

PERSPECTIVES

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TOWARD A METABOLIC THEORY OF ECOLOGY

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Abstract. Metabolism provides a basis for using first principles of physics, chemistry, and biology to link the biology of individual organisms to the ecology of populations, communities, and ecosystems. Metabolic rate, the rate at which organisms take up, transform, and expend energy and materials, is the most fundamental biological rate. We have developed a quantitative theory for how metabolic rate varies with body size and temperature. Metabolic theory predicts how metabolic rate, by setting the rates of resource uptake from the environment and resource allocation to survival, growth, and reproduction, controls ecological processes at all levels of organization from individuals to the biosphere. Examples include: (1) life history attributes, including development rate, mortality rate, age at maturity, life span, and population growth rate; (2) population interactions, including carrying capacity, rates of competition and predation, and patterns of species diversity; and (3) ecosystem processes, including rates of biomass production and respiration and patterns of trophic dynamics.

Data compiled from the ecological literature strongly support the theoretical predictions. Eventually, metabolic theory may provide a conceptual foundation for much of ecology, just as genetic theory provides a foundation for much of evolutionary biology.

Key words: allometry; biogeochemical cycles; body size; development; ecological interactions; ecological theory; metabolism; population growth; production; stoichiometry; temperature; trophic dynamics.

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INTRODUCTION

The complex, spatially and temporally varying structures and dynamics of ecological systems are largely consequences of biological metabolism. Wherever they occur, organisms transform energy to power their own activities, convert materials into uniquely organic forms, and thereby create a distinctive biological, chemical, and physical environment.

Metabolism is the biological processing of energy and materials. Organisms take up energetic and material resources from the environment, convert them into other forms within their bodies, allocate them to the fitness-enhancing processes of survival, growth, and reproduction, and excrete altered forms back into the environment. Metabolism therefore determines the demands that organisms place on their environment for all resources, and simultaneously sets powerful constraints on allocation of resources to all components of fitness. The overall rate of these processes, the metabolic rate, sets the pace of life. It determines the rates of almost all biological activities.

Recent progress in understanding how body size, temperature, and stoichiometry affect biological structure and function at the molecular, cellular, and whole-organism levels of organization raises the prospect of developing a metabolic theory of ecology. Metabolism is a uniquely biological process, but it obeys the physical and chemical principles that govern the transformations of energy and materials; most relevant are the laws of mass and energy balance, and thermodynamics. Much of the variation among ecosystems, including their biological structures, chemical compositions, energy and material fluxes, population processes, and species diversities, depends on the metabolic characteristics of the organisms that are present. Much of the variation among organisms, including their life history characteristics and ecological roles, is constrained by their body sizes, operating temperatures, and chemical compositions. These constraints of allometry, biochemical kinetics, and chemical stoichiometry lead to metabolic scaling relations that, on the one hand, can be explained in terms of well-established principles of biology, chemistry, and physics and, on the other hand, can explain many emergent features of biological structure and dynamics at all levels of organization.

THEORETICAL FOUNDATIONS

Virtually all characteristics of organisms vary predictably with their body size, temperature, and chemical composition (e.g., Bartholomew 1981, Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Niklas 1994, Gillooly et al. 2001, 2002, Sterner and Elser 2002). For more than a century, biologists have been investigating the mechanistic processes that underlie these relationships. Recent theoretical advances have shown more explicitly how these biological characteristics can be quantified, related to each other, and explained in terms

of basic principles of biology, chemistry, and physics (e.g., Peters 1983, Sterner 1990, Elser et al. 1996, 2000a, West et al. 1997, 1999a, b, 2001, Enquist et al. 1999, Gillooly et al. 2001, 2002). Together, the older conceptual and empirical foundations and the more recent theoretical advances provide the basis for a metabolic theory of ecology. This theory explicitly shows how many ecological structures and dynamics can be explained in terms of how body size, chemical kinetics, and resource supply affect metabolism. Through variation in the rates and biochemical pathways of metabolism among different kinds of organisms and environmental settings, metabolic theory links the performance of individual organisms to the ecology of populations, communities, and ecosystems.

Metabolism and metabolic rate

Metabolism is a complex network of biochemical reactions that are catalyzed by enzymes, allowing the concentrations of substrates and products and the rates of reactions to be regulated. A chart of the chemical reactions of metabolism shows a bewildering number of substrates, enzymes, and pathways. Nevertheless, the core of metabolism consists of a small number of reactions that form the basis of the TCA (tricarboxylic acid) cycle (Morowitz et al. 2000). The vast majority of organisms use the same basic biochemistry, but the rates of resource uptake, transformation, and allocation vary.

When we speak of energy and energetics, we refer to potential energy: the energy contained in photons or chemical bonds. Some fraction of this energy is converted by the reactions of photosynthesis and respiration into biologically useful forms that are used to perform the work of biosynthesis, membrane transport, muscle contraction, nerve conduction, and so on. We use the term kinetics to refer to kinetic energy, the energy of molecular motion. Kinetics affect biological processes largely through the influence of temperature on metabolic rate.

The metabolic rate is the fundamental biological rate, because it is the rate of energy uptake, transformation, and allocation. For a heterotroph, the metabolic rate is equal to the rate of respiration because heterotrophs obtain energy by oxidizing carbon compounds as described by the reaction: $\text{CH}_2\text{O} + \text{O}_2 \rightarrow \text{energy} + \text{CO}_2 + \text{H}_2\text{O}$. For an autotroph, the metabolic rate is equal to the rate of photosynthesis because this same reaction is run in reverse using energy (i.e., photons) provided by the sun to fix carbon (Farquhar et al. 1980). It has proven challenging to measure metabolic rate accurately and consistently. Ideally, it would be measured as heat loss by direct calorimetry, which would quantify the energy dissipated in all biological activities. However, because of the fixed stoichiometry of respiratory gas exchange, it is nearly as accurate and much more practical to measure the rate of carbon dioxide uptake in plants or the rate of oxygen consumption in

aerobic prokaryotes and eukaryotes (Withers 1992). Physiologists typically measure the basal or standard metabolic rate, the minimal rate of an inactive organism in the laboratory. Basal rates are invariably less than the actual or field metabolic rates of free-living organisms, which must expend additional energy for foraging, predator avoidance, physiological regulation, and other maintenance processes, and still more energy for growth and reproduction. In most organisms, however, the average daily energy expenditure or the long-term sustained rate of biological activity is some fairly constant multiple, typically about two to three, of the basal metabolic rate (Taylor et al. 1982, Schmidt-Nielsen 1984, Nagy 2001; Savage et al., *in press b*).

In addition, most organisms exhibit phenotypic plasticity in the expression of metabolism. They can vary the rate and pathways of metabolism to some extent to adjust for variations in resource supply, such as fluctuating quantity and quality of food resources, or in resource demand, such as the costs of reproduction or of maintaining homeostasis in the face of altered environmental temperature, osmotic concentration, or elemental chemical composition. For example, during periods of resource shortages, many organisms are able to lower metabolic rates and resource requirements by reducing activity and entering some form of diapause or torpor. Even these phenotypic variations, however, occur within constraints on metabolic rate due to three primary factors: body size, temperature, and stoichiometry.

Body size

Since early in the 20th century, it has been known that almost all characteristics of organisms vary predictably with body size. Huxley (1932) is credited with pointing out that most size-related variation can be described by so-called allometric equations, which are power functions of the form

$$Y = Y_0 M^b. \quad (1)$$

They relate some dependent variable, Y , such as metabolic rate, development time, population growth rate, or rate of molecular evolution, to body mass, M , through two coefficients, a normalization constant, Y_0 , and an allometric exponent, b . Most of these biological scaling exponents have the unusual property of being multiples of $1/4$, rather than the multiples of $1/3$ that would be expected from Euclidean geometric scaling. Thus, for example, Kleiber (1932) showed that whole-organism metabolic rate, I , scales as

$$I = I_0 M^{3/4} \quad (2)$$

where I_0 is a normalization constant independent of body size. This same relation, with different values for the normalization constant, describes: (1) basal metabolic rate, the minimal rate of energy expenditure necessary for survival under ideal conditions; (2) field metabolic rate, the actual rate of energy expenditure by a

free-living organism in nature, which ideally would include allocation to growth and reproduction sufficient to maintain a stable population; and perhaps also (3) maximal metabolic rate, the rate of energy flux during maximal sustained activity (Savage et al., *in press b*).

Recently, West et al. (1997, 1999a, b) showed that the distinctively biological quarter-power allometric scaling could be explained by models in which whole-organism metabolic rate is limited by rates of uptake of resources across surfaces and rates of distribution of materials through branching networks. The fractal-like designs of these surfaces and networks cause their properties to scale as $1/4$ powers of body mass or volume, rather than the $1/3$ powers that would be expected based on Euclidean geometric scaling (Savage et al., *in press b*).

Temperature

It has been known for more than a century that biochemical reaction rates, metabolic rates, and nearly all other rates of biological activity increase exponentially with temperature. These kinetics are described by the Boltzmann factor or the Van't Hoff-Arrhenius relation

$$e^{-E/kT} \quad (3)$$

where E is the activation energy, k is Boltzmann's constant, and T is absolute temperature in K (Boltzmann 1872, Arrhenius 1889). The Boltzmann factor specifies how temperature affects the rate of reaction by changing the proportion of molecules with sufficient kinetic energy, E , which here we measure in electron volts (1 eV = 23.06 kcal/mol = 96.49 kJ/mol).

This relationship holds only over the temperature range of normal activity, which for most organisms lies between 0° and 40°C (Thompson 1942, Schmidt-Nielsen 1997). Normal operating temperature varies among species and taxonomic or functional groups. Any given species usually operates over some subset of this temperature range, although there are exceptions. For example, most aquatic organisms do not experience temperatures above 25°–30°C, endothermic birds and mammals maintain relatively high and constant temperatures (36°–40°C), some ectotherms can tolerate only a very narrow range of temperatures, and some microbes from extreme environments such as hot springs and hydrothermal vents can live at temperatures that approach or exceed 100°C. With some qualifications, then, the exponential form (3) describes the temperature dependence of whole-organism metabolism of virtually all organisms, from unicellular microbes to multicellular plants and animals (Gillooly et al. 2001). Nearly all other biological rates and times, including individual and population growth rates, and development times and life spans, show a similar temperature dependence (Gillooly et al. 2001, 2002; Savage et al., *in press a*). Interestingly, the empirically estimated activation energies for all of these processes are similar, and within the range of activation energies typically

observed for the biochemical reactions of metabolism (0.60–0.70 eV, Gillooly et al. 2001). This suggests that metabolism is the underlying process that governs most biological rates.

Stoichiometry

In its narrow sense, stoichiometry is concerned with the proportions of elements in chemical reactions. In broader applications, such as to ecology, stoichiometry refers to the quantities, proportions, or ratios of elements in different entities, such as organisms or their environments (e.g., Reiners 1986, Elser et al. 1996, 2000a, Sterner and Elser 2002). Protoplasm, and the different structural and functional materials that comprise living biomass, have characteristic ratios of the common elements such as H, O, C, N, P, Na, Cl, S, Ca, and K. N is found primarily in proteins; P in nucleic acids, ADP and ATP, phospholipids, and skeletal structure; Na or K in intracellular solutes, and so on. All organisms have internal chemical compositions that differ from those in their environment (Lotka 1925), so they must expend metabolic energy to maintain concentration gradients across their surfaces, to acquire necessary elements, and to excrete waste products.

Fundamental stoichiometric relationships dictate the quantities of elements that are transformed in the reactions of metabolism. Biochemistry and physiology specify the quantitative relationship between the metabolic rate and the fluxes of elemental materials through an organism. The metabolic rate dictates the rates at which material resources are taken up from the environment, used for biological structure and function, and excreted as “waste” back into the environment. Far from being distinct ecological currencies, as some authors have implied (e.g., Reiners 1986, Sterner and Elser 2002), the currencies of energy and materials are inextricably linked by the chemical equations of metabolism. These equations specify not only the molecular ratios of elements, but also the energy yield or demand of each reaction. Ecological stoichiometry is concerned with the causes and consequences of variation in elemental composition among organisms and between organisms and their environments (Sterner and Elser 2002). Despite the overall similarity in the chemical makeup of protoplasm, organisms vary somewhat in stoichiometric ratios within individuals, among individuals of a species, and especially between different taxonomic and functional groups. For example, in unicellular organisms and small metazoans, which have high rates of biosynthesis, a significant portion of total body phosphorus is found in ribosomal RNA (Sutcliffe 1970, Elser et al. 2000b, Sterner and Elser 2002). Larger vertebrate organisms, with lower rates of biosynthesis, require much less RNA, but require much more phosphorus for skeletal structure. Vertebrates, with bones and muscles, contain proportionately more P and N and less C than plants, which use cellulose and lignin

as primary structural materials and have high ratios of C relative to N and P (Elser et al. 2000a).

The elemental composition of an organism is governed by the rates of turnover within an organism and the rates of flux between an organism and its environment. The concentrations of elements in ecosystems are therefore directly linked to the fluxes and turnover rates of elements in the constituent organisms. There may be reciprocal limitation, so that concentrations of some elements, such as N in soils and P in lakes, are regulated by a balance between the rate of supply from abiotic and biotic sources and the rate of uptake by organisms. On the one hand, environmental concentrations can limit metabolic rates, and thereby growth rates, reproductive rates, and standing stocks of organisms. For example, plants can be limited by nitrogen, water, iron, and phosphorus. Under controlled laboratory conditions, plant growth rates have been shown to vary linearly with N concentration (Ingestad 1979). Similarly, fertilization and irrigation experiments have repeatedly shown that growth rates of plants in the field are limited by nitrogen or water (Field and Mooney 1986; see review in Tilman 1988). On the other hand, sizes of pools and rates of turnover in organisms can regulate environmental concentrations of elements and compounds, sometimes within narrow limits (Vitousek 1982). This is the case for CO₂ concentration in the atmosphere, which is regulated in part by the balance between photosynthesis and respiration in the biosphere (Falkowski et al. 2000, Chapin et al. 2002), and for the concentrations of C, N, and P found in the organic matter of oceans and lakes, which is regulated in part by nutrient metabolism of the biota (Redfield 1958).

ALTERNATIVE EXPRESSIONS FOR BIOLOGICAL RATES

The joint effects of body size, M , and temperature, T (in K), on individual metabolic rate, I , can be described by combining Eqs. 2 and 3 (Gillooly et al. 2001). This gives

$$I = i_0 M^{3/4} e^{-E/kT} \quad (4)$$

where i_0 is a normalization constant independent of body size and temperature. We can take logarithms of both sides of this equation and rearrange terms to yield

$$\ln(IM^{-3/4}) = -E(1/kT) + \ln(i_0). \quad (5)$$

Note that in Eq. 5, we have “mass-corrected” metabolic rate, I , by incorporating the logarithm of mass raised to the $3/4$ power. This method facilitates quantitative evaluation of the mass and temperature dependence predicted by Eq. 4, by incorporating the predicted scalings into the analysis and into the y-axis of bivariate plots. Eq. 5 predicts that the natural logarithm of mass-corrected whole-organism metabolic rate should be a linear function of inverse absolute temperature ($1/kT$). The slope of this relationship gives the activation energy of metabolism, E , and the intercept

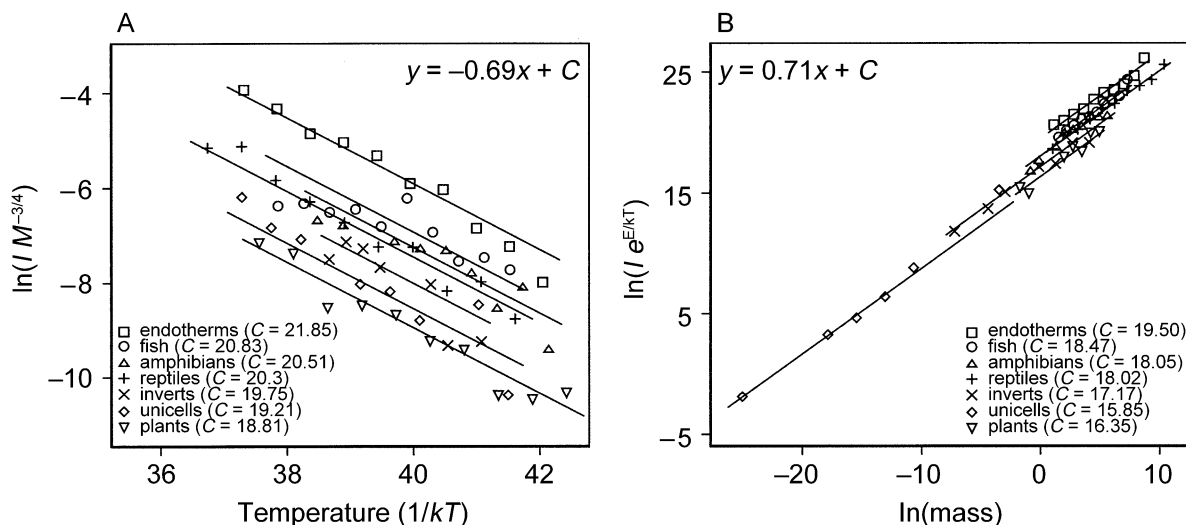


FIG. 1. Temperature and mass dependence of metabolic rate for several groups of organisms, from unicellular eukaryotes to plants and vertebrates (from Gillooly et al. 2001). (A) Relationship between mass-corrected metabolic rate, $\ln(IM^{-3/4})$, measured in watts/ $g^{3/4}$, and temperature, $1/kT$, measured in K. The overall slope, calculated using ANCOVA, estimates the activation energy, and the intercepts estimate the normalization constants, $C = \ln(i_0)$, for each group. The observed slope is close to the predicted range of 0.60–0.70 eV (95% CI, 0.66–0.73 eV; SI conversion, 1 eV = 96.49 kJ/mol). (B) Relationship between temperature-corrected metabolic rate, $\ln(Ie^{E/kT})$, measured in watts, and body mass, $\ln(M)$, measured in grams. Variables are M , body size; I , individual metabolic rate; k , Boltzmann's constant; T , absolute temperature (in K). E is the activation energy. The overall slope, calculated using ANCOVA, estimates the allometric exponent, and the intercepts estimate the normalization constants, $C = \ln(i_0)$, for each group. The observed slope is close to the predicted value of $3/4$ (95% CI, 0.69–0.73). For clarity, data from endotherms ($n = 142$), fish ($n = 113$), amphibians ($n = 64$), reptiles ($n = 105$), invertebrates ($n = 20$), unicellular organisms ($n = 30$), and plants ($n = 67$) were binned and averaged for each taxonomic group to generate the points depicted in the plot.

gives the natural logarithm of the normalization constant, $\ln(i_0)$. Plotted in this way (Fig. 1), it is clear that data for all groups are well-fitted by a common slope, $E \approx 0.69$ eV (1 eV = 96.49 kJ/mol), including endotherms in hibernation and torpor. Excluding these endotherms, we obtain an average value of $\bar{E} \approx 0.63$ eV. Both of these values are within the range (0.60–0.70 eV) commonly reported for aerobic respiration (Gillooly et al. 2001).

Using the value of $E = 0.63$ eV, we can “temperature-correct” metabolic rates to isolate the effects of mass:

$$\ln(Ie^{E/kT}) = (3/4)\ln(M) + \ln(i_0). \quad (6)$$

We use this same value of $E = 0.63$ eV for subsequent temperature corrections. Eq. 6 predicts a linear relationship between the logarithm of temperature-corrected metabolic rate and the logarithm of mass. Plotting the same metabolic rate data in this alternative way (Fig. 1), we see that the fitted slope (0.71) is close to the value of $3/4$ predicted by the theory, and that different groups show consistent differences in intercepts or normalization constants, $\ln(i_0)$.

The explanatory power of Eq. 4 is substantial, with body size predicting $\sim 100,000$ -fold variation in rates over the 20 orders-of-magnitude size range from the smallest unicellular microbes to the largest vertebrates and trees, and with temperature predicting ~ 30 -fold

variation over the biologically relevant temperature range from 0° to 40°C.

There are, of course, quantitative deviations of individual data values around the regression lines and from the predictions of the models. For example, there exists an ~ 20 -fold variation in the normalization constants for basal metabolism, i_0 , across all taxonomic groups. The residual variation offers clues to the other factors, in addition to body size and temperature, that affect metabolic and ecological processes. We will show that some of the remaining variation in ontogenetic growth rates and litter decomposition rates is related to elemental stoichiometry.

These methods of “mass correction” and “temperature correction” will be applied repeatedly in subsequent sections of the paper to investigate other biological rates and times. Slightly different versions of Eqs. 5 and 6 are required for mass-specific metabolic rate and most other biological rates, which are predicted to scale as $M^{-1/4}$, and for biological times, which are expected to scale as $M^{1/4}$. For simplicity, in most subsequent equations, we will use \propto instead of $=$ and will leave out symbols for the normalization constants. We emphasize, however, that these coefficients are important, because they differ in systematic ways among different biological traits, taxa of organisms, and kinds of environments.

INDIVIDUAL PERFORMANCE AND LIFE HISTORY

The combined effect of body size and temperature on whole-organism metabolic rate, I , is given in Eq. 4. Because the mass-specific rate of metabolism, B , is simply I/M , it follows that B scales as

$$B \propto M^{-1/4} e^{-E/kT}. \quad (7)$$

Other biological rates, from heart rate to development rate, and even the rate of molecular evolution (J. F. Gillooly and A. P. Allen, *unpublished data*), also vary with mass as $M^{-1/4}$ and with the Boltzmann factor. Biological times, t_B , such as turnover times for metabolic substrates and generations of individuals, are the reciprocal of rates and therefore scale as

$$t_B \propto M^{1/4} e^{E/kT} \quad (8)$$

(Gillooly et al. 2002). These equations express relationships that have been studied for many decades. It has long been known that large organisms require more resources, but flux them through at slower rates than do smaller organisms. Both overall resource requirements and flux rates are higher at higher temperatures. Elephants require more food, but reproduce more slowly and live longer than mice. Microbial activity and rates of litter decomposition are higher in warm, tropical environments than cold, subarctic ones. The advantage of this framework, however, is that the equations combine the effects of size and temperature in a single quantitative expression. This makes possible precise comparisons across organisms that differ substantially in body size and operating temperature, including species in different taxonomic or functional groups or diverse environments. When such comparisons are made, the commonalities of life and their ecological manifestations are revealed.

Individual biomass production

Organisms devote some fraction of their metabolism to catabolism and activities associated with maintenance, and the remainder to anabolism and activities associated with production of new biomass for growth and reproduction. Empirically, rates of whole-organism and mass-specific biomass production, P and P/M , respectively, scale similarly to whole-organism and mass-specific rates, so $P \propto M^{3/4} e^{-E/kT}$ and $P/M \propto M^{-1/4} e^{-E/kT}$. This supports the theoretical conjecture that some constant fraction of metabolism tends to be allocated to production. It follows that, to the extent organisms have similar metabolic rates after adjusting for body size and temperature, they should also have similar rates of production. This prediction is confirmed by plotting maximal rates of temperature-corrected whole-organism production against body mass for a wide variety of aerobic eukaryotes, including plants and animals, ectotherms and endotherms (Fig. 2). Note that all values cluster closely around the same allometric relationship, which extends over nearly 20 orders of mag-

nitude in body mass and has a slope almost exactly equal to the predicted $3/4$. Trees and vertebrates of the same body mass, operating at the same body temperature, produce new biomass through some combination of growth and reproduction, at very similar rates. The same applies to fish and terrestrial insects. Of course there is residual variation, some probably related to stoichiometric resource requirements, and the remainder to other taxon- or environment-specific factors. But the degree of commonality is impressive.

Ontogenetic growth

The rate of metabolism sets the pace of life, including the life history schedule. For example, time to hatching of eggs in diverse animals, including zooplankton, insects, fish, amphibians, and birds, varies with size and temperature according to Eq. 8 (West et al. 2001, Gillooly et al. 2002). Fig. 3 is a plot of development rates as a function of temperature and mass for eggs of zooplankton in the laboratory and fish in the field. Note that the mass-corrected rates as a function of temperature have slopes corresponding to activation energies of 0.73 and 0.68 eV (1 eV = 96.49 kJ/mol), close to the range of estimated activation energies for aerobic metabolism (Gillooly et al. 2001). The temperature-corrected rates as a function of mass have slopes corresponding to allometric exponents of -0.27 and -0.24 , bracketing the theoretically predicted value of $-1/4$. Much of the variation within these two groups probably can be explained by stoichiometric resource limitation. This was shown for development of zooplankton from hatching to maturity, in which residuals around the regression were positively correlated with body phosphorus concentration (Gillooly et al. 2002), as expected from the relationships between growth rate and RNA concentrations (Sutcliffe 1970, Elser et al. 2000b).

Survival and mortality

Ecologists have traditionally viewed survival times and their inverse, mortality rates, as being highly variable and consequences of extrinsic environmental conditions, such as predation, disease, and resource competition, rather than intrinsic properties of individual organisms (e.g., Charnov 1993, Kozłowski and Weiner 1997, Stearns et al. 2000). However, because most populations are neither continuously increasing nor decreasing, mortality rates must very nearly equal fecundity rates, and fecundity is fueled by biomass production. Metabolic theory therefore predicts that Eq. 7 should account for much of the variation in field mortality rates, Z . Mortality rates of free-living marine fish stocks support this prediction (Fig. 4; see also Peterson and Wroblewski 1984). The slope of the size-corrected relationship between mortality rate and temperature gives an activation energy of 0.47 eV, which is somewhat lower than the predicted range of 0.60–0.70 eV. The slope of temperature-corrected mortality rate as a

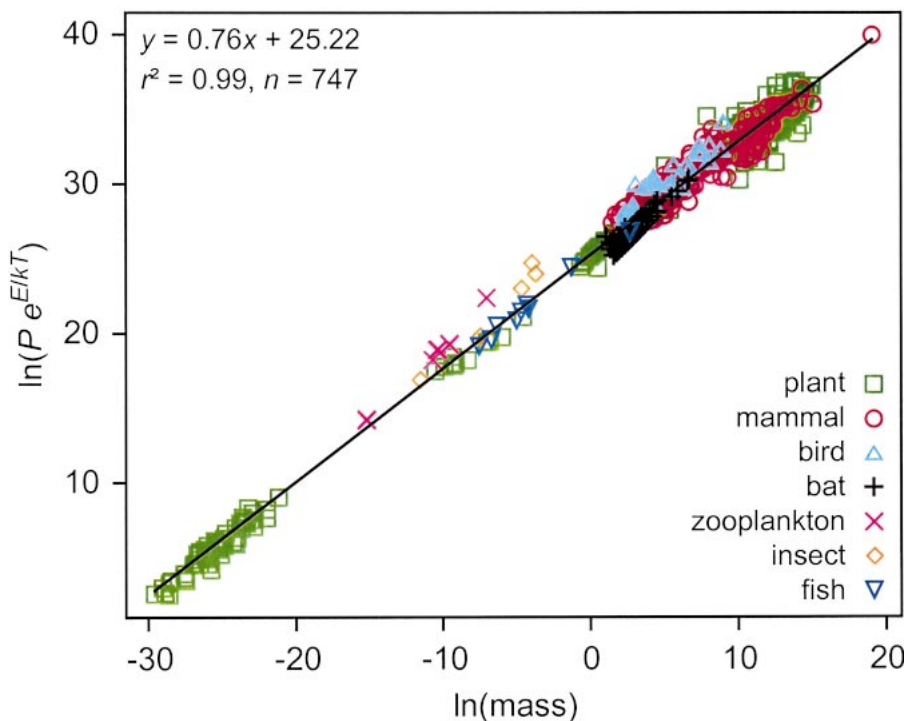


FIG. 2. Mass dependence (mass measured in grams) of temperature-corrected maximal rates of whole-organism biomass production ($Pe^{E/kT}$, measured in grams per individual per year) for a wide variety of organisms, from unicellular eukaryotes to plants and mammals (from Ernest et al. 2003). Data, which span >20 orders of magnitude in body size, have been temperature corrected using Eq. 6. The allometric exponent, indicated by the slope, is close to the predicted value of $3/4$ (95% CI, 0.75–0.76).

function of body mass, -0.24 , is almost identical to the predicted exponent of $-1/4$ (Savage et al., *in press a*).

We offer two complementary, non-mutually exclusive hypotheses for the body size and temperature dependence of field mortality rates. First, the cumulative effects of metabolism with age may affect the ability of individual organisms to resist ecological causes of death, whether they be biotic or abiotic in origin. Studies of aging have led to a theory of senescence that attributes aging and eventual death to cumulative damage at the molecular and cellular levels by the free radicals produced as byproducts of aerobic metabolism (Gerschman et al. 1954, Hartman 1956, Cadenas and Packer 1999). **Second, the size and temperature dependence of field mortality rates suggest that Eq. 5 characterizes rates of ecological interactions that lead to death, including competition, predation, parasitism, and disease.** As we will show, the rates of these interactions do indeed show the predicted temperature dependence.

Stoichiometry

At the individual level, energy and materials are linked by the chemical equations of metabolism, by the composition of organelles and other constituents of protoplasm, and by fundamental constraints on struc-

ture and function at cellular to whole-organism levels of organization. Many of these constraints are related directly to metabolism. The average rate of turnover of an element (i.e., the inverse of residence time) is equal to the whole-organism flux divided by the whole-organism pool or storage. The fluxes (per individual rates of uptake and loss) of most elements vary with body size in direct proportion to whole-organism metabolic rate, as $F \propto M^{3/4}$ (e.g., Peters 1983). Pools of the commonest constituents of protoplasm, including carbon, hydrogen, oxygen, and water, usually scale linearly with body mass, i.e., as $S \propto M^1$. So, for these common elements, turnover rate, on average, scales as $F/S \propto M^{3/4}/M^1 = M^{-1/4}$. However, this is not true of all element pools, especially those that have some special function in metabolism. Metabolism of eukaryotes takes place primarily in organelles: chloroplasts, mitochondria, and ribosomes, which are, respectively, the sites of photosynthesis, respiration, and protein synthesis. These organelles are effectively invariant units; their structure and function are nearly identical across taxa and environments. The reaction rate per organelle is independent of body size (but not temperature), so the rate of whole-organism metabolism depends on the total numbers of organelles. Consequently, numbers of these organelles per individual scale as $M^{3/4}$, and concentrations or densities of the organelles scale as $M^{-1/4}$.

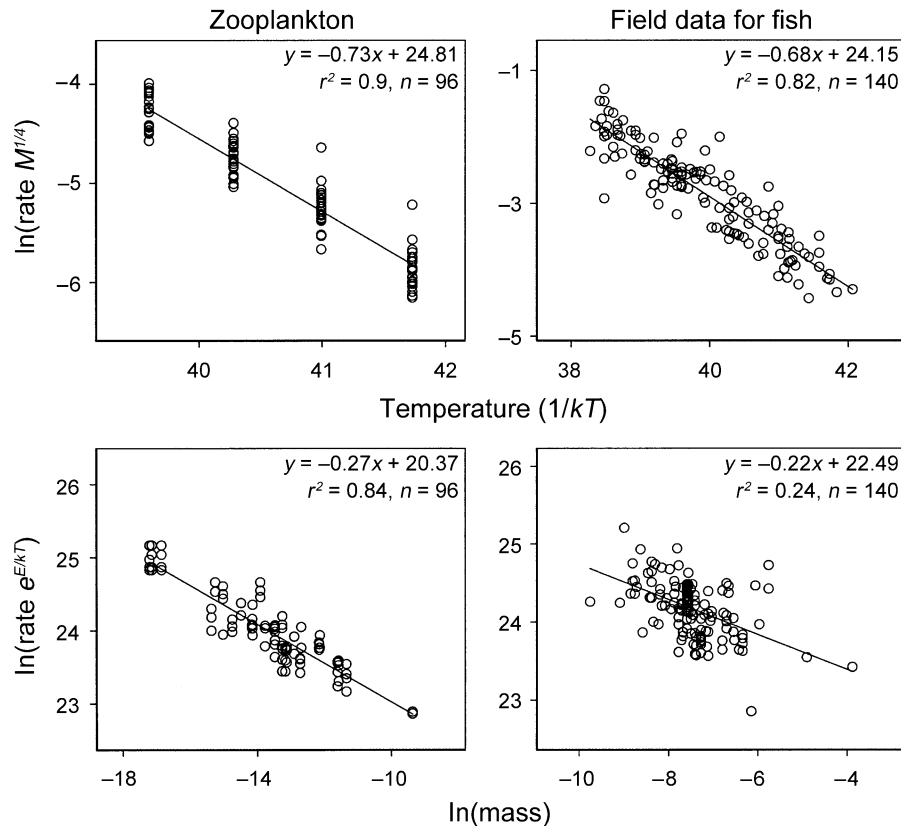


FIG. 3. Temperature (measured in K) and mass (measured in grams) dependence of developmental rates for eggs of zooplankton in the laboratory (data from Gillooly and Dodson 2000) and fish in the field (data from Pauly and Pullin 1988). Hatching time data have been converted to rates (1/time) and plotted as functions of temperature (upper panels, where the rate is measured in $\text{g}^{1/4}/\text{day}$) and mass (lower panels, where the rate is measured as 1/day), as described in the section *Ontogenetic growth*. The activation energy and allometric exponent, as indicated by the slopes in the upper and lower panels, respectively, are similar to the predicted values of 0.60–0.70 eV (95% CIs from left to right, 0.68–0.78 eV and 0.62–0.73) and $-1/4$ (95% confidence intervals, from left to right, -0.24 to -0.29 and -0.16 to -0.29).

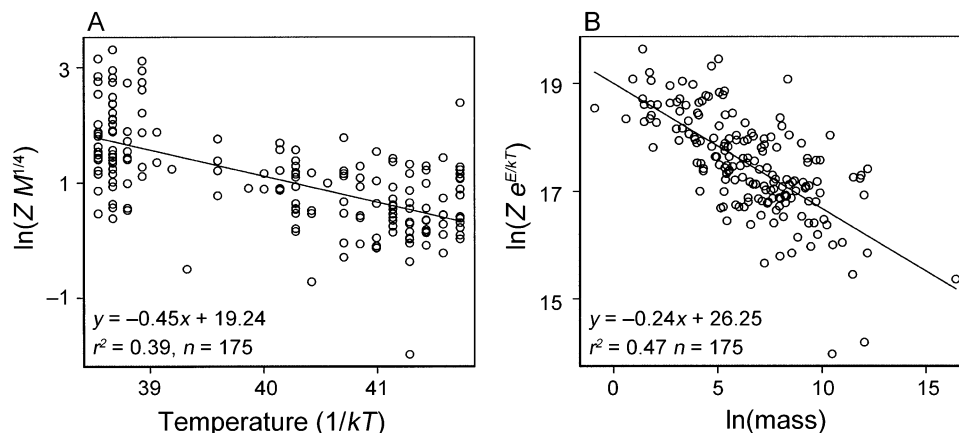


FIG. 4. Temperature (measured in K) and mass (measured in grams) dependence of fish mortality rates in the field (data from Pauly 1980). (A) Relationship between mass-corrected mortality rate, $\ln(ZM^{1/4})$, measured in $\text{grams}^{1/4}$ per year, and temperature, $1/kT$ (measured in K). The activation energy, indicated by the slope, is lower than the predicted range of 0.60–0.70 eV (95% CI, -0.37 to -0.54). (B) Relationship between temperature-corrected mortality rate, $\ln(Ze^{E/kT})$, measured as 1/year, and body mass, $\ln(M)$, measured in grams. The allometric exponent, indicated by the slope, is close to the predicted value of $-1/4$ (95% CI, -0.20 to -0.27).

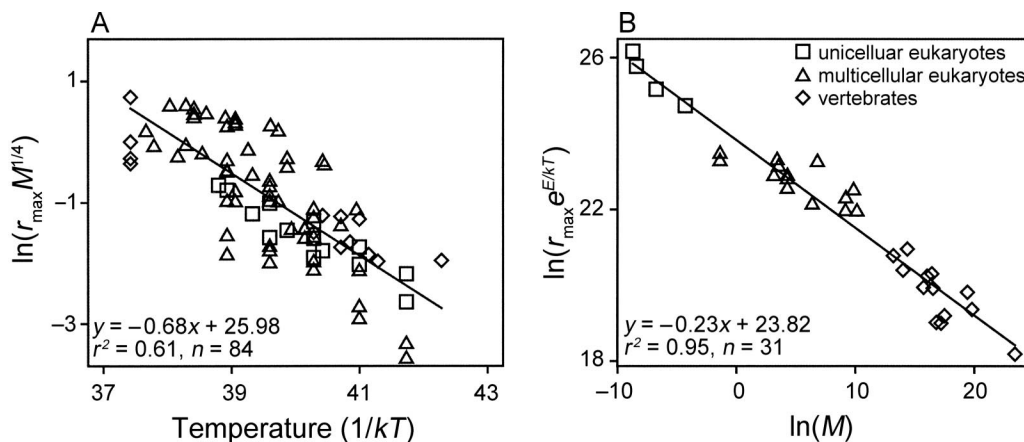


FIG. 5. Temperature (in K) and mass (measured in grams) dependence of maximal rates of population growth, r_{\max} , for a wide variety of organisms (A and B, respectively; data sources are listed in Savage et al., *in press a*). Data are plotted as in Figs. 3 and 4; r_{\max} is measured in $g^{1/4}$ per day in (A) and as 1/day in (B). There are fewer data points in (B) because there are multiple temperature points for a species of a given mass. The activation energy and allometric exponent, indicated by the slopes in (A) and (B), respectively, are close to the predicted values of 0.60–0.70 eV (95% CI, 0.56–0.80) and $-1/4$ (95% CI, -0.21 to -0.25), respectively.

(Niklas and Enquist 2001, West et al. 2002; J. F. Gillooly and A. P. Allen, *unpublished data*). This has been shown to be true for mitochondria (West et al. 2002), chloroplasts (Niklas and Enquist 2001), and RNA (Foss and Forbes 1997). Thus, element pools associated with organelles such as these should scale with body size as $S \propto M^{3/4}$, and turnover rates of these pools should be independent of body size ($F/S \propto M^{3/4}/M^{3/4} = M^0$).

The extent to which whole-body stoichiometry is determined by these pools, and thus varies with body size, will depend on their sizes relative to other pools. For example, whole-body phosphorus concentrations should decline with increasing body size in growing unicellular organisms because they contain relatively high concentrations of phosphorus in RNA relative to phosphorus in other pools. However, whole-body phosphorus concentrations in most multicellular organisms should vary little with body size because most phosphorus is found in other pools that do not scale with body size (J. F. Gillooly and A. P. Allen, *unpublished data*). Similar reasoning should apply to the concentrations of nitrogen in plants, because a significant fraction is found in chloroplasts.

POPULATION AND COMMUNITY DYNAMICS

We can extend this framework to population and community levels of ecological organization. Many features of population dynamics and community organization are due to effects of body size, temperature, and stoichiometry on the performance of individual organisms.

Population growth rates and r_{\max}

Population dynamics can be complex and unpredictable, but the potential for exponential growth that underlies these fluctuations has been called the one

unequivocal law of population ecology (Turchin 2001). The maximal rate of exponential increase, r_{\max} , is predicted to scale according to Eq. 7. This follows from the fact that reproduction is fueled by metabolism, and that mass-specific production rates and mortality rates follow Eq. 7. In fact, metabolic rates of microbes are often determined by measuring maximal population production P_{tot} or maximal population growth rates, r_{\max} .

The $-1/4$ mass dependence of r_{\max} has been well documented empirically (Slobodkin 1962, Blueweiss et al. 1978), but what about the temperature dependence? Fig. 5 shows that Eq. 5 describes tightly constrained variation in r_{\max} across a wide variety of organisms, from unicellular eukaryotes to mammals. The commonality is impressive, especially because these organisms have very different modes of reproduction and occur in a wide variety of environments (Savage et al., *in press a*).

This finding suggests that some interpretations of differences in life history and resulting population processes should be reexamined. For example, differences between populations in life history, including the classical r and K strategies, have often been viewed as adaptations to particular environmental conditions. Metabolic theory shows that smaller organisms, and those operating at higher temperatures, tend to have higher r_{\max} values than larger, colder organisms, simply as a consequence of allometric and kinetic constraints. We hasten to add, however, that this does not necessarily mean that size- and temperature-related differences between populations in life histories are not adaptive. Organisms can respond to selection resulting from different environments by changing body size. For example, strong selection, perhaps for high reproductive rates in the absence of predators, apparently

causes rapid dwarfing of elephants and other large mammals on islands (e.g., Lister 1989, Roth 1990, Brown 1995). Some organisms can also change temperature adaptively. For example, many terrestrial ectothermic animals exhibit some kind of behavioral thermoregulation: they seek out warm microenvironments to elevate body temperatures and increase rates of production for growth and reproduction.

Population density

It is straightforward to solve the equation for population growth rate for the steady state when the number of individuals, N , is not changing ($dN/dt = 0$). The equilibrium number of individuals or carrying capacity, K , is predicted to vary as

$$K \propto [R]M^{-3/4}e^{E/KT} \quad (9)$$

linearly with the supply rate or concentration of the limiting resource $[R]$, as a power function of body mass, and exponentially with temperature (Savage et al., *in press a*). The qualitative effects of resource supply and body size are not surprising: more individuals with increased resource or decreased size. The effect of temperature, however, may not be so intuitive. Increasing the temperature actually reduces the carrying capacity, because the same supply of energy supports a smaller number of individuals, each fluxing energy and materials at a higher rate. This prediction of an inverse Boltzmann relationship between equilibrium abundance and environmental temperature for ectotherms is supported by the analysis of Allen et al. (2002).

If resource supply rate $[R]$ and temperature T are held constant, then population density should vary inversely with body size, as $M^{-3/4}$. This is the basis for deriving a resource-based thinning law of plant ecology in which the number of stems, N , is predicted to vary with plant mass as $N \propto M^{-3/4}$, or with stem diameter, D , as $N \propto D^{-2}$ (Enquist et al. 1998, Belgrano et al. 2002; see also Lonsdale 1990). The theory assumes that sessile plants grow until limited by competition for resources, and that individual resource requirements scale as $M^{3/4}$. The theory accurately predicts thinning trajectories in even-aged stands, which follow a $M^{-3/4}$ or D^{-2} power law. A more complex model that incorporates growth and mortality predicts size–frequency distributions of the trees in steady-state forests with stable age and size distributions (G. B. West, B. J. Enquist, and J. H. Brown, *unpublished data*). This model predicts the same scaling of number of stems of a given size as a function of plant mass or stem diameter ($N \propto M^{-3/4} \propto D^{-2}$). Data from forests throughout the world show size distributions that are very similar to the predicted scaling (Enquist and Niklas 2001).

Eq. 9 predicts that carrying capacity or equilibrium population density should also scale as $M^{-3/4}$ in mobile animals if one again assumes that the rate of resource supply is held constant. One potentially confounding

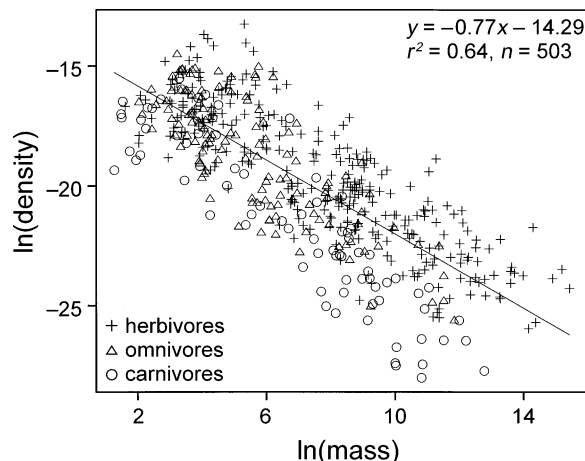


FIG. 6. Mass dependence of population density in terrestrial mammals (data sources are listed in Ernest et al. [2003], including data from Damuth [1987]). Density was measured as no. individuals/km², and mass was measured in grams. Data were analyzed without temperature correction because mammals have very similar body temperatures. The slope of this relationship gives an allometric exponent close to the predicted value of $-3/4$ (95% CI, -0.72 to -0.82). There is considerable variation in the densities of mammals of similar size, which is not surprising since the data are for all kinds of mammals from throughout the world. So, for example, some of the residual variation is related to trophic level: carnivores with lower rates of resource supply tend to have lower population densities than herbivores.

issue is the unit of analysis. The theory predicts how many individuals of a given size can be supported, but the data are often compiled by species. For example, Damuth (1981, 1987; see also Carbone and Gittleman 2002) showed empirically that population densities of species of terrestrial mammals from all over the world scaled as $M^{-3/4}$. There are, however, at least two orders of magnitude variation in the population densities of species of any given size (Fig. 6). Most of this variation can almost certainly be attributed to variation in resource supply. The data come from a wide variety of environments that differ considerably in resource availability, and from mammal species that vary in diet from herbivores to carnivores. So to test the theory properly, the densities of all coexisting species within a trophic group and body size category should be summed, as is done for trees in forest communities.

The $M^{-3/4}$ scaling of equilibrium population density with body size raises interesting theoretical questions. Because the number of individuals per unit area, N , scales as $M^{-3/4}$ and whole-organism metabolic rate scales as $M^{3/4}$, total energy use per unit area for a size class is $M^{-3/4} M^{3/4} \propto M^0$. Within a functional group sharing a common resource, the rate of energy flux per unit area of the combined populations of different-sized organisms is predicted to be independent of size. This energy equivalence argument can also be turned around. Whenever total population density scales empirically as $M^{-3/4}$, the resulting invariance in energy

TABLE 1. Studies in which relevant components of competitive or predator–prey interactions have been studied at different temperatures so as to allow estimation of the activation energy, E .

Study	Interspecific interaction	Taxon	Measure	E (eV)
Burnett (1951)	parasitism	wasp/sawfly	rate of parasitism	0.81
Spitze (1985)	predation	fly larvae/zooplankton	attack rate	0.56
Eggleston (1990)	predation	crab/oyster	attack rate	0.80
Luecke and O'Brien (1983)	predation	zooplankton	feeding rate	0.81
Verity (1985)	grazing	zooplankton/phytoplankton	grazing rate	0.57
Park (1954)	competition	beetle	time to competitive exclusion	0.64

Note: Although the number of measurements is usually small, resulting in wide confidence intervals, note that the values of E vary around the theoretically predicted range of 0.60–0.70 eV. SI conversion: 1 eV = 23.06 kcal/mol = 96.49 kJ/mol.

flux implies that resources are available to and are used by each body size class at equal rates. Why should this be so? The resource-based thinning theory for plants reasonably assumes that sessile individuals of different size compete for the same limiting resources (light, water, nutrients). So far, however, we have no comparable theory to explain why the rate of supply of usable energy should be approximately constant for differently sized mammals or other mobile animals that utilize a broad spectrum of resources.

Interspecific interactions

Since the theoretical studies of Lotka (1925) and Volterra (1926) and the classical experiments of Gause (1934), Park (1948), and Huffaker (1958), ecologists have tried to understand how pairs of competing species or of predators and prey coexist with stability in the same environment. The experimental studies found that coexistence was difficult to obtain in simple laboratory environments: one of the populations almost invariably went extinct. For example, in Park's (1954) classic experiments with flour beetles, by varying the temperature, he was able to reverse the outcome of competition, changing which species survived and which went extinct. Less appreciated is the fact that time to competitive exclusion across three temperatures was inversely related to temperature with an activation energy of 0.64 eV (1 eV = 96.49 kJ/mol), nearly identical to the average for individual metabolism. A number of other interaction rates and times, including rates of parasitism and predator attack rates, show similar temperature relations (Table 1; see also Tilman et al. 1981, Dunson and Travis 1991). Metabolic theory predicts the pace of these interactions, because rates of consumption and population growth are determined by rates of individual metabolism and have the same body size and temperature dependence.

Species diversity

The scaling of rates of ecological interactions has important implications for coexistence and species diversity. The qualitative empirical patterns of biodiversity would suggest that the processes that generate and maintain species richness scale similarly to other bi-

ological rates, as in Eq. 7. Other things being equal, there are more species of small organisms than large ones and more species in warm environments than cold ones.

The fact that species diversity varies inversely with body size suggests that metabolism plays a central role (e.g., Hutchinson and MacArthur 1959, May 1978, 1986, 1988, Brown 1995). As recently as a decade ago, the available evidence suggested that the highest diversity occurred in small, but not the smallest, organisms (i.e., in small insects; see May 1978, 1986). Recent data, however, reveal enormous microbial diversity and suggest that species richness may continue to increase with decreasing body size right on down to the smallest prokaryotes and perhaps even to viruses (e.g., Pace 1997).

It has long been known that diversity of most taxonomic and functional groups is highest in the tropics, but this has usually been attributed to higher productivity (resource availability) or reduced seasonality, rather than to the kinetic effect of higher temperatures (e.g., Brown and Lomolino 1998; but see Rohde 1992). We have recently shown, however, that species richness in many groups of plants and animals has the same Boltzmann relationship to environmental temperature that metabolic rate does (Eq. 3; see Allen et al. 2002). This result holds true not only along latitudinal gradients, but also along elevational gradients where variables such as photon flux, seasonal changes in day length, and biogeographic history are held relatively constant (Fig. 7). The implication is that much of the variation in species diversity is directly attributable to the kinetics of biochemical reactions and ecological interactions.

The temperature dependence of population growth and interspecific interactions brings into question explanations for diversity that invoke long time lags (e.g., Hutchinson 1961, Bell 2001, Hubbell 2001). The highest diversity on earth is found in warm, productive environments, such as tropical rain forests and coral reefs, where the kinetics of interactions might be expected to lead to rapid exclusion. We hypothesize that diversity is largely a consequence of evolutionary processes that obey Eqs. 7 and 8: small or warm organisms

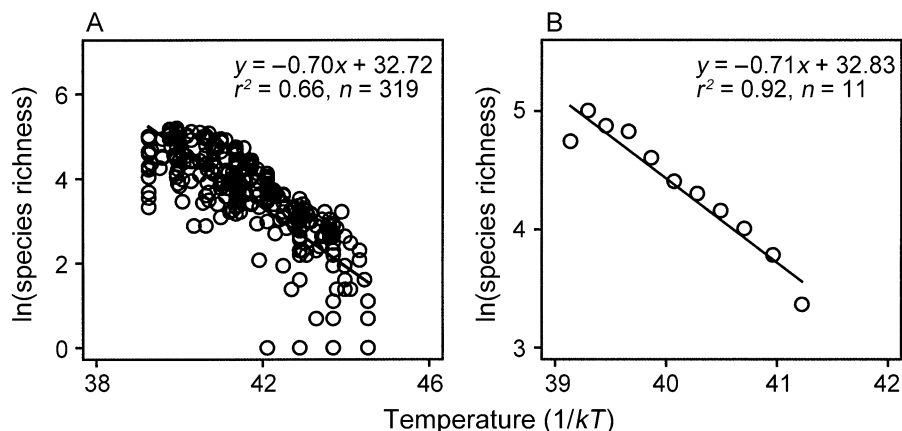


FIG. 7. Temperature dependence (temperature measured in K) of amphibian species richness in two geographic gradients (Allen et al. 2002). (A) A latitudinal gradient in North America (data from Currie 1991). (B) An elevational gradient over 2600 m on Volcan Barva in Costa Rica (data from Duellman 1988). The slopes indicate nearly identical effects of temperature on diversity in the two gradients, with activation energies close to the predicted value of 0.60–0.70 eV (95% confidence intervals, from left to right, 0.63–0.77 and 0.55–0.87).

having faster ecological dynamics than large or cold ones should also have faster evolutionary dynamics, resulting in higher rates of speciation and a higher standing stock of species. We have shown that Eq. 7 predicts rates of molecular evolution for a variety of genes and genomes for ectotherms and endotherms (J. F. Gillooly and A. P. Allen, *unpublished data*). Van Valen (1973) attributed the origin and maintenance of biodiversity largely to the “Red Queen” phenomenon, rates of species interaction and coevolution. We agree, and conjecture that the Red Queen runs according to Eq. 7: faster in warmer environments and smaller organisms.

Although this conjecture is consistent with many facts about biodiversity, it raises additional questions. First, how can the kinetic effects of high temperature be distinguished from the resource supply effects of high productivity, which also increases with increasing temperature? Second, how do faster rates of interspecific interaction and evolution result in higher standing stocks of species? This conjecture also raises the question of why ectotherms, whose body temperatures and metabolic rates vary with environmental temperature, and endotherms, which have relatively high and constant body temperatures, show qualitatively similar geographic patterns of diversity. One hypothesis would again invoke the Red Queen and suggest that species diversity of endotherms is due largely to interactions with ectotherms: food resources, competitors, predators, parasites, and diseases. Alternatively, biodiversity gradients may be driven largely by ecosystem productivity for endotherms, and by temperature effects on biochemical kinetics for ectotherms. Consistent with this latter hypothesis, average population densities of ectotherms, but not endothermic mammals, decline exponentially with temperature toward the warm tropics (Allen et al. 2002). Clearly, much additional work on

the relationship between metabolism and biodiversity is needed, but a metabolic perspective has sharpened many of the questions and has suggested where to look for some of the answers.

ECOSYSTEM PROCESSES

Some of these questions can be addressed by probing more deeply the effects of biological metabolism on the fates of energy and materials in ecosystems. Biologically regulated whole-ecosystem stores and fluxes of elements and compounds, such as phosphorus, nitrogen, and carbon, are simply the sums of the stores and fluxes of the constituent organisms. Metabolic theory therefore makes explicit predictions about the contribution of biota to biogeochemical cycles. Specifically, Eq. 7 provides the basis for predicting how size, temperature, and stoichiometry determine magnitudes of stores and rates of flux within and between compartments such as primary producers, herbivores, predators, and detritivores.

Standing stock of biomass

It is straightforward to derive an expression for standing stock biomass. Eq. 9 gives the effects of body mass and temperature on equilibrium population density (number of individuals per unit area). Multiplying this expression by the body size per individual, M , gives the corresponding equation for standing stock or stored biomass, W , per unit area:

$$W \propto [R]M^{1/4}e^{E/kT}. \quad (10)$$

The rate of supply of limiting resource, $[R]$, has direct linear effects on both carrying capacity and biomass. Total biomass increases nonlinearly with increasing body size and decreasing temperature. Large and/or cold organisms retain more resources in their bodies because they flux them more slowly through their met-

abolic pathways, and vice versa for small and/or hot organisms.

Energy flux and biomass production

At steady state, the rate of resource uptake by consumers or “predators” is some constant fraction of the rate of production of producers or “prey.” As individuals, both producers and consumers flux energy with the whole-organism and mass-specific scalings given in Eqs. 4 and 7. However, the rate of energy flux for populations should show a different mass dependence, but not temperature dependence, because of the scaling of population density and biomass. Rate of flux per unit area, F_{tot} , can be derived by multiplying Eq. 4, for the whole-organism metabolic rate per individual, by $M^{-3/4}$, the number of individuals per unit area (from Eq. 9). The result is

$$F_{\text{tot}} \propto [R]M^0 e^{-E/KT}. \quad (11)$$

The rate of biological energy flux or productivity per unit area of an ecosystem is therefore predicted to be independent of body size but to increase with increasing temperature. Enquist et al. (1998; also Niklas and Enquist 2001) show that across diverse ecosystems, rates of primary production, measured as rates of whole-plant xylem flux, are independent of plant size as predicted by Eq. 11. The data of Enquist et al. (1998; Fig. 4) show about two orders of magnitude variation in rates of productivity, which is small in comparison to the nearly 12 orders of magnitude variation in plant mass. Most of the variation in productivity is probably due to both temperature and stoichiometry. The data set includes ecosystems from around the world with substantially different temperatures and energy, water, and nutrient availability. The size invariance explicit in Eq. 11 means that ecosystems with similar temperature regimes and rates of resource supply, such as adjacent forests and grasslands, should have nearly equal rates of primary production. Clearly, however, the forests contain much more stored biomass, as predicted by Eq. 10.

One complication is that plant metabolic rate is the rate of photosynthesis: the rate of conversion of solar energy into organic compounds. Photosynthesis consists of multiple biochemical reactions, some of which are temperature dependent and have a range of activation energies (0.35–0.65 eV; Bernacchi et al. 2001), and some of which are dependent only on light (Farquhar et al. 1980). Terrestrial plants maximize photosynthesis in different environments by differentially partitioning proteins among enzymatic reactions based on their respective temperature and light dependencies (Farquhar et al. 1980, Field and Mooney 1986). Less well understood, however, is how photosynthesis at the level of individual plants is manifested in global patterns of plant production. We find that the activation energy for terrestrial net primary production (gross plant production minus plant respiration) across the

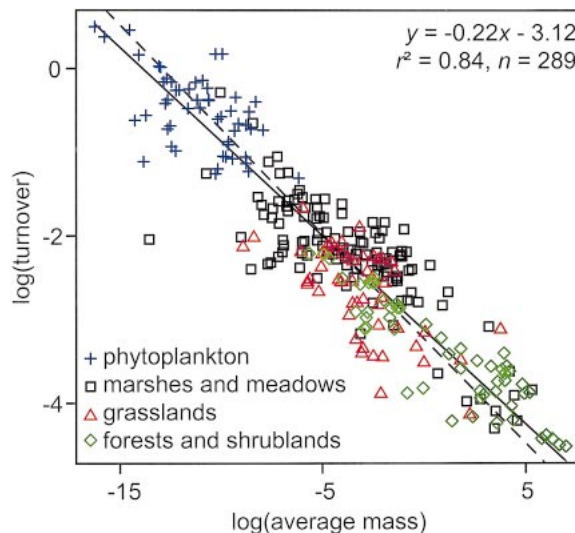


FIG. 8. Relationship of carbon turnover rate (measured as $[\text{day}]^{-1}$) to average plant size for plant biomass (measured in grams) in aquatic and terrestrial ecosystems (analysis by A. P. Allen, J. F. Gillooly, and J. H. Brown, *unpublished manuscript*; carbon turnover data from Cebrian [1999] and for plant size data from Belgrano et al. [2002]). Data have not been temperature corrected, because environmental temperatures were not reported. The slope of the relationship (solid line) gives an allometric exponent close to the predicted value of $-1/4$ (dashed line; 95% CI, -0.21 to -0.24).

globe is well described by a Boltzmann relationship with an activation energy of ~ 0.33 eV (A. P. Allen, J. F. Gillooly, and J. H. Brown, *unpublished manuscript*). This value is approximately half the magnitude of the activation energy for respiration or secondary production (≈ 0.63 eV). This has important consequences for carbon cycles and organic matter storage (e.g., Schlesinger 1991).

Biomass turnover and energy flux

In the ecological literature, especially in applied disciplines such as fisheries, production is often expressed as the production/biomass ratio, P_{tot}/W , of total population production, P_{tot} , to standing stock biomass, W . Given that $P_{\text{tot}} = PN$, and that $W = NM$, this quantity must scale as

$$P_{\text{tot}}/W \propto M^{-1/4} e^{-E/KT} \quad (12)$$

the same as mass-specific metabolic rate (Eq. 7). Empirical studies have shown this predicted size dependence for populations of different species (Peters 1983). For a steady-state population, production reflects the replacement of individuals lost due to mortality, so production must scale with body size and temperature the same as mortality rate, Z , consistent with Eqs. 7 and 12 and the empirically observed scaling (Savage et al., *in press a*; Fig. 4). Furthermore, because rates of biomass production and consumption must be equal at steady state, Eqs. 7 and 12 also predict rates

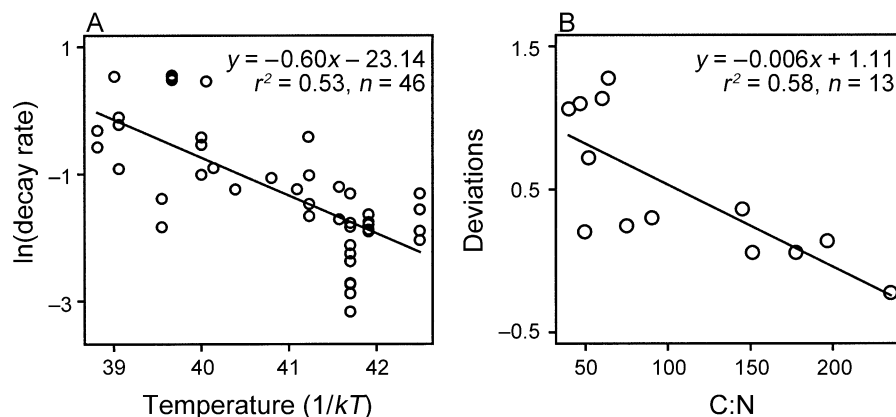


FIG. 9. Temperature dependence (temperature in K) of short-term root decay rate (measured as $[\text{day}]^{-1}$) as characterized by the rate constant, k (analysis by A. P. Allen, J. F. Gillooly, and J. H. Brown, *unpublished manuscript*; data from Silver and Miya [2001]). (A) The observed activation energy, as indicated by the slope, is within the range of values (0.60–0.70 eV) predicted on the basis of metabolic rate (95% CI, 0.43–0.76). (B) Plotting the residuals about the regression line in (A) as a function of C:N shows that much of the variation is due to stoichiometry ($P < 0.05$).

of biomass turnover. Fig. 8 (from A. P. Allen, J. F. Gillooly, and J. H. Brown, *unpublished manuscript*; data from Cebrian 1999) shows that carbon turnover rates in a broad assortment of terrestrial and aquatic ecosystems scale with average plant size as $M^{-0.22}$. Not only is this very close to the predicted $M^{-1/4}$, but also size varies over ~ 20 orders of magnitude and accounts for 84% of the variation in these data. Thus retention times for carbon and nutrients must show the reciprocal relation, as in Eq. 8. Temperature and nutrient supply undoubtedly explain much of the remaining variation.

Empirical studies also support the predicted temperature dependence. Total ecosystem respiration from a broad assortment of terrestrial ecosystems around the world, measured by eddy covariance towers as nighttime CO_2 flux, varies with temperature as predicted based on individual metabolism. The average activation energy from 19 sites was 0.62 eV, within the predicted range of 0.60–0.70 eV (Enquist et al. 2003). Similarly, Fig. 9 shows that temperature alone accounts for 53% of the variation in short-term rates of decomposition from sites around the world (A. P. Allen, J. F. Gillooly, and J. H. Brown, *unpublished manuscript*; data from Silver and Miya 2001). The activation energy is 0.60 eV, not significantly different from the range 0.60–0.70 eV predicted on the basis of aerobic metabolism. Furthermore, 58% of the residual variation can be explained by stoichiometry (in this case, the C:N ratio of the litter; see Fig. 9).

This metabolic framework also could be applied to address more precisely and quantitatively the questions raised by Odum (1969) in his classic paper on “The Strategy of Ecosystem Development.” For example, it should be possible predict the dynamics of succession: how productivity, biomass, and material turnover rates change with increasing plant size during transition from herbaceous-dominated to tree-dominated ecosystems following either natural disturbances, such as forest

fires, or human perturbations, such as abandonment of agricultural fields. Metabolic theory also provides a framework for more explicitly incorporating stoichiometry and understanding the effects of limited water and nutrients on variation in productivity and other processes across biomes and geographic gradients. Regression models that incorporate these variables are able to account for much of the observed variation (e.g., Lieth 1973), but it should be possible to replace these with mechanistic analytical models based on first principles.

Trophic dynamics

Another major focus of ecosystem science has been the structure and dynamics of food webs, which depict the flows of energy and materials through ecosystems due to trophic interactions. Metabolism has usually been incorporated into food web theory only to the extent of showing that the fluxes of energy and materials obey the laws of thermodynamics and conservation of energy, mass, and stoichiometry (but see Kerr and Dickie 2001). It should be possible to do much more, in particular to use metabolic theory to understand the abundance, biomass, energy use, and elemental chemical composition of species populations or entire functional groups in terms of the effects of body size, temperature, and stoichiometry on metabolic rate. We illustrate the possibilities with two examples.

Ecologists have long depicted trophic organization as pyramids of energy, biomass, or abundance. Each layer of a pyramid corresponds to a successively higher trophic level, starting with primary producers and going up through herbivores, primary carnivores, and so on. Metabolic theory makes quantitative predictions for how body size, temperature, and stoichiometry affect the pools and fluxes of biomass and energy. At steady state, the Second Law of Thermodynamics demands that there be less available energy at higher trophic

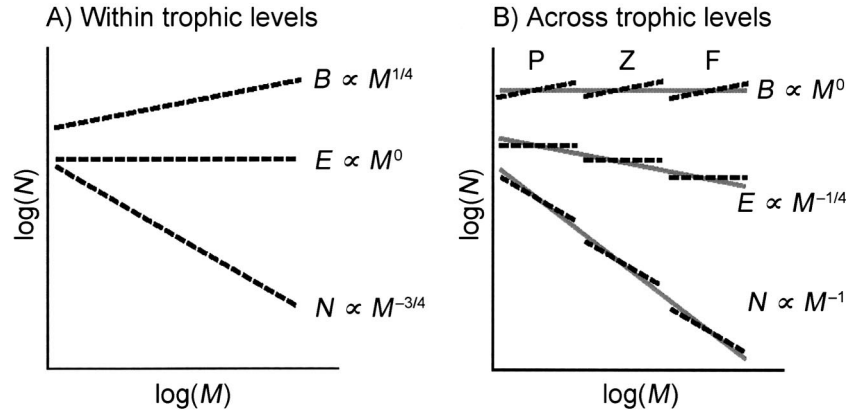


FIG. 10. A simple graphical model to explain the invariance of biomass as a function of body size of pelagic organisms in ocean and lake ecosystems (from Brown and Gillooly 2003), where M is body mass, E is activation energy of metabolism, B is mass-specific rate of metabolism, and N is number of individuals. If the ratio of predator size to prey size is 10 000, and 10% of energy is transferred between successive trophic levels, Eq. 13 predicts allometric scaling of total abundance, energy use, and biomass (A) within trophic levels (dashed lines: $M^{-3/4}$, M^0 , $M^{1/4}$, respectively) and (B) across trophic levels (continuous lines: M^{-1} , $M^{-1/4}$, M^0 , respectively) from phytoplankton (P) to zooplankton (Z) to planktivorous fish (F).

levels because, first, energy is lost within a trophic level due to respiration and heat production, and second, energy is lost between trophic levels due to inefficiencies in transferring the biomass produced at one trophic level, designated 0, to the next higher trophic level, designated 1. The loss of energy between two adjacent trophic levels can be characterized by a Lindeman efficiency, α , the ratio of total metabolic energy fluxes at trophic level 1 to those at level 0. So, from Eq. 4 it follows that $\alpha = i_1 N_1 M_1^{3/4} e^{-E/kT} / i_0 N_0 M_0^{3/4} e^{-E/kT}$, where i_0 and i_1 are the normalization constants for field metabolic rate, and N_0 , N_1 , M_0 , and M_1 are the population densities and body masses at trophic levels 0 and 1, respectively. Assuming that the system is in steady state and that temperatures and normalization constants do not differ between trophic levels, this simplifies to $\alpha = N_1 M_1^{3/4} / N_0 M_0^{3/4}$, and α must always be < 1 . Given these same assumptions, we can also derive comparable relations for abundance, $N_1/N_0 = \alpha (M_0/M_1)^{3/4} < (M_1/M_0)^{-3/4}$; and for biomass, $W_1/W_0 = \alpha (M_0/M_1)^{-1/4} < (M_1/M_0)^{-1/4}$. Thus, it is impossible to observe inverted pyramids of energy flux, but possible to observe inverted pyramids of abundance if the higher trophic level is composed of organisms of sufficiently smaller size; e.g., phytophagous insects feeding on trees. It is also possible to observe inverted pyramids of biomass if the higher trophic level is composed of organisms of sufficiently larger size, e.g., whales feeding on plankton. Note that the more explicit version incorporating normalization constants and temperature dependence can be used to give a more exact prediction, as when, for example, a trophic level is composed primarily of endotherms with elevated body temperatures. Usually, however, the simpler inequalities will be conservative, because the organisms at higher trophic levels tend to have somewhat higher normalization con-

stants for metabolic rate and because some of the energy goes directly to decomposers rather than to traditional “consumers” at higher trophic levels.

A second and related example concerns the relationship between body size, biomass, and abundance in pelagic ecosystems. Since the 1970s, ecologists have noted the empirical pattern that in both freshwater and marine ecosystems, total standing biomass, W , is invariant with respect to body size (i.e., $W \propto M^0$) across all pelagic organisms from unicellular plankton to the largest animals. Consequently, abundance varies with body size as $N \propto M^{-1}$ (e.g., Sheldon and Parsons 1967, Sheldon et al. 1972, 1977, Peters 1983, Cyr 2000; see also Kerr and Dickie 2001, Cohen et al. 2003). A simple model can explain this pattern (Fig. 10; see also Brown and Gillooly 2003). There are powerful body size constraints on the flow of energy in pelagic ecosystems. Primary producers are minute unicellular algae and prokaryotes, whereas successive trophic levels consist of organisms of increasing size, zooplankton, planktivorous fish, and so on. If the size of the unicellular algae at trophic level 0 is equal to M_0 and β is the average ratio of predator body size to prey body size, then the dependence of trophic level on mass can be described by the equation $\tau = \log_\beta(M/M_0) = \log(M/M_0)/\log(\beta)$, where $\tau = 0$ is the trophic level for algae of size M_0 . If we further assume that the total rate of metabolism at trophic level 0 is equal to $i_0 N_0 M_0^{3/4} e^{-E/kT}$, and that τ and the Lindeman efficiency α are constants across trophic levels, then the total rate of metabolism for organisms of size M is

$$I_{\text{tot}} = (i_0 N_0 M_0^{3/4} e^{-E/kT}) \alpha^\tau$$

$$= (i_0 N_0 M_0^{3/4} e^{-E/kT}) \left(\frac{M}{M_0} \right)^{\log(\alpha)/\log(\beta)}.$$

Following Eq. 4, the total number of organisms of a given size is the following:

$$N = \frac{I_{\text{tot}}}{I} = N_0 \left(\frac{M}{M_0} \right)^{[\log(\alpha)/\log(\beta)] - 3/4} \quad (13)$$

Within a trophic level, where resource supply is relatively constant, Eq. 13 predicts that abundance should decrease with size as $M^{-3/4}$, as has been observed empirically (e.g., Belgrano et al. 2002, Li 2002). Between trophic levels, the transfer of energy, characterized by the Lindeman efficiency α , has been estimated empirically to be $\sim 10\%$ (Lindeman 1942). The range of body sizes within a trophic level, and the difference in average size between trophic levels, is about four orders of magnitude. Consequently, $(\log \alpha)/(\log \beta) \approx -1/4$ in Eq. 11, and abundance declines with body size as $M^{-1/4-3/4} = M^{-1}$ across all trophic levels and the entire spectrum of body sizes (Brown and Gillooly 2003). It follows that energy flux, F , declines with body mass as $M^{(\log \alpha)/(\log \beta)} = M^{-1/4}$, and that biomass scales as M^0 and therefore is invariant (Fig. 10).

We do not yet have a mechanistic theory to explain why α is often $\sim 10^{-1}$ or why β is often $\sim 10^4$. The fraction of metabolic energy allocated to biomass production by the lower trophic level sets an upper limit on α , because production at the lower trophic level fuels metabolism at the next highest trophic level (Kerr and Dickie 2001). This is only an upper limit, however, because it does not include energy losses incurred by the higher trophic level due to foraging and assimilation. The fact that $\beta \sim 10^4$ in size-structured pelagic ecosystems is intriguing (see also Kerr and Dickie 2001, Cohen et al. 2003). The quarter-power allometry implies that predator-prey body size ratios potentially can be explained in terms of metabolic constraints.

CONCLUSIONS AND CAVEATS

We close with a few words about the strengths and limitations of the theory that we have presented. First, we should be explicit about what we mean by a mechanistic theory of ecology. We consider it to be a mechanistic, quantitative, synthetic framework that (1) characterizes the effects of body size and temperature on the metabolism of individual organisms, and (2) characterizes the effects of metabolism of individual organisms on the pools and flows of energy and matter in populations, communities, and ecosystems. Many parts of this framework were established decades ago. Our work has built upon this foundation, primarily by developing mechanistic models that explain quarter-power allometric scaling in biology, combining the effects of body size and temperature on metabolic rate in a single expression, and showing how the metabolism of individual organisms affects the structure and dynamics of ecological systems. Other parts of the framework are still incomplete. Many other investigators are contributing to the emerging theory. Nevertheless, in its current state metabolic theory appears to predict the magnitudes and to elucidate the mechanisms of many empirical phenomena in ecology.

Second, metabolic theory suggests that energy and materials (or energy and stoichiometry) are not fundamentally different ecological currencies that operate independently of each other to affect the structure and dynamics of ecological systems. They are inextricably linked. The fluxes, stores, and transformations of energy and materials are stoichiometrically constrained by the biochemistry and physiology of metabolism. Energy is required to perform biological work, including acquiring and transforming material resources. Materials, both carbon compounds and elemental nutrients, are required to synthesize the chemical compounds that are the basis of all biological structures and functions. At all levels, from individual organisms to ecosystems, the processing of energy and materials is linked due to metabolic constraints.

Third, metabolic processes relate the structure and function of individual organisms to the roles of organisms in ecosystems. On the one hand, many of these linkages are not yet well understood. Both more and better data and new and better theories are needed. On the other hand, much progress can be made using existing data and theories. We have shown how the same principles of allometry, kinetics, and stoichiometry can be used to understand quantitatively the fluxes of both energy and materials in different kinds of organisms and in different kinds of ecosystems. This is because the biogeochemical processes in ecosystems are largely consequences of the collective metabolic processes of the constituent organisms.

Fourth, we envision a metabolic theory that would eventually provide a conceptual basis for ecology similar to that which genetic theory provides for evolution. Metabolism, like inheritance, is one of the great unifying processes in biology, making connections between all levels of organization, from molecules to ecosystems. Metabolic theory would by no means be the only ecological theory nor would it account for all important patterns and processes. It does, however, provide a conceptual framework for ecological energetics and stoichiometry. It does account for much of the variation in ecological rates and times. It is based on first principles of energy, mass, and stoichiometric balances, thermodynamics, biochemical energy transformations, chemical reaction kinetics, and fractal-like biological designs. It uses the biological processing of energy and materials to make linkages between individual organisms and the ecology of populations, communities, and ecosystems.

Fifth, metabolic theory is emphatically not a "theory of everything." As presently formulated, its domain is restricted to effects of allometry, kinetics, and stoichiometry on the biological processing of energy and materials. Within this domain, it appears to explain much of the variation in pools, rates, and times. As our figures show, however, it cannot explain all of the variation. The existence of residual variation calls attention to the importance of other variables and processes

not included in either the specific models or the general theory. A strength of the theory, however, is that it makes explicit quantitative predictions based on first principles. The residual variation can then be measured as departures from these predictions, and the magnitude and direction of these deviations may provide clues to their causes. Additionally, much of ecology lies outside the domain of metabolic theory. There are many phenomena for which metabolic processes either do not apply or play at most a small contributing role. Examples include species–area and species–time relationships, distributions of abundances among coexisting species of similar size, temperature and resource requirements, and the Taylor power law relationship between mean and variance of population size over time or space.

Finally, in this paper we have been concerned only with basic science, with developing a conceptual framework for ecology based on first principles of biology, physics, and chemistry. This is not the place to apply the theory to practical problems of environmental policy and management. It should be apparent, however, that there are many such applications, from wildlife, fisheries, and forest management to global change ecology. The theory helps one to understand some of the changes that have occurred as humans have altered size distributions of organisms, environmental temperatures, and chemical stoichiometry of ecosystems. The theory offers a predictive framework for assessing and responding to human-induced changes in the abundance, distribution, and diversity of organisms, and the fluxes of energy and materials in ecological systems.

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