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Effects of network and dynamical model structure on species persistence in large model food webs

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ORIGINAL PAPER

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Abstract Four models of network structure are combined with models of bioenergetic dynamics to study the role of food web topology and nonlinear dynamics on species coexistence in complex ecological networks. Network models range from the highly structured niche model to loosely constrained energetically feasible random networks. Bioenergetic models differ in how they represent primary production, functional responses, and consumption by generalists. Network structure weakly influenced the ability of species to coexist. Species persistence is strongly affected by functional responses and generalists' consumption rates but weakly affected by models and amounts of primary production. Despite these generalities, specific mechanisms that determine persistence under one dynamical regime, such as top-down control by consumers, may play an insignificant role under different dynamical conditions. Future research is needed to strengthen the weak empirical basis for various functional forms and parameter values that strongly influence whether species can coexist in complex food webs.

Keywords Food web · Bioenergetic dynamics · Stability · Persistence

Introduction

The study of food webs or networks of consumer–resource interactions has long been a central topic of ecological research (Dunne 2006). Despite the many technical problems in gathering and interpreting food web data (Borer et al. 2002; Cohen et al. 1993), there are clear patterns in food web structure that span a diverse range of habitats around the globe (e.g., Camacho et al. 2002; Dunne 2006; Dunne et al. 2004; Neutel et al. 2002; Williams et al. 2002; Williams and Martinez 2000). Recently, many of these patterns have been reproduced with simple static structural models (Cattin et al. 2004; Stouffer et al. 2005; Williams and Martinez 2000), but the understanding of the biological mechanisms responsible for these patterns has been slower to develop.

In general, explanatory models of food web structure are either based on evolutionary theory (Amaral and Meyer 1999; Camacho and Sole 2000; Rossberg et al. 2006a, b) or on structural constraints arising from population dynamics (Montoya and Sole 2003; Pimm 1984; Yodzis 1981). Recently, a number of models have combined evolution-like processes with population dynamics to produce food webs with some properties that are similar to empirical systems (Caldarelli et al. 1998; Drossel et al. 2001, 2004; Loeuille and Loreau 2005; Yoshida 2003). These models are generally quite complex, and the relative importance of evolutionary and dynamical processes within these models is unclear. In addition, rigorous statistical comparison of these models with empirical data along the lines of that carried out in some structural model studies (Rossberg et al. 2006a, b; Williams and Martinez 2000) has been lacking.

The search for the understanding of the mechanisms that give rise to the observed food web structures is closely related to the long-standing problem of explaining the

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stability and resilience of ecosystems and the mechanisms that allow so many species to coexist (McCann 2000). Models of the population dynamics of complex systems have long played a key role in this debate (May 1972), and are still widely used in research in this area (Brose et al. 2006b; Garcia-Domingo and Saldana 2007; Kondoh 2003; Martinez et al. 2006; Uchida and Drossel 2007). Models that combine the evolutionary process with population dynamics and also models that only consider population dynamics implicitly assume that the ability of species to coexist in a complex network depends both on the topology of the network and the basic rules of species growth and interaction that are formalized in the dynamical model. The goal of this study is to elucidate the relative importance of these two factors in more detail than has been done previously and to better understand how these factors affect species coexistence in complex food webs.

The effects of network structure on species persistence are assessed for a range of network structural models and variations in structural properties such as omnivory, trophic level, and the fractions of top and basal species. The influence of a range of features of dynamical models is also explored, including the effects of various models of primary production, different functional responses, and the behavior of generalists. The methodology used combines a range of topological models of species-rich food webs with a nonlinear model of energy capture, flow, and dissipation in those networks (Brose et al. 2006b; Martinez et al. 2006). Recent studies have addressed some of the structural and dynamical model variants considered here (Brose et al. 2006b; Garcia-Domingo and Saldana 2007; Uchida and Drossel 2007), but the range of structural and dynamical models considered here provides a more comprehensive treatment of the role of network and dynamical model structure in the persistence of species in large model food webs than these earlier studies. This work also incorporates recent advances in the parameterization of bioenergetic models, including size-structured networks and allometrically scaled parameters, which enhance the empirical realism of the models.

This work addresses a number of issues relating to the persistence and stability of species populations in food webs that have been discussed in the literature. One recent study of species' persistence in large model food webs (Brose et al. 2006b) used a subset of all possible model webs with a fixed number of basal species to control for possible effects of variations in a system's total potential productivity. The work presented here clarifies the roles of the number of basal species and the total possible energy supply in determining network persistence and allows a more consistent analysis of the dependence of species' persistence on productivity.

Early theoretical work (Pimm and Lawton 1978) argued that omnivory could be a destabilizing influence in food webs, while more recent theoretical studies of three species systems (McCann and Hastings 1997) and experimental work (Fagan 1997) have argued that omnivory plays an important role in stabilizing food webs. Omnivory in combination with weak links was also found to be stabilizing in four-species models with Lotka–Volterra dynamics (Emmerson and Yearsley 2004). The universality of omnivory as a stabilizing influence was questioned in a recent comprehensive analysis of the role of omnivory in three-species models (Vandermeer 2006), which found that in different situations omnivory is either stabilizing or destabilizing. A generally stabilizing effect of omnivory could help explain its relatively common occurrence in empirical food webs (Williams and Martinez 2004a; Thompson et al. 2007). The relative frequency of a simple omnivorous trophic module or motif has been shown to vary widely across empirical food webs (Bascompte and Melian 2005) and on average not be significantly more common than in randomized networks (Milo et al. 2002), though a recent study found that the omnivory motif is overrepresented in the majority of food webs in a larger set of empirical data (Stouffer et al. 2007). None of these studies addressed the effect of omnivory on the persistence of species in systems with large numbers of species, an issue that is addressed in this work.

The length of food chains and the distribution of abundance among trophic levels in a food web have also been studied as possibly influencing the stability and persistence of species in food webs. It has long been argued that observed food chains are short because of lower energy availability at higher trophic levels (Hutchinson 1959). An alternative mechanism is that perturbations take longer to recover in long food chains (Pimm and Lawton 1977), suggesting that long chains will be relatively rare. A recent review (Post 2002) found that no single process determines food chain length and the number of trophic levels but that both resource availability and dynamical stability provide important constraints, along with ecosystem size, predator–prey size ratios, disturbance, and community history. In contrast to earlier theoretical studies based on systems with a small number of species, the work described here addresses the role of trophic structure and primary productivity on the ability of species to coexist in multispecies food web models.

Materials and methods

The models used here allow the study of the effects of network structure, primary production, and interspecies interaction rules on the ability of species to coexist in complex food webs. They combine static models of food web structure with nonlinear models of energy flow along the trophic links in the food web. Time series of species abundances and energy flows along the various links are recorded, and the fraction of species that remain above a biomass threshold during the simulation is used as a measure of species' persistence in the combined structural–dynamical model.

Models of network structure Four different models of network structure are considered, varying from minimally constrained random networks to highly structured networks that are quite similar to empirically observed food webs. Input parameters to all models include species richness (S) and directed connectance (C) where $C=L/S^2$ and L is the number of feeding links in the food web. All models were constrained to produce energetically feasible food webs by requiring that every species have at least one path connecting it to a basal species. The basic rules of each of the models are described below; details of their implementation can be found in the online appendix.

The niche model (Williams and Martinez 2000), the most empirically successful of the structural models used here, achieves its success by constraining the network's structure in three ways. First, species are hierarchically ordered on a one-dimensional niche axis, so that a species is far more likely to consume an organism lower in the hierarchy. Second, the distribution of the number of resources of each consumer has a specific functional form (Stouffer et al. 2005). Finally, species are constrained to consume from a contiguous niche in the one-dimensional niche space.

The generalized cascade model (Stouffer et al. 2005) retains the hierarchical ordering and the distribution of the number of resource of each consumer used in the niche model. It discards the niche model's contiguity constraint and instead allows a consumer to utilize with equal probability any resource equal to or below itself in the hierarchy.

The cascade model (Cohen et al. 1990; Williams and Martinez 2000) retains the strict trophic hierarchy of the niche and generalized cascade models but uses a different resource probability distribution. This resource distribution produces a significantly worse match to the empirical data than either the niche model (Williams and Martinez 2000) or the generalized cascade model (Stouffer et al. 2005).

The simplest model, the random model, removes all these constraints by establishing any of S^2 potential links among all S nodes with probability C (Erdos and Renyi 1959) and selecting among these networks only those that are energetically feasible.

The possible influence of various quantitative properties of network structure on persistence was evaluated. Results addressing influences of the following properties are presented: FractionBasal and FractionTop, the proportions of basal (without prey), and top (without predators) species, respectively; TopGen, the mean generality of the top species where generality is defined as the number of prey divided by L/S; VulSD, the standard deviation of vulnerability, which measures the variation in the number of predators of each species (Williams and Martinez 2000); TrophicLevel, the mean trophic level of all species computed using the short-weighted trophic level algorithm (Dunne et al. 2004; Williams and Martinez 2004a); and Omnivory, the fraction of species that are omnivores, species that have a noninteger trophic level and consume more than one species.

Bioenergetic model The flow of energy along the links in the food web is simulated with a multispecies, allometrically scaled consumer–resource model (Brose et al. 2006b; Williams et al. 2007; Williams and Martinez 2004b; Yodzis and Innes 1992). This approach is intermediate in complexity, capturing interspecies interactions more accurately than the Lotka–Volterra models typically used in studies of species-rich systems but simplifying the system by using allometric scaling and ignoring many processes to avoid a proliferation of parameters and model complexity (Yodzis and Innes 1992).

As in earlier work, the biological rates of production, metabolism, and maximum consumption are scaled with the species' body mass (Brown et al. 2004; Enquist et al. 1999; Yodzis and Innes 1992). All primary producers are assumed to have the same body mass, and time is scaled with the growth rate of a primary producer, species k (Brose et al. 2006a). The governing equations for the rate of change of biomass of each species are

$$\frac{\mathrm{d}B_i}{\mathrm{d}t'} = B_i G_i\left(\vec{B}\right) - \sum_{j=\text{predators}} x_j y_{ji} B_j F_{ji}\left(\vec{B}\right) \Big/ e_{ji} \tag{1a}$$

for primary producers and

$$\frac{\mathrm{d}B_i}{\mathrm{d}t'} = -x_i B_i + x_i B_i \sum_{j=\text{prey}} y_{ij} F_{ij}\left(\vec{B}\right) - \sum_{j=\text{predators}} x_j y_{ji} B_j F_{ji}\left(\vec{B}\right) \Big/ e_{ji} \tag{1b}$$

for consumer species. In these equations, B_i is the biomass of species i, and t' is the rescaled time. There are three metabolic parameters: x_i is the mass specific metabolic rate of species i relative to the chosen time scale of the system, and 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). Two parameters are related to assimilation efficiency: e_{ij} is the assimilation efficiency, equal to the fraction of the biomass of species j lost due to consumption by species i that is actually metabolized. The function $G_i\left(\vec{B}\right)$ is the normalized growth rate of primary producer population i, and the function $F_{ij}\left(\vec{B}\right)$ is the normalized multispecies functional response of consumer i and resource j. Both are potentially functions of the biomasses of all of the populations in the system.

The metabolic parameters are given by

$$x_i = \frac{a_{Ti}}{a_{rk}}\left(\frac{M_k}{M_i}\right)^{0.25}, \tag{2}$$

$$y_{ij} = \frac{a_{Ji}}{a_{Ti}}. \tag{3}$$

In these equations, M_i is the mass of an individual of species i, and M_k is the mass of the primary producer used for normalizing the model's time scale. The constants a_T, a_r, and a_J, all with units of (mass$^{0.25}$ time^{-1}), are determined from the allometric scaling of metabolism, production, and maximum consumption, respectively, and have been determined from empirical data. Their values vary between metabolic groups of organisms including plants, invertebrates, and ectotherm and endotherm vertebrates but remain the same for species within the same metabolic group despite dramatic variation in mean body mass (Brown et al. 2004; Ernest et al. 2003; Yodzis and Innes 1992). Details of the derivation of these equations are given in the online appendix.

Several further simplifications are made to reduce the size of the parameter space being explored. All species are assumed to have a constant consumer–resource body size ratio Z (Brose et al. 2006b) along the shortest path to a basal species so the mass of species i is $M_i=M_kZ^T$ where T is the length of the shortest path from consumer to resource. Using the shortest path to basal species to scale body size gives sensible body sizes in all structural models. The short-weighted or prey-averaged trophic level used in other work can have very large values in random networks due to the extreme looping in those networks, which gives unreasonably large body sizes to many species. Within a food web, all species are assumed to be a single metabolic type, invertebrates, and $a_r=1$, $a_T=0.314$, and $y_{ij}=8$ (Brose et al. 2006b). The consumer–resource body size ratio is set to $Z=100$. The assimilation efficiency $e_{ij}=0.45$ for consumption of primary producers and $e_{ij}=0.85$ for other feeding links (Yodzis and Innes 1992). Initial B_i of each species is randomly selected between 0.1 and 1.

Primary producer growth rate Three models of the primary producer's growth rate $G_i\left(\vec{B}\right)$ are compared. The simplest model, the commonly used logistic model, assumes that each basal species independently has a growth rate $G_i\left(\vec{B}\right) = (1 - B_i/K_i)$ where K_i is the carrying capacity of species i. To minimize parameters, a single parameter K sets the per-species carrying capacity, and $K_i=K$. This formulation has the problem that the carrying capacity of the system and the system-wide maximum possible rate of primary production are dependent on the number of primary producers in the system (Kondoh 2003). Since it is possible that many system properties depend on the rate of primary production, it is useful to control for this effect (Brose et al. 2006b). In this study, the effects of two different models that define a system-wide productivity are tested. One defines a system-wide carrying capacity K, and the carrying capacity of each primary producer is $K_i = K/n_\mathrm{p}$, where n_p is the number of primary producers. The other employs a simple Lotka–Volterra competition model, which allows the primary producers to compete for a system-wide carrying capacity K: $G_i\left(\vec{B}\right) = \left(1 - \sum_{producers} a_{ij}B_j \Big/ K\right)$. All simulations were done using a neutrally stable competition model in which all $a^{ij}=1$. Preliminary experiments with a model with weak competitive exclusion in the absence of consumer species ($a^{ii}=1$ and all other $a^{ij}=1.05$) found that the top-down effects of the consumer species typically allow multiple resource species to coexist where in their absence only a single competitive dominant species would remain. A more detailed exploration of the many possible scenarios is beyond the scope of this study.

Multispecies functional response Adding a simple model of predator interference (Beddington 1975; DeAngelis et al. 1975) and type III effects (Real 1977, 1978) to the classic multispecies type II functional response (Murdoch 1973) gives a functional response of the form

$$F_{ij}\left(\vec{B}\right) = \frac{\left(B_j/B_{0ij}\right)^{1+q}}{1 + d_iB_i + \sum_{k=\mathrm{prey}} \left(B_k/B_{0ik}\right)^{1+q}}. \tag{4}$$

In this equation, B_i is the biomass of species i, B_{0ij} is the half-saturation biomass of predator i consuming prey j, q is a positive constant controlling the strength of the type III functional response (Real 1977; Williams and Martinez 2004b), and d_i is a positive constant that controls the amount of predator interference (Beddington 1975; DeAngelis et al. 1975). This is the simplest model of predator interference, with interference only occurring within the predating species rather than between all predators that share the same prey (Arditi and Michalski 1996). Based on previous explorations of the effects of functional response parameter values (e.g., Williams and Martinez 2004b; Martinez et al. 2006) and a large amount of ecological theory (see e.g., Gentleman et al. 2003), we explored the effects of three different functional responses by choosing the following parameters: the Holling type II response, $q=0$ and $d=0$; a weak Holling type III response, $q=0.2$ and $d=0$; and a Beddington–DeAngelis response with an empirically reasonable amount of predator interference, $q=0$ and $d=0.5$ (Skalski and Gilliam 2001).

Assuming that there is a reference value B_0 and defining $\omega_{ij} = \left(B_0/B_{0ij}\right)^{1+q}$, the functional response (Eq. 4) can be rewritten as

$$F_{ij}\left(\vec{B}\right) = \frac{\omega_{ij}B_j^{1+q}}{B_0^{1+q} + d_iB_iB_0^{1+q} + \sum_k \omega_{ik}B_k^{1+q}} \tag{5}$$

which is the form used by Brose et al. (2006b) and an extension of the form used in some earlier studies (McCann and Hastings 1997; McCann et al. 1998). The parameters ω_{ij} are the relative half-saturation densities or relative inverse attack rate in a Holling type II response (Holling 1959), usually interpreted as the relative preference of consumer i for resource j (Chesson 1983; McCann and Hastings 1997). This model has passive switching, driven only by the different relative abundances of the resources (Gentleman et al. 2003).

Some previous studies (Brose et al. 2006b; McCann and Hastings 1997; McCann et al. 1998; Williams and Martinez 2004b) have used the constraint $\sum_{j=\mathrm{prey}} \omega_{ij} = 1$. In this case, if all the ω_{ij} of a consumer are equal, $\omega_{ij} = 1/n_{ri}$ where n_{ri} is the number of resources of species i, and $B_{0ij} = n_{ri}^{1/(1+q)}B_0$. If B_0 is a fixed system-wide parameter, generalist species (species with larger n_{ri}) have higher half saturation densities B_{0ij} than specialists. It is easiest to understand the consequences of this difference between specialists and generalists by considering the case of the Holling type II response ($q=d=0$). If only one of a consumer's resources has a nonzero abundance, $F_{ij}\left(\vec{B}\right) = B_j/\left(n_{ri}B_0 + B_j\right)$. This means that faced with an equal abundance of a single resource, a generalist (large n_{ri}) will consume that resource at a lower rate than a specialist (small n_{ri}). Similarly, and again with $q=d=0$, equal abundance of resource species and total resource biomass $B_{\mathrm{TOT}} = \sum_{k=\mathrm{prey}} B_k$, the total rate of consumption is $F_{\mathrm{TOT}} = \sum_j F_{ij}\left(\vec{B}\right) = B_{\mathrm{TOT}}/\left(n_{ri}B_0 + B_{\mathrm{TOT}}\right)$. This shows that given equal prey abundances, the total rate of consumption of a generalist (large n_{ri}) will be lower than that of a specialist (small n_{ri}). In this study, this model is referred to as the weak generalist model.

An alternative model that preserves the assumption that each consumer has uniform relative consumption across all resources is to make each consumer's behavior toward its resources independent of the consumer's generality. This is accomplished by setting all ω_{ij} to the same constant value rather than to a value that is a function of n_i. By using $\omega_{ij}=1$, the half-saturation densities B_{0ij} are equal to the reference value B_0. In this case, a specialist and generalist will consume at the same rates when they encounter the same total density of their resource species. To contrast this behavior to the model described above, this model is referred to as the strong generalist model.

The effects of these four different network models, three models of primary production, three functional response models, and two models of the behavior of generalists were studied in a fully factorial design with 200 replicates of each of the 72 combinations of independent variables. Network persistence was measured as the fraction of species with biomasses above a threshold value ($B_i > 10^{-15}$) at $t=4{,}000$. As expected and as found previously (Brose et al. 2006b), simulations with longer time series yield qualitatively similar results but with slightly lower persistence values, and using higher or lower extinction thresholds slightly decrease or increase persistence, respectively. A sample time series that allows the effect of variations in time series duration or extinction threshold to be considered is shown in Supplementary Appendix A.3.

Results

Effects of structural and dynamical models on network persistence The effects of network topology, resource model, functional response, and generalist model on network persistence are given in Table 1 and show that persistence is by far most strongly affected by the choice of functional response, with the choice of the generalist model having the second strongest effect. In contrast, variations in network structural and resources model have much smaller effects on system persistence.

The effects of structural model for each functional response are shown in Fig. 1a. Persistence is strongly affected by the functional response, with type II response having low persistence and the weak ($q=0.2$) type III response consistently having fairly high persistence. Network structure has a modest effect on persistence for the less persistent type II and predator interference response models but has only a very small effect on persistence for models using the weak type III response.

The large effect of the generalist strength on persistence occurs in all structural models (Fig. 1b). For all structural models, systems with weak generalists consistently have higher persistence. This effect is less in random model systems than in systems using the other structural models, as shown in Fig. 1b and also by the relatively large second-order effect (MODEL×GEN) in Table 1.

The individual effects of functional response and generalist strength on persistence is shown in Fig. 1c.

Table 1 Results of an analysis of variance of structural and dynamical first- and second-order effects on persistence

Source	Sum-of-squares	*df*	Mean square	*F* ratio
MODEL	9.0800	3.0000	3.0270	155.01
PROD	16.403	2.0000	8.2010	420.05
FNRESP	622.31	2.0000	311.16	15936
GEN	241.56	1.0000	241.56	12372
MODEL × PROD	8.5260	6.0000	1.4210	72.781
MODEL × FNRESP	2.5660	6.0000	0.42800	21.902
MODEL × GEN	14.900	3.0000	4.9670	254.37
PROD × FNRESP	5.1180	4.0000	1.2800	65.534
PROD × GEN	1.5360	2.0000	0.76800	39.333
FNRESP × GEN	36.384	2.0000	18.192	931.74

Analysis of variance, $r^2 = 0.78$

MODEL Structural model, *PROD* model of primary production, *FNRESP* functional response, *GEN* generalist behavior

Again, the large effect of both the functional response and the generalist strength is clear. For all models of functional response, the strength of generalists has a strong effect on persistence. Weak generalists are essential for species coexistence when interactions are governed by a type II response. In contrast, when the weak type III response is used, a fairly large fraction of species persist with either generalist model, and the variation in persistence with generalist strength is smaller than variation with the other functional responses, reflecting the relatively large second-order effect (FNRESP × GEN) in Table 1.

Effect of carrying capacity on network persistence and stability The effect of varying carrying capacity was tested in systems with niche model structure and type III functional responses (Fig. 2). We describe this effect within this combination of the structural model and functional response because of its dynamic interest and close correspondence with empirical data (Williams and Martinez 2000, 2004b; Martinez et al. 2006) combined with the qualitative consistency with other combinations of independent variables (results not shown). With all three models of primary productivity, increasing carrying capacity has a strong effect on system persistence (Fig. 2a). For all primary production models, when carrying capacity is small, system persistence rises as carrying capacity increases. At larger values of carrying capacity, persistence levels off and drops slightly in some systems. At low K, systems have less persistence when generalists are weak because the weak generalists are less able to capture energy and so more likely to starve to extinction. At higher values of K, systems with strong generalists have lower persistence because their strength more likely drives their prey to extinction.

While larger carrying capacities had little effect on persistence, there is a dramatic increase in biomass variability as measured by the coefficient of variation of biomass as the carrying capacity increases (Fig. 2b). This effect is consistently larger in systems with strong generalists. These results show that in the models tested here, enrichment modeled as increased carrying capacity generally destabilizes systems but does not drive species to extinction. Figure 2b also shows that systems with strong generalists are generally less stable than those with weaker generalists.

Effect of network structural properties on persistence Table 2 shows the results of linear regressions of network persistence against various structural properties of the initial network. Results are only shown for niche model networks with weak type III functional response, which are averaged across all models of primary production but separate out results for models with strong and weak generalists. The results show that the sensitivity of persistence to initial network property depends strongly on whether the dynamical model has weak or strong generalists. In models with strong generalists, networks with larger numbers of top species and top species that are more generalist tend to have lower persistence, while these properties play a much smaller role when the generalists are weak. In models with weak generalists, networks with more basal species or shorter mean trophic level tend to be more persistent, but neither of these properties play a strong role in determining the persistence of species in network models with strong generalists. Finally, the fraction of species that are omnivores does not strongly affect the persistence of species in any of these model scenarios.

These regression trends are independent of the model of and amount of primary production used in the simulations (results not shown). Two of the primary production models set a system-wide carrying capacity that partially controls for variations in the number of basal species. This means that the dependence of persistence on basal fraction is not a result of the increased potential productivity in systems with more basal species.

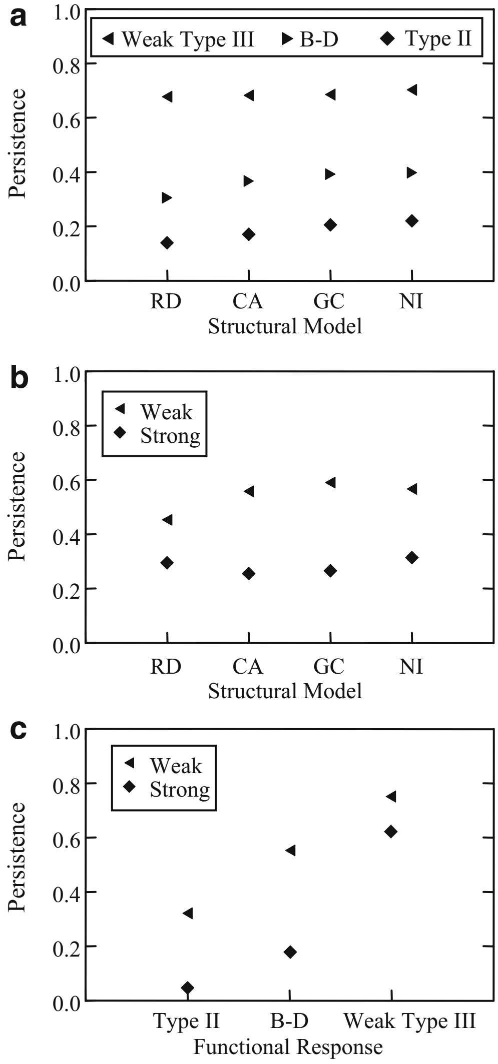

Fig. 1 The variation of species persistence with structural model, functional response and generalist model. Data points present means for all simulations within the class described averaged over all combinations of independent variables not mentioned in the class description. For example, persistence of niche model networks with type II responses in **a** averages over networks with both types of generalist models. In all figures, the initial network models had inputs of $S=30$ and $C=0.15$. Functional responses are the type II, a weak type III and Beddington–DeAngelis response with moderate predator interference (B–D). **a** Persistence vs. structural model for each functional response. **b** Persistence vs. structural model for each generalist model. **c** Persistence vs. functional response for each generalist model. *RD* Random model, *CA* cascade model, *GC* generalized cascade model, *NI* niche model

Discussion

The relationship between stability and persistence Throughout the long complexity–stability debate, researchers have explicitly or implicitly assumed a correlation between model stability and the ability of species to coexist. This relationship is fundamental to the interpretation of model results such as those presented here. Examples include the claim that "destructive oscillations in populations" occur in simple communities (Elton 1958), and the argument that systems with large amplitude fluctuations that sometimes have small population magnitudes will be more subject to species loss due to demographic stochasticity (McCann and Hastings 1997). By imposing an extinction threshold, the models explored here are effectively subject to stochastic extinctions. Still, when carrying capacity is increased under a wide range of conditions, there is increased instability as measured by biomass variability but near-constant persistence of species (Fig. 2). This occurs because increased biomass fluctuation amplitude does not lead to increased extreme low biomass values. Thus, increased instability as measured by fluctuation amplitude does not lead to increased extinctions, and the presumed relationship be-

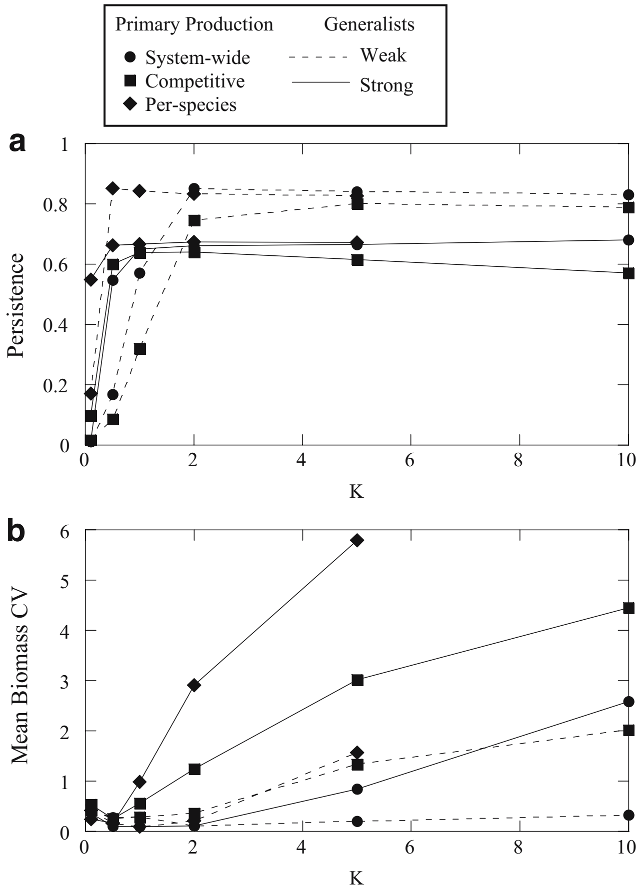

Fig. 2 **a** Mean persistence and **b** biomass coefficient of variation vs. *K* (carrying capacity) for three models of primary production and two models of generalist behavior. *K* is the total carrying capacity for the competitive or system-wide models and is the carrying capacity of each basal species for the per-species model. Each data point is the average across 200 different niche model networks with initial $S=30$ and $C=0.15$ employing weak type III ($q=0.2$) functional responses

Table 2 Results from linearly regressing persistence against initial network properties in systems employing all models of production and created by the niche model with $S=30$, $C=0.15$, and $q=0.2$ (weak type III functional response)

Property	Strong generalists		Weak generalists	
	Slope	r^2	Slope	r^2
FractionTop	−1.68	0.30	−0.81	0.12
TopGen	−0.07	0.18	−0.018	0.019
VulSD	−0.755	0.17	−0.449	0.11
FractionBasal	0.657	0.031	1.23	0.20
TrophicLevel	−0.041	0.008[a]	−0.146	0.21
Omnivory	−0.011	0[b]	−0.305	0.025

Consumers are parameterized as invertebrates with a predator–prey body size ratio=100. FractionTop is the fraction species that have no consumers. TopGen is the normalized mean generality of top species (mean number of top species' resource species divided by the total number of species). VulSD is the standard deviation of the normalized mean number of each species' consumers. FractionBasal is the fraction species that have no resource species. Omnivory is the fraction of species that feed on more than one trophic level. All slopes are significantly different from zero except [a] is marginally significant and [b] is not significantly different from 0

tween stability and persistence does not occur in these models.

Structural models and persistence In the wide range of species-rich dynamical models explored here, network topology does not provide a strong constraint on the ability of species to coexist. Even when network structure is random, the dynamical models used here can produce networks in which a high fraction of species are persistent. This surprising result suggests that studies of this sort must go beyond looking at species persistence to consider more sophisticated measures of network function, such as the biomass structure of the network, system-wide rates of primary productivity, and energy dissipation. Recently, a number of coupled evolution-dynamical models (Caldarelli et al. 1998; Drossel et al. 2001; Drossel et al. 2004; Loeuille and Loreau 2005; Yoshida 2003) use interspecies dynamics to select which network structures will persist into future generations. Given that species persistence (Fig. 1) is similar across the different network models studied here, using dynamical models to select more persistent network structures may not be a very discriminating process for evolving network structure.

Role of omnivory The role of omnivory in larger model systems has not previously been examined, and the results reported here (Table 2) show no effect of omnivory on the ability of species to coexist in niche model food webs. The structural models produce webs with a fairly wide range of omnivory, but there is no sign of a relationship between the fraction of omnivores and species' persistence across the levels of omnivory produced in these models. The lack of effect might be due to the use of the shortest path to basal species to scale body size, which allows omnivores to have destabilizing consumption relationships in which they consume larger prey. This result is broadly in agreement with recent results for three species systems (Vandermeer 2006) in which there is no clear relationship between omnivory and system stability. It contradicts some earlier studies that found a positive relationship between omnivory and stability or persistence (Fagan 1997; McCann and Hastings 1997).

Role of the functional response Earlier studies have highlighted the importance of small changes in the functional response to the dynamics of small (two- and three-species) systems (Fussman and Blasius 2005; Williams and Martinez 2004b) and shown that the functional response can have important impacts on species coexistence in larger systems (Brose et al. 2006b). The results presented here show again that the choice of functional response type can have a dramatic impact on the ability of species to coexist in large model food webs, especially when the strong generalist model is used (Fig. 2). Getting a better understanding of these aspects of the dynamics will be vital for furthering our understanding of the functioning of complex food webs.

The models of functional response explored here are a tiny range of the possibilities. Processes drawn from the foraging theory such as active prey switching and adaptive foraging (Gentleman et al. 2003; Kondoh 2003; Post et al. 2000; Uchida and Drossel 2007), other functional forms designed to better represent spatially inhomogeneous processes (Nachman 2006) and to more accurately model the behavior of individuals (Jeschke et al. 2002), are all likely to have significant effects on the energy flow dynamics. Some of these possibilities have already been shown to significantly influence the ability of species to coexist in multitrophic food webs (Drossel et al. 2004; Kondoh 2003; Uchida and Drossel 2007). The broad range of relatively unexplored possibilities shows that there is still much work to be done to understand the connections between individual behavior, community structure, and ecosystem properties. However, our results do extend earlier findings (Williams and Martinez 2004b; Yodzis and Innes 1992) that a variety of type III and predator interference responses can provide more stable or persistent dynamics than type II responses.

Role of the generalist strength The relative intensity of specialists and generalists plays an important role in both the ability of species to coexist in a food web. Systems in which generalists are strong consumers have fewer persistent species than systems with weak generalists (Fig. 1b and c). The size of this effect depends somewhat on the functional response with less dependence of persistence on the strength of generalists occurring in systems using a weak type III response. This seems to contradict an earlier study (Uchida and Drossel 2007) in which their “classical population dynamics” model (similar to the strong generalist model) was more persistent than their “population dynamics without adaptive foraging” model (similar to the weak generalist model). There are two likely reasons for this. First, these alternate models have mean a_{ij} values that are half the value used here, so their stronger consumers are not as strong and the weaker consumers are significantly weaker than those used here. This might make their weaker consumers be unable to bring sufficient energy to higher trophic levels to sustain those species. Second, the basic dynamics and parameterization of their model are very different, and their model includes a strong “competition strength within species” term.

Interdependence of the functional response and generalist model Earlier work (Brose et al. 2006b; Martinez et al. 2006) found the persistence of species in systems with strong (q=1) type III, weak (q=0.2) type III, and predator interference functional responses to be quite similar. This is surprising given the very different mechanisms at work in the type II and predator interference responses. The type III response releases resources from predation when they are rare and so drastically reduces the likelihood that they will be driven extinct. In contrast, the predator interference response lowers the per capita rate of predation when the predator is common, independent of the abundance of the prey. Along similar lines, Brose et al. (2006b) found that the increased persistence of systems with strong type III and predator interference responses compared to systems with type II responses was quite small.

The work here tests a wider range of model features than previous studies and finds that the level of persistence seen in earlier studies using similar techniques (Brose et al. 2006b; Martinez et al. 2006) only occurs when using a model with generalists that are relatively weak consumers compared to specialists. When generalists are strong, very few species persist in systems with type II responses, and compared to systems with weak generalists, persistence is strongly diminished for the predator interference functional responses and slightly diminished for the weak type III response (Fig. 1c).

These systems’ sensitivity to the relative strength of predation of generalists and specialists demonstrates that these behaviors are important for understanding the persistence and functioning of complex food webs. These two models of generalist behavior are two simple cases in a large universe of possibilities, and both assume that a consumer has equal attack rates toward all its resources. Exploring models in which a consumer attacks and captures different resources at different rates and exploring the effects of active prey switching (Kondoh 2003; Post et al. 2000) in multispecies food webs are two important areas for future research. It would be interesting to use the available empirical data to address both whether the attack rate is a function of consumer generality and whether attack rate scales with consumer body size. Unfortunately, empirical data for addressing these questions are sparse. For example, a recent compilation of type II functional response parameter values found only 123 predator–prey pairs with attack rate and handling time data (Beckerman et al. 2006).

Interdependence between structure and dynamics No consistent patterns emerged linking particular structural properties of networks to the ability of species in the network to coexist. Instead, there is interplay between structure and dynamics such that certain structural features are important to species coexistence under certain dynamical regimes. When generalists are weak consumers, persistence is driven primarily by bottom-up effects and is dependent on the fraction of basal species and the overall trophic height of the network, with broader, shorter systems (systems with more basal species and lower mean trophic level) being more persistent (Table 2, Martinez et al. 2006). In contrast, persistence in systems with strong generalists is more controlled by top-down effects. In this case, networks are more persistent when they have fewer top species, and those top species are less general (Table 2). Persistence of the model systems was largely independent of productivity above a small minimum of productivity. This result reproduces the empirical findings reviewed by Post (2002) “that resource availability limits food-chain length only in systems with very low resource availability.”

Conclusions

These models highlight a number of issues that arise when considering the interplay between structure and dynamics in complex food webs. First, across the range of network structures studied here, network structure does not have a large effect on the ability of species to persist in complex food webs. Second, a number of effects that have been identified as important in small systems, such as the role of omnivory and food chain length, play more ambiguous roles in larger systems. This points out the important complementary role of studies such as this one that examine the effect of embedding processes originally identified in small systems within larger systems (Brose et al. 2005). Third, structure and dynamics are often strongly interlinked, such that specific mechanisms that play a role in determining persistence under one dynamical regime, such as top-down effects when generalists are strong consumers, do not play a significant role under different dynamical conditions. Finally, species persistence is strongly affected by the form of the functional response and the relative rate of consumption of generalists but not by the model of primary production or total system productivity. These components of the dynamical model represent different aspects of the behavior of species and their interactions. Incorporating more realistic models of the population-level consequences of individual behavior and predator–prey interactions into models of ecological networks is an important area for further research. Despite the model's sensitivity to the functional responses used, their form and parameterization are not well supported by empirical data. Better data on functional response forms in natural systems and on attack rates and the variation of attack rate between generalists and specialists are needed to accurately represent and parameterize these dynamically vital model components.

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