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

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 ($≈ 0.6$ 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 $P ≈ M^{3/4}$ (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: $E = N B_0 e^{−E_a/kT} M^{3/4} ≈ M^2$. (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
\[ E = NB_0 M^{3/4} \]. 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 indistin-
guishable 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.

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

<table>
<thead>
<tr>
<th>Group</th>
<th>Spp. number</th>
<th>Scaling exponent</th>
<th>95% CI</th>
<th>Normalization constant</th>
<th>95% CI</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Production</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plants</td>
<td>387</td>
<td>0.759</td>
<td>0.76–0.75</td>
<td>10.15</td>
<td>10.18–10.12</td>
<td>0.995</td>
</tr>
<tr>
<td>Mammals</td>
<td>305</td>
<td>0.755</td>
<td>0.78–0.73</td>
<td>10.25</td>
<td>10.29–10.21</td>
<td>0.910</td>
</tr>
<tr>
<td>Birds</td>
<td>33</td>
<td>0.740</td>
<td>0.85–0.63</td>
<td>10.66</td>
<td>10.79–10.53</td>
<td>0.858</td>
</tr>
<tr>
<td>Fish</td>
<td>9</td>
<td>0.761</td>
<td>0.84–0.68</td>
<td>10.85</td>
<td>11.03–10.67</td>
<td>0.984</td>
</tr>
<tr>
<td>Animals</td>
<td>361</td>
<td>0.719</td>
<td>0.74–0.70</td>
<td>10.30</td>
<td>10.34–10.26</td>
<td>0.934</td>
</tr>
<tr>
<td>All organisms</td>
<td>748</td>
<td>0.757</td>
<td>0.75–0.76</td>
<td>10.24</td>
<td>10.21–10.27</td>
<td>0.988</td>
</tr>
<tr>
<td>Population energy use</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plants</td>
<td>365</td>
<td>0.0005</td>
<td>0.02–0.009</td>
<td>4.25</td>
<td>4.30–4.21</td>
<td>0.0</td>
</tr>
<tr>
<td>Mammals</td>
<td>547</td>
<td>0.0018</td>
<td>0.06–0.06</td>
<td>2.66</td>
<td>2.72–2.60</td>
<td>0.0</td>
</tr>
</tbody>
</table>

Figure 1 Relationship between body mass
(kg) and temperature-corrected whole-
organism biomass production (\( P_{E/\Delta T} \)).
Before temperature correction, annual bio-
mass production units are: kg individu-
als\(^{-1}\)year\(^{-1}\). Data plotted for 387 plants,
305 mammals, 33 birds, nine fish, five
insects, eight zooplankton and one protist
(Paraphysomonas imperforata). Regressions cal-
culated 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.
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 (ANOVA $F_{1,908} = 0.02, P = 0.89$). The normalization constants varied significantly among groups (ANOVA $F_{1,909} = 1294, P < 0.0001$), 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 a c. 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$^{-2}$).

**Figure 2** Relationship between body mass (kg) and temperature-corrected population energy use ($B_0M^{3/4}Ne^{-Ea/kT}$). 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.

**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.
quantifying the importance of other factors affecting but also to provide a baseline for assessing and to not only scale from individual to ecosystem processes, study shows how metabolism can be used at broad-scales predictions concerning specific ecosystems. However, this into general processes, it can be difficult to make conditions. While macroecological studies provide insights history, interspecific interactions and environmental con-

ments. 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/supportmat/ELE/ELE526/ELE526sm.htm
Appendix S1 Supplementary methods

ACKNOWLEDGEMENTS
We are grateful to C. Carbone and A. P. Allen for discussion and K. E. Jones for discussion and assistance. This project was conducted as part of the Working Group in Body Size in Ecology and Paleoecology: linking pattern and process across taxonomic, spatial and temporal scales (F. A. Smith, Project Leader). The working group was supported by the National Center for Ecological Analysis and Synthesis, a centre funded by NSF (grant #DEB-0072909), the University of California, and UC Santa Barbara. In addition, SKME was supported by a biocomplexity grant from NSF (DEB-0083422).

REFERENCES


