

Diversity, Complexity, and Persistence in Large Model Ecosystems

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ABSTRACT

Research on how vast numbers of interacting species manage to coexist in nature reveals a deep disparity between the ubiquity of complex ecosystems and their theoretical improbability. Here, we show how integrating models of food-web structure and nonlinear bioenergetic dynamics bridges this disparity and helps elucidate ecological complexity. Network constraints including the trophic hierarchy, contiguity, and looping formalized by the “niche model” are shown to greatly increase persistence in complex model ecosystems. Behavioral nonlinearities including interference between consumers and reduced consumption of rare resources formalized by predator interference and new “type II.2” functional responses further increase the diversity of dynamically interacting species. Integrating these empirically observed regularities yields remarkably comprehensive, extensible, and ecologically realistic models that revise the role of omnivory and emphasize the importance of network structure, short food chains, and behavioral ecology. These models also provide a powerful framework for adding non-trophic effects and developing field experiments and hypotheses.

INTRODUCTION

One of the most important and least settled questions in ecology concerns the roles of diversity and complexity in the functioning of ecosystems (McCann 2000). Scientists still have difficulty explaining why diversity in terms of vast numbers of species and complexity in terms of species' myriad interactions are so ubiquitous in ecological systems (McCann 2000; Kondoh 2003). Early attempts found that diversity and complexity increased ecosystem stability because the addition of consumers can prevent their prey from competitively excluding other prey (Paine 1966) and more feeding links among more species generally reduced the risk of species' dependence on few resources (MacArthur 1955). Later, influential models of ecosystems demonstrated that diversity and complexity may actually destabilize ecosystems, either through increasing the chance of positive feedback loops (May 1973) or through additional omnivorous interactions increasing the time needed for perturbed species to return to equilibrium (Pimm & Lawton 1978).

While much early work emphasized equilibrium-based modeling and comparative empiricism applied to large ecosystems, later research placed more emphasis on nonlinear modeling and experimental empiricism focused on small modules within ecosystems. These recent models and experiments find increases in complexity, such as the addition of weak and omnivorous interactions (McCann & Hastings 1997; McCann *et al.* 1998; Fussman & Heber 2002), and increases in diversity, such as increases in numbers of species and functional groups (Naeem *et al.* 1994; Tilman *et al.* 2001) to be stabilizing. Other work has confirmed the theoretically destabilizing effects of large amounts of complexity in experimental communities (Fox & McGrady-Steed 2002). These findings leave much disparity between the improbability of diverse complex ecosystems in theory and their pervasiveness in nature. In particular, it is unclear whether the stabilizing effects of omnivory, (McCann & Hastings 1997) weak links, (McCann *et al.* 1998; Berlow 1999) and diversity in small modules (Naeem *et al.* 1994) and single trophic levels (Tilman *et al.* 2001) also apply to large networks with several trophic levels.

Here, we address these issues by examining persistence in nonlinear dynamical models of large complex ecological networks that replace limiting and unrealistic modeling assumptions e.g., food webs are random networks and populations are at equilibrium (May 1973; Yodzis 2000), with more mechanistic and empirically consistent biological diversity and complexity (Yodzis & Innes 1992; McCann *et al.* 1998). Currently, few analyses of such models examine the nonlinear dynamics of more than ten species. Here, we present results from integrated models of ecosystem structure and dynamics with up to fifty species and systematically analyze the larger parameter space that such higher dimensionality creates. The structural "niche model" component successfully predicts the network structure of the largest and most complex food webs in the primary literature (Williams & Martinez 2000; Camacho *et al.* 2002; Williams *et al.* 2002). The dynamical bioenergetic model component successfully simulates persistent and non-persistent stable, cyclic, and chaotic dynamics (Williams & Martinez *in press*) that are often found in nature (Kendall *et al.* 1998).

We refer to the number of species as the diversity of the network, while linkage density is referred to as the networks' complexity. Function refers to processes associated with species' interactions including rates of consumption and preferences for different prey. We explore the interplay of structure and nonlinear dynamics by systematically varying diversity, complexity, and function in order to "elucidate the devious strategies which make for stability in enduring natural systems." (May 1973) Our exploration expands on previously proposed strategies and

shows how recently discovered structural and functional properties of ecological networks appear to promote stability and persistence in large complex ecosystems.

METHODS

Our bioenergetic network models are constructed in two steps. The first step specifies the structure of a food web network using one of three different stochastic models. The second step uses a nonlinear bioenergetic model to compute the dynamics of the network.

Structural Models and Food-Web Topology.

All three structural models require the number of species in the system (S) and the density of trophic links (L) in terms of directed connectance ($C = L/S^2$) as input parameters, but vary in the degree to which they constrain network organization. In the random model (Cohen *et al.* 1990; Solow & Beet 1998), any link among S species occurs with the same probability equal to C of the empirical web. This creates webs as free as possible from biological structuring while maintaining observed S and C . The modified (Williams and Martinez 2000) cascade model (Cohen *et al.* 1990) creates a hierarchical structure by assigning each species a random value drawn uniformly from the interval $[0,1]$ and giving each species a probability $p = 2CS/(S-1)$ of consuming only species with values less than its own. The niche model (Williams & Martinez 2000) similarly assigns each species a randomly drawn “niche value.” The species are constrained to consume all species within one beta-distributed range of values whose mean = C and whose uniformly and randomly chosen center is less than the consumer’s niche value. Some niche model networks contain energetically unsustainable closed loops such as pairs of mutual predators that are preyed on but have no prey themselves. These networks are most common in small systems with low connectance and are not considered here.

When describing food webs, several conventions are employed. Top species have resources but no consumers. Intermediate species have resources and consumers. Basal species have consumers but no resources. Omnivores feed from more than one trophic level and herbivores eat only basal species. To remove the confounding variability of the number of basal species, omnivory and herbivory are the fraction of consumers that are omnivores and herbivores respectively. Similarly, to better measure the trophic height of the consumers independent of the fraction of basal species, mean trophic level is the mean of all consumer species’ trophic levels. Among a variety of definitions of trophic level, we use a modification of previous trophic level definitions (Levine 1980; Adams *et al.* 1983) that weights each consumer’s prey equally (Williams & Martinez 2004). A species’ connectivity is its total number of links (both incoming and outgoing) divided by the mean connectivity ($2L/S$) of the network.

Bioenergetic Model of Nonlinear Food-web Dynamics

The dynamic model closely follows previous work (Yodzis & Innes 1992; McCann & Yodzis 1995; McCann & Hastings 1997; McCann *et al.* 1998) but is generalized to n species and arbitrary functional responses. Extending the earlier notation (Yodzis & Innes 1992) to n -species systems, the variation of B_i , the biomass of species i , over time t , is given by

$$B_i'(t) = G_i(B) - x_i B_i(t) + \sum_{j=1}^n (x_i y_{ij} \alpha_{ij} F_{ij}(B) B_j(t) - x_j y_{ji} \alpha_{ji} F_{ji}(B) B_j(t) / e_{ji}). \quad (1)$$

The first term $G_i(B) = r_i B_i(t) (1 - B_i(t) / K_i)$ is the gross primary production rate of species i where r_i is the intrinsic growth rate that is non-zero only for basal species, and K_i is the carrying capacity; the second term is metabolic loss where x_i is the mass-specific metabolic rate; the third

and fourth terms are gains from resources and losses to consumers respectively, where y_{ij} is the maximum rate at which species i assimilates species j per unit metabolic rate of species i ; α_{ij} is the relative preference of species i for species j compared to the other prey of species i . α_{ij} is normalized so that the sum of α_{ij} ($0 \leq \alpha_{ij} \leq 1$) across all j is 1 for consumer species and 0 for basal species; $F_{ij}(B)$, a non-dimensional functional response that may depend on resource and consumer species' biomasses, gives the fraction of the maximum ingestion rate of predator species i consuming prey species j ; e_{ij} is the conversion efficiency with which the biomass of species j lost due to consumption by species i is converted into the biomass of species i . Dividing the last term by e_{ij} converts the biomass assimilated by consumer j into biomass lost by resource i . Non-zero α_{ij} 's are assigned according to the topology specified by the structural models. The many parameters in these equations have been estimated from empirical measurements (Yodzis & Innes 1992) and there are wide ranges of biologically plausible values.

While a wide variety of functional responses have been proposed in the literature (Holling 1959b; Hassell & Varley 1969; Beddington 1975; DeAngelis *et al.* 1975; Skalski & Gilliam 2001), our model uses two different families of functional responses (F_H and F_{BD} , Fig. 1) that have both mechanistic and empirical justifications (Skalski & Gilliam 2001). The first (F_H , (Williams & Martinez *in press*),) is based on a parameterized form (Real 1977, 1978) of Holling's (Holling 1959a, b) type II and III responses and generalizes earlier multiple species type II responses (McCann *et al.* 1998; Fussman & Heber 2002). F_H of predator i consuming prey j is

$$F_{Hij}(B) = \frac{B_j(t)^{1+q_{ij}}}{\sum_{k=1}^n \alpha_{ik} B_k(t)^{1+q_{ij}} + B_{0ji}^{1+q_{ij}}}, \quad (3)$$

where B_{0ji} is the half saturation density of species j when consumed by species i and q_{ij} controls the form of F_H . The functional response decelerates and accelerates feeding on relatively rare and abundant resources as q increases and decreases, respectively (Fig. 1). The range $0 < q_{ij} \leq 1$ generalizes F_H so that it can smoothly vary from standard type II responses ($q_{ij} = 0$) used in many earlier studies (Yodzis & Innes 1992; McCann & Yodzis 1995; McCann & Hastings 1997; McCann *et al.* 1998; Post *et al.* 2000; Fussman & Heber 2002) to the standard type III response ($q_{ij} = 1$) (Real 1977, 1978; Yodzis & Innes 1992) that stabilizes two-species systems (DeAngelis *et al.* 1975; Murdoch & Oaten 1975; Hassell 1978; Yodzis & Innes 1992).

The F_{BD} response models predator interference (Skalski & Gilliam 2001) by extending earlier models (Beddington 1975; DeAngelis *et al.* 1975) to consumers of multiple species. F_{BD} of predator i consuming prey j is

$$F_{BDij}(B) = \frac{B_j(t)}{\sum_{k=1}^n \alpha_{ik} B_k(t) + (1 + c_{ij} B_i(t)) B_{0ji}} \quad (4)$$

Similar to F_H (3), F_{BD} includes a control parameter $c_{ij} \geq 0$ that quantifies the intensity of predator interference. When $c_{ij} = 0$, F_{BD} is the standard type II response with no predator interference, and empirical studies suggest $c \approx 1$ (Skalski & Gilliam 2001).

Predator interference and type III responses are known to stabilize small food web modules (DeAngelis *et al.* 1975; Murdoch & Oaten 1975; Hassell 1978; Yodzis & Innes 1992) but have not previously been used to study the dynamics of relatively species-rich systems. In addition, small deviations from the type II response such as our "type II.2 response" ($q = 0.2$)

have only recently been introduced and applied to food-web models with 10 or fewer species (Williams & Martinez *in press*).

We simplify the dynamical model through our choice of parameter values. First, we choose a single value for each of the parameters $K_i=1$, $r_i=1$, $x_i=0.5$, $y_{ij} = 6$, $e_{ij}=1$, and $B_{0ij}=0.5$ for each set of a model's iterations. Simulations that draw these parameters from normal distributions with specified mean and standard deviation ($e_{ij}>1$ not allowed) gave similar results to fixed parameter simulations (results not shown). Second, even though functional responses could be different for each link in the network (Williams & Martinez *in press*), we specify a single value of q_{ij} or c_{ij} , so each link within a network is of the same type.

Unless stated otherwise, we assume that predator species have equal preference (α_{ij}) for all their prey. If n_i is the number of prey that species i consumes, $\alpha_{ij} = 1/n_i$ for each species j in the diet of species i . We also systematically vary the α_{ij} of omnivores to examine the effects of skewing diets to higher or lower trophic level prey. The range of α_{ij} is defined by a preference skewness $k = \alpha_{imax}/\alpha_{imin}$, where α_{imax} and α_{imin} are the preferences for the prey items of species i with the maximum and minimum trophic level (TL_{max} and TL_{min}) respectively. For each prey species j of species i , we define $b_{ij} = 1 + (k - 1)(TL_j - TL_{min}) / (TL_{max} - TL_{min})$, where TL_j is the trophic level of prey item j . The preference of species i for prey item j is then $\alpha_{ij} = b_{ij} / \sum_l b_{il}$,

where the sum is across all prey items of species i . When $k = 1$, all prey preferences of an omnivore are equal; when $k < 1$, low trophic level prey are preferred and when $k > 1$, high trophic level prey are preferred.

Each simulation begins by building an initial random, cascade, or niche model web of a certain size (S_0) and connectance (C_0). The integrated structure-dynamic model then computes which species persist with positive biomass greater than an extinction threshold of 10^{-15} after 4000 time steps. Following any extinctions, a "persistent web" with S_P species and connectance C_P remains. As the structural models are stochastic, this procedure is repeated a large number of times so that statistical properties of the integrated structure-dynamic model is ascertained. Both the functional response control parameters and a predator's preferences among prey are varied to study effects of food-web dynamics on persistence and food-web structure. For each model iteration, we define absolute persistence $P_A = S_P$ and relative persistence as $P_R = S_P/S_0$. Overall persistence P is the mean value of P_R across a set of iterations. Topological properties of the persistent webs were compared to different versions of niche webs. Here, we focus on the distribution of trophic levels and connectivity among species by examining the fractions of top, intermediate, basal, omnivorous, and herbivorous species, mean trophic level, and the standard deviation of the connectivity of each species.

RESULTS

We analyzed the behavior of our dynamic network models with respect to the combined variation of several key parameters. The models' high dimensionality prevents full examination of all the combinations of parameter values that were analyzed. Instead, we present a sequence of results that describes the effects of varying a few parameters and then fix these parameters and analyze effects of varying other parameters. Fixing the parameters at different values quantitatively changes the results. Therefore, we focus on overall behaviors that resist qualitative changes due to alternative choices.

Perhaps most importantly, varying topology and the functional response control parameters profoundly affect persistence. Figure 2a shows the effect of varying q and c on 30-

species webs with an intermediate level (Williams & Martinez 2000) of $C_0 = 0.15$ for food webs with initial topologies built using the random, cascade and niche models. All other input parameters are constant across all trials of the stochastic models unless otherwise indicated. Most or all species go extinct in every trial of random webs and q and c have little if any effect on their relative persistence ($P < 0.05$). The structural constraints provided by the cascade model and especially the niche model increase P by more than an order of magnitude. In addition to this enormous effect of network structure, a large change in persistence occurs when q is increased from 0 to 0.1. In this range, cascade-web P increases 32% from 0.34 to 0.44 and niche-web P increases 44% from 0.43 to 0.62. Compared to cascade webs, niche webs are 27% to 50% more robust for any fixed q from 0 to 0.3 and more strongly increase in persistence for $q > 0$. Figure 2b shows that predator interference causes a similar change in the persistence of 30-species webs when c varies across a biologically reasonable (Skalski & Gilliam 2001) range. The effect of c on persistence is similar to the effects of q but, unlike q 's asymptotic effects, increasing c continually increases persistence across the whole range of values examined. Due to the similar effects of q and c , we present further results only for intermediately robust responses with $q = 0.2$ or $c = 1.0$, a choice that highlights the effects of altering other model parameters in a representative manner.

Relative persistence ($P_R = P_A / S_0$) of niche-model webs decreases linearly both with increasing initial network size (S_0) and with increasing initial connectance (C_0) (Fig. 3) as shown by linear regressions of P_R as a function of the product $S_0 C_0$, the network's initial value of L/S . For the type II.2 response ($q=0.2$) with constant $C_0 = 0.15$, $P_R = 0.87 - 0.05 S_0 C_0$ ($\mathbf{R}^2=0.48$, $n=2500$); with constant $S_0 = 30$, $P_R = 0.93 - 0.06 S_0 C_0$ ($\mathbf{R}^2=0.23$, $n=3500$). Despite the negative effect of S_0 on P_R , absolute persistence (P_A) increases with S_0 from roughly 11 when $S_0 = 15$ to approximately 25 when $S_0 = 50$.

We compared variation in C_P with S_P among persistent webs that were initially constructed with the niche model to two other sets of model webs (Fig. 4). These sets were created by starting with a set of niche webs using fixed parameters $S_0 = 30$ and $C_0 = 0.15$ and then randomly deleting species (Solé & Montoya 2001; Dunne *et al.* 2002a) to create networks with the same S as the persistent webs. Two deletion algorithms were used. One deletes species entirely at random and the other randomly deletes only non-basal species (Dunne *et al.* 2002a). C of niche webs increases with the number of entirely random deletions but varies little when basal species are protected. Despite the strong negative effects of C_0 on P , C_P of the most robust webs ($S_P > 21$, $P_R > 0.7$) is typically greater than the C of niche webs subjected to random deletions (Fig. 4). This suggests that structurally peculiar subsets of niche webs with relatively high C yield remarkably persistent networks (Dunne *et al.* 2002a).

Both S and C affect many topological properties of empirical and niche-model webs (Williams & Martinez 2000; Camacho *et al.* 2002; Dunne *et al.* 2002b; Williams *et al.* 2002). We examined how dynamic extinctions affect network topology by controlling for these effects and comparing the persistent webs with two sets of 1000 niche webs (Fig. 5a-e). One set had the initial values of $S_0 = 30$ and $C_0 = 0.15$ as inputs and non-basal species were randomly deleted until $S = S_p$. This compares persistent webs of a certain size to similarly sized niche webs subjected to randomized extinctions that leave C relatively unchanged ($C \approx C_0 \approx C_P$, Fig 4). The second set was created using the values $S = S_P$ and $C = C_P$ as inputs into the niche model, allowing comparison between persistent webs of a certain size and similarly sized niche webs not subject to extinctions.

Compared to either set of niche webs, persistent webs consistently have higher fraction of basal species and consumers with lower mean trophic levels, especially in larger most persistent webs ($S_P > 25$, Fig. 5a-b). Both of these properties vary with S_P in the same direction but less strongly as the properties vary with S in niche webs. The fractions of consumer species that are omnivores or herbivores are higher in the persistent webs than in the niche webs (Fig 5c-d). This helps explain persistent webs' lower mean trophic levels. The differences in herbivore and basal species richness tend to lose their statistical significance as webs get smaller, while the differences in mean trophic level also get smaller but remain significant. The fraction of omnivorous consumers was often slightly (5-10%) though not significantly higher in the highly robust persistent webs ($S_P > 25$), whereas there was a slight deficit of omnivores in less robust persistent networks ($S_P < 15$). The standard deviations of node connectivity were similar between persistent and niche webs but random deletions increased these deviations above those in persistent webs (Fig. 5e). This similarity also applies to the standard deviation of the number of incoming and outgoing links taken separately, properties previous termed the generality and vulnerability, respectively (Williams & Martinez 2000).

We examined omnivory more finely by altering the skewness of omnivores' preference for prey at different trophic levels. Such skewness has profound effects on overall persistence, P (Fig. 6), similar to the effects of varying the functional-response parameter q . Niche webs are most persistent ($P \approx 0.42$ when $q = 0$ and $P \approx 0.64$ when $q = 0.2$) when omnivores prefer lower trophic-level resources but avoid near exclusive consumption of the lowest trophic-level resources ($0.2 < \text{skewness} < 0.8$). Persistence drastically falls to as low as $P \approx 0.25$ when $q = 0$ and $P \approx 0.34$ when $q = 0.2$ as omnivores more strongly prefer upper trophic-level resources (skewness = 10).

DISCUSSION

Effects of Structure on Dynamics

Our results generally illuminate how the structure of ecological networks may influence their function by examining the effects of diversity and complexity on *in silico* ecosystem dynamics. One early and remarkably durable theory based on linear stability analyses of random networks (May 1973) proposed that S and C have hyperbolically negative effects on stability. Qualitatively similar effects occur in our nonlinear analyses of more ecologically realistic networks, but the effects are linear rather than hyperbolic (May 1973), perhaps due to the differences between linear stability and nonlinear persistence. C affects persistence much more strongly than does S . This is illustrated by the regressions in which variance in C explains over twice as much variance of P_R as does variance in S . This greater importance of C than S to persistence had been previously noted but the negative effects of C observed here are opposite the previously noted positive effects (Dunne *et al.* 2002a; Fussman & Heber 2002; Kondoh 2003). Analyzing the effects of deleting species or otherwise challenging persistent webs to study their robustness may clarify this discrepancy.

Beyond the classic effects of S and C on dynamics, our study illustrates the overriding importance of the overall arrangement of links among species. Random webs have almost no persistence while the hierarchal ordering of the cascade model vastly increases persistence. The contiguous niches and looping (Neutel *et al.* 2002) in the niche model appears confer even more persistence on food-web networks. The hierarchical ordering of the cascade and niche models is easily interpreted as a mechanistic formalization of energy flowing from plants to upper trophic

levels. Models that ignore such distinctions between plants and animals by making all species capable of growing without consuming other species (Kondoh 2003) fail to detect the significance of nonrandom and hierarchical network structure (Brose *et al.* 2003). Niche space as formalized by the niche model is much less easily interpreted and deserves more study to understand which evolutionary, ecological, and mathematical factors underlie the improved the model's improved empirical fit (Williams & Martinez 2000) and persistence (Fig. 2).

Effects of Dynamics on Structure

This work illuminates how the functioning of ecological networks influences their structure by examining the effects of nonlinear dynamics on the topology of complex food webs. Importantly, we show for the first time that the stabilizing effects of both predator interference and respective decelerated and accelerated feeding on rare and abundant resources found in small modules of two species also apply to much larger networks with 30 or more species. This enables large complex food webs to sustain many more species than networks governed by standard type II responses. This remarkable persistence greatly increases the potential to add other ecological processes such as facilitation, age-structured populations, migration, and environmental stochasticity to models of large ecological networks, which should further facilitate exploration of their effects on ecological structure and dynamics. We also show that small and perhaps empirically undetectable changes in functional responses foster greatly increased persistence in model ecosystems (Williams & Martinez *in press*). This suggests that tiny amounts of prey switching behavior of consumers (Post *et al.* 2000; Kondoh 2003) or refuge seeking behavior of resources (Holling 1959a; Sarnelle 2003) has large effects on the structure and dynamics of complex ecological networks. This suggestion complements recent empirical findings (Skalski & Gilliam 2001; Sarnelle 2003), suggesting these functions as some of nature's more prevalent and important stabilizing strategies.

More effects of network function on network structure are seen in comparisons between persistent webs and webs generated by structural models free from explicit dynamics. Persistent webs typically have C similar to that in niche webs whose consumers are randomly deleted but lower than that in niche webs subjected to random deletions of any species. More strikingly, persistent webs have higher fractions of basal species and consumers with lower mean trophic levels than do niche webs. This is consistent with the niche model's overestimation of empirically observed food-chain lengths (Williams & Martinez 2000) assuming that empirical webs have more persistent topologies than do niche webs. While the SD of node connectivity shows few differences between niche webs subjected to dynamic loss of species and random loss of consumers, more detailed investigation of degree distributions (Dunne *et al.* 2002b) could illuminate differences hidden by our relatively coarse analysis.

Given the niche model's overestimation of the mean trophic level of consumers in large persistent webs by almost a whole level (Fig 5a) and its underestimation of the fraction herbivores by ~ 0.07 (Fig 5c), we tested the niche model against these properties of the seven empirical webs originally compared to the niche model (Williams & Martinez 2000). Table 1 shows that the niche model consistently overestimates mean trophic level by 0.2-2.4 levels and underestimates the fraction of herbivores by 0.01-0.32. Apparently, dynamics alters these properties of niche webs to become even more similar to empirically observed properties.

The empirically observed fraction of basal species is well explained by the niche model (Williams & Martinez 2000), so the higher fraction of basal species observed in the dynamically constrained networks (Fig 5b) appears to conflict with empirical findings. This discrepancy may

be due to highly aggregated and poorly described basal species in the empirical data. For example, basal species in the St. Martin island food web (Goldwasser & Roughgarden 1993) are categories of plant material such as seeds, leaves, etc. Many basal taxa in the Bridge Brook Lake (Havens 1992) food web are trophically identical, suggesting that the trophic links are poorly resolved (Martinez *et al.* 1999). Therefore, the fraction of basal species in the observed trophic-species networks and the niche model's fit to these fractions could be methodological artifacts of taxonomic and trophic resolution. The importance basal species to persistence emphasizes the need for high quality data resolved evenly at all trophic levels (Cohen *et al.* 1993). Alternatively, artifacts of the dynamical model might cause the discrepancy (Brose *et al.* 2003). Our models assume that basal species do not compete for shared resources. Adding competition among basal species might lower the fraction of basal species in the persistent webs.

Omnivory

One of the more confusing interdependencies between food-web structure and dynamics concerns the issue of omnivory. There is a close positive and confounding relationship between omnivory and C in earlier studies, (McCann & Hastings 1997; Fussman & Heber 2002) since increasing C typically makes consumers more omnivorous and increasing omnivory typically increases C . We help clarify this issue by controlling for the strong effects of C on persistence (Fig 4b) and showing that the prevalence of omnivorous consumers in persistent webs is usually similar to that in niche webs (Fig 5d), which is usually much less than in cascade webs (Williams & Martinez 2000). If structural omnivory had an unusually strong positive effect on persistence, one would expect higher omnivory in the most persistent niche webs and more persistence in cascade webs. This is not generally supported by our results.

Contemporary modeling studies also tend to confound increasing omnivory with lowering consumers' trophic levels by increasing omnivory in a restricted fashion. That is, omnivory that lowers a consumer's trophic level is typically created by adding short paths that enable carnivores to consume primary production (McCann & Hastings 1997; Fussman & Heber 2002). Omnivory that increases a consumer's trophic level, for example, by adding a carnivorous links to an herbivore's diet, is typically avoided. Omnivores that prefer higher trophic level prey strongly decrease persistence compared to omnivores lacking such preference, while variable preference for low levels has much less effect (Fig. 6). These findings, combined with consumers' lower trophic levels and higher prevalence of basal species and herbivores in the most persistent niche webs, suggest that shortening food chains and reducing trophic levels account for the stabilizing effects previously attributed to omnivory. In contrast, omnivory strongly decreases persistence in food webs when omnivores engage in the empirically unusual (Williams & Martinez 2002) destabilizing behavior of preferring prey at higher trophic levels.

CONCLUSION

Our analyses address several historically perplexing aspects of the remarkable complexity and persistence of natural ecosystems and show how more empirically prevalent aspects of ecological interactions (Williams & Martinez 2000; Skalski & Gilliam 2001; Williams & Martinez 2002; Sarnelle 2003) may confer persistence on large complex ecosystems. Both food-web structure as characterized by the relatively successful the niche model and food-web function as characterized by decelerated consumption of rare resources (Sarnelle 2003), predator interference (Skalski & Gilliam 2001), and omnivores' preferences for lower trophic-level prey (Williams & Martinez 2002) greatly increase the diversity and complexity that persists in

ecological networks. While all models are simplifications of nature, formal inclusion of these frequently observed regularities indicate that our ecological models may be the most biologically informed and empirically well-corroborated in terms of their detailed diversity, complexity, structure, function, and dynamics. Some of the increased persistence resulting from including these factors appears to have been mistakenly attributed to unqualified omnivory. The strong effects of predator interference and decelerated and accelerated feeding on relatively rare and abundant resources, respectively, suggests that other behaviors that reduce consumption of rare resources, e.g., prey switching (Post *et al.* 2000; Kondoh 2003), will also stabilize large complex networks. In contrast, responses that increase consumption of rarer and higher trophic level resources, e.g. economic exploitation of relatively rare carnivorous fishes (Pauly *et al.* 2002), can be expected to decrease persistence.

The persistent models described here provide new tools to explore non-trophic processes including invasions, extinctions, experimental manipulations, environmental variability, and spatial processes. Such processes could be simulated by manipulating our model's parameters e.g., stochastically varying basal species' carrying capacity, and adding different functions e.g., density-dependent migration. More study of these models as well as empirical and especially experimental tests of their findings could significantly refine our results. Such combined studies could do much to bring about exciting new insights regarding the trophic and non-trophic interactions in the large complex networks that sustain the stunning, yet tragically diminishing, levels of diversity in nature.

ACKNOWLEDGEMENTS

Jennifer A. Dunne, Ulrich Brose, and Jessica Green are greatly appreciated for comments on the manuscript. NSF provided support for RJW and NDM. NDM especially thanks the NSF funded IGERT Program in Nonlinear Systems and hospitality of the Telluride House, both at Cornell University, for support. Portions of this research were completed during research visits by RJW and NDM to the Santa Fe Institute. Correspondence and Requests for materials should be addressed to: E-mail: neo@rmbf.org, Telephone: 510-295-7624, Fax: 970-349-7481.

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Table 1. Errors of niche model predictions of the fraction of herbivores (Herbivory) and mean trophic level (TL) of consumers in empirical food webs. S is the number of trophic species. C is directed connectance. Error is measured both as the difference between the model's mean property and the empirically observed property (in parentheses) and in more rigorously comparable terms of the number of model standard deviations that the empirically observed property differs from the model's mean (Williams & Martinez 2000).

| Food Web Name | S | C | Herbivory | TL of consumers |
|-------------------|-----|-------|---------------|-----------------|
| St. Martin Island | 42 | 0.12 | -2.7 (-0.15) | 1.4 (0.79) |
| Bridge Brook L. | 25 | 0.17 | -3.9 (-0.19) | 1.5 (1.23) |
| Coachella Valley | 29 | 0.31 | -1.3 (-0.04) | 0.6 (1.24) |
| Chesapeake Bay | 31 | 0.072 | -0.2 (-0.01) | 0.6 (0.21) |
| Skipwith Pond | 25 | 0.32 | -7.8 (-0.29) | 0.1 (2.39) |
| Ythan Estuary | 78 | 0.061 | -4.1 (-0.20) | 1.6 (0.60) |
| Little Rock L. | 92 | 0.12 | -12.7 (-0.32) | 2.5 (1.52) |
| | | | | |
| Mean | | | -4.62 (-0.17) | 1.17 (1.14) |
| Std error | | | 1.65 (0.04) | .30 (0.27) |

Figure Legends

Figure 1. Illustration of the effects of control parameters q and c on fractions of maximal consumption rates (F) according to the F_H and F_{BD} functional responses in equations 3 and 4, respectively. Note that F_{BD} also depends on the density of consumers that pushes the half saturation density (B_0) of the dotted $c = 1$ line left or right as the consumer density decreases or increases, respectively.

Figure 2. Mean overall persistence (P) of model food webs vs. functional response control parameter for networks built using the random (\diamond), cascade (\square) and niche (\circ) models. In (a) q controls the parameterized Holling (type II to “type II.3”) functional response (Eq. 3); in (b) c controls the Beddington-DeAngelis (BD) predator interference functional response (Eq. 4). All networks initially have $S_0 = 30$ and $C_0 = 0.15$. Values shown are averages of 500 trials.

Figure 3. Mean overall persistence (P) of model food webs vs. (a) initial network size S_0 for niche model networks with $C_0 = 0.15$, and (b) initial network connectance C_0 for niche model networks with $S_0 = 30$. The dynamical model uses (\circ) the parameterized Holling type II.2 functional response where $q = 0.2$ (Eq. 3) and (\square) the Beddington-DeAngelis (BD) predator interference functional response with $c = 1$ (Eq. 4). Values shown are averages of 500 trials. The regression lines are (a) Type II.2: $P = 0.874 - 0.00770S_0$, $r^2 = 0.996$; BD: $P = 0.799 - 0.00682S_0$, $r^2 = 0.992$ and (b) Type II.2: $P = 0.927 - 1.923C_0$, $r^2 = 0.998$; BD: $P = 0.862 - 1.799C_0$, $r^2 = 0.997$.

Figure 4. Mean connectance C of model food webs versus dynamically persistent network size S (\times), with error bars showing plus and minus two standard errors of the estimated mean. The points without error bars show the mean connectance of 1000 niche model networks that have species deleted at random (\circ) or have consumer species deleted at random (\square). All initial networks are built using the niche model with $S_0 = 30$, $C_0 = 0.15$, and the dynamical model uses our Holling “type II.2” functional response where $q = 0.2$ (Eq. 3).

Figure 5. Mean and variation of model food-web properties versus persistent network size S (\times). Error bars show plus and minus two standard errors of the estimated mean. Points without error bars show the mean property value in 1000 niche model networks with the same size and connectance as the dynamical model networks (\circ) and in 1000 niche model networks with the same initial size and connectance as the dynamically constrained networks that then had consumer species deleted at random (\square). Properties shown are (a) fraction of basal species, (b) trophic level, (c) fraction of consumers that are omnivores, (d) fraction of consumers that are herbivores, and (e) standard deviation of node connectivity. Initial networks are built using the niche model with $S_0 = 30$, $C_0 = 0.15$, and the dynamical model uses our Holling “type II.2” functional response with $q = 0.2$ (Eq. 3).

Figure 6. Mean ($n=500$) overall persistence P of model food webs vs. skewness k of the prey preference of omnivores. When $k = 1$, all prey preferences of an omnivore are equal; when $k < 1$, low trophic level prey are preferred and when $k > 1$, high trophic level prey are preferred (see methods). All networks initially have $S_0 = 30$, $C_0 = 0.15$, and the dynamical model uses parameterized Holling type II ($q = 0$) and II.2 ($q = 0.2$) functional responses (Eq. 3).

Figure 1

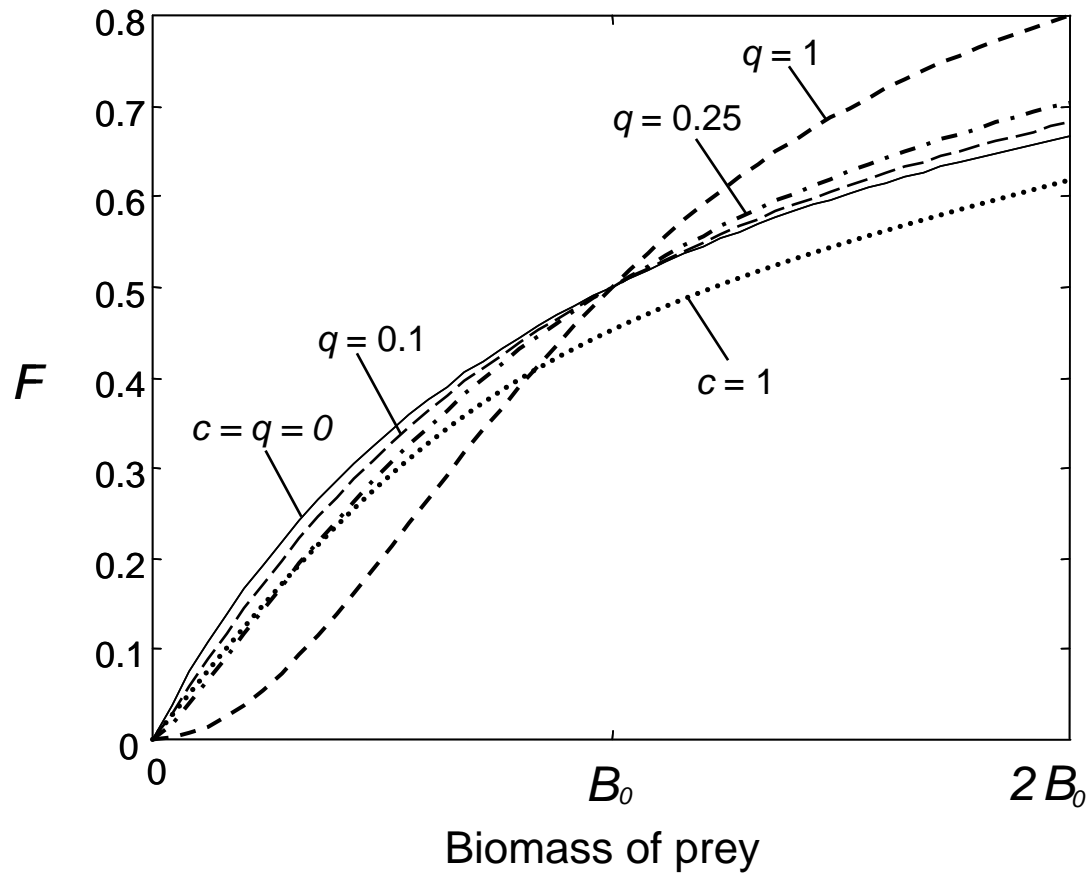


Figure 2

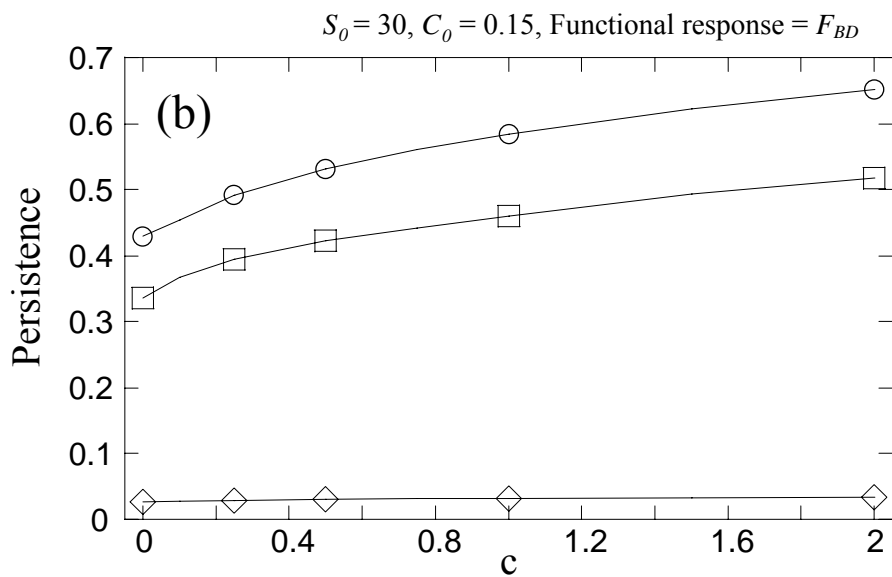
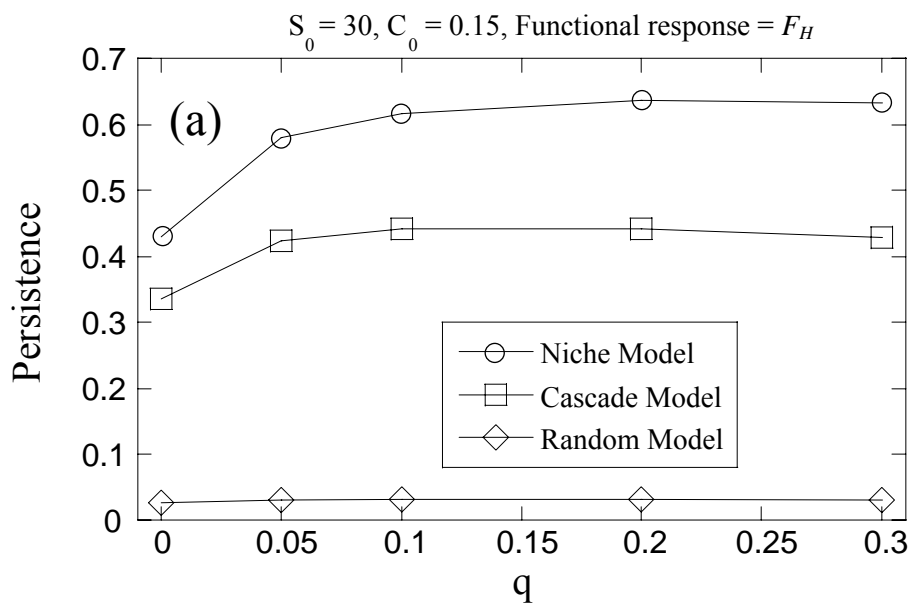


Figure 3

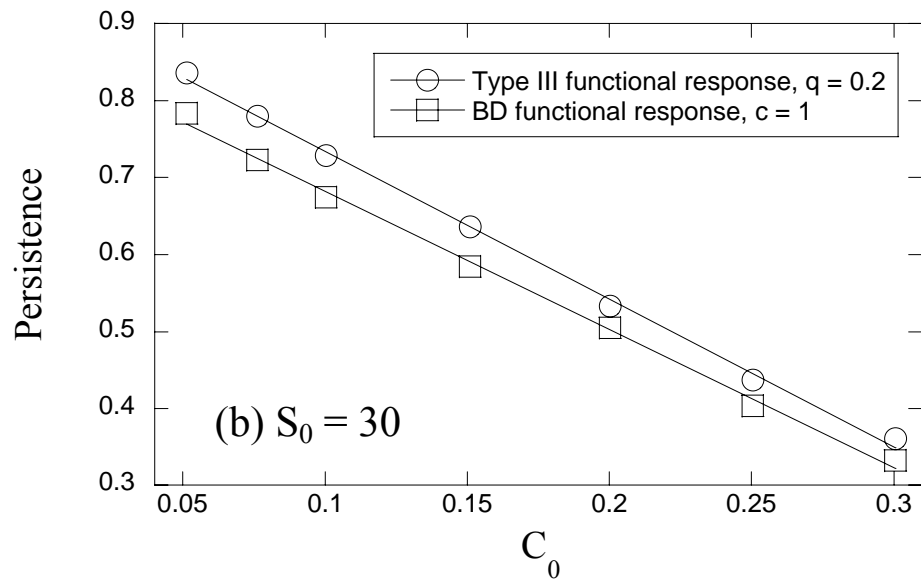
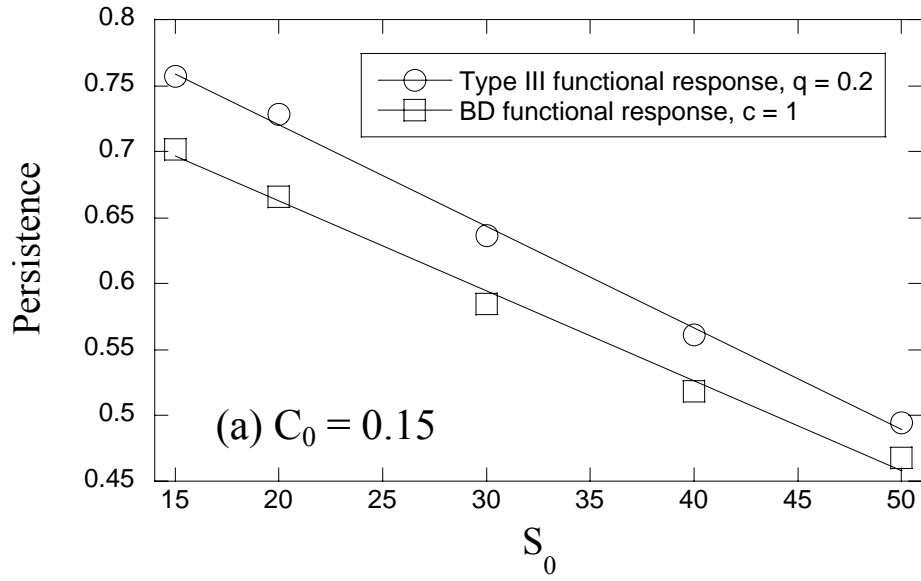


Figure 4

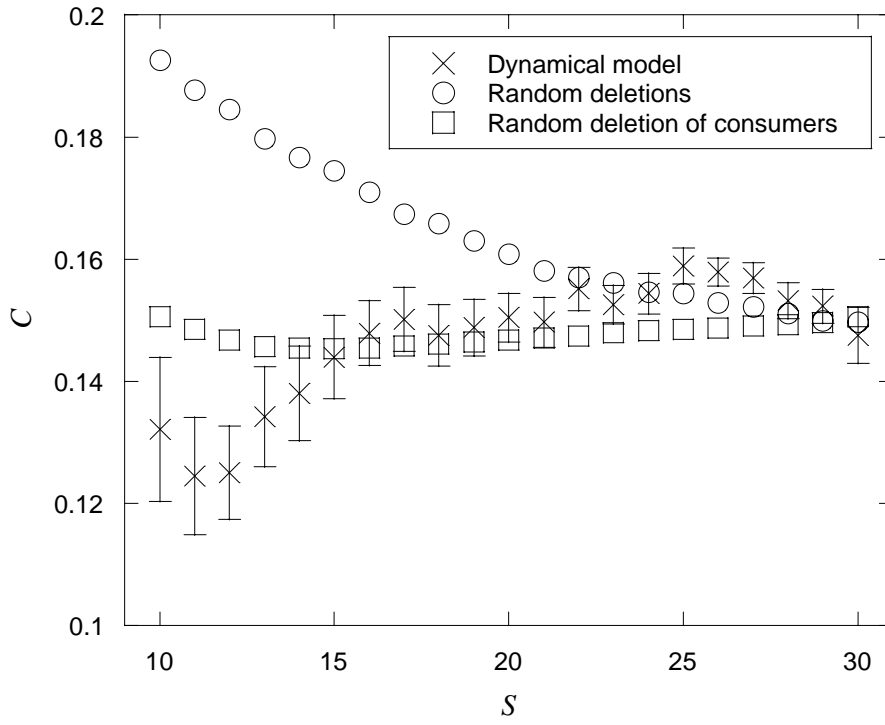


Figure 5

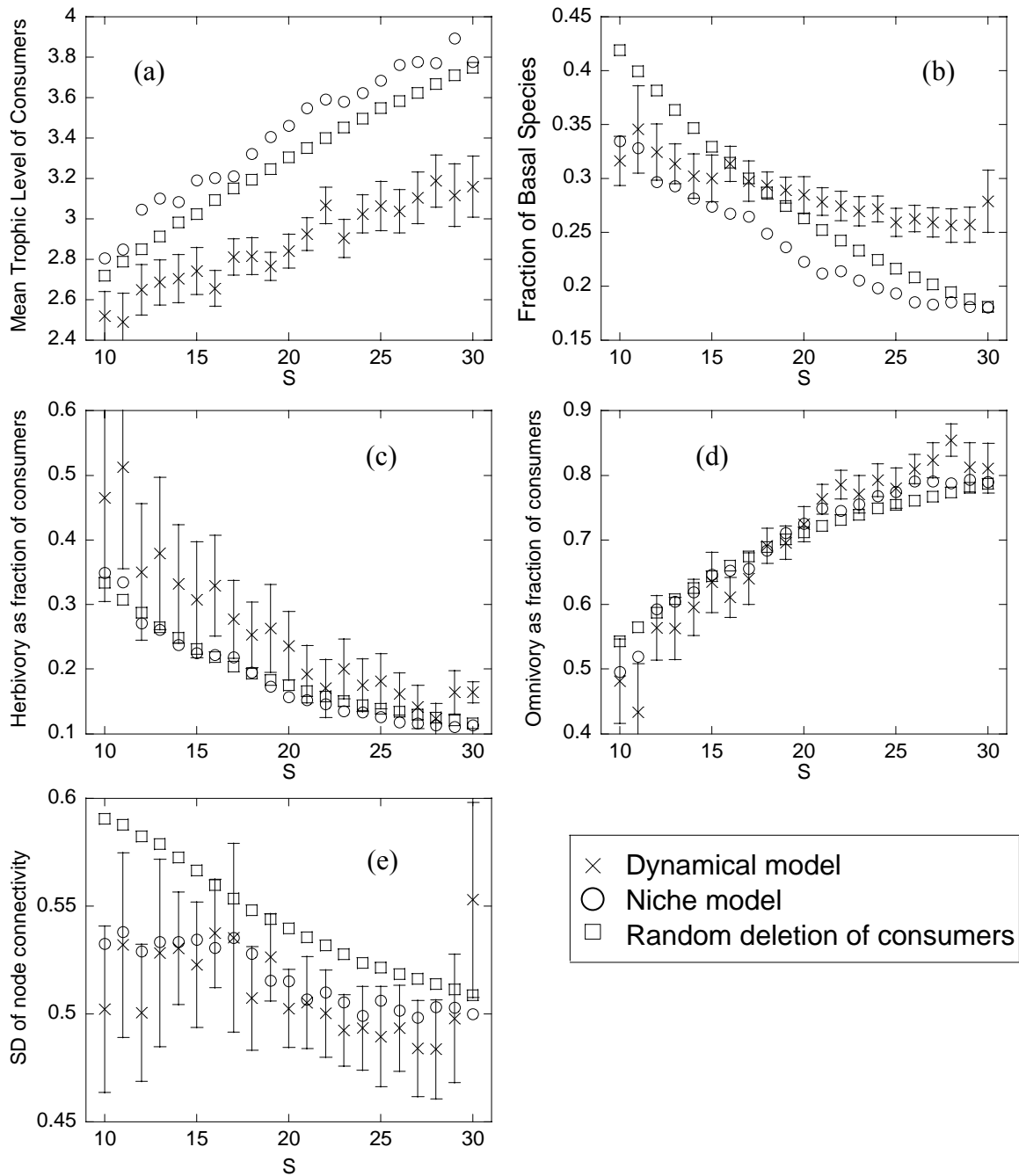


Figure 6.

