Diversity, Complexity, and Persistence in Large Model Ecosystems

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Research on how vast numbers of interacting species manage to coexist in
nature reveals a deep disparity between the ubiquity of complex ecosys-
tems and their theoretical improbability. Here, we show how integrat-
ing models of food-web structure and nonlinear bioenergetic dynamics
bridges this disparity and helps elucidate the relationship between eco-
logical complexity and stability. Network structure constraints, including
trophic hierarchy, niche contiguity, and looping formalized by the "niche
model," greatly increase persistence in complex model ecosystems. Be-
havioral nonlinearities, particularly competition among consumers and
reduced consumption of rare resources, formalized by predator inter-
ference and new "Type II.2" functional responses, further encourage
persistence of species in complex food webs. Trophic dynamics are also
shown to feed back to network structure, resulting in more accurate
topologies than those achieved by simple structural models alone. Thus,
integrating structure and dynamics of ecological networks yields remark-
ably comprehensive and ecologically plausible models that highlight the

importance of network structure, short food chains, and behavioral ecology for ecosystem persistence and stability, and also alters our understanding of the role of omnivory in food webs. This modeling approach provides a potentially powerful framework for exploring the impacts of perturbations on ecosystems, and can be altered to include non-trophic processes, spatial effects, and evolutionary dynamics.

> *Our ultimate goal is to use these consumer-resource models as building blocks for the construction of plausible models of more complicated systems involving many interacting species. In that setting, one needs to be parsimonious with respect to detail, but we hope to do so without too great a sacrifice in realism.*
> —Yodzis and Innes, 1992

1 INTRODUCTION

One of the most important and least settled questions in ecology concerns the roles of diversity and complexity in the functioning and stability 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 ubiquitous in ecological systems (McCann 2000; Kondoh 2003; Brose et al. 2003). Early theoretical considerations suggested that the presence of more feeding links among more species generally reduces the risk of species' dependence on a few resources (MacArthur 1955). By the late 1950s the notion that "complexity begets stability" was considered by many to be a basic ecological theorem (Hutchinson 1959). However, the apparent inevitability of this relationship was severely challenged by simple mathematical models of food-web dynamics which showed that diversity and complexity destabilize idealized 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 and Lawton 1978). Much of the work since those early modeling studies has focused on trying to parse conditions under which ecologists should expect to see (or not see) a positive relationship between diversity/complexity and stability (for review, see Dunne et al. 2005).

Most early work emphasized equilibrium-based modeling (e.g., May 1973) and comparative empiricism (as reviewed in Pimm et al. 1991) with a focus on whole-system analysis (i.e., many species at multiple trophic levels). Later research placed more emphasis on nonlinear modeling and experimental empiricism, with both approaches focusing on parts of ecosystems—small food-web modules in the case of modeling, and single trophic levels in biodiversity/ecosystem function experiments. In general, the nonlinear modeling approach has suggested that increases in complexity, such as the addition of weak or omnivorous interactions (McCann and Hastings 1997; McCann et al. 1998; Fuss-

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man and Heber 2002) stabilize ecosystems. Similarly, experimental work suggests that increases in diversity, in terms of numbers of species and functional groups (Naeem et al. 1994; Tilman et al. 2001), also stabilizes ecosystems. However, one of the few experimental tests of complexity/stability in speciose, multi-trophic level communities showed that complexity, defined in terms of species richness and number of interactions, destabilized microcosm assemblages (Fox and McGrady-Steed 2002). This and other studies suggest that there is still an important disparity to be addressed between the improbability of diverse, complex, stable ecosystems in theory and their pervasiveness in nature. In particular, it is unclear whether the stabilizing effects of omnivory (McCann and Hastings 1997), weak links (McCann et al. 1998; Berlow 1999), and diversity (Naeem et al. 1994; Tilman et al. 2001) found in small modules or single trophic levels also apply to large networks with many species at multiple trophic levels.

Here, we address these issues by examining species persistence in nonlinear dynamical models of large complex ecological networks. Our model (Williams and Martinez 2004b) builds on research that replaces unrealistic modeling assumptions prevalent in early studies (e.g., food webs are random networks, populations are at equilibrium—May 1973), with more empirically supported and mechanistically based assumptions (Yodzis and Innes 1992; McCann et al. 1998). This recent approach to modeling explicitly incorporates the nonlinearities, non-equilibrium behavior, and non-random topologies that many ecologists now believe characterize natural ecosystems. However, few analyses have examined the nonlinear dynamics of model systems with more than ten species (but see Drossel et al. 2001; Kondoh 2003).

We present results from an integrated model of ecosystem structure and dynamics, which is used to examine food-web networks with up to fifty species. The structural "niche model" component successfully predicts the network structure of the largest and most complex food webs in the primary literature (Williams and Martinez 2000; Camacho et al. 2002; Dunne et al. 2004). The dynamical bioenergetic model component (based on Yodzis and Innes 1992) successfully simulates persistent and non-persistent stable, cyclic, and chaotic dynamics (Williams and Martinez 2004b) that are often found in nature (Kendall et al. 1998). We explore the interplay of structure and nonlinear dynamics by systematically varying diversity, complexity, and function to "elucidate the devious strategies which make for stability in enduring natural systems" as suggested by May (1973). Diversity refers to the number of species in a food web, and complexity is quantified as connectance, the proportion of potential links in a food web which are actually realized (links/species^2). Function refers to processes associated with species' interactions including rates of consumption and preferences for different prey. The relatively high dimensionality of the model makes it impossible to fully explore the parameter space here. However, by focusing on key aspects of the model that speak most closely to ongoing theory and experimentation, we arrive at several intriguing, if provisional, insights. In general, the model suggests that recently discovered network structure proper-

ties, as well as longer-standing functional properties of ecological interactions, appear to promote stability and persistence in large complex ecosystems.

2   METHODS

Our bioenergetic network model constructs food webs in two steps. The first step specifies the structure of a food-web network using one of three different stochastic models, which are described briefly below and in more detail in chapter 2 (Dunne this volume; Williams and Martinez 2000; Dunne et al. 2004). The second step uses a nonlinear bioenergetic model to compute the dynamics of the network (Williams and Martinez 2004b). This integrated approach allows us to explore the impact of structure on dynamics as well as the impact of dynamics on structure.

2.1   STRUCTURAL MODELS AND FOOD-WEB TOPOLOGY

All three structural models require the number of species in the system (S) and the number 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 and 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 and Martinez 2000) similarly assigns each species a randomly drawn "niche value." The species consume all species with niche values within one contiguous range. The size of the range is chosen from a beta distribution with a mean $= C$. The range is located by uniformly and randomly assigning its center to be less than the consumer's niche value. Because the center can be close to the consumer's niche value, the strict hierarchy of the cascade model is relaxed, and cannibalism and looping can occur. Niche model networks that contain energetically unsustainable closed loops such as pairs of mutual predators with no other prey items (which sometimes occurs in low diversity, low-connectance webs) are eliminated from analysis.

When describing food webs, we employ several conventions. 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 frac-

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tion 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 and Martinez 2004a). A species' connectivity is its total number of links (both incoming and outgoing) divided by the mean connectivity $(2L/S)$ of the network.

2.2   BIOENERGETIC MODEL OF NONLINEAR FOOD-WEB DYNAMICS

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

$$B_i'(t) = G_i(B) - x_i B_i(t) + \sum_{j=1}^{n} \left(\frac{x_i y_{ij} \alpha_{ij} F_{ij}(B) B_i(t) - x_j y_{ji} \alpha_{ji} F_{ji}(B) B_j(t)}{e_{ji}} \right).$$
(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. The rate y_{ij} is the maximum at which species i assimilates species j per unit metabolic rate of species i. The term α_{ij} is the relative preference of species i for species j compared to the other prey of species i and is normalized so that the sum of $\alpha_{ij}(0 \leq \alpha_{ij} \leq 1)$ across all j is 1 for consumer species and 0 for basal species. Non-zero α_{ij}'s are assigned according to the topology specified by the structural models. A non-dimensional functional response, $F_{ij}(B)$, that may depend on resource and consumer species' biomasses (Box 1), gives the fraction of the maximum ingestion rate of predator species i consuming prey species j. The term 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. Parameter values in these equations have been estimated from empirical measurements (Yodzis and Innes 1992) and there are wide ranges of biologically plausible values.

    The form of the functional response $F_{ij}(B)$ can have a large impact on predator-prey dynamics. While a variety of functional responses have been proposed in the literature, our model uses two basic families of functional responses (F_H and F_{BD}, Box 1; Martinez and Williams 2004b) that have both mechanistic and empirical justifications (Skalski and Gilliam 2001). The F_H functional response (Box 1, eq. (2)) is based on a parametrized form (Real 1977, 1978; Yodzis and Innes 1992) of Holling's type II and III responses (Holling 1959a,b). F_H generalizes earlier multispecies type II responses (McCann et al. 1998; Fussman and

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Heber 2002). Type II responses have been used in many studies of the dynamics of small food-web modules (Yodzis and Innes 1992; McCann and Yodzis 1995; McCann and Hastings 1997; McCann et al. 1998; Post et al. 2000; Fussman and Heber 2002). The F_{BD} response (Box 1, eq. (3)) models predator interference (Skalski and Gilliam 2001) by extending earlier models (Beddington 1975; DeAngelis et al. 1975) to consumers of multiple species. Predator interference and type III responses are known to stabilize small food-web modules (DeAngelis et al. 1975; Murdoch and Oaten 1975; Hassell 1978; Yodzis and 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" ($q = 0.2$), intermediate between type II and III responses, are a recent innovation, but have only been applied to food-web models with 10 or fewer species (Williams and Martinez 2004b).

We simplify the dynamical model through our choice of parameter values. First, we set a single value for the parameters $K_i = 1, r_i = 1, x_i = 0.5, y_{ij} = 6, e_{ij} = 1$, and $B_{0ij} = 0.5$. Simulations that draw these parameters from normal distributions with specified means and standard deviations ($e_{ij} > 1$ not allowed) gave similar results to fixed parameter simulations (results not shown). Second, even though functional responses can differ for each link in the network (Williams and Martinez 2004b), 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 $k = \alpha_{i\,\max}/\alpha_{i\,\min}$, where $\alpha_{i\,\max}$ and $\alpha_{i\,\min}$ are the preferences for the prey items of species i with the maximum and minimum trophic levels $TL_{\max}$ 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/dynamics model then computes which species persist with positive biomass greater than a local extinction or "exclusion" threshold of 10^{-15} after 4000 time steps. Following any exclusions, a "persistent web" with S_P species and connectance C_P remains. The initial biomasses of species are stochastic (uniformly random between 1 and 10^{-15}), as are elements of the structural models. Therefore, we repeated this procedure a large number of times so that statistical properties of the integrated structure-dynamic model resulting from systematically varied parameters can be ascertained. In particular, we systematically varied di-

Box 1. Functional response modeling
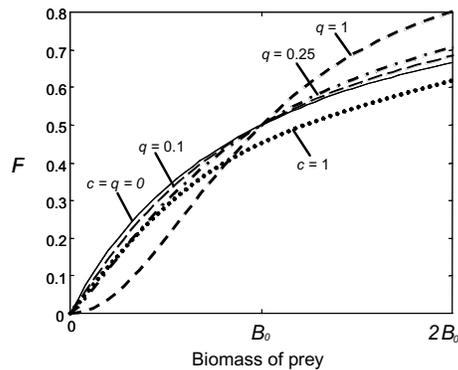
The effects of control parameters q (F_H, eq. (2)) and c (F_{BD}, eq. (3)) on fractions of maximal consumption rates (F) are shown. Where $q_{ij} = c_{ij} = 0$, the functional response is a standard type II response, and where $q_{ij} = c_{ij} = 1$, the functional response is a standard type III or predator interference response, respectively. F_H of predator i consuming prey j is

$$F_{Hij}(B) = \frac{B_j(t)^{1+q_{ij}}}{\sum_{k=1}^{n} \alpha_{ik} B_k(t)^{1+q_{ij}} + B_{0ji}^{1+q_{ij}}} \qquad (2)$$

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, as shown in the figure above. The range $0 < q_{ij} \leq 1$ generalizes F_H so that it can smoothly vary from standard type II ($q_{ij} = 0$) to standard type III responses ($q_{ij} = 1$).

F_{BD} of predator i consuming prey j is

$$F_{BDij}(B) = \frac{B_j(t)}{\sum_{k=1}^{n} \alpha_{ik} B_k(t) + (1 + c_{ij} B_i(t)) B_{0ji}} . \qquad (3)$$

Similar to F_H, F_{BD} has a control parameter $c_{ij} \geq 0$ that quantifies the intensity of predator interference. Empirical studies suggest $c \approx 1$ (Skalski and Gilliam 2001). Note that F_{BD} 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.

versity (S_0), complexity (C_0), the functional response control parameters (q_{ij} and c_{ij}), and a predator's preferences among prey (α_{ij}) to study effects of food-web structure on dynamics and persistence, as well as effects of dynamics on food-web

structure. For each model iteration, absolute persistence $P_A = S_P$ and relative persistence $P_R = S_P/S_0$ are calculated. Overall persistence P is the mean value of P_R across a set of iterations. Topological properties of the persistent webs are then compared to different versions of niche model 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.

3   RESULTS

We analyzed the behavior of the dynamic network model with respect to the combined variation of several key parameters. The model's high dimensionality, resulting from the model's many parameters, prevents full examination of all the combinations of parameter values. 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 changes the results quantitatively. Therefore, we report overall behaviors that resist qualitative changes due to alternative choices.

Perhaps most importantly, varying network structure and the functional response control parameters profoundly affects persistence. Figures 1(a) and 1(b) show the effect of varying q and c on 30-species webs with an intermediate level 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 (fig. 1(a)). 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 1(b) shows that predator interference causes a similar change in the persistence of 30-species webs when c varies across a biologically reasonable range (Skalski and Gilliam 2001). 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. 1(c) and 1(d)) as shown by linear regressions of P_R as a
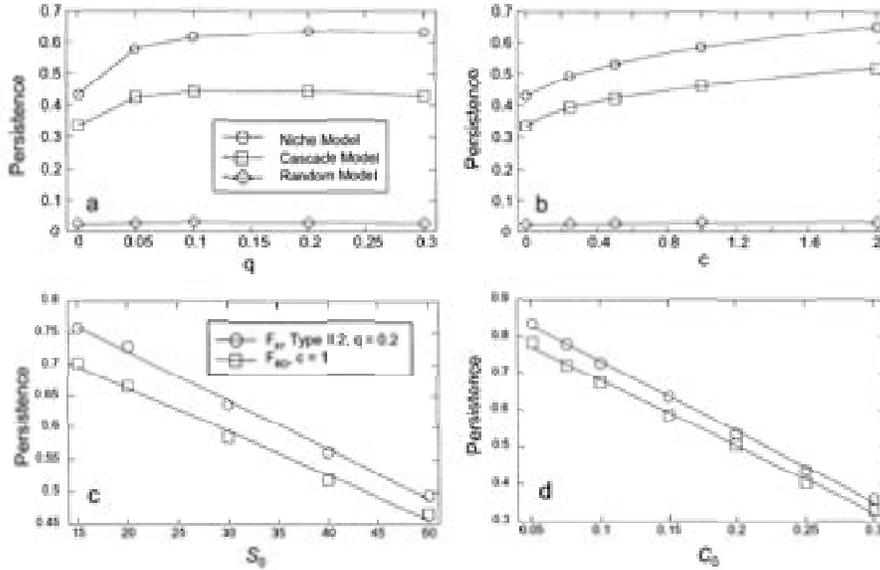
FIGURE 1   1(a) and 1(b): Mean overall persistence of model food webs vs. functional response control parameter for networks built using the niche, cascade, and random models. In (a) q controls the parametrized Holling functional response (F_H, Box 1, eq. (2)); in (b) c controls the Beddington-DeAngelis predator interference functional response (F_{BD}, Box 1, eq. (3)). All networks initially have $S_0 = 30$ and $C_0 = 0.15$. 1(c) and 1(d): Mean overall persistence of niche model food webs versus (c) initial network size S_0 for networks with $C_0 = 0.15$, and (d) initial network connectance C_0 for networks with $S_0 = 30$. Responses shown for a single value of the two types of functional responses, Type II.2, F_H, $q = 0.2$; and Type BD, F_{BD}, $c = 1$. The regression lines are (c) 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 (d) Type II.2: $P = 0.927 - 1.923C_0$, $r^2 = 0.998$; BD: $P = 0.862 - 1.799C_0$, $r^2 = 0.997$. Values shown and used for regression analyses are averages of 500 trials.

function of the product S_0C_0, the network's initial value of L/S. For the type II.2 response ($q = 0.2$) with constant $C_0 = 0.15$, $P_R = 0.87 - 0.05S_0C_0(R^2 = 0.48, n = 2500)$; with constant $S_0 = 30$, $P_R = 0.93 - 0.06S_0C_0(R^2 = 0.23, n = 3500)$. 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. 2). 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 and 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 "consumer" species (Dunne et al. 2002a). The value C of niche webs increases with the number of entirely random deletions but varies little when basal species are protected (fig. 2). 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. 2). 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 and 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. 2). 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. 2). 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 consumers with lower mean trophic levels, and higher fractions of basal species, especially in the largest, most persistent webs ($S_P > 25$, fig. 3(a) and 3(b)). These properties of persistent webs 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 herbivores or omnivores are higher in the persistent webs than in the niche webs (fig. 3(c) and 3(d)). This helps explain the lower mean trophic levels of persistent webs. 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 standard deviations above those in persistent webs (fig. 3(e)). This similarity also applies to the standard deviation of the number of incoming and outgoing links taken separately, properties previously referred to as generality and vulnerability, respectively (Williams and Martinez 2000). Overall, these results indicate that more persistent webs are shorter and fatter than niche webs, since persistent webs have more basal and herbivore species as well as consumers with lower trophic levels.

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. 4), similar to the effects of varying the functional
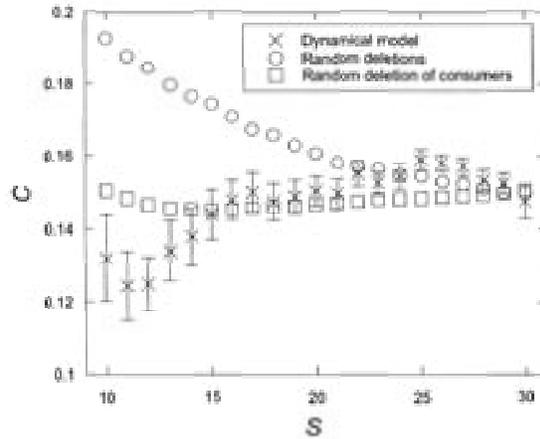
FIGURE 2   Mean connectance C of model food webs versus dynamically persistent network size S, with error bars showing plus and minus two standard errors of the estimated mean. The points without error bars show the mean connectance of 1000 niche model networks that have species deleted at random or have consumer species deleted at random. 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 $q = 0.2$ (Box 1, eq. (2)).

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 ($0.2 <$ skewness < 0.8). Persistence drastically falls to as low as $P \approx 0.25$ when $q = 0$ and $P \approx 0.34$ when $q = 0.2$ when omnivores more strongly prefer upper trophic-level resources (skewness $= 10$).

4   DISCUSSION

4.1   EFFECTS OF STRUCTURE ON DYNAMICS

Our results illustrate how the structure of ecological networks may influence their function by showing the effects of diversity and complexity on *in silico* ecosystem dynamics. May's early and remarkably durable theory based on linear stability analyses of random networks proposed that S and C have hyperbolically negative effects on stability (May 1973). Qualitatively similar effects occur in our nonlinear analyses of more ecologically realistic networks, but the effects are linear rather than hyperbolic, perhaps due to the differences between linear

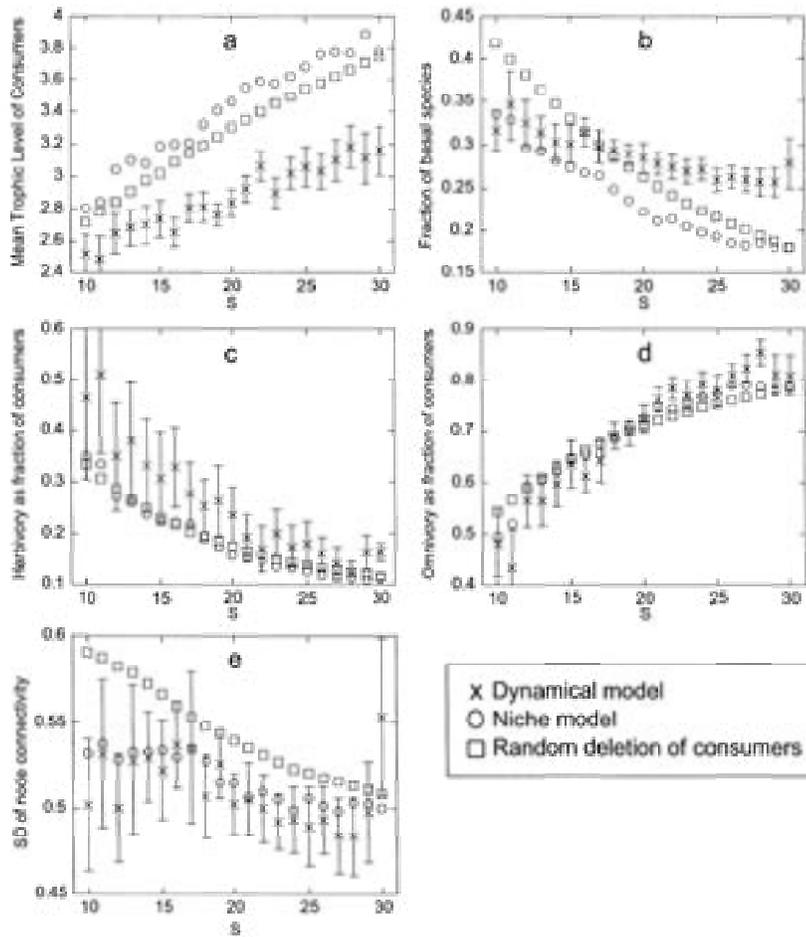**174**   Diversity, Complexity, and Persistence in Large Model Ecosystems

FIGURE 3   Mean and variation of model food-web properties versus persistent network size S. 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 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. Properties shown are (a) mean trophic level of consumers, (b) fraction of basal species, (c) fraction of consumers that are herbivores, (d) fraction of consumers that are omnivores, 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 $q = 0.2$ (Box 1, eq. (2)).
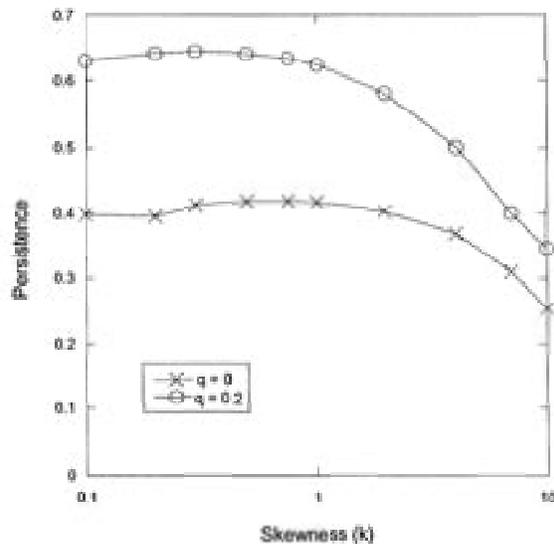
FIGURE 4   Mean ($n = 500$) overall persistence of model food webs vs. skewness k of the prey preference of omnivores. When $k = 1$, all prey preferences of an omnivore are equal; when $k < 1$, low trophic level prey are preferred and when $k > 1$, high trophic level prey are preferred (see methods). All networks initially have $S_0 = 30$, $C_0 = 0.15$, and the dynamical model uses parametrized Holling Type II ($q = 0$) and II.2 ($q = 0.2$) functional responses (Box 1, eq. (2)).

stability and nonlinear persistence. Connectance (C) affects persistence much more strongly than does diversity (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 and 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 arrangement of links among species (fig. 5). Random webs have almost no persistence, and the hierarchical ordering of the cascade model vastly increases persistence. The contiguous niches, cannibalism, and looping in the niche model allow even more persistence in 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.

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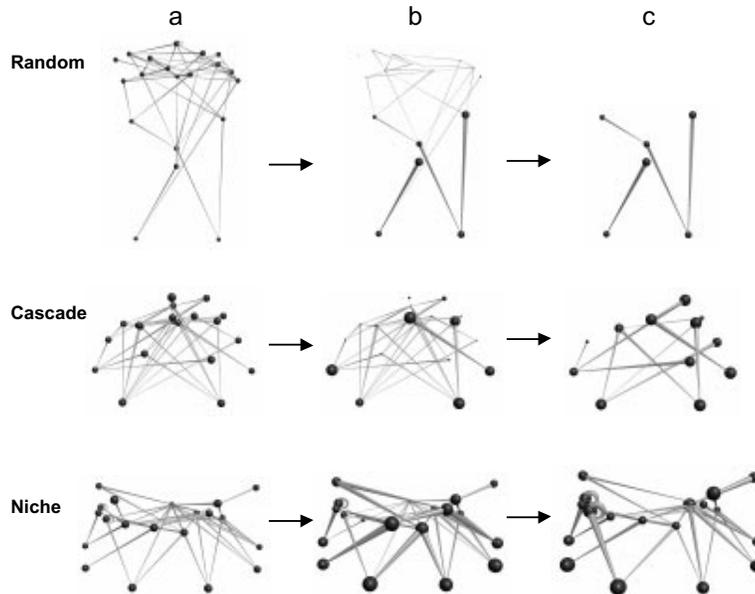

FIGURE 5   (a) Screen shots showing images of examples of random, cascade, and niche model food webs, each with $S_0 = 20$ and $C_0 = 0.15$. The dynamical model is then run on each structure. (b) Shows a moment while dynamics are running, and (c) shows a moment of the final persistent dynamical structure for each food web. The relative persistence ($P_r = S_p/S_o$) for each web is $P_{\text{random}} = 0.30$, $P_{\text{cascade}} = 0.60$, $P_{\text{niche}} = 0.90$. Images were produced with FoodWeb3D, written by R.J. Williams and provided by the Pacific Ecoinformatics and Computational Ecology Lab (www.foodwebs.org).

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 model's improved empirical fit (Williams and Martinez 2000; Dunne et al. 2004) and increased persistence (figs. 1 and 5).

4.2   EFFECTS OF DYNAMICS ON STRUCTURE

This research also illuminates how the functioning of ecological networks influences their structure by examining the effects of nonlinear dynamics on the topology of complex food webs. We show for the first time that the stabilizing

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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 (e.g., changes from $q = 0.0$ to $q = 0.2$, Box 1) foster greatly increased persistence in model ecosystems (Williams and Martinez 2004b). This suggests that tiny amounts of prey switching behavior by consumers (Post et al. 2000; Kondoh 2003) or refuge-seeking behavior by resource taxa (Holling 1959a; Sarnelle 2003) can have large effects on the structure and dynamics of complex ecological networks, and may act 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 biomass dynamics. Persistent webs typically have similar C to that in niche webs whose consumers are randomly deleted, but have lower C 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 and Martinez 2000), assuming that empirical webs have more persistent topologies than do niche webs. While the standard deviation 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. 3(a)) and its underestimation of the fraction of herbivores by ~0.07 (fig. 3(c)), we tested the niche model against these properties of the seven empirical webs originally compared to the niche model (Williams and Martinez 2000). Table 1 shows that the niche model consistently overestimates the 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 produce network structures even more similar to empirically observed properties. The empirically observed fraction of basal species is well explained by the niche model (Williams and Martinez 2000), so the higher fraction of basal species observed in the dynamically constrained networks (fig. 3(b)) 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 and Roughgarden 1993) are categories of plant material such

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 and Martinez 2000).

Food Web	S	C	Herbivory	TL Consumers
St. Martin Island	42	0.12	-2.7 (-0.15)	1.4 (0.79)
Bridge Brook Lake	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 Lake	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)	0.30 (0.27)

as seeds and leaves. Many basal taxa in the Bridge Brook Lake (Havens 1992) food web are trophically identical in terms of having the exact same set of consumers, 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 of basal species for 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.

4.3   THE ROLE OF 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 and Hastings 1997; Fussman and 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. 2) and showing that the prevalence of omnivorous consumers in persistent webs is usually similar to that in niche webs (fig. 3(d)), which is much less than in cascade webs (Williams and Martinez 2000). If structural omnivory has 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 and Hastings 1997; Fussman and Heber 2002). Omnivory that increases a consumer's trophic level, for example, by adding 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. 4). 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 and Martinez 2004a) destabilizing behavior of preferring prey at higher trophic levels.

5   CONCLUSIONS AND FUTURE DIRECTIONS

Our analyses address several historically perplexing aspects of the remarkable complexity and persistence of natural ecosystems and show how more empirically prevalent aspects of trophic interactions (Williams and Martinez 2000; Skalski and Gilliam 2001; Sarnelle 2003; Williams and Martinez 2004a) may confer persistence on large complex ecosystems. Both food-web structure, characterized by the empirically successful the niche model, and food-web function, characterized by decelerated consumption of rare resources (Sarnelle 2003), predator interference (Skalski and Gilliam 2001), and omnivores' preferences for lower trophic-level prey (Williams and Martinez 2004a), greatly increase the diversity and complexity that persists in ecological networks. 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, for example, 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, such as economic exploitation of relatively rare carnivorous fishes (Pauly et al. 2002), can be expected to decrease persistence of species within ecosystems.

Perhaps even more important than these results is that the models described here provide new, more sophisticated, and flexible tools for exploring crucial issues such as the impacts of various types of perturbations on ecosystem structure

and nonlinear dynamics, as well as the influence of structure and dynamics on mitigating ecosystem responses to perturbations. For example, integrated structure/dynamics models can be used to explore which properties of species (e.g., trophic level, generality, vulnerability) make them more effective invaders and which properties of complex networks (e.g., connectance, distribution of species among trophic levels) make them more resistant to invasions. Similarly, this modeling approach can be used to explore which properties of species, interactions, or networks are likely to make ecosystems more or less robust to biodiversity loss (Solé and Montoya 2001; Dunne et al. 2002a). Climate change impacts can be investigated by simulating the effects of temperature change on metabolic rates. The dynamic consequences of consumer-resource (predator-prey) body-size ratios can be explored by examining the effects of metabolic rates that reflect body-size ratios and metabolic types (i.e., ectotherm, endotherm, vertebrate, and invertebrate) found in natural systems. These and other research questions represent important future directions for structure/dynamics modeling that could be explored with relatively minor modifications of the methods described here.

With more significant modifications, our modeling approach can be used to explore other processes such as behavior modification, detrital loops, adaptation, coevolution, mutualism, and competition. Addressing these types of issues would involve moving from food webs containing only trophic interactions to broader ecological networks that include non-trophic interactions. For example, the consequences of resource sharing and competition among basal species can be explored by replacing the independent logistic growth of basal species with basal growth that is dependent on explicit dynamics of flows into and out of limiting nutrient pools, including differential uptake by plants according to their growth and relative consumption rates (Brose et al. in press). Another major modification would be to add explicit detrital dynamics to account for biomass shed and excreted by organisms. That organic matter becomes available to microbes and other detritivores, which are consumed by higher trophic level organisms, and whose activity helps determine nutrient availability for photosynthetic species. Such modifications of the model presented here will likely involve new functional responses characterizing consumption as a function of nonliving resources. Other changes in functional responses can allow exploration of nontrophic influences (e.g., ecological engineering, Jones et al. 1997; indirect effects, Peacor and Werner 2001) and evolution rates (Yoshida et al. 2003) on consumption rates and population dynamics. The addition of nutrient and detrital dynamics should also provide a powerful framework for exploring network evolution (McKane and Drossel Chapter 9). By modeling the emergence of biological innovation within an interaction network, feedbacks through short and long chains of direct and indirect effects help determine the success or failure of new traits and species, and alter the structure and dynamics of the network.

This basic model could also be altered to account for spatially explicit processes. The simplest approach is to add functions such as density-dependent migration. More ambitiously, complex networks could be made spatially explicit

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by placing the networks within cells in a landscape. Migration could occur between adjacent cells and network structure in a cell could depend on the spatial ranges of species and other network nodes. This *trophic circulation model* approach would be analogous to better known global circulation models of weather and climate. Similar *NPZ* models (Franks and Walstad 1997) are already used by oceanographers to model the nonlinear dynamics of nutrients, phytoplankton, and zooplankton in a spatially explicit manner (Franks 2002). However, such models, focused on relatively simple modules, face the classic problem of dynamical instability (Denman 2003). Our results suggest that scaling up beyond simple spatially explicit modules may be achieved by incorporating realistic network structure, non-type II responses, and omnivory skewed towards lower trophic levels. While the vast number of parameters and computational intensity required may hinder scaling up within a spatially explicit framework, rapid advances in informatics and computing may facilitate advances in the near future (Green et al. 2005).

Regardless of how they are modified or augmented, models of complex systems are still simplifications of nature. In order to create a plausible and useful simplification of natural systems, we base our integrated structure/dynamics model on simple empirical regularities and processes that are well documented in the literature. This strategy has produced novel insights into the complexity and stability of diverse, multi-trophic level ecosystems and should continue to facilitate research that includes other well-documented regularities and processes. We encourage the continued exploration of high diversity model systems that go beyond traditional module or single trophic-level approaches. Such models of complex systems have greater fidelity to the diversity in natural ecosystems that field ecologists study every day. More research based on these types of models as well as empirical and experimental tests of their findings could significantly extend and refine our understanding of the persistence and stability of complex networks of species. Such integrated studies can facilitate exciting new insights regarding trophic and non-trophic processes in the complex ecosystems that sustain the stunning, yet tragically diminishing, levels of diversity in nature.

Models that incorporate more detail than ours quickly require so much information about any given real population that very substantial empirical programs are needed to provide it. That is not to say that such models or such programs are to be avoided: quite to the contrary, often they are necessary. However, when constraints of time or research resources call for maximum realism from minimum data, plausible models such as we have discussed here may be a valid recourse.
—Yodzis and Innes, 1992

6   ACKNOWLEDGMENTS

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