

REPORT

Thermodynamic and metabolic effects on the scaling of production and population energy use

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Abstract

Ecosystem properties result in part from the characteristics of individual organisms. How these individual traits scale to impact ecosystem-level processes is currently unclear. Because metabolism is a fundamental process underlying many individual- and population-level variables, it provides a mechanism for linking individual characteristics with large-scale processes. Here we use metabolism and ecosystem thermodynamics to scale from physiology to individual biomass production and population-level energy use. Temperature-corrected rates of individual-level biomass production show the same body-size dependence across a wide range of aerobic eukaryotes, from unicellular organisms to mammals and vascular plants. Population-level energy use for both mammals and plants are strongly influenced by both metabolism and thermodynamic constraints on energy exchange between trophic levels. Our results show that because metabolism is a fundamental trait of organisms, it not only provides a link between individual- and ecosystem-level processes, but can also highlight other important factors constraining ecological structure and dynamics.

Keywords

Allometry, annual biomass production, cross-taxonomic comparison, energy use, macroecology, metabolism, scaling, trophic energy transfer.

INTRODUCTION

Linking physiological traits of individual species with the function of ecosystems is a major theme in current ecological research (e.g. Lawton & Jones 1995). With increasing concern about global warming, habitat fragmentation and introductions of exotic species, it is imperative to understand how changes in species composition scale up to affect large-scale ecosystem processes (Vitousek 1990; Lawton & Jones 1995; Hector *et al.* 2001). Field studies have demonstrated how the physiology of a species can influence ecosystem properties such as nutrient cycling, productivity and species richness (e.g. Vitousek 1990; Elser *et al.* 2000). While these approaches suggest a link among these ecological properties, there is still no generally agreed upon theoretical framework that quantitatively links the physiological traits of individual species to ecosystem-level rate processes.

Metabolism – the rate at which energy and material resources are taken up from the environment, transformed within an organism, and allocated to maintenance, growth and reproduction – is a fundamental physiological trait. Recently, it has been shown that a simple model (West *et al.* 1997, 1999; Gillooly *et al.* 2001) can explain the joint effects of body size and temperature on whole-organism metabolic rate (B) for plants and animals. In this model, whole organism metabolic rate scales with mass because of the fractal-like geometry of distribution networks within organisms, whereas temperature, described by the Boltzmann factor, affects the rates of chemical processes involved in metabolism. This model is represented as $B = B_0 M^{3/4} e^{-E_a/kT}$, where B_0 is the taxon-specific, but mass and temperature independent metabolic normalization constant; M is body mass; $e^{-E_a/kT}$ is the Boltzmann factor where E_a is the average activation energy of metabolism (c. 0.6 eV, but ranges from 0.4 to 0.8 eV), k is Boltzmann's constant (8.62×10^{-5} eV Kelvin⁻¹), and T is absolute temperature in Kelvin.

Through this relationship with body size and temperature, metabolic rate can affect currencies of ecological interest. For example, the rate of biosynthesis or whole organism biomass production (P) reflects the allocations of metabolic products to growth and reproduction, consequently, this relationship scales as $P \propto M^{3/4}$ (Brody 1945; Charnov 2001; Niklas & Enquist 2001). As production fuels ontogenetic and population growth, it is central to life history and population ecology. Another crucial ecological variable, population-level energy use (E) is influenced by metabolic rate through the interaction between the energetic requirements of the individual (B) and the number of individuals in a population (N), resulting in the empirically supported relationship: $E = NB \propto M^{-3/4} M^{3/4} \propto M^0$. (Damuth 1981; Enquist *et al.* 1998; Savage *et al.* in press).

The relationship for population energy use depends upon the supply of energy to species within functional groups. The number of individuals that can be supported depends directly on the rate of energy supply and inversely on the rate of energy used by individuals of a species (B) (Damuth 1987; Allen *et al.* 2002). It has been known since Lindeman (1942) that thermodynamic constraints on energy flow through trophic webs reduce the energy supplied to successive trophic levels. Empirical measurements of the transfer efficiency of energy between trophic levels often range from 5 to 15% (e.g. Lindeman 1942; Slobodkin 1962; Burness *et al.* 2001), though there is considerable variability (Turner 1970; Slobodkin 2001). Therefore, decreasing energy availability to species at successive trophic levels should result in successively lower population-level energy use, with plants > herbivores > omnivores > carnivores.

While production and population-level energy use have been studied for a variety of organisms, there are few cross-taxonomic comparisons. As a result it is currently unclear how rates of production and population-level energy use scale with body size across functionally and taxonomically different organisms. Here, using data for plants and animals, we explore the above relationships for how organismal metabolism and Lindeman constraints on trophic energy transfer affect individual biomass production and population-level energy use, two properties with important implications for ecosystem function.

METHODS

We collected data from the literature on whole-organism maximal annual biomass production for a diverse assortment of plants, animals and unicellular algae and protists (see compiled datasets for literature sources: Niklas 1994; references listed in Enquist & Niklas 2001; Jones *et al.* 2003; Ernest in press; bird data used in Ricklefs 2000 and obtained from author; Savage *et al.* in press). For photosynthetic organisms, we obtained annual net primary production data for individuals of 387 species, including phytoplankton, algae, angiosperms and gymnosperms. For endotherms (34 birds, 305 mammals), which produce new biomass mainly through reproduction, we used data on life history characteristics to estimate the maximum quantity of biomass reared by an adult during a year. For the remaining 23 species of animals (eight zooplankton, nine fish, five insects and one protist), individual biomass production was estimated from population measurements of the per capita maximum rate of increase, r_{\max} , and average adult body size.

We investigated population energy use using data collected for plants (365 spp.) and mammals (547 spp.), the two groups for which we could obtain high-quality data for many species (Damuth 1987; Enquist & Niklas 2001). Population-level energy use (Watts km⁻²) was calculated

from density and body size data using the equation $E = NB_0M^{\delta/4}$. As we did not have metabolic rates for each species, we estimated metabolic rate from published metabolic relationships for plants and mammals (Nagy *et al.* 1999; Gillooly *et al.* 2001).

Production and population energy use were corrected for differences in operating temperatures among the groups (Gillooly *et al.* 2001; Allen *et al.* 2002). For plants, the Willmott and Matsuura global temperature database (http://climate.geog.udel.edu/~climate/html_pages/README.ghcn_ts2.html) was used to calculate an average growing season temperature (20 °C, May–Sept) over the latitudinal range corresponding to the plant data (35°S and 66.22°N). For fish, insects, zooplankton and the protist *Paraphysomonas imperforata*, environmental temperatures were gathered directly from the data sources listed in Savage *et al.* (in press). Average body temperatures were used for birds (40 °C) and mammals (37 °C). We examined the effect of

trophic level on population energy use using the data for plants and mammals. For mammals, trophic level was determined using published dietary information (Nowak 1999; American Society of Mammalogists 2003). For additional information, see Supplementary material.

RESULTS

The scaling exponents of annual biomass production for plants, birds, fish and mammals were statistically indistinguishable from the expected values (Table 1; Fig. 1). When groups were compared with each other using ANCOVA, the exponents of the groups were statistically indistinguishable (ANCOVA $F_{3,726} = 0.07$, $P = 0.98$). While the normalization constants varied significantly among groups (ANCOVA $F_{3,729} = 42.60$, $P < 0.0001$), they varied by less than an order of magnitude (Table 1). The largest difference between groups, plants and fish, was only five-fold. Despite

Group	Spp. number	Scaling exponent	95% CI	Normalization constant	95% CI	r^2
Production						
Plants	387	0.759	0.76–0.75	10.15	10.18–10.12	0.995
Mammals	305	0.755	0.78–0.73	10.25	10.29–10.21	0.910
Birds	33	0.740	0.85–0.63	10.66	10.79–10.53	0.858
Fish	9	0.761	0.84–0.68	10.85	11.03–10.67	0.984
Animals	361	0.719	0.74–0.70	10.30	10.34–10.26	0.934
All organisms	748	0.757	0.75–0.76	10.24	10.21–10.27	0.988
Population energy use						
Plants	365	0.0005	0.02––0.009	4.25	4.30–4.21	0.0
Mammals	547	0.0018	0.06––0.06	2.66	2.72–2.60	0.0

Table 1 Regression statistics for annual biomass production and population-level energy use. The group ‘animals’ includes mammals, birds, fish, zooplankton, insects and the protist *Paraphysomonas imperforata*

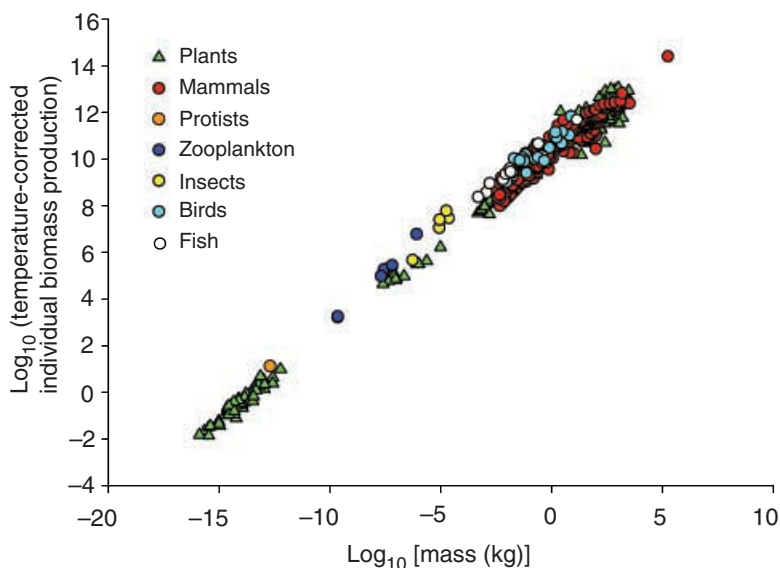


Figure 1 Relationship between body mass (kg) and temperature-corrected whole-organism biomass production ($P e^{E/kT}$). Before temperature correction, annual biomass production units are: kg individuals⁻¹ year⁻¹. Data plotted for 387 plants, 305 mammals, 33 birds, nine fish, five insects, eight zooplankton and one protist (*Paraphysomonas imperforata*). Regressions calculated for plants, mammals, birds, fish, animals (which includes mammals, birds, fish, zooplankton, insects and the protist) and all organisms combined. All groups, except the composite group of animals, have a slope statistically indistinguishable from 0.75. Regression statistics are given in Table 1.

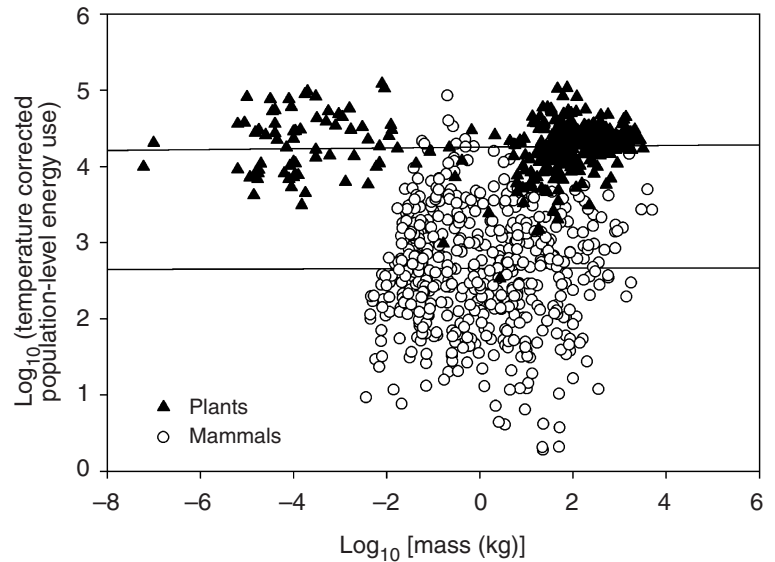


Figure 2 Relationship between body mass (kg) and temperature-corrected population energy use ($B_0 M^{3/4} N e^{-E_a/kT}$). Before temperature correction, population-level energy use units are: Watts km^{-2} . Slopes for both groups were indistinguishable from zero but the intercepts differed by almost 1.5 orders of magnitude.

differences across groups, when all organisms are pooled, the slope is still indistinguishable from 0.75 (Table 1).

Population energy use was invariant with respect to body size (Table 1; Fig. 2) and the allometric exponent was again indistinguishable between plants and mammals (ANCOVA $F_{1,908} = 0.02$, $P = 0.89$). The normalization constants varied significantly among groups (ANCOVA $F_{1,909} = 1294$, $P < 0.0001$), indicating that on average the energy use of a plant of a given body size was 1.5 orders of magnitude higher than those of equivalently sized mammals.

When population-level energy use within mammals is compared across trophic levels, each trophic level exhibits a log-normal distribution of energy use (Kolmogorov–Smirnov normality test: all $P > 0.15$) with ≈ 10 -fold difference between herbivores and carnivores with omnivores approximately halfway in between (arithmetic means from log-normal distributions: herbivores: 2617 W km^{-2} , omnivores: 1457 W km^{-2} , carnivores: 264 W km^{-2}).

DISCUSSION

Similarities in production rates across such diverse taxa as plants, mammals, birds and fish indicate that there is little variation between groups in the rate at which an individual of a given size and temperature produces biomass. The similarity in biomass production is especially interesting because of differences among taxa in how production is allocated, with indeterminate growers allocating mostly to ontogenetic growth and determinate growers allocating mostly to reproduction (Harper 1977; Peters 1983; Charnov 2001).

Clearly, in addition to the differences between these groups in how production is allocated, there are a wide array

of differences in life history variables within and among functional or phylogenetic groups that reflect evolutionary constraints on resource allocation to growth and reproduction (Gotelli & Pyron 1991; Charnov 1993; Purvis & Harvey 1995). At this broad scale, however, the effects of body size and temperature appear to dominate. The variation across all organisms in production was less than the 20-fold difference in standard basal metabolic rates (Gillooly *et al.* 2001). Because metabolism is allocated to a combination of growth, reproduction and maintenance, and growth and reproduction are accounted for in production, the larger differences in metabolic rates may reflect the physiological costs of maintenance. This is consistent with the possibility that energetic costs of maintenance differ substantially among groups, depending in part on the mechanisms of resource uptake from the environment and distribution within organisms. Vertebrates may have higher maintenance costs than plants because they actively move to forage and use energetically expensive pumps (peristalsis of gut, beating of heart) to transport resources within the body (Schmidt-Nielsen 1997). In contrast, plants are sessile and rely on more 'passive' pumps (diffusion of respiratory gases, osmotic pressure to move fluids) to transport materials (Raven *et al.* 1992). Energetic costs of production are similar across all organisms because the same basic biochemical reactions are used to synthesize similar compounds, but the rate of biosynthesis varies with body size and temperature. These results also support the suggestion that while endothermic birds and mammals process energy at higher rates than ectotherms, they also spend proportionally more energy on thermoregulation and maintenance (Schmidt-Nielsen 1997).

In contrast to production, there were large differences between plants and mammals in population-level energy use

(Fig. 2). This difference may reflect thermodynamic constraints on energy flow between trophic levels as proposed by Lindeman (1942) and others (e.g. Odum 1957; Slobodkin 1962). In terrestrial ecosystems, where producers and consumers occupy the same range of body sizes, diminished energy availability to successive trophic levels reduces both the number of individuals and the biomass that can be supported per unit area (Odum 1959). This is certainly the case within mammals. When population-level energy use is examined, trophic groups exhibited a *c.* 10-fold difference. For mammals, at least, thermodynamic constraints on energy transfer interact with metabolism to affect resource availability at successive trophic levels. Interestingly, plants differed from mammals in population-level energy use by approximately 1.5 orders of magnitude (*c.* 2–3% transfer efficiency), which is less than the 10% transfer efficiency observed in many other studies. However, many studies on transfer efficiencies are from aquatic ecosystems. The efficiency of energy transfer from terrestrial plants to mammals may be lower, because the tissue of terrestrial plants contains indigestible components such as cellulose and lignin that cannot be digested without behavioural and physiological adaptations that include reliance on symbiotic microbes (Robbins 1983).

Interestingly, a recent paper on the scaling of carnivore density (Carbone & Gittleman 2002) reported that the standing biomass of predators represented *c.* 1% of the standing biomass of their prey. This differs markedly from our estimate of $\sim 10\%$ for energy flow. However, their study differed from ours in the scale examined and the focal currency. In addition, it focuses on biomass of only the primary prey species instead of general energetic requirements. Further research integrating these approaches should yield more insight into trophic energy flow in mammalian systems.

Our results offer insights into linkages between the metabolic rates of individuals and the ecological roles of organisms in populations and ecosystems. One challenge for using metabolism to link the processing of energy and materials from individuals to ecosystems will be to understand processes that cause variation around, or deviations from, theoretically predicted relationships. For example, population-level energy use is influenced not only by metabolism but also by factors such as trophic-level energy supply, resource specialization, evolutionary history, interspecific interactions and environmental conditions. While macroecological studies provide insights into general processes, it can be difficult to make predictions concerning specific ecosystems. However, this study shows how metabolism can be used at broad-scales to not only scale from individual to ecosystem processes, but also to provide a baseline for assessing and quantifying the importance of other factors affecting

individual performance, population performance and ecosystem function.

SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE526/ELE526sm.htm>

Appendix S1 Supplementary methods

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