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CHAPTER 2

HOMAGE TO YODZIS AND INNES 1992: SCALING UP FEEDING-BASED POPULATION DYNAMICS TO COMPLEX ECOLOGICAL NETWORKS

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2.1 INTRODUCTION

Scientists have long strived to simplify and abstract nature into fundamental categories and statements that could yield understanding of, and predictive insight into, the phenomena they study. Only a few of such abstractions survive the test of time and continue to yield both broad and deep scientific insights. Here, we explore an ecological abstraction that many ecologists including ourselves have found very useful and especially insightful. While it is only one of many abstractions of population growth in nature, we focus on it here because it appears likely to survive the difficult and important transition from modeling a few trophically interacting species to modeling the large complex networks more like those we see in nature. To survive this mission, we desire maximum correspondence with nature and empirical tractability combined with minimal complexity. That is, we want abstractions based on the fewest but most useful and easily measured parameters in order to minimize the costs of complexity while trying to model it.

This abstraction is the bioenergetic approach of Yodzis and Innes (1992) that provided an important foundation for many further advances by Peter Yodzis and other colleagues, especially his former student Kevin McCann (McCann and Yodzis 1994, 1995, McCann and Hastings 1997, McCann et al. 1998) plus further developments by many others (e.g., Fussman et al. 2000, Post et al. 2000, Callaway and Hastings 2002, Brose et al. 2003, Williams and Martinez 2004, Bascompte et al. 2005, Shurin and Seabloom 2005). At its core, the advance of Yodzis and Innes (1992) was to distinguish two fundamental aspects of organisms as central to the modeling of their feeding interactions and population dynamics: body size and metabolic type. The relevance of body size to “metabolism” or the energetic maintenance cost of staying alive has recently become a spectacularly successful and currently highly active research program (Whitfield 2004). Much earlier, Yodzis and Innes (1992) realized that the combination between the biological importance and empirical ease of measuring body size made it an ideal variable to incorporate into population dynamics. The other distinction, that of metabolic type, recognizes that all bodies are not the same and that, in particular, fundamental distinctions among plants, invertebrates and endotherm, and ecotherm vertebrates needed to be made in order for body size to reasonably predict both the metabolic and maximum assimilation rates of organisms. Once such distinctions were made, each group of organisms could be simply modeled as an undifferentiated stock of biomass that grows and shrinks depending on losses to predation and metabolic costs and gains from animal feeding activities and plant net primary production.

Though important and productive, the Yodzis and Innes approach is highly abstract and rather difficult to comprehend in an intuitive manner. For example, in the more useful nondimensional form of the model, several parameters, such as maximum assimilation rates, are numbers “per,” or relative to, metabolic rate. Having struggled to embrace, employ, and expand the Yodzis and Innes approach, we have discovered important clarifications and characterizations of their approach. This chapter redescribes their approach and how it can be more rigorously applied to networks with many more species and also to more mechanistic treatment of basal species such as plants that consume abiotic resources in order to grow.

2.2 HISTORY OF CONTINUOUS TIME PREDATOR-PREY POPULATION DYNAMIC MODELS

Historically, predator-prey population dynamics have been modeled with continuous time models that describe infinitesimally small changes of species i over time in population numbers or biomasses, B_i, by differential equations for $\mathrm{d}B_i/\mathrm{d}t$. The prey population biomass, B_i, has an intrinsic growth, G_i, and loses biomass to consumption by the predator population. The predator population of species j, B_j, gains biomass by consumption and loses biomass due to respiration and death. This yields the following set of differential equations:

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = B_i G_i(B_i) - B_j F_{ji}(B_i) \tag{2.1}$$

$$\frac{\mathrm{d}B_j}{\mathrm{d}t} = -B_j T_j + B_j e_{ji} F_{ji}(B_i) \tag{2.2}$$

where F_{ji} is the functional response that quantifies the dependence of per capita of species j (unit B_j) consumption on the density of prey species i. The product of predator density, B_j, with per capita consumption, F_{ji}, yields the total consumption. T_j is the sum of the metabolic and death rates of predator j and e_{ji} is the efficiency of predator j at converting the biomass of prey i that predator j kills or otherwise removes from prey i into predator j's biomass. Early attempts used linear interaction terms to describe the increase in per capita consumption with prey density:

$$F_{ji} = a_{ji} B_i \tag{2.3}$$

This "Lotka-Volterra" functional response assumes that the per capita consumption does not saturate at high prey densities, which causes an infinite linear increase of consumption with prey density. In response to this ecologically unrealistic assumption, many empirical and theoretical studies described multiple forms of functional responses (Holling 1959, Real 1977, Murdoch and Oaten 1975, Beddington 1975, DeAngelis et al. 1975, Arditi and Akcakaya 1990). All these studies described nonlinear functional responses with consumption saturation at high prey densities (see examples below). These functional responses can be prey-dependent (i.e., depend on the density of the prey), predator-dependent (i.e., depend on the density of the predator), or ratio-dependent (i.e., depend on the ratio of the predator to the prey). Implementations of these nonlinear functional responses in population-dynamic models of the form (Eqs. (2.1, 2.2)) are known as McArthur-Rosenzweig models

(Rosenzweig and MacArthur 1963). These models improve the Lotka-Volterra model by using more realistic nonlinear functional responses, but just as in Lotka-Volterra models, the parameters describing the species' metabolic rates, their maximum consumption (the saturation level of the functional response), intrinsic production-biomass ratios of the prey population, and biomass conversion efficiencies are parameters that are estimated independently and are unrelated to species' traits.

In their seminal work, Yodzis and Innes (1992) used allometric relationships to relate production, metabolic, and maximum consumption rates to the species' body masses and their metabolic categories. This approach yields a model that is intermediate in its level of detail, more constrained by known biological properties of the system than some of the highly abstract models (e.g., Lotka-Volterra and Rosenzweig-McArthur) that are studied, but less constrained than a model tailored to a specific system. The use of allometric scaling introduced empirical realism and parameter interdependence into the models, which substantially reduced the space of possible parameter combinations. Awareness of this interdependence helped show that parameter combinations of species' metabolic rates and maximum consumption rates that were previously thought possible were shown to be impossible (e.g., compare McCann and Yodzis 1995 with Hastings and Powell 1991).

2.3 MULTISPECIES VERSION OF THE BIOENERGETIC MODEL OF YODZIS AND INNES (1992)

The bioenergetic model of Yodzis and Innes (1992) is of the interaction between one consumer and one resource. Here, we extend their formulation to multispecies systems that may have multiple primary producers. For species that are primary producers, their population's rate of change of biomass over time is given by

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = B_i G_i(\vec{B}) - \sum_{j=\text{predators}} B_j F_{ji}(\vec{B})/f_{eji}. \tag{2.4}$$

For species that are consumers, the rate of change of the biomass of its population is given by

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = -B_i T_i + B_i \sum_{j=\text{prey}} e_{ij} F_{ij}(\vec{B}) - \sum_{j=\text{predators}} B_j F_{ji}(\vec{B})/f_{eji} \tag{2.5}$$

In these equations, B_i is the biomass of population i, G_i is the mass-specific net growth rate of primary producer population i and is potentially a function of the biomasses of any or even all of the populations in the system, T_i is the mass-specific respiration rate, F_{ij} is the rate of consumption of population j by population i (i.e., the rate population j loses biomass due to consumption activities of i such as herbivory, predation, infection), e_{ij} is an assimilation efficiency equal to the fraction of the biomass of species j lost due to consumption by species i that is actually metabolized, and f_{eij} is ingestion efficiency equal to the fraction of biomass lost from resource j that is actually ingested by consumer i (e.g., some carnivores do not consume the whole of a kill nor do parasitoids consume all of a host). Assimilation efficiency is separated from ingestion efficiency because the former can theoretically be allometrically scaled while the latter is less systematic and contingent on natural history of consumption such as that between a nematode that causes a disease that kills a host and a different nematode that parasitizes a host without killing it. The former nematode has a much lower f_{eij} than the latter.

Equation 2.4 states that the rate of change of the primary producer's biomass is made up of two components. The first term is the gain in biomass from the species' intrinsic net growth that includes biomass gain from primary production and biomass loss from metabolism. The second term is the loss of biomass from consumption by each predator of the species. Similarly, the rate of change of a consumer's biomass (Eq. (2.5)) is made up of three parts. The first term is the loss in biomass from the consumer metabolizing energy for respiration. The second term is the gain in biomass from consuming various resource species. The third term is the loss of biomass from consumption by each predator or other consumer (herbivore, parasites, etc.) of the species.

The rate of ingestion of resource j by consumer i is given by a multispecies functional response which saturates at some maximum ingestion rate. It is convenient to assume that the functional response has the form

$$F_{ij}(\vec{B}) = J_{ij}\widehat{F}_{ij}(\vec{B}) \tag{2.6}$$

where J_{ij} is the maximum ingestion rate of prey item j by consumer i and $\widehat{F}_{ij}(\vec{B})$, the normalized functional response, is a function that ranges between zero and one and is potentially a function of the biomasses of all species in the system.

The mass-specific growth rate is assumed to be of the form

$$G_i(\vec{B}) = r_i\widehat{G}_i(\vec{B}) \tag{2.7}$$

where r_i is the maximum mass-specific growth rate and $\widehat{G}_i(\vec{B})$, the normalized growth rate, is a function whose maximum value is equal to one and is potentially a function of the biomasses of all species in the system.

Using these expressions for the functional response and growth rate, the two equations for the rate of change of biomass (Eqs. (2.4, 2.5)) can be written as

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = r_iB_i\widehat{G}_i(\vec{B}) - \sum_{j=\text{predators}} B_jJ_{ji}\widehat{F}_{ji}(\vec{B})/f_{eji} \tag{2.8}$$

for primary producers; and

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = -B_iT_i + B_i\sum_{j=\text{prey}} e_{ij}J_{ij}\widehat{F}_{ij}(\vec{B}) - \sum_{j=\text{predators}} B_jJ_{ji}\widehat{F}_{ji}(\vec{B})/f_{eji} \tag{2.9}$$

for consumer species.

Yodzis and Innes (1992) introduced allometric scaling relationships for the physiological rates for the model described in Eqs. (2.8) and (2.9). These rates are the intrinsic growth rate of the resources, the respiration rate of consumers, and the maximum consumption rate of a resource by a consumer. To simplify the model, all rates are assumed to scale as $M_i^{0.75}$, where M_i is the body mass of species *i*. Yodzis and Innes (1992) simply described M_i as "adult body masses for the populations." No reference is made as to whether this is the mean, median, or more sophisticated estimate of the body mass that accurately characterizes a population with variable body sizes within this model. Further progress on this fundamental question has occurred only recently (Savage 2004, Economo et al. 2005). In any case, all rates are normalized to the chosen species' body mass. These mass-specific rates scale with $M_i^{-0.25}$ $(=M_i^{0.75}/M_i)$.

The mass-specific respiration rate, T_i, is given by

$$T_i = a_{Ti} M_i^{-0.25} \tag{2.10}$$

The mass-specific maximum assimilation rate, $e_{ij}J_{ij}$, is given by

$$e_{ij}J_{ij} = f_{Jij} a_{Ji} M_i^{-0.25} \tag{2.11}$$

The mass-specific maximum growth rate of a producer species is given by

$$r_i = f_{ri} a_{ri} M_i^{-0.25} \tag{2.12}$$

The constants a_T, a_r, and a_J, all with units of (mass$^{0.25}$time^{-1}) have been determined from empirical data. Throughout the model, biomass is used as a surrogate for energy, so rates of energy respiration are converted to rates of biomass loss due to respiration and variations in energy content per unit biomass in different organisms within a metabolic type are ignored. However, these constants do vary between metabolic groups of organisms including plants, invertebrates, and ectotherm and endotherm vertebrates but still remain the same for species within the same metabolic group despite dramatic variation in mean body mass (Yodzis and Innes 1992, Ernest et al. 2003, Brown et al. 2004). These values are not universal for the whole system when the system is made up of species with different metabolic types. The constants f_{Jij} and f_{ri} are fractional quantities whose value may be specified for each specific population or feeding interaction in a particular ecological context.

One of the least intuitive aspects of this model concerns the model's timescale. Yodzis and Innes (1992) normalize time to the growth rate of the single primary producer in their model. Here, time is normalized to the growth rate of a chosen primary producer *k* (Eq. (2.12)) by introducing a new nondimensional time variable t':

$$t = \frac{t'}{r_k} = \frac{t'}{f_{rk} a_{rk} M_k^{-0.25}} \tag{2.13}$$

This means that a unit of time is defined as the inverse of the growth rate of primary producer *k*. This time varies greatly, for example, between phytoplankton and redwood species. Once species k is chosen and time is scaled accordingly, several constants are defined as follows:

$$r_i = \frac{f_{ri} a_{ri}}{f_{rk} a_{rk}} \left(\frac{M_k}{M_i} \right)^{0.25} \tag{2.14}$$

$$x_i = \frac{a_{Ti}}{f_{rk} a_{rk}} \left(\frac{M_k}{M_i} \right)^{0.25} \tag{2.15}$$

$$y_{ij} = \frac{f_{Jij} a_{Ji}}{a_{Ti}} \tag{2.16}$$

The first parameter r_i is the relative mass-specific growth rate of producer species i normalized with the growth rate of the chosen producer species k. Similarly, x_i is the mass-specific metabolic rate of species i relative to the chosen timescale of the system. Finally, the nondimensional constant y_{ij} is the maximum ingestion rate (biomass per unit time) of prey species j by predator species i relative to the metabolic rate of species i (biomass per unit time).

This allows the governing Eqs. (2.8, 2.9) to be written as

$$\frac{\mathrm{d}B_i}{\mathrm{d}t'} = r_i B_i \hat{G}_i(B) - \sum_{j=\text{predators}} x_j y_{ji} B_j \hat{F}_{ji}(B) / f_{eji} e_{ji} \tag{2.17}$$

for primary producers; and

$$\frac{\mathrm{d}B_i}{\mathrm{d}t'} = -x_i B_i + x_i B_i \sum_{j=\text{prey}} y_{ij} \hat{F}_{ij}(B) - \sum_{j=\text{predators}} x_j y_{ji} B_j \hat{F}_{ji}(B) / f_{eji} e_{ji} \tag{2.18}$$

for consumer species.

Overall, the formulation of this population dynamic model by Yodzis and Innes (1992) is based on three steps: (1) the parameters of the simple but highly abstract population dynamic model (Eqs. (2.8, 2.9)) are reformulated as mass-specific parameters (2.10–2.12). This allows seeding the model based on regressions that yield key parameters as a function of species' body mass; (2) time is nondimensionalized using the inverse of the maximum growth rate of producer k (2.13), so the model's time scale is expressed relative to the growth rate of that producer; (3) the mass-specific growth and metabolic rates of the model are normalized by the time scale (Eqs. (2.14, 2.15)), while the maximum ingestion rate is normalized by the metabolic rate (Eq. (2.16)). These three steps yield a population dynamic model with mass-specific parameters using a time-scale based on the growth rate of a chosen primary producer (Eqs. (2.17, 2.18)).

2.3.1 Parameter values

Key parameters include three very general constants; a_i for each metabolic category of the species, three fractions f_i with values between zero and one that depend on the specific ecological circumstances of the system being modeled, and the efficiency e_{ij} that simply depends on whether the resource is a plant or animal. The values given in Yodzis and Innes are collected below.

	Endotherm	Vertebrate ectotherm	Invertebrate	Phytoplankton
$a_T(\mathrm{kg}^{0.25}\mathrm{year}^{-1})$	54.9	2.3	0.5	
$a_J(\mathrm{kg}^{0.25}\mathrm{year}^{-1})$	89.2	8.9	9.7	
$a_r(\mathrm{kg}^{0.25}\mathrm{year}^{-1})$	34.3	6.6	9.2	0.4

	Plant resource	Animal resource
e_{ij}	0.45	0.85
f_r		Of the order 0.1
f_J		1.0 (endotherms), 0.2 (ectotherms), 0.3 (invertebrates)
f_e		1 for grazers and parasites; < 1 for some carnivores

To fully specify the model, the normalized growth function and functional response need to be defined.

2.4 GROWTH RATE MODELS

The simplest resource growth model is unconstrained exponential growth, in which case $\hat{G}_i(B) = 1$. The more advanced and commonly used logistic growth model which decreases the growth of a species as it reaches and exceeds its carrying capacity is given by

$$\hat{G}_i(B) = 1 - B_i/K_i \tag{2.19}$$

where K_i is the system's carrying capacity for producer species i. These two growth models are specific in two ways: (i) they describe net-growth that includes gross primary production as well as metabolism, and (ii) they do not account for effects of shared-resource consumption such as competition amongst primary producers in a multispecies community. To address (ii) in a community with multiple primary producer species (Brose et al. 2005), growth can be modeled as a function of the consumption of l limiting physical resources R_l (Tilman et al. 1997, Huisman and Weissing 1999):

$$\hat{G}_i(B, R) = \mathrm{MIN}\left(\frac{R_1}{K_{1i} + R_1}, \ldots, \frac{R_l}{K_{li} + R_l}\right) \tag{2.20}$$

K_{li} is the half saturation constant for resource l, and MIN is the minimum operator specifying that the least available resource relative to its half saturation constant limits growth of the producer. These half saturation constants indicate the nutrient concentration at which the consumer attains half its maximum rate of nutrient consumption. The variation of resource l's density with time is given by a two-term equation where the first calculates abiotic effects on resources concentration and the second term calculates effects of biotic consumption:

$$\frac{\mathrm{d}R_l}{\mathrm{d}t} = D(S_l - R_l) - \sum_{i=\text{producers}} (c_{li}\hat{G}_i(R)B_i) \tag{2.21}$$

where c_{li} is the fraction of resource l in the biomass of producer species i. The resource dynamics depend on a turnover rate D that is one divided by the mean residence time of the nutrient in its abiotic matrix (e.g., water, soil). Resource l is added to the matrix with a supply concentration of S_l, and its removal depends on the current resource content of the system, R_l. This Monod model of growth is well-established in plant ecology and the producer species compete by utilizing shared physical resources (Miller et al. 2005). The competition hierarchy is based on the half saturation constants, where lower K_{li} indicate "utilization efficiencies" or higher consumption rates at nonsaturating resource concentrations for primary producer species i consuming the physical resource l.

2.5 FUNCTIONAL RESPONSES

We discuss here multispecies versions of a few of the many models of functional response that have been studied. It is well known that the stability of small systems is quite sensitive to the choice of the functional response (e.g., DeAngelis et al. 1975, Murdoch and Oaten 1975, Yodzis and Innes 1992), and preliminary work shows that large systems are similarly sensitive (Williams and Martinez 2004). For more complete reviews of this very important and difficult topic, see Gentleman et al. (2003) and Jeschke et al. (2002).

2.5.1 Type II multispecies functional responses

Holling (1959) described the changing feeding rate of a predator in response to variations in prey density. In his type II functional response model, the predator divides its time between searching for prey, during which prey is captured at some fixed rate, and processing captured prey, during which time no searching takes place. If a is the rate of capture rate (units 1/time), b is the handling time (units: time/prey), and D is the prey density (number of individuals), then the rate of consumption of the predator, F, is the maximum amount potentially captured divided a term that decreases this rate as handling time increases above zero:

$$F = \frac{aD}{1 + abD} \tag{2.22}$$

Murdoch (1973) generalized Holling's (1959) type II functional response to predators with multiple prey by lowering the maximum possible amount captured of a single species by a term in the denominator that sums the time needed to handle all prey species captured:

$$F_{ij} = \frac{a_{ij} D_j}{1 + \sum_k a_{ik} b_{ik} D_k} \tag{2.23}$$

Here F_{ij} is the rate at which species j is consumed by the predator i, D_j is the density of species j, a_{ij} is rate at which the predator i attacks species j and b_{ij} is the time it takes predator i to handle prey item j.

Defining $c_{ij} = 1/b_{ij}$ as the maximum rate at which predator i can consume prey j in the absence of other prey and $D_{0ij} = 1/a_{ij}b_{ij}$ as the half-saturation density of predator i on prey j in the absence of other prey, this can be rewritten as

$$F_{ij} = \frac{c_{ij} D_j / D_{0ij}}{1 + \sum_k D_k / D_{0ik}} \tag{2.24}$$

2.5.2 Non-type II multispecies functional responses

If the attack rate is a function of the density of the prey, then the model of predation can relax predation pressure on rare prey more than the type II model. This can give rise to a sigmoidal, or type III functional response (Holling 1959). Predator interference can also modify the attack rate. In this case the attack rate decreases with increasing prey density (Beddington 1975, DeAngelis et al. 1975) compared to the rate given by the type II model. In general, rather than being constant, the attack rate a in (2.22) or a_{ij} in (2.23) is made a function of the predator and prey densities $\hat{a}_{ij}(D_i, D_j)$, but otherwise the functional response given in (2.22) or (2.23) is unchanged.

2.5.3 Type III

Real (1977) introduced a generalized type III functional response by defining $\hat{a}_{ij} = a_{ij} D_j^q$. When $q = 0$ in the equation below, (Eq. (2.25)) reduces to the attack rate used in the standard type II response (Eq. (2.22)). Using the half-saturation density of the prey as a natural scale for a feeding interaction suggests using an attack rate of the form $\hat{a}_{ij} = a_{ij}(D_j/D_{0ij})^q$. The functional response is then

$$F_{ij} = \frac{c_{ij}(D_j/D_{0ij})^{1+q}}{1 + \sum_k (D_k/D_{0ik})^{1+q}} \tag{2.25}$$

2.5.4 Predator interference

Beddington (1975) and DeAngelis et al. (1975) independently proposed a functional response in which predators spend some of their foraging time interacting with members of their own species, which reduces the rate at which predators capture prey. Assuming that this effect is the same for all prey species and that $a_{ij,\text{Interference}} = a_{ij,\text{NoInterference}}/(1 + d_i N_i)$ where d_i is a positive constant that describes the amount of interference and N_i is the number of individuals of predaceous species i, the resulting functional response is

$$F_{ij} = \frac{c_{ij}(D_j/D_{0ij})^{1+q}}{1 + d_i D_i + \sum_k (D_k/D_{0ik})^{1+q}}. \tag{2.26}$$

The preceding functional responses are for the rate at which a predator consumes individual prey items. By redefining the various parameters as per unit biomass rather than per individual, the functional response (Eq. (2.26)) can be rewritten in the form used in Eq. (2.6):

$$F_{ij} = J_{ij}\widehat{F}_{ij}(\vec{B}) = J_{ij}\frac{(B_j/B_{0ij})^{1+q}}{1 + d_i B_i + \sum_k (B_k/B_{0ik})^{1+q}} \tag{2.27}$$

Here B_i is the biomass of species i, B_{0ij} is the half-saturation biomass of predator i consuming prey j, and J_{ij} is the maximum rate at which predator i can consume prey j (biomass per unit time).

It is informative to look at the role of the various parameters in this functional response in determining prey preference. Following the analysis of Chesson (1983) and Gentleman et al. (2003), and using the notation introduced above for biomass-based functional response (Eq. (2.27)), a predator's relative preference of one resource over another is defined as

$$p_{ijk} = \frac{F_{ij}/B_j}{F_{ik}/B_k} = \frac{J_{ij}B_j^q/B_{0ij}^{1+q}}{J_{ik}B_k^q/B_{0ik}^{1+q}},$$

where the predator is species i and the two prey species are j and k. The term "switching" is used to describe situations in which the preference changes with changes in the relative resource density B_j/B_k. In the terminology of Gentleman et al. (2003), when $q = 0$ the response is class 1 and has no switching, and when $q \neq 0$, the response is class 2 and has passive switching.

For the type II response (q = 0), the preference is

$$p_{ijk} = \frac{J_{ij}/B_{0ij}}{J_{ik}/B_{0ik}}$$

This shows that a resource species is preferred either because its consumer species has a greater maximum rate of intake of the resource species or the consumer has a smaller half-saturation density for the resource. When the passive switching of a type III response is added, a resource will also be preferred when it has a higher relative density.

Table 2.1. Mathematical expression and their descriptions

Expression	Description
dB_i/dt	Change in population density of species *i* with time *t*
B_i	Population density of species *i*
G_i	Mass-specific net growth of species *i*
T_i	Mass-specific respiration (metabolic growth rate)$^{-1}$ of species *i*
r_i	Maximum mass-specific growth rate of species *i*
F_{ij}	Functional response = the fraction of the maximum consumption rate of the population of species *i* by the population of species *j* (i.e., per capita consumption of *j* by *i*)
e_{ij}	Assimilation efficiency = fraction of the biomass of species *j* lost due to feeding by species *i* that is metabolized by species *i*
f_{eij}	Ingestion efficiency = fraction of biomass of species *j* lost due to feeding by species *i* that is ingested by species *i*
a_{ji}	Attack rate of *j* on *i*
(B^{V})	Biomass loss from metabolism
J_{ij}	The population of species *i*'s maximum rate of ingesting the population of species *j*
G_i	Normalized growth rate of species *i*
M_i	Adult body mass among the population of species *i*
a_{Ti}	Mass to respiration conversion constant for species *i*
a_{Ji}	Mass to assimilation conversion constant for species *i*
a_r,	Mass to growth conversion constant for species *i*
f_J, f_r	Fractional constants
x_i	Constant mass-specific metabolic rate of species *i* relative to the maximum growth rate of a chose producer species
y_{ij}	Maximum ingestion rate of resources species *j* by consumer species *i* relative to metabolic rate of species *i*
r_i	Relative mass-specific growth rate of producer species *i*
K_i	System's carrying capacity for resource I
R_l	Limiting physical resources
l	A particular resource
c_{li}	Fraction of resource *l* that comprises the biomass of producer species *i*
D	(Eq. (2.21)) turnover rate of resources
D	(Eq. (2.22)) prey density
d	Positive constant describing amount of interference (Eq. (2.26))
B_{0ij}	Half-saturation biomass of predator I consuming prey j
q	Control parameter within functional response equations

2.6 CONCLUSION

With this modeling framework that extends Yodzis and Innes (1992) nonlinear approach to many species systems and functional responses, a new frontier of more empirically-based theoretical explorations of the structure and dynamics of complex networks is opened to researchers. Early explorations have shown, for example, that 50-species networks that allow most species to persist have food-web structure more like the empirically corroborated "niche model" than the ecologically unrealistic "cascade" and "random" models (Martinez et al. 2006). Such explorations have also shown how small variations in functional responses have dramatic effects on the stability and persistence of species within the simulated networks (Williams and Martinez 2004). Body-size ratios have also been shown to have similarly dramatic effects which help explain a recently discovered systematic difference between the body-size ratios of endotherm and ectotherm vertebrate predators (Brose et al. in review). Furthermore, this framework has been applied to the analysis of keystone effects which found that increased nutrient supply can systematically increase the strength of interactions measured by simulating the removal of keystone species from complex ecological networks (Brose et al. 2005). This of course points the way towards more compelling theoretical investigations of applied issues such as the effects of biodiversity loss and species invasions (Gibbs 2003) but such applications are not without significant problems (Paine 2004, Martinez and Dunne 2004).

Addressing these and many other challenges of modeling and managing ecosystems will involve a great deal of work to understand the sensitivity of simple and complex models to their many parameters described here. These parameters are needed to base models firmly on ecological observations while attempting to predict ecosystem behavior. Others have found that even more parameters are needed to successfully apply Yodzis and Innes' approach to even simple 2-species systems in chemostats (Shertzer et al. 2002). This means that more work is needed beyond understanding and empirically-basing model parameters before application of such models to specific complex ecological systems. For example, beyond the evolution parameters incorporated by Shertzer et al. (2002), better models of multispecies functional responses are needed (Gentleman et al. 2003). The specific functional response or responses used in the model and the values of the various parameters these responses introduce should be based on empirical knowledge of the system of interest. In addition, the approach presented here could also easily be extended to include the effects of temperature variation on system stability using the methods developed in Vasseur and McCann (2005). While conducting such work is clearly a hugely difficult and important challenge, we thank Peter Yodzis and his coworkers for making spectacularly important contributions to addressing the challenge and providing some of the most creative and rigorous foundations for current and future research on complex ecosystems.

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