Food-Web Structure and Dynamics:
Reconciling Alternative Ecological Currencies

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1 INTRODUCTION

There is a longstanding history of research on trophic relationships in ecology. Historically, most researchers have adopted one of two distinct ecological currencies to develop theoretical foundations and test theories against data.

Community ecologists have traditionally used the currency of abundance, N, to characterize the structure and dynamics of food webs. They have typically taken single species, or small groups of ecologically similar "trophic species," as the fundamental units of analysis. They have based their conceptual approaches on the theories of population dynamics, species interactions, and evolution by natural selection. Together these theories comprise the concept of Malthusian-Darwinian dynamics, which represents the outcome of three kinds of fundamental individual- and population-level processes:

1. Facultative adaptive changes in performance of individuals. These are of two basic types: (a) shifts in diet and other patterns of food acquisition by con-

sumers, including changes in the kinds of prey items in the diet e.g., as predicted by models of optimal foraging and search images (see Krebs and Davies 1978), and changes in rates of food intake, e.g., as predicted by models of functional responses and satiation (see Holling 1959); and (b) shifts in behavior of prey to avoid predators, including such things as aggregation, microhabitat selection, and alteration in the timing of activity.

2. Numerical responses of populations. These include the wide range of population dynamics for coupled resource-consumer systems that have been described empirically and modeled theoretically (e.g., MacArthur 1955; Yodzis and Innes 1992; McCann et al. 1998; Turchin 2003).

3. Evolutionary adaptive shifts in resource-consumer interactions. These include such things as behavioral and evolutionary adaptations of consumers to utilizing new resources and increasing intake and assimilation of particular food types, and adaptations of prey to altering exposure, apparency, palatability, and digestability by predators.

Community ecologists have traditionally used these Malthusian-Darwinian dynamic concepts and more explicit N-currency models to address questions about the lengths, species diversities, and trophic structures of food chains, and the topology and dynamical stability of species interaction networks.

Ecosystem ecologists, on the other hand, have traditionally used the currency of energy, E, to characterize trophic relationships. They have typically considered trophic levels, dietary guilds, or functional groups—and not species populations—as the fundamental units of analysis. They have developed theories and models based on the physical principles of thermodynamics and mass, energy, and stoichiometric balance. They have typically addressed questions about fates of energy and materials in ecosystems, such as how differences in abiotic conditions and biotic composition affect the fluxes and pools of energy, water, and nutrients and the trophic structure and dynamics of particular terrestrial, freshwater, and marine ecosystems.

These two contrasting N- and E-currency approaches reflect longstanding historical specializations and divisions within ecology. The theoretical foundations of the N-currency approach were developed by Alfred Lotka (1925), Vito Volterra (1926), Charles Elton (1933), and Robert MacArthur (1955), among others. This seminal work laid the foundation for a flurry of activity in the 1970s and 1980s in which publications by Cohen (1977; Cohen and Briand 1984), May (1986), and Pimm and Lawton (1980; Pimm 1982; Lawton 1989) figured prominently. Theoretical foundations of the E-currency approach were most clearly articulated in Raymond Lindeman's classic paper on the trophic-dynamic aspect of ecology (Lindeman 1942). This approach was subsequently adopted and elaborated in a major research effort led by Eugene Odum (1955), Howard Odum (1957), Frank Golley (1960), Charles Kendeigh (1961), and their students. Despite the efforts of Lotka (1925), Elton (1933), and Hutchinson (1959), among others, a synthesis of these two divergent perspectives has yet to materialize.

Brown (1981) has attributed this longstanding division to the contrasting perspectives of Eugene Odum and Robert MacArthur, the two most influential ecologists throughout the last half of the twentieth century. Fundamental differences in the approaches of these two schools of ecology led to spirited, sometimes heated debate. Each school pointed to cases where the other's theories seemed to conflict with empirical data and the intuition of field naturalists.

Within the last decade or so, there has been renewed interest in achieving a more synthetic framework for trophic ecology (Yodzis and Innes 1992; Hall and Raffaelli 1993; Polis and Winemiller 1996; Kerr and Dickie 2001; Drossel and McKane 2003; Berlow et al. 2004; Williams and Martinez 2004). In particular, there has been progress made in linking the N and E currencies (Yodzis and Innes 1992; McCann et al. 1998; Kerr and Dickie 2001).

We believe recent advances toward a metabolic theory of ecology (e.g., Allen et al. 2002; Gillooly et al. 2002; Brown et al. 2004; Savage et al. 2004; Allen et al. 2005) can build on this progress and thus provide a means of achieving greater synthesis. In particular, metabolic theory has developed models that predict the combined effects of three variables on metabolic rate—body size, temperature, and stoichiometry—based on first principles of biology, physics, and chemistry (West et al. 1997; Gillooly et al. 2001). They yield explicit, quantitative expressions that directly link the ecological currencies of abundance and energy. As we demonstrate below, extensions of these models also predict rates of population growth and interspecific interactions because metabolic rate ultimately governs these processes.

2 CONCEPTUAL CHALLENGES IN TROPHIC ECOLOGY

Trophic interactions are often represented as simplified abstractions referred to as food webs. A food web depicts trophic interactions among species as a network of connected, interacting nodes. However, there are many different definitions for nodes or their interactions. A node can represent a single species population or an aggregation of multiple species that together comprise a guild, functional group, or trophic level.

Aggregation avoids the monumental tasks of identifying all of the species in the food web, determining their abundances, and characterizing their diets. Trophic interactions among nodes may be represented either qualitatively, based on the presence or absence of interactions between nodes, or quantitatively. Quantitative representations depict the magnitudes of interactions among nodes as flows of energy or biomass, E, or as changes in numbers of individuals, N.

More standardized definitions and measurements in describing food webs would be helpful in achieving a more unified conceptual approach to trophic ecology. Qualitative models achieve notational and computational simplicity, but at the expense of sacrificing details necessary to ensure that Malthusian-Darwinian dynamics and mass and energy balance are upheld. N-currency models are con-

sistent with Malthusian-Darwinian dynamics, but may violate mass and energy balance. For example, N-currency models do not account for the differential contributions to predators of prey that vary in body size and elemental composition. E-currency models, on the other hand, enforce mass and energy balance, but do not account for adaptive shifts in diet with changes in the abundances of alternative prey, or for varying impacts of consumption of alternative prey on population sizes and growth rates of predators. These examples illustrate both the strengths and weaknesses of N- and E-currency approaches. Neither is sufficient to capture all of the principles that govern the dynamics of food webs in nature. We therefore suggest that trophic ecology would benefit from integrating N-currency and E-currency approaches.

So, how are these currencies integrated? Is it possible to move toward an approach to food webs that explicitly incorporates both approaches? We believe metabolic theory offers some potential for doing so. It could be helpful in developing models of trophic ecology that characterize the nodes, and their interactions, in terms of both abundance and energy. Using metabolic theory, interactions can be measured in terms of the birth, growth, and death of individual organisms, or in terms of the production and consumption of energy and materials.

Metabolic theory has two main components. The first is a characterization of how three variables, body size, temperature, and stoichiometry, affect the metabolic rates of individual organisms, and hence rates of resource acquisition and allocation (West et al. 1997; Gillooly et al. 2001). The second is a characterization of how energy and materials combine to affect the pools and fluxes of resources in organisms and their environments (Brown et al. 2004; Savage et al. 2004; Allen et al. 2005). Thus, metabolic theory provides a means of linking Malthusian-Darwinian dynamics to the flow of energy and materials through food webs.

3 THEORETICAL FRAMEWORK: A SIMPLE MODEL

We illustrate a potential application of metabolic theory to food webs by presenting simple formulations that describe the storage and flux of energy and materials within and between two nodes in a food web (fig. 1). We develop a model that builds on the pioneering work of Yodzis and Innes (1992; see also Peters 1983; Kerr and Dickie 2001). Yodzis and Innes developed a two-species consumer-resource model, which incorporated the quarter-power allometries in food requirements, energy expenditure, and population dynamics in population interaction models. We build on some of these ideas by explicitly incorporating the effects of temperature and stoichiometry on interactions between nodes, and then making explicit the relationships between N and E currencies in these trophic interactions.

In developing this model, we make two simplifying assumptions. First, we assume that the food web is at steady state, which implies that the abundances
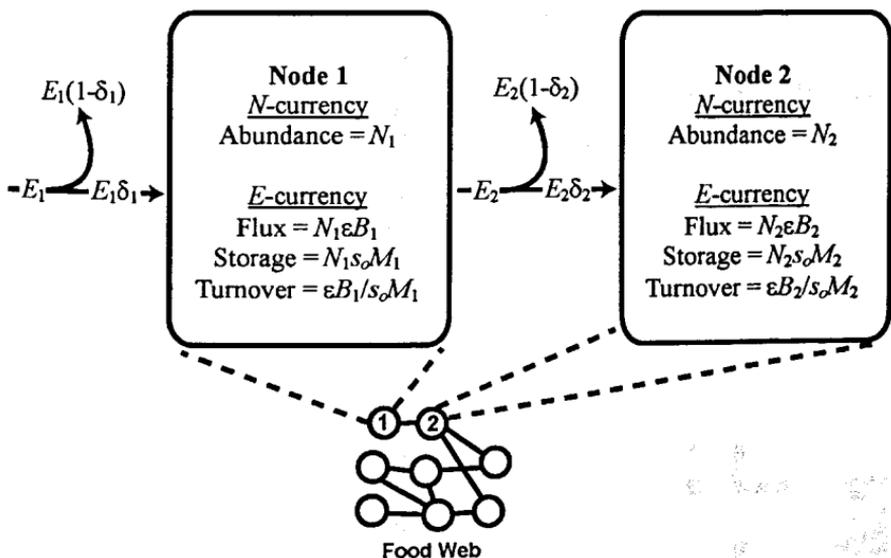
FIGURE 1 Depiction of just two nodes in a food web, predator and prey, and interactions between these nodes. The focus on just two nodes is intended to show how metabolic theory can be used to model the storage and flux of energy and materials within and between nodes of a food web in terms of both the number of individuals and energy. The paired symbols N_1 and N_2 represent abundances, E_1 and E_2 represent energy supply rates, B_1 and B_2 represent metabolic rates, δ_1 and δ_2 represent energy assimilation efficiencies for nodes 1 and 2 (i.e., prey and predators, respectively). The parameter ε denotes the fraction of metabolic energy allocated to growth, and the parameter s_o denotes the energy content of biomass. Both parameters are assumed to be the same for predators and prey in our simplified formulation.

of prey and predators remain constant through time. Second, we assume that the composition of biomass at the two nodes is identical, thus avoiding the necessity to write explicit expressions for all the substances fluxing between nodes. These two assumptions allow us to impose mass and energy balance, and to thus explicitly link individuals to the structure and function of the community.

Given these assumptions, the model derivation proceeds as follows. First, we use the size and temperature dependence of individual metabolic rate, B, to obtain expressions for the flux, turnover, and storage of energy and materials in individual organisms. Second, we derive N-currency expressions for the abundances of prey and predators, assuming that all of the biomass produced by prey at node 1 is used to fuel the metabolism of predators at node 2. Third, by imposing mass and energy balance on this system using the two simplifying assumptions discussed above, we derive expressions for energy flux that inte-

grate both ecological currencies, N and E. And finally, fourth, we quantify the relationships between these two currencies based on the size and temperature dependence of individual metabolic rate.

3.1 LINKING METABOLIC RATE TO INDIVIDUAL-LEVEL ENERGY STORAGE AND FLUX

Metabolic rate is the fundamental biological rate. It is the rate of transformation of energy and materials within an organism. As a consequence of mass and energy balance, metabolic rate determines the rate of uptake of energy and materials from the environment and the allocation of these resources to survival, growth, and reproduction. The combined effects of body size and temperature on mass-specific metabolic rate, B/M (watts/g), can be expressed as

$$\frac{B}{M} = b_0 M^{-1/4} e^{-e_a/kT} \tag{1}$$

where b_0 is a normalization constant independent of body size and temperature (watts/g$^{3/4}$), and M is individual body mass (g) (Gillooly et al. 2001). The Boltzmann or Arrhenius factor, $e^{-E_a/kT}$, characterizes the exponential effects of temperature on metabolic rate, where E_a is the activation energy of heterotrophic metabolism ($\sim$0.65 eV), k is Boltzmann's constant (8.62 $\times$ 10^{-5} eV/K), and T is absolute temperature in kelvin degrees.

The amount of energy stored in an organism, S (joules), can be expressed as

$$S = s_0 M \tag{2}$$

where s_0 is a normalization constant independent of body size and temperature that characterizes the number joules of energy contained in a gram of biomass. Energy flux in the form of biomass, F (watts), can be expressed as

$$F = \varepsilon B = \varepsilon b_0 M^{3/4} e^{-E_a/kT} \tag{3}$$

where ε is the fraction of metabolic energy allocated to growth. Empirical data indicate that the parameter ε is a constant independent of body size and temperature (Ernest et al. 2003). For what follows, we will assume that b_0, s_0, ε, T, and E_a are identical for prey and predators. We will also assume that the body sizes of prey and predator, M_1 and M_2, are identical for all organisms comprising each of the two nodes. These assumptions can be relaxed without substantively changing our conclusions, but yield more complicated expressions.

3.2 EXPRESSIONS FOR ABUNDANCE USING THE N-CURRENCY

For illustrative purposes, we model changes in the abundances of prey and predators, N_1' and N_2' (individuals/m^2), through time, t (sec), using a pair of coupled

differential equations:

$$\frac{dN_1'}{dt} = r_1 N_1' \left(1 - \left(\frac{N_1'}{N_1^*}\right)\right) - f_1(N_1', N_2') \tag{4}$$

and

$$\frac{dN_2'}{dt} = f_2(N_1', N_2') \tag{5}$$

where r_1 is the intrinsic rate of population increase for prey (1/sec), and N_1^* is the carrying capacity for prey, at steady state, when predators are absent ($N_2' = 0$). The functions $f_1(N_1', N_2')$ and $f_2(N_1', N_2')$ can take a variety of forms depending on the numerical and functional responses of predators to prey. Regardless of the functional forms of $f_1(N_1', N_2')$ and $f_2(N_1', N_2')$, the only biologically plausible solutions to these equations are those where the steady-state abundance of prey in the presence of predators, N_1, is less than the steady -tate abundance of prey in the absence of predators, N_1^* (i.e., $N_1 \leq N_1^*$). This is because $f_1(N_1, N_2) \geq 0$ due to consumption of prey by predators.

3.3 EXPRESSIONS FOR ENERGY FLUX THAT INTEGRATE THE N- AND E-CURRENCIES

We express fluxes between nodes in terms of energy by assuming that the prey and predator populations maintain steady-state abundances of N_1 and N_2, respectively, and by assuming that predators consume all of the biomass produced by prey at node 1 (fig. 1). At node 1, total energy flux, B_1^{Tot} (watts/m²), is described by the following expression:

$$B_1^{\text{Tot}} = N_1 B_1 = N_1(1 - \varepsilon)B_1 + N_1 \varepsilon B_1 = \delta_1 E_1 \tag{6}$$

where B_1 is the metabolic rate of an individual at node 1, $N_1(1 - \varepsilon)B_1$ is the total metabolic energy allocated to maintenance, $N_1 \varepsilon B_1$ is the total metabolic energy allocated to growth, E_1 is the energy supply rate to node 1 (watts/m²), and δ_1 is the dimensionless efficiency of energy assimilation by individuals at node 1. Assuming that predator abundance is controlled by energy supply from node 1, total energy flux at node 2, B_2^{Tot} (watts/m²), is equal to

$$B_2^{\text{Tot}} = N_2 B_2 = \delta_2 E_2 = \delta_2(N_1 \varepsilon B_1) = \delta_2 \varepsilon \delta_1 E_1 \tag{7}$$

where B_2 is the metabolic rate of an individual at trophic level 2, $E_2 = N_1 \varepsilon B_1$ is the energy supply rate to node 2, and δ_2 is the dimensionless efficiency of energy assimilation by individuals at node 2. Equation (6) shows that total energy flux by prey at node 1 is equal to the sum of the individual fluxes (i.e., metabolic rates) at that node. This sum is in turn constrained by the energy supply rate, E_1. Equation (7) shows that the total energy flux by predators at node 2 is constrained by the rate of biomass production by prey at node 1, $N_1 \varepsilon B_1$.

3.4 LINKING THE N- AND E-CURRENCY MODELS

Having defined expressions that link the flux and storage of energy in individual organisms to body size and temperature (eqs. (1)–(3)), that link interactions between predators and prey to their abundances (eqs. (4) and (5)), and that link abundance to energy availability (eqs. (6) and (7)), we can now explicitly characterize how body size and temperature constrain relationships between abundance and energy availability at a node through their effects on individual metabolic rate. Specifically, the abundances of prey and predator nodes can respectively be quantified by the following expressions:

$$N_1 = \frac{\delta_1 E_1}{B_1} = \frac{\delta_1 E_1}{b_0} M_1^{-3/4} e^{E_a/kT} \tag{8}$$

and

$$N_2 = \frac{\delta_2 E_2}{B_2} = \frac{\delta_2 \varepsilon \delta_1 E_1}{B_2} = \frac{\delta_2 \varepsilon \delta_1 E_1}{b_0} M_2^{-3/4} e^{E_a/kT} . \tag{9}$$

Equations (8) and (9) impose constraints on steady-state solutions to eqs. (4) and (5) based on the size and temperature dependence of individual metabolic rate (eq. (1)), and resource availability in the environment, E_1. Holding resource availability constant, these equations also predict how increases in both temperature and body size reduce carrying capacity at a node through their effects on the energetic demands of individuals (Savage et al. 2004; Allen et al. 2005).

Using the equations above, we can now express biomass storage in terms of the size and temperature dependence of individual metabolic rate. Following eqs. (2), (8), and (9), energy storage in the form of biomass (J/m^2) is equal to

$$S_1 = N_1 S_0 M_1 = \delta_1 E_1 s_0 \left(\frac{M_1}{B_1} \right) = \delta_1 E_1 \frac{s_0}{b_0} M_1^{1/4} e^{E_a/kT} \tag{10}$$

and

$$S_2 = N_2 S_0 M_2 = \delta_2 \varepsilon \delta_1 E_1 s_0 \left(\frac{M_2}{B_2} \right) = \delta_2 \varepsilon \delta_1 E_1 \frac{s_0}{b_0} M_2^{1/4} e^{E_a/kT} . \tag{11}$$

Equations (10) and (11) demonstrate the fundamental importance of mass-specific metabolic rate (B_1/M_1) and (B_2/M_2) in controlling the storage of biomass at nodes. More specifically, they show how storage increases allometrically with increasing body size, and declines exponentially with increasing temperature, due to the effects of these variables on metabolic rate (Allen et al. 2005).

Together, eqs. (1)–(11) link the N and E currencies within and between the nodes of food webs through their relationships to individual level metabolic rate, and the primary factors controlling metabolic rate, body size and temperature. In doing so, they provide a means of capturing both Malthusian-Darwinian dynamics, characterized by the currency of N, and the laws of thermodynamics and mass and energy balance, characterized by the currency of E.

4 REFLECTIONS AND CONCLUSIONS

The model presented above makes a number of simplifying assumptions so as to reduce the complexity to a bare minimum. In particular, the model derivation assumes that the nodes are at dynamic equilibrium, in other words, steady state. The model predicts how steady-state values of N and E will change in response to spatial or temporal changes in abiotic environmental variables, such as resource supply and temperature, and to shifts in biotic composition, such as changes in body size distributions or in replacements of ectotherms by endotherms at a node. So, for example, if the nodes are comprised of ectotherms, an increase in environmental temperature due to global warming will exponentially increase all rates of population change and energy flux as described by eq. (1).

However, it is important to recognize that metabolic rate, and thus body size and temperature, also constrain parameters governing nonequilibrium dynamics. Specifically, the intrinsic rate of population increase (r_1 in eq. (4)), the rate of individual mortality, and the rate of ontogenetic growth are all similarly constrained by metabolic rate and, therefore, show the same size and temperature dependence as in eq. (1) (West et al. 2001; Gillooly et al. 2002; Savage et al. 2004). So, for example, a shift in body size at a node, such as may occur by the invasion and replacement by a smaller species, should alter both N- and E-currency rates as given by eq. (1). It is conceptually straightforward, but computationally more complicated, to increase the model's realism by incorporating these more complex dynamics.

More explicitly linking the two fundamental currencies, N and E, may yield new insights into some longstanding questions in trophic ecology. For example, interaction strengths between nodes are often measured in terms of N. However, understanding the consequences of these interactions for energy flow through food webs requires expressing interaction strength in terms of E. The currency chosen to evaluate interaction strength can have profoundly different implications. So, for example, consumption of a rare prey species may be an unimportant N-currency interaction for an abundant predator species if this prey simply supplies energy (biomass) and there are alternative prey species available. On the other hand, consumption of this rare prey may represent an important E-currency interaction if it provides the sole or primary supply of an essential nutrient for the predator species.

Energy and material flow impose important structural (topological) and dynamical constraints on attributes of entire food webs, such as the number of trophic levels (Lindeman 1942) and size-abundance relationships within and across trophic levels (Kerr and Dickie 2001; Jennings and Mackinson 2003; Brown et al. 2004). So, for example, there has been an ongoing debate as to whether food chain length is limited by attenuation of energy supply or dynamical population instability at higher trophic levels (Post et al. 2000). Arguments have traditionally been made by efforts to show that one or the other phenomenon could limit the persistence of the highest trophic level, rather than by examining

the joint effect of N- and E-currencies and ensuring that the fundamental principles of population persistence and mass and energy balance are both obeyed. Additionally, the body sizes of the organisms occupying different nodes or trophic levels have enormous implications for the rates of flows and the sizes of pools for both N- and E-currencies. For example, plant communities subject to similar abiotic conditions but comprised of different-sized individuals, such as an adjacent forest and early successional old field, are predicted by metabolic theory and observed empirically to have similar rates of energy flux (productivity) but dramatically different energy storage pools and, hence, correspondingly different energy turnover rates (Allen et al. 2005). For another example, the biomass invariance observed empirically across pelagic marine food chains (e.g., Sheldon et al. 1977; Kerr and Dickie 2001) can potentially be explained as a straightforward consequence of the effect on energy flux of the approximately four orders of magnitude increase in body size between successive trophic levels (Brown and Gillooly 2003; Brown et al. 2004).

We believe that the approach taken here offers potential for a more synthetic approach to trophic ecology for two reasons. First, by explicitly linking Malthusian-Darwinian dynamics to mass and energy balance, the structure and dynamics of food webs can be better conceptualized theoretically and better studied empirically. Second and more generally, this approach serves to break down the specialization that has historically separated community and ecosystem ecology. This separation was due largely to treating the N- and E-currencies as separate and distinct entities. The emerging metabolic theory of ecology makes explicit the linkages between N and E by quantifying the material and energetic demands of survival, growth, and reproduction.

REFERENCES

Allen, A. P., J. F. Gillooly, and J. H. Brown. 2005. "Linking the Global Carbon Cycle to Individual Metabolism." *Functional Ecology* 19:202–213.

Allen, A. P., J. H. Brown, and J. F. Gillooly. 2002. "Global Biodiversity, Biochemical Kinetics, and the Energetic-Equivalence Rule." *Science* 297:1545–1548.

Allen, A. P., J. F. Gillooly, and J. H. Brown. 2005. "Linking the Global Carbon Cycle to Individual Metabolism." *Functional Ecology* 19(2):202–213.

Berlow, E., A-M. Neutel, J. E. Cohen, P. deRuiter, B. Ebenman, M. Emmerson, J. W. Fox, V. A. A. Jansen, J. I. Jones, G. D. Kokkoris, D. O. Logofet, A. J. McKane, J. M. Montoya, and O. Petchey. 2004. "Interaction Strengths in Food Webs: Issues and Opportunities." *J. Animal Ecol.* 73:585–598.

Brown, J. H. 1981. "Two Decades of Homage to Santa-Rosalia: Toward a General Theory of Diversity." *Amer. Zool.* 21:877–888.

Brown, J. H. and J. F. Gillooly. 2003. "Ecological Food Webs: High-Quality Data Facilitate Theoretical Unification." *PNAS* 100:1467–1468.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. "Toward a Metabolic Theory of Ecology." *Ecology* 85:1771–1789.

Cohen, J. 1977. "Food Webs and the Dimensionality of Trophic Niche Space." *Proc. Natl. Acad. Sci. USA* 74:4533–4536.

Cohen, J., and F. Briand. 1984. "Trophic Links of Community Food Webs." *Proc. Natl. Acad. Sci. USA* 81:4105–4109.

Drossel, B., and A. J. McKane. 2003. "Modelling Food Webs." In *Handbook of Graphs and Networks: From the Genome to the Internet*, ed. S. Bornholdt and H. G. Schuster, 1–34. Berlin: Wiley.

Elton, C. 1933. *The Ecology of Animals*. London: Methuen.

Ernest, S. K. M., B. J. Enquist, J. H. Brown, E. L. Charnov, J. F. Gillooly, V. M. Savage, E. P. White, F. A. Smith, E. A. Hadley, J. P. Haskel, S. K. Lyons, B. A. Maurer, K. J. Niklas, and B. Tiffney. 2003. "Thermodynamic and Metabolic Effects on the Scaling of Production and Population Energy Use." *Ecol. Lett.* 6:990–995.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. "Effects of Size and Temperature on Metabolic Rate." *Science* 293:2248–2251.

Gillooly, J. F., E. L. Charnov, G. B. West, V. M. Savage, and J. H. Brown. 2002. "Effects of Size and Temperature on Developmental Time." *Nature* 417:70–73.

Golley, F. B. 1960. "Energy Dynamics of a Food Chain of an Old-Field Community." *Ecol. Monogr.* 30:187–206.

Hall, S. J., and D. G. Raffaelli. 1993. "Food Webs: Theory and Reality." *Adv. Ecol. Res.* 24:187–237.

Holling, C. S. 1959. "Some Characteristics of Simple Types of Predation and Parasitism." *Canadian Entomologist* 91:385–398.

Hutchinson, G. E. 1959. "Homage to Santa Rosalia or Why are There so Many Kinds of Animals." *Amer. Natur.* 93:145–159.

Jennings, S., and S. Mackinson. 2003. "Abundance-Body Mass Relationships in Size-Structured Food Webs." *Ecol. Lett.* 6:971–974.

Kendeigh, S. C. 1961. *Animal Ecology*. Englewood Cliffs, NJ: Prentice-Hall.

Kerr, J. T., and L. M. Dickie. 2001. *Biomass Spectrum*. New York: Columbia University Press.

Krebs, J. R., and N. B. Davies 1978. *Behavioural Ecology: An Evolutionary Approach*. Oxford: Blackwell Scientific.

Lawton, J. H. 1989. "Food Webs." In *Ecological Concepts*, ed. J. M. Cherrett, 43–78. Oxford: Blackwell.

Lindeman, R. L. 1942. "The Trophic-Dynamic Aspect of Ecology." *Ecology* 23:399–417.

Lotka, A. J. 1925. *Elements of Physical Biology*. Baltimore, MD: Williams & Wilkins.

MacArthur, R. H. 1955. "Fluctuations of Animal Populations, and a Measure of Community Stability." *Ecology* 36:533–536.

May, R. M. 1986. "The Search for Patterns in the Balance of Nature: Advances and Retreats." *Ecology* 67:1115–1126.

McCann, K., A. Hastings, and G. R. Huxel. 1998. "Weak Trophic Interactions and the Balance of Nature." *Nature* 395:794–798.

Odum, E. P. 1955. "Trophic Structure and Productivity of a Windward Coral Reef Community on Eniwetok Atoll." *Ecol. Monogr.* 25:291–320.

Odum, H. T. 1957. "Trophic Structure and Productivity of Silver Springs, Florida." *Ecol. Monogr.* 27:55–112.

Peters, R. H. 1983. *The Ecological Implications of Body Size*. Cambridge, MA. Cambridge University Press.

Pimm, S. L. 1982. *Food Webs*. London: Chapman and Hall.

Pimm, S. L., and J. H. Lawton. 1980. "Are Food Webs Divided into Compartments?" *J. Animal Ecol.* 49:879–898.

Polis, G., and K. Winemiller, eds. 1996. *Food Webs: Integration of Patterns and Dynamics*. New York: Chapman and Hall.

Post, D. M., M. L. Pace, and N. G. Hairston, Jr. 2000. "Ecosystem Size Determines Food-Chain Length in Lakes." *Nature* 405:1047–1049.

Savage, V. M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. "Effects of Body Size and Temperature on Population Growth." *Amer. Natur.* 163:430–441.

Sheldon, R. W., W. H. Sutcliffe, and M. A. Paranjape. 1977. "Structure of Pelagic Food-Chain and Relationship between Plankton and Fish Production." *J. Fish. Res. Board of Can.* 34:2344–2353.

Turchin, P. 2003. *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton, NJ: Princeton University Press.

Volterra, V. 1926. "Fluctutations in the Abundance of a Species Considered Mathematically." *Nature* 118:558–560.

West, G. B., J. H. Brown, and B. J. Enquist. 1997. "A General Model for the Origin of Allometric Scaling Laws in Biology." *Science* 276:122–126.

Williams, R., and N. Martinez. 2004. "Limits to Trophic Levels and Omnivory in Complex Food Webs: Theory and Data." *Amer. Natur.* 163:E458–E468.

Yodzis, P., and S. Innes. 1992. "Body Size and Consumer-Resource Dynamics." *Amer. Natur.* 139:1151–1175.