

Allometry and Metabolic Scaling in Ecology

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Body size affects the structure and function of all levels of biological organization. In ecological systems, body size strongly influences individuals (e.g. rates of individual growth, reproduction and mortality), populations (e.g. population growth rate, abundance and space use), communities (e.g. community abundance, food-web structure and interspecific interactions) and ecosystems (e.g. flux, storage and turnover of materials and energy). This is because individual metabolic rate – the rate at which an organism takes up and utilizes energy and materials – is largely controlled by body size. Here we review how body-size allometries at the individual level affect the structure and function of populations, communities and ecosystems. We use these results to identify and highlight exciting new applications of allometric theory in ecology.

Introduction

Body size has a major impact on the structure and function of populations, communities and ecosystems through its effects on the physiology of individuals.

More than two decades ago, George Bartholomew (1982) contended that ‘... the most important attribute of an animal, both physiologically and ecologically, is its size. Size constrains virtually every aspect of structure and function and strongly influences the nature of most inter- and intraspecific interactions.’ Well before this, body size was recognized as an important biological variable by

eminent scientists including Otto Snell, D’arcy Thompson and Julian Huxley, who first coined the term ‘allometry’ to describe the study of relationships between body size and other variables (Huxley, 1932). These early efforts set the stage for the use of allometric equations to quantify relationships of body size to a wide variety of organismal traits, including metabolic rate (Box 1). In the early 1980s, a number of influential books summarized and highlighted the pervasive effects of body size on the physiology, life history and ecology of animals (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984). Shortly thereafter, Karl Niklas demonstrated that similar allometric principles apply to plants (Niklas, 1994). In general, this body of work supports Bartholomew’s 1982 contention by showing that many key features of organisms are governed by metabolic rate, and thus by body size, through its effects on metabolic rate. See also: [Ecological Consequences of Body Size; Huxley, Julian Sorrell](#)

Inspired by this work, Brown *et al.* (2004) proposed the Metabolic Theory of Ecology (MTE). MTE describes how metabolic rate – the rate at which an organism takes up and expends energy for survival, growth and reproduction – can be used as a basis for predicting how animals, plants and unicells interact with each other and their environments. The theory, which is composed of a series of related mathematical models, yields first-order quantitative predictions for many important ecological rates and states, from individual life history to population dynamics to nutrient cycling in ecosystems. Albeit controversial, this theory is at the centre of current research on the role of allometry in ecology. Therefore, in this review, we focus mainly on how MTE has applied and extended allometric scaling principles to better understand individual-level rate processes, which in turn affect the structure and dynamics of populations, communities and ecosystems. We review current developments in the field, and suggest some promising areas for future research.

Metabolic Rate

Metabolic rate is the rate at which an organism transforms organic molecules for maintenance, growth and reproduction. For a plant, it is the rate of photosynthesis, whereas

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Box 1 Understanding allometry

An allometric relationship is one in which a trait (Y) scales with body mass (M) according to the following general equation:

$$Y = y_0 M^b \quad [1]$$

Here, y_0 is a normalization constant that represents the value of Y at $M = 1$ and b , is a scaling exponent whose value defines the behaviour of Y as M increases (Figure 1a). In some cases, proxies such as length or height are used in place of mass.

To facilitate the visualization and statistical analysis of allometric relationships and because it is mathematically appropriate, it is standard to log-transform both sides of equation [1]:

$$\log(Y) = b \log(M) + \log(y_0) \quad [2]$$

This transformation yields a linear relationship between $\log(Y)$ and $\log(M)$ with a slope equal to the scaling exponent b and an intercept equal to the logarithm of the normalization constant, y_0 (Figure 1b). Allometric relationships are typically plotted in this form.

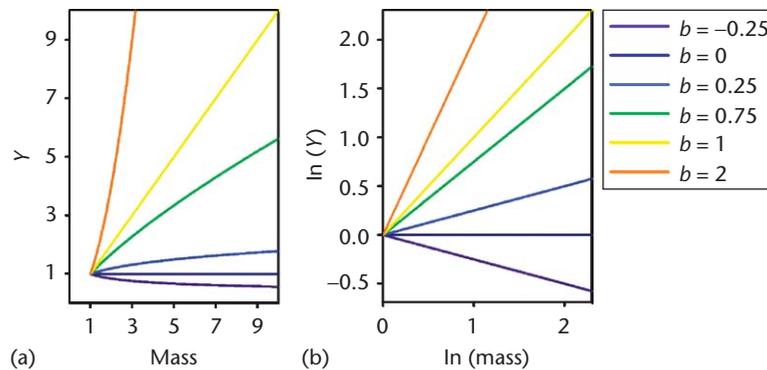


Figure 1 Schematic diagram illustrating allometric relationships with different exponents, b , and a constant normalization constant ($y_0 = 1$) on both (a) arithmetic and (b) logarithmic scales.

for an animal, it is the rate of respiration. Metabolic rate acts as a primary functional link between an organism and its biotic and abiotic environment by determining an organism's energetic and nutritional requirements, its excretion rate and its energy availability for altering the physical environment and interacting with other organisms (Brown *et al.*, 2004). **See also:** [Vertebrate Metabolism](#)

Individual metabolic rate (B) scales as a power function with body mass (M) with an exponent (b) that is generally close to $3/4$ (Peters, 1983; Schmidt-Nielsen, 1984; Glazier, 2005). Power-function scaling of metabolic rate with size appears to apply almost universally to living organisms, having been documented in animals, plants and unicells (Gillooly *et al.*, 2001). Importantly, however, there exists significant variation in the scaling exponent b and the 'normalization constant' B_0 (see **Box 1**) within species over ontogeny and among species and environments (e.g. Gillooly *et al.*, 2001; Anderson and Jetz, 2005; Glazier, 2005). **See also:** [Ecological Consequences of Body Size](#); [Vertebrate Metabolic Variation](#); [Vertebrate Metabolism](#)

An ongoing challenge for physiologists has been to provide a mechanistic explanation for allometric scaling relationships in general, and $3/4$ -power scaling of individual metabolic rate in particular (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984). In 1997, West, Brown and Enquist proposed a model to explain how the $3/4$ -scaling of metabolic rate arises from the structure and dynamics of

distribution networks common to most living organisms (e.g. the cardiovascular system and plant vascular systems; West *et al.*, 1997). This model, and more generally the mechanisms underlying allometric scaling, remain a topic of debate in the literature (e.g. Dodds *et al.*, 2001) and have catalysed further research on the topic. Recent work has shown, for example, that some of the assumptions of the original model can be relaxed to accommodate variation in the scaling exponent with body size (Savage *et al.*, 2008), diverse architectures of plant taxa (Price *et al.*, 2007) and size-dependent variation in metabolic scope among mammal species (Gillooly and Allen, 2007). Importantly, these model extensions can yield predictions that deviate from the 'canonical' scaling exponent of $3/4$. Further efforts along these lines are clearly warranted and promise to yield important insights into the mechanisms responsible for variation in scaling exponents, b , and normalization constants, B_0 , among taxa and environments.

Individuals

Most allometric applications in ecology are independent of the mechanisms controlling b . Consequently, empirical support for a scaling exponent of approximately $3/4$ for metabolic rate, B , provides a sufficient foundation for understanding other allometric scaling relationships,

including those relevant for predicting species' life histories. Given this scaling exponent for individual metabolic rate, the metabolic rate per unit mass (i.e. mass-specific metabolic rate), B/M , should scale approximately as $M^{-1/4}$. Thus, other rate processes fuelled by metabolic rate (e.g. growth rate) should also scale approximately as $M^{-1/4}$. Conversely, since times are inversely proportional to rates, it follows that many biological times (e.g. lifespan) should scale approximately as $M^{1/4}$. A comprehensive review of biological rates and times supports both of these 'quarter-power scaling' predictions (Savage *et al.*, 2004b). More generally, these findings support an important proposition of MTE: the size-dependence of metabolic rate similarly affects diverse rate processes in animals, plants and unicells (e.g. rates of growth, reproduction and survival) because *all* biological rate processes are ultimately fuelled by metabolism (Calder, 1984; Charnov, 1993; Niklas, 1994; Brown *et al.*, 2004). **See also:** [Ecological Consequences of Body Size](#)

With respect to growth, MTE has been used to better understand the energetics of ontogenetic development both within species and across major taxonomic groups (Gillooly *et al.*, 2008; Hou *et al.*, 2008; Moses *et al.*, 2008). As expected given quarter-power scaling of metabolic rate, biological rates and times associated with ontogenetic growth and development, including embryonic development, tend to exhibit quarter-power scaling (Savage *et al.*, 2004b). For example, after controlling for the exponential temperature-dependence of biological rates, the times to first heartbeat in embryos, hatching and first reproduction exhibit remarkably similar quarter-power scaling relationships for diverse endothermic and ectothermic taxa (**Figure 2a**; Gillooly *et al.*, 2008). The normalization constants (i.e. fitted intercepts) are also similar, which indicates that the size- and temperature-corrected rates of metabolism and the energetics of biomass production are similar among taxa and ontogenetic stages (Gillooly *et al.*, 2008). By imposing mass- and energy-balance on the consumption and subsequent assimilation of resources used to fuel growth, these models have recently been extended to yield novel predictions for how resource allocation to growth and maintenance changes over ontogeny (Hou *et al.*, 2008).

Resource allocation to reproduction is also strongly influenced by body size through its effects on metabolic rate. For example, in plants, individual-level rates of seed production are related to size because biomass production is ultimately constrained by the rate of photosynthesis and hence by the amount of leaf tissue maintained in the plant (Niklas and Enquist, 2003). For animals, rates and times associated with reproduction are often well described by allometric models that assume quarter-power scaling. These include rates of reproduction and times such as interbirth interval, gestation period and age at weaning (Peters, 1983; Calder, 1984; Charnov, 1993). Integrated over an entire lifespan, reproductive effort appears to be size-invariant for diverse vertebrates, including female mammals and lizards, which produce a total mass of offspring that is approximately 1.4 times their own body

weight irrespective of body size (Charnov *et al.*, 2007). This ratio is one of many life-history invariants that can be predicted by combining allometric theory with principles of optimal fitness (Charnov, 1993). **See also:** [Ecological Consequences of Body Size](#); [Life History Theory](#)

Lifespans and mortality rates of species in their natural environments are also influenced by body size through its effects on metabolic rate. Species from most taxonomic groups, including plants, adhere to the predicted quarter-power scaling of mortality rate (**Figure 2b**) (McCoy and Gillooly, 2008). This finding is perhaps surprising given that mortality is often considered to be driven mainly by extrinsic factors (e.g. disease and predation) and thus to be independent of metabolic rate. Residual deviations about these allometric relationships may partly reflect these extrinsic factors, as well as life-history trade-offs to maximize fitness. As this example demonstrates, much remains to be learned about how physiological, ecological and evolutionary processes combine to determine variation in the pace of life among diverse organisms.

Populations

Recent MTE work indicates that body size imposes substantial constraints on population dynamics as a direct consequence of how it affects individual-level life history parameters. For example, the intrinsic rate of population increase, r_{\max} , is predicted to scale as $M^{-1/4}$ (Savage *et al.*, 2004a) because r_{\max} is ultimately controlled by individual-level rates of birth, growth and mortality, all of which exhibit quarter-power scaling. Savage *et al.* (2004a) tested this prediction using empirical data and showed that, after accounting for temperature, r_{\max} does indeed adhere to approximate quarter-power scaling with mass for diverse endothermic and ectothermic taxa (**Figure 3a**). More generally, these findings emphasize that body size plays a primary role in the ecology and evolution of species because r_{\max} controls a population's ability to recover from disturbance, to expand into newly available habitats and to compete with other species. **See also:** [Demographic Concepts](#); [Population Dynamics: Introduction](#)

Population density at carrying capacity, K (individuals/area), is another key feature of populations that is constrained by body size through its effects on metabolic rate, B . In particular, given that B dictates the resource demands of an individual and scales as $M^{3/4}$, population density should scale as $M^{-3/4}$ if abundance is matched to some constant supply rate of limiting resources in the environment, R (i.e. $K \propto R/B \propto M^{-3/4}$) (Allen *et al.*, 2002; Savage *et al.*, 2004a). Consistent with this prediction, $M^{-3/4}$ scaling is frequently observed for the population density of both terrestrial and marine populations (**Figure 3b**; Damuth, 1987). A related prediction is that residual variation about the $M^{-3/4}$ scaling relationship should be attributable to differences in resource availability, R , for populations in different environments or niches. **See also:** [Ecological Consequences of Body Size](#)

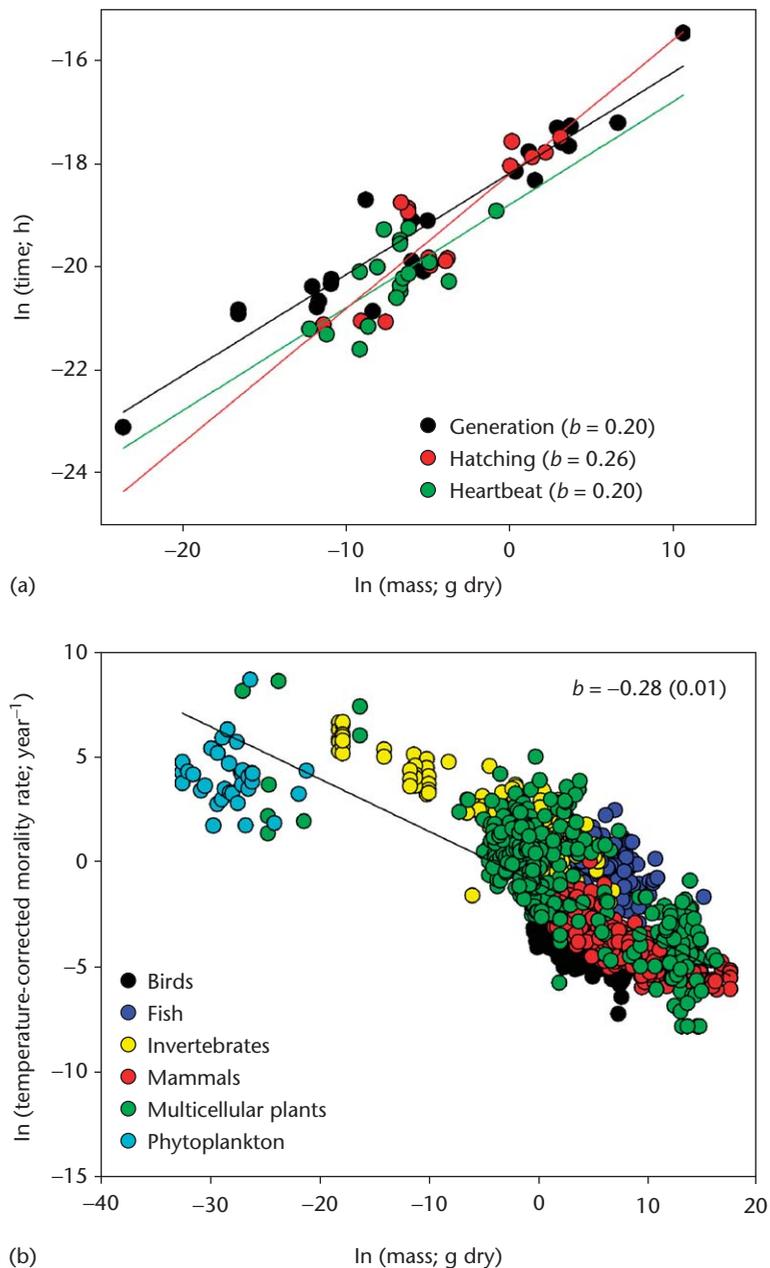


Figure 2 Allometries of life-history variables: (a) temperature-corrected, normalized development times (time to first heartbeat, time to hatching and generation time), where similar intercepts reflect the observation that the time to any specified developmental endpoint is similarly constrained by body mass (adapted from Gillooly *et al.* (2008), copyright 2008 by The Royal Society), and (b) temperature-corrected mortality rates (adapted from McCoy and Gillooly (2008), with permission of Blackwell Publishing). See original publications for explanation of normalization and temperature correction.

Analyses of global compilations of mammalian data indicate that field population densities in areas of suitable habitat, which may often be less than the theoretical maximum K , exhibit $M^{-3/4}$ scaling for mammals that vary in size from mouse to elephant (Damuth, 1987). These results suggest that mammals of different size are 'energetically equivalent' because population energy flux is calculated as the product of metabolic rate and population density, and the size-dependencies for these two variables

cancel out. Energetic equivalence is unexpected given that mammals encompassing this size range occupy different trophic levels, utilize different resources and therefore presumably experience different levels of resource availability (R). In seeming contrast to these findings, population densities of species within a specified area often appear to exhibit only a weak relationship to body size (White *et al.*, 2007). Together, these results reveal intriguing results that highlight the importance of size as well as

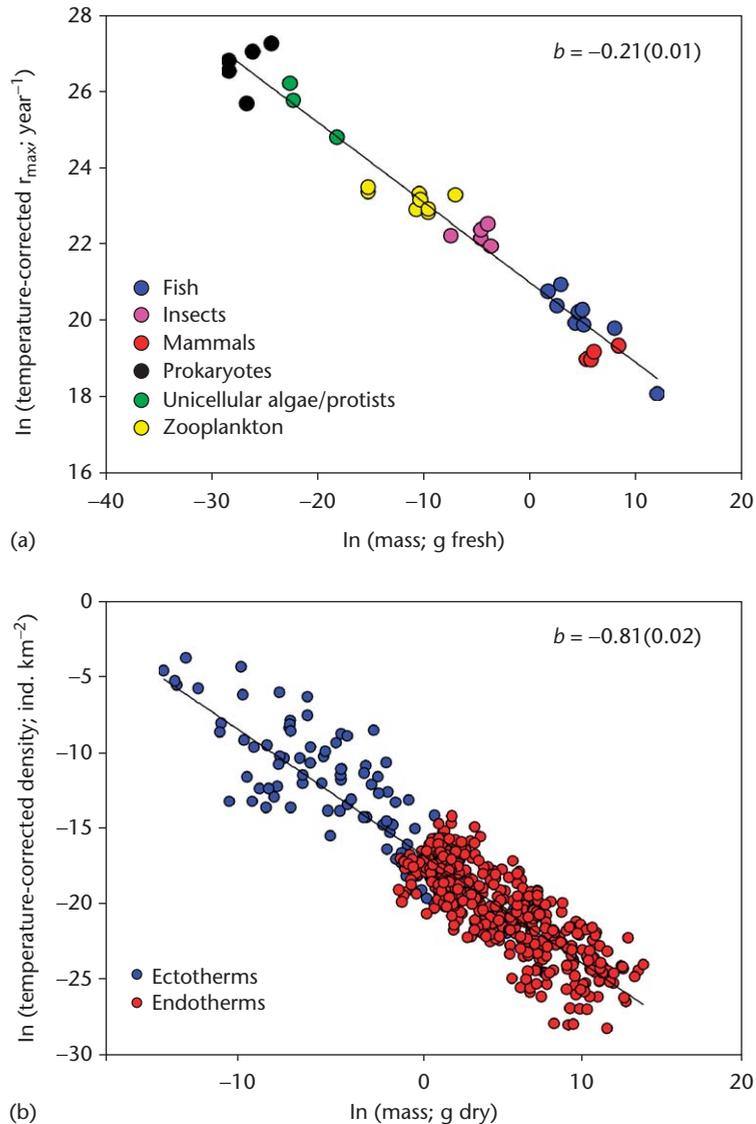


Figure 3 Allometries of population dynamics: (a) temperature-corrected intrinsic rate of population increase, r_{\max} (adapted from Savage *et al.* (2004a), Copyright 2004 by The University of Chicago) and (b) temperature-corrected population density (adapted from Allen *et al.* (2002); used with permission from AAAS). See original references for explanation of temperature correction.

limitations in our current understanding of the mechanisms linking size to population densities.

A related issue concerns individual space-use, which is also influenced by body size. In particular, range size appears to scale approximately as M^1 (Peters, 1983) rather than the reciprocal of population density ($\propto M^{3/4}$). Differences in the scaling of population density and home range size have been attributed to greater range overlap for larger-bodied species (Jetz *et al.*, 2004) and/or size-dependent changes in resource availability (Haskell *et al.*, 2002). An improved understanding of how size affects spatial distributions of individuals across landscapes may, in part, be achieved by considering the allometry of resource use, movement and behaviour. Such research takes on practical importance when one considers that larger-bodied species

appear to require larger minimum geographic range sizes and to be more susceptible to extinction (Liow *et al.*, 2008). Although the interacting effects of density, mobility and behaviour preclude a simple allometry of susceptibility to extinction, body size may be one key determinant of species' ability to persist through climate change and habitat loss. **See also:** [Biodiversity – Threats; Ecological Consequences of Body Size](#)

Communities

Body size fundamentally influences community structure through its effects on individual turnover in populations, individual-level resource demands and interspecific

interactions. For example, body size influences the size distribution of individuals in a community through its effects on mortality and movement rates. When abundance data at a given trophic level are aggregated across species, one often observes $M^{-3/4}$ scaling of density (Marquet *et al.*, 1990). This community-level form of energetic equivalence is only expected after demographic equilibrium has been reached between individual recruitment and size-dependent mortality rates (Kerkhoff and Enquist, 2007) for individuals and species that compete for common resources (e.g. trees competing for light and space, filter-feeding mollusks competing for particulate matter). Thus, deviations from $M^{-3/4}$ may be indicative of recent disturbance, variation among size classes with respect to exogenous sources of mortality, or resource use or availability.

Community structure is also characterized by aggregating abundance and biomass data across species and trophic levels. Here again, body size plays an important role. Owing to the second law of thermodynamics, which imposes mass and energy balance on energy and material fluxes, energy expenditure must decline as one moves to successively higher levels in the trophic 'pyramid'. Thus, in terrestrial ecosystems, it is not surprising that standing biomass typically declines at higher trophic levels. However, in pelagic ecosystems, where the base of the trophic pyramid is typically occupied by small species, total biomass in different size classes, ranging from phytoplankton to whales, is often remarkably similar (Peters, 1983; Brown and Gillooly, 2003; Cohen *et al.*, 2003). This alternative 'biomass equivalence rule', which implies M^{-1} scaling of density, can be viewed as a direct consequence of quarter-power scaling of metabolic rate. Specifically, in pelagic systems body sizes systematically increase, and hence mass-specific metabolic rates systematically decrease, as one moves to higher trophic levels. In particular, quarter-power scaling of metabolic rate yields biomass equivalence (i.e. M^{-1} scaling of density) given the reasonable assumptions of a 10^4 -fold difference in body size, and a 10% energy transfer efficiency, between adjacent trophic levels (Brown and Gillooly, 2003; Brown *et al.*, 2004). Thus, allometry can be used to better understand differences in the allometric scaling of density both within and between trophic levels (Figure 4). See also: Food Webs

Finally, body size plays a key role in mediating inter-specific interactions, and hence food-web structure. Predators with larger body sizes move more quickly but less frequently, expend more energy in search of prey, and consume more prey biomass per individual but not per population (Carbone and Gittleman, 2002). Also, because of the efficiency of biomass conversion, predator populations must feed on prey populations with greater productivity. Predator size also influences the types and sizes of prey that predators can consume. For example, using an energetics approach to costs associated with search and handling time, Carbone *et al.* (1999) demonstrated that, beyond a size threshold of approximately 25 kg, mammalian predators must shift from small-sized invertebrates to prey of a size comparable to that of the predator. Using a similar approach, Petchey *et al.* (2008) have had some success in characterizing interaction links among species in food webs by assuming that predators choose prey at an optimum size to maximize energy gain. This study highlights the promise of combining allometric scaling relationships with other areas of theory to better understand the structure and dynamics of communities. See also: Food Webs; Foraging

Ecosystems

The contribution of biota to the cycling of energy and materials in ecosystems is, in part, a function of the size distributions of the individuals and species that comprise an ecosystem as well as their respective metabolic rates. This concept can be understood by thinking of biogeochemical cycling in terms of how size-dependent changes in the metabolic rates of individuals contribute to the flux, storage and turnover of energy and elements in ecosystems.

Fluxes of energy and elements at the individual level are controlled by metabolic rate and therefore often exhibit the same $M^{3/4}$ scaling as metabolic rate. Fluxes that exhibit $M^{3/4}$ scaling include carbon uptake and release in plants and animals (Ernest *et al.*, 2003), nitrogen fluxes by insect and mammalian herbivores (Meehan and Lindroth, 2007; Habeck and Meehan, 2008) and water fluxes by mammals

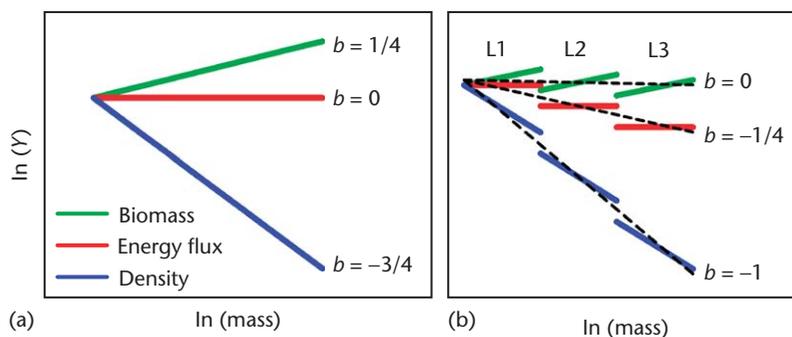


Figure 4 Theoretically predicted allometric structuring of density, energy flux and biomass, (a) within a single trophic level and (b) in an idealized food-web community with 10^4 -fold differences in body size between trophic levels (L1, L2 and L3) and a 10% efficiency of energy transfer from one trophic level to the next. Adapted from Brown and Gillooly (2003), Copyright 2003 by The National Academy of Sciences of the USA.

(Nagy and Bradshaw, 2000) and plants (Enquist *et al.*, 1998). These $M^{3/4}$ scaling relationships for fluxes are controlled by metabolic rate, B . When combined with $M^{-3/4}$ scaling for carrying capacity (K ; see earlier), this relationship implies that population- and ecosystem-level fluxes can be independent of body size and standing biomass (Enquist *et al.*, 1998; **Figure 5a**). Substantial changes in biomass and abundance can therefore occur with little or no effect on total ecosystem flux (Ernest *et al.*, 2009).

Storage of energy and elements, including limiting nutrients such as nitrogen and phosphorus, have also been

shown to exhibit predictable scaling relationships with body size and metabolic rate. Intriguingly, biomass concentrations of elements associated with structure (e.g. carbon in wood and phosphorus in bone) appear to be largely independent of body mass (i.e. scale as M^0). In contrast, concentrations of elements associated with metabolically active biomass constituents (e.g. chloroplast-associated nitrogen in leaves, ribosome-associated phosphorus in ribosomes) appear to scale as $M^{-3/4}$, arising from the scaling of mass-specific metabolic rate (Allen and Gillooly, 2009). Consequently, when one compares

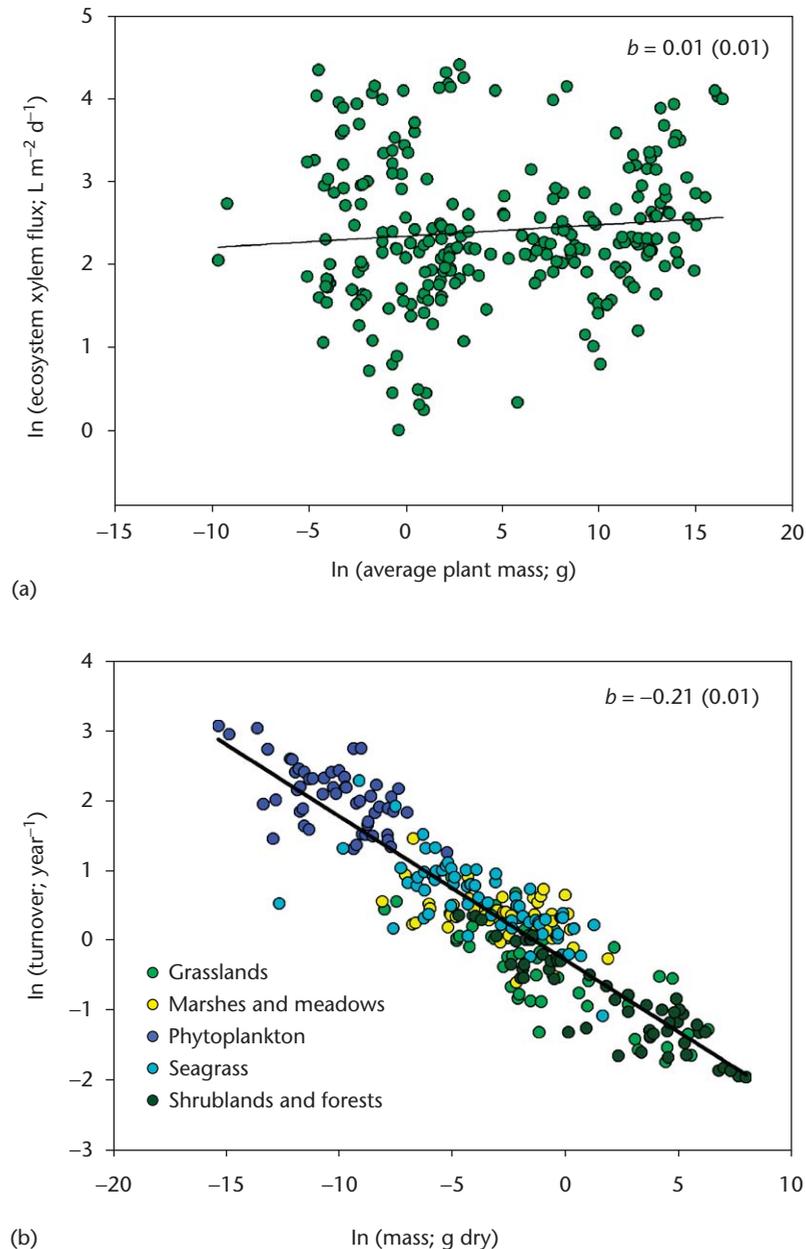


Figure 5 Allometries of ecosystem properties: (a) whole-ecosystem xylem flux as a function of average plant mass (reprinted by permission from Enquist *et al.* (1998), copyright 1998; <http://www.nature.com/nature/index.html>) and (b) biomass turnover in plant communities (adapted from Allen *et al.*, 2005, with permission of Wiley-Blackwell).

ecosystems that vary substantially in average plant size and standing biomass (i.e. tundra to forest), the total quantities of nitrogen and phosphorus increase somewhat less than linearly with total standing biomass (Kerkhoff and Enquist, 2006). As this example demonstrates, size, as well as total standing biomass, can be important in determining element storage in ecosystems. **See also:** [Biological Stoichiometry](#)

Together, flux and storage control the turnover rate (=flux/storage) of elements in tissues and the turnover rate of biomass in individuals. As outlined earlier, rates of individual growth, reproduction, mortality and the intrinsic rate of population increase all scale allometrically as $M^{-1/4}$. As a result, the turnover rate of biomass in ecosystems exhibits quarter-power scaling with average plant mass (**Figure 5b**; Allen *et al.*, 2005). These findings emphasize that much of the observed variation in rates of biomass turnover among biomes (e.g. grasslands, shrublands and forests) can be predicted based on the size-dependence of metabolic rate. Size-dependent changes in turnover rates of biomass and individuals may also contribute to the observation that *species* turnover through time is generally faster for communities composed of smaller-bodied organisms (Schoener, 1983), for example, during early stages of succession when plants are relatively small and short lived (Anderson, 2007). We have much to learn about the role of body size in community- and ecosystem-level dynamics. Improved understanding may, in part, be achieved by considering linkages between size, individual energetics and elemental composition, and how these linkages affect nutrient dynamics in ecosystems (Allen and Gillooly, 2009).

Conclusions

Body size sets an organism's metabolic rate and thereby controls its rates of growth, reproduction and mortality. Consequently, body size plays a key role in a broad range of ecological phenomena, from life-history variation among individuals and species, to the regulation of populations, to the structure and dynamics of communities and ecosystems. Such allometric relationships are applicable across a wide range of taxa; however, we note that most of the allometries described here have not yet been tested for insects and other invertebrates. Thus, allometric models provide a baseline for understanding the structure and function of complex ecological systems, and a means of quantitatively linking different levels of biological organization from cells to ecosystems.

New and exciting avenues of research on allometry in ecology are being developed. Many of these advances combine allometric theory with other bodies of theory to gain a more complete understanding of ecological and even evolutionary dynamics. In the past five years, allometric theory has been combined with food web theory (Petchey *et al.*, 2008), Hubbell's neutral theory of biodiversity

(Ernest *et al.*, 2009), ecological stoichiometry theory (Allen and Gillooly, 2009) and Kimura's neutral theory of molecular evolution (Gillooly *et al.*, 2005). In each case, the new, more synthetic theory has yielded novel, quantitative predictions for the structure and function of ecological systems. Research of this sort serves to link disparate biological disciplines, from physiology to ecology and evolution. For example, recent work has highlighted the importance of considering allometry in animal behaviour, evolutionary processes (Gillooly *et al.*, 2005) and even the organization and functioning of human societies (Hamilton *et al.*, 2007). Thus, research on allometry in ecology is rapidly expanding and promises to yield significant insights into ecological patterns and mechanisms in the coming years. **See also:** [Biological Stoichiometry](#); [Food Webs](#); [Molecular Evolution: Neutral Theory](#)

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