries question the extent to which MTE, as we have presented it, is truly mechanistic. We have three responses.

The first is that there is considerable variation in what scientists consider to constitute a mechanism; one person's mechanism is another's empirical phenomenology. This is a long-standing problem. For example, physicists still don't completely understand the mechanistic basis of gravity, even though the force of gravity can be characterized by analytical equations and used as a first principle to make useful, accurate predictions about everything from satellite orbits to biomechanical properties of bones. We freely admit that there is abundant room for additional research on mechanisms: from (1) how the kinetics of the multiple biochemical reactions of metabolism determine the observed activation energies at whole-organism and ecological levels of organization; to (2) how the kinetics of species interaction, evolution, coevolution, speciation, and extinction cause the observed temperature dependence in biogeographic gradients of species diversity. We hope other research groups will investigate some of the mechanisms and we welcome all contributions to producing a more complete and mechanistic conceptual framework for MTE.

The second response is that mechanisms are described in much more detail in our other publications. Most equations in Brown et al. (2004) are the result of mathematical models described in separate publications. These models make explicit mechanistic connections between the metabolic processes of individual organisms and their ecological and evolutionary consequences.

The third response is that empirical support for these models and, in particular, for the predicted scalings with size and temperature, suggests that metabolic rate is indeed the most fundamental biological rate, and that its manifestations ramify to affect all levels of biological organization, from molecules to ecosystems. Data sources and statistical procedures are not described in Brown et al. (2004), but are documented in the original papers. It is important to recognize that the figures in Brown et al. (2004) are not just descriptive statistical regression equations. Two points should be emphasized: (1) theoretically predicted values for allometric exponents and activation energies, based on metabolic processes within individual organisms, are incorporated directly into the analyses and into the plots of the data; and (2) support for model predictions comes not only from the high proportions of variation explained by the regression equations (high values of r^2), but more importantly from the fact that 95% confidence intervals for the slopes almost always include the predicted allometric exponents and activation energies.

What about all the variation?—The authors of the commentaries represent a wide spectrum of biologists and ecologists, from those who seek unifying principles, to those who emphasize diversity and complexity. Both approaches are valid—indeed both are required to keep the science focused, balanced, realistic, and progressing. We are at one end of the spectrum, unabashedly seeking unifying theory. For those who are more concerned about the variation, we have three comments.

First, the influence of metabolism on ecology is most apparent when comparisons can be made across wide ranges of body size and temperature, where the pervasive influences of allometry and kinetics are strong. When body mass differs by only two- or threefold, or temperature varies by only a degree or two, other factors can assume equal or greater importance. Many of these factors are outside the domain of metabolic theory. For example, allometry and kinetics are of little value in explaining coexistence and species diversity of herbs in an old field or warblers in a forest, because there is little variation in both body size and temperature. In effect, these variables are ''controlled'' by the design of the study, thereby allowing other factors to be evaluated. Nevertheless, many systems studied by population and community ecologists have sufficient variation in body size and temperature for metabolic theory to be directly applicable. For example, our model can explain ~90% of the variation in growth rates of zooplankton (Gillooly et al. [2002]; see also egg-hatching rates in Brown et al. 2004: Fig. 3). The magnitudes of intra- and interspecific variation in body mass and seasonal variation in environmental temperature make these results directly relevant to population and community dynamics of zooplankton in temperate lakes.

The second comment is that effects of allometry and kinetics on individual organisms and ecological systems are powerful and pervasive. The very fact that body size and temperature account for most of the variation in log-scaled ''microbe to monster'' and ''oceans to forests'' plots is evidence that the allometry and kinetics of metabolic rate are fundamental to biology and ecology. These processes are still operating even when their influences may be obscured by variation due to other processes. Suppose that we want to understand the processes involved in secondary succession from an old field to a forest. Then, the influence of plant size on species interactions and ecosystem processes assumes major importance. Or suppose that we want to predict the ecological consequences of a rise in average environmental temperature by 2°C. The actual responses will undoubtedly be complicated by time lags, transient dynamics, initial species composition, effects of limiting material resources, and other variables. Despite these sources of variation, however, metabolic theory provides a good starting point: it predicts that rates of individual-, population-, community-, and ecosystem-level processes will increase as described by the Boltzmann factor with an activation energy of 0.6–0.7 eV (1 eV = 96.49 kJ/mol).

The third point, also made in several commentaries, is that a theory soundly based on first principles, provides a baseline—a point of departure—from which to understand the residual variation. Deviations from predictions can be grouped loosely into four categories: (1) measurement errors or other biases in the data; (2) effects of factors not included in the model or theory; (3) exceptions that ''prove the rule'' by showing how violating specific model assumptions leads to predictable deviations; and (4) discrepancies that expose serious flaws in the assumptions or operations of the model. Having a theoretically predicted baseline helps one to evaluate these possibilities.

Specifics.—Most commentaries raise specific issues that warrant attention, but we address only two here.

First, Cyr and Walker (2004) extol the virtues of the dynamic energy budget (DEB) approach of Kooijman, Nisbet, and collaborators (e.g., Kooijman 2000, Nisbet et al. 2000). DEB models do indeed describe growth and reproduction of individuals in terms of metabolic processes and first principles of energy and material balance. And they do indeed incorporate more detail—many more variables and functions—than our deliberately simple MTE. How much complexity in a model is desirable or necessary is in part a matter of taste, and in part a matter of the purpose for which the model is used. We view the DEB and MTE approaches as complementary. They make different trade-offs between specificity and generality, and consequently have different strengths, weaknesses, and applications.

Second, Sterner (2004) asks whether ''one cardinal equation of macroecology, $X = M^{3/4}e^{-E/kT}R$ + error . . . '' with a ''. . . single linear term in R is enough to do the job'' (where R is the ''amount'' of some limiting material resource). This is a straw man. We never claimed that this is the ''one cardinal equation of macroecology.'' We explicitly stated that many ecological phenomena, including macroecological species–area and species–abundance relationships, are outside the purview of MTE. We did not suggest that the unexplained variation should be regarded as ''error.'' We explicitly noted that residual variation may be due to deterministic influences of stoichiometry, phylogenetic or functional group affinity, environment, and other factors that are not included in our models. We did not say that resource limitation is due to a single reagent and is linear with respect to R and ''organism nutrient content.'' We do agree with Sterner that ''there is quite a bit more work to do'' on ecological stoichiometry and its relationship to energetics, and for this reason we deliberately omitted a term for resource abundance from our models (our Eqs. 4–8) for rates and times at the individual organism level. We did include a linear term, R, in our Eqs. 9–11 for abundance, biomass, and productivity at the population to ecosystem levels. These models can be taken as testable hypotheses for the effects of limiting material resources, together with body size and temperature, on these ecological variables. The chemical compositions of the fluxes and pools of material resources are central to organismal metabolism and must be an essential ingredient of any complete MTE. Our earlier work has concentrated on allometry and kinetics. As indicated in Brown et al. (2004), we have begun to address many of the interrelationships between energy and materials in both organisms and ecosystems. A major research program of Sterner, Elser, and others has concentrated on ecological stoichiometry, and represents a major contribution (e.g., Elser et al. 2000, Sterner and Elser 2002). However, we strongly disagree with Sterner that ''we are beyond that . . . previous era in ecology, where bioenergetics was *the* hoped for organizing concept.'' Just change *the* (our italics) to *a*. Energetics, updated, based more firmly on first principles, and interrelated to stoichiometry, is *a* powerful organizing concept for ecology.

We end by emphasizing that MTE is not intended to be the theory of everything that is interesting and important in ecology. Nor is it intended to account for all of the variation among living things and ecological systems. Within its domain, however, MTE offers mechanistic explanations for linking many ecological patterns and processes to biological, physical, and chemical constraints on individual organisms. MTE suggests that underlying the diversity of living things and the complexity of ecological systems are fundamental unities, some of which reflect how first principles of biology, physics, and chemistry govern the fluxes and pools of energy and materials within organisms and between organisms and their environments.

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