School and Workshop on
Structure and Function of Complex Networks

16 - 28 May 2005

Diversity, Complexity and Persistence in
Large Model Ecosystems

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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 the relationship between ecological 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. Behavioral nonlinearities, particularly competition among consumers and reduced consumption of rare resources, formalized by predator interference 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 remarkably 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 alter 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 respects to detail, but we hope to do so without too great a sacrifice in realism.
-Yodzis and Innes 1992

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 few resources (MacArthur 1955). By the late 50's 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 & 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.* in press).

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 & Hastings 1997; McCann *et al.* 1998; Fussman & 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 & 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 & 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 & 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 & Martinez 2000; Camacho *et al.* 2002; Dunne *et al.* 2002ab, 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 & Martinez 2004) 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 properties, as well as longer-standing functional properties of ecological interactions, appear to promote stability and persistence in large complex ecosystems.

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 the chapter on "Ecological network structure" (Dunne, this volume, Box 1; Williams & Martinez 2000; Dunne et al. 2004). The second step uses a nonlinear bioenergetic model to compute the dynamics of the network (Williams & Martinez 2004). This integrated approach allows us to explore the impact of structure on dynamics as well as the impact of dynamics on structure.

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 & 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 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 (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 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 2004a) . A species' connectivity is its total number of links (both incoming and outgoing) divided by the mean connectivity (2*L*/*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 earlier notation (Yodzis & Innes 1992) to *n*-species systems, variation of B_i, the biomass of species *i*, over time *t*, is given by

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

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. 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* and is normalized so that the sum of α_{ij} ($0 \le \alpha_{ij} \le 1$) across all *j* is 1 for consumer species and 0 for basal species. Non-zero α_{ij}'s are

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assigned according to the topology specified by the structural models. $F_{ij}(B)$, a non-dimensional functional response 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. 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 & 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 & Williams 2004b) that have both mechanistic and empirical justifications (Skalski & Gilliam 2001). The F_H functional response Box 1, eq. 2) is based on a parameterized 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 & Heber 2002). Type II responses have been used in many studies of the dynamics of small food-web modules (Yodzis & Innes 1992; McCann & Yodzis 1995; McCann & Hastings 1997; McCann *et al.* 1998; Post *et al.* 2000; Fussman & Heber 2002). The F_{BD} response (Box 1, eq. 3) models predator interference (Skalski & 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 & 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" ($q = 0.2$), 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 & Martinez 2004b).

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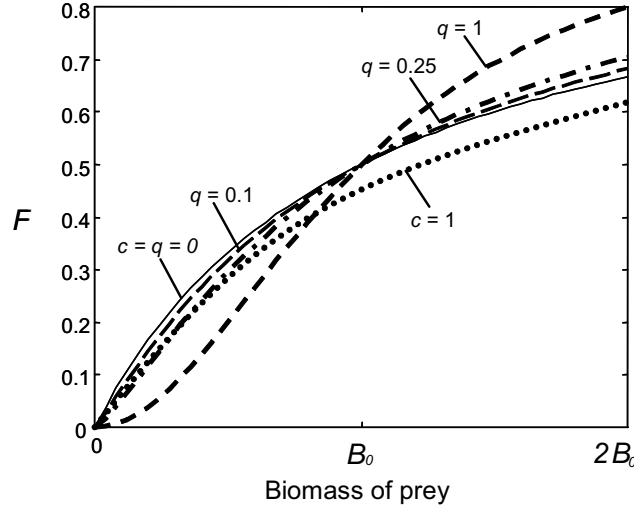
The effects of control parameters q (F_H, equation 2) and c (F_{BD}, equation 3) on fractions of maximal consumption rates (F) are shown. Where $q_{ij} = c_{ij} = 0$, the functional response is a standard type II response, and where $q_{ij} = c_{ij} = 1$, the functional response is a standard type III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

F_H of predator i consuming prey j is

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

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

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

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 & 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.

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 & 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 $k = \alpha_{imax}/\alpha_{imin}$, 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/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 diversity (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.

RESULTS

We analyzed the behavior of the dynamic network models with respect to the combined variation of several key parameters. The models' high dimensionality, resulting from the models' 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 1a and 1b 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.1a). 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 1b shows that predator interference causes a similar change in the persistence of 30-species webs when c varies across a biologically reasonable range (Skalski & 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.
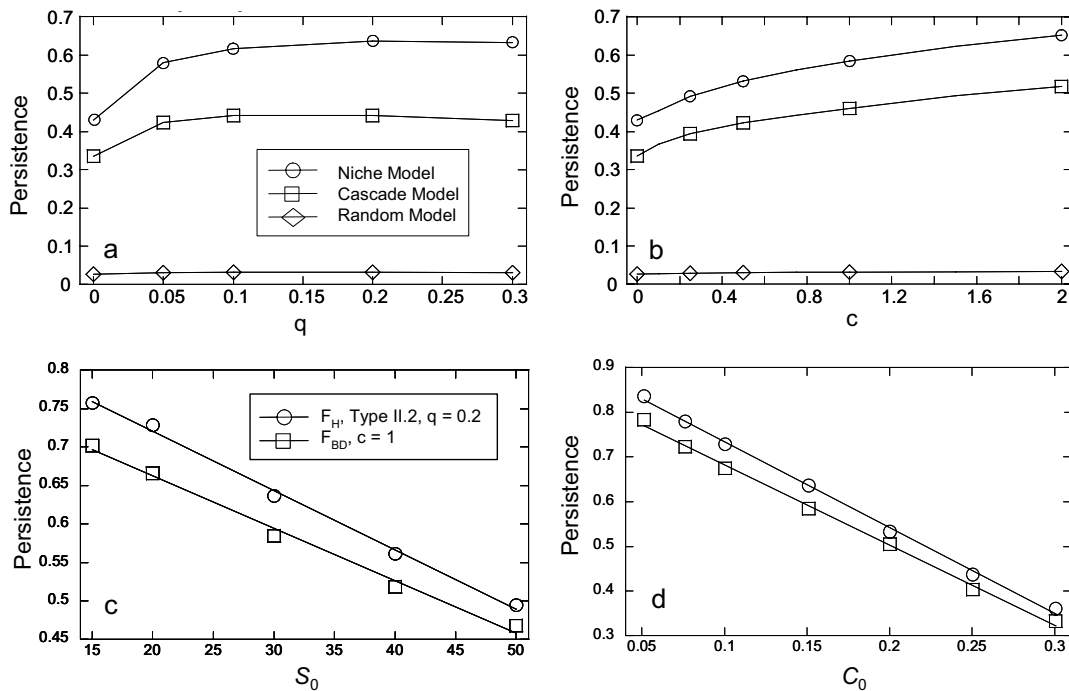

Figure 1. 1a and 1b: Mean overall persistence of model food webs vs. functional response control parameter for networks built using the niche, cascade, and random

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models. In (a) q controls the parameterized Holling functional response (F_H, Eq. 2); in (b) c controls the Beddington-DeAngelis predator interference functional response (F_{BD}, Eq. 3). All networks initially have $S_0 = 30$ and $C_0 = 0.15$. 1c and 1d: 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.

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. 1c, 1d) as shown by linear regressions of P_R as a 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 $C_0 = 0.15$, $P_R = 0.87 - 0.05 \, S_0 \, C_0$ (R^2=0.48, n=2500); with constant $S_0 = 30$, $P_R = 0.93 - 0.06 \, S_0 \, C_0$ (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 & 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) . 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).
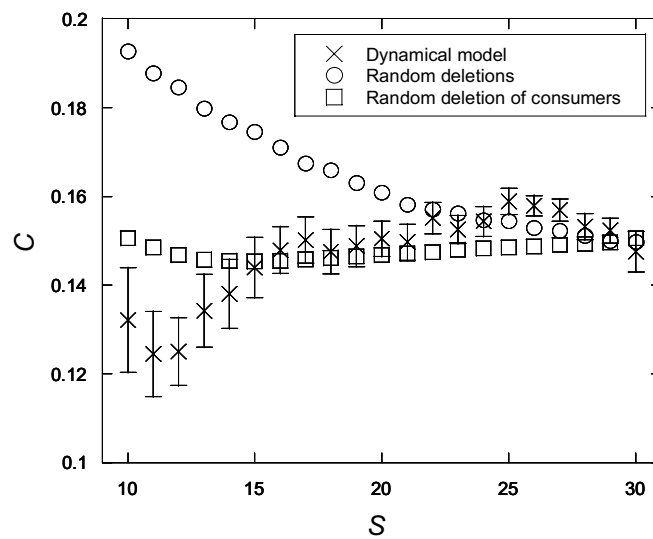
Figure 2. Mean connectance C of model food webs versus dynamically persistent network size S ($\times$), with error bars showing plus and minus two standard errors of the estimated mean. The points without error bars show the mean connectance of 1000 niche model networks that have species deleted at 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. 2).

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. 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.
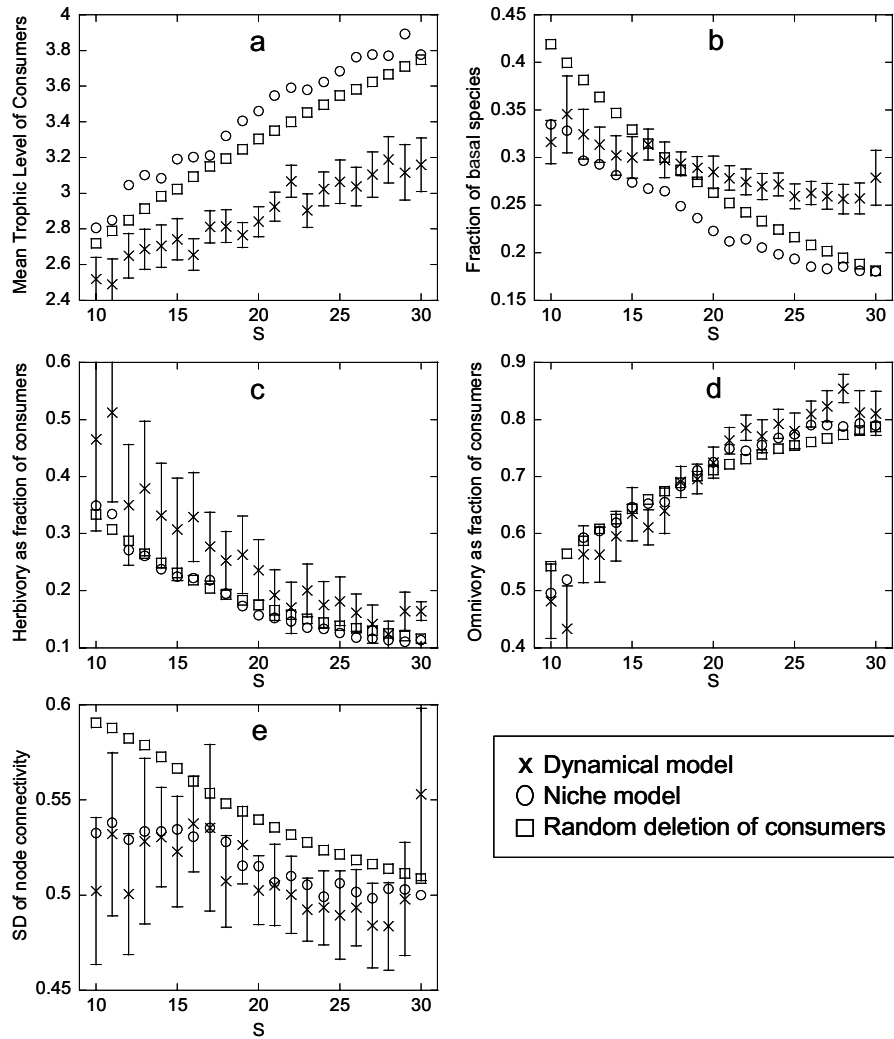
Figure 3. Mean and variation of model food-web properties versus persistent network size S (×). Error bars show plus and minus two standard errors of the estimated mean. Points without error bars show the mean property value in 1000 niche model networks with the same size and connectance as the dynamical 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) fraction of basal species, (b) mean trophic level of consumers, (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. 2).

Compared to either set of niche webs, persistent webs consistently have higher fractions of basal species and consumers with lower mean trophic levels, especially in the largest, most persistent webs ($S_P > 25$, Fig. 3a, 3b). 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 omnivores or herbivores are higher in the persistent webs than in the niche webs (Fig. 3c, 3d). This helps explain the lower

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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. 3e). 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 & 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.
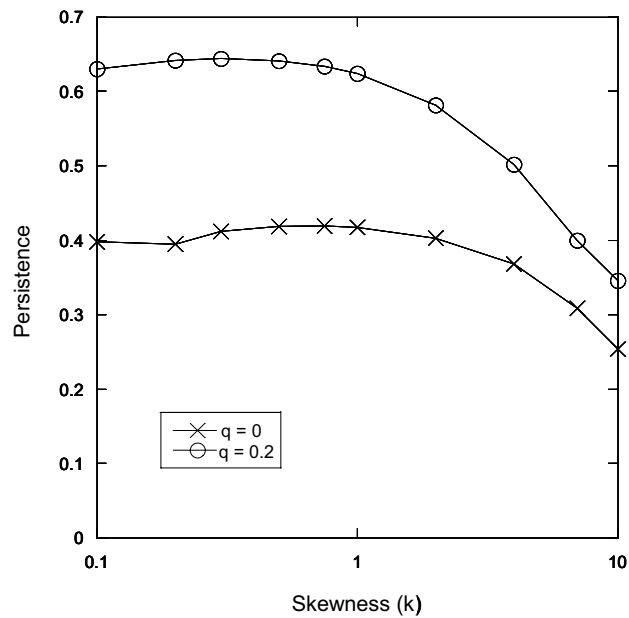

Figure 4. Mean (n=500) overall persistence of model food webs vs. skewness k of the prey preference of omnivores. When $k = 1$, all prey preferences of an omnivore are equal; when $k < 1$, low trophic level prey are preferred and when $k > 1$, high trophic level prey are preferred (see methods). All networks initially have $S_0 = 30$, $C_0 = 0.15$, and the dynamical model uses parameterized Holling Type II ($q = 0$) and II.2 ($q = 0.2$) functional responses (Eq. 2).

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 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).

DISCUSSION

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 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 & 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 hierarchal 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. 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 & Martinez 2000, Dunne et al. 2004) and increased persistence (Figs. 1, 5).

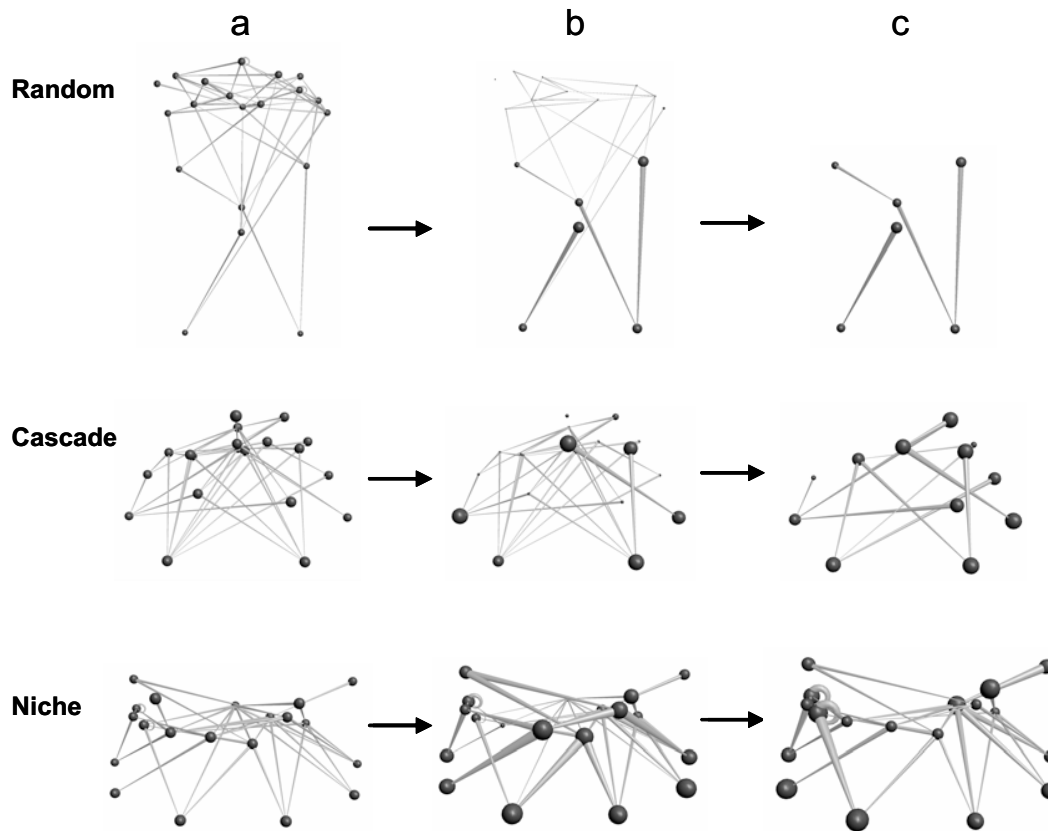Figure 5. (5a) Screen shots showing images of an example random, cascade, and niche model food web, each with S_0=20 and C_0=0.15. The dynamical model is then run on each structure. (5b) shows a moment while dynamics are running, and (5c) shows a moment of the final persistent dynamical structure for each food web. The relative persistence ($P_r = S_p/S_o$) for each web is P_{random} = 0.30, $P_{cascade}$ = 0.60, P_{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).

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. 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 (e.g., changes from q = 0.0 to q = 0.2, Box 1) foster greatly increased persistence in model ecosystems (Williams & Martinez 2004b) . This suggests that tiny amounts of prey

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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 & 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.

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)

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).

Given the niche model's overestimation of the mean trophic level of consumers in large persistent webs by almost a whole level (Fig. 3a) and its underestimation of the fraction of herbivores by ~0.07 (Fig. 3c), 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 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 & Martinez 2000), so the higher fraction of basal species observed in the dynamically constrained networks (Fig. 3b) 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 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.

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 & 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. 2) and showing that the prevalence of omnivorous consumers in persistent webs is usually similar to that in niche webs (Fig. 3d), which is much less than in cascade webs (Williams & 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 & 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. 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 & Martinez 2004a) destabilizing behavior of preferring prey at higher trophic levels.

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 & Martinez 2000; Skalski & Gilliam 2001; Sarnelle 2003, Williams & 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 & Gilliam 2001), and omnivores' preferences for lower trophic-level prey (Williams & 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, 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 of species within ecosystems.

Perhaps even more important than these *results* is that the models described here provide new, more sophisticated and flexible *tools* to explore 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, etc.) make them more effective invaders and which properties of complex networks (e.g., connectance, distribution of species among trophic levels, etc.) 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 & 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, co-evolution, 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 depending 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 & Werner 2001) and evolution rates (Yoshida *et al.* 2003) on consumption rates and population dynamics. Addition of nutrient and detrital dynamics should also provide a powerful framework for exploring network evolution (McKane & Drossel, this volume). 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 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 & 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.* in press).

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

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Simple rules yield complex food webs

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Several of the most ambitious theories in ecology[1–14] describe food webs that document the structure of strong and weak trophic links[9] that is responsible for ecological dynamics among diverse assemblages of species[4,11–13]. Early mechanism-based theory asserted that food webs have little omnivory and several properties that are independent of species richness[1–4,6]. This theory was overturned by empirical studies that found food webs to be much more complex[5,7–9,14–18], but these studies did not provide mechanistic explanations for the complexity[9]. Here we show that a remarkably simple model fills this scientific void by successfully predicting key structural properties of the most complex and comprehensive food webs in the primary literature. These properties include the fractions of species at top, intermediate and basal trophic levels, the means and variabilities of generality, vulnerability and food-chain length, and the degrees of cannibalism, omnivory, looping and trophic similarity. Using only two empirical parameters, species number and connectance, our 'niche model' extends the existing 'cascade model'[3,19] and improves its fit ten-fold by constraining species to consume a contiguous sequence of prey in a one-dimensional trophic niche[20].

We compare the abilities of two earlier models, the random and cascade models[3,19], and our new niche model to predict a dozen properties for each of seven food webs. The parameters of all models are set to synthesize webs with the empirically observed species number and connectance level. We compare model predictions with the largest and highest-quality empirical food webs that include autotrophs and were originally documented to study food web structure comprehensively (Table 1). Three are from freshwater habitats: Skipwith Pond, Little Rock Lake and Bridge Brook Lake;

Table 1 Basic properties of empirical food webs

Name	Taxa	S	L/S	$C(L/S^2)$
Skipwith Pond	35	25	7.9	0.32
Little Rock Lake	181	92	10.8	0.12
Bridge Brook Lake	75	25	4.3	0.17
Chesapeake Bay	33	31	2.2	0.072
Ythan Estuary	92	78	4.8	0.061
Coachella Valley	30	29	9.0	0.31
St Martin Island	44	42	4.9	0.12

'Taxa' refers to the original names for groups of organisms found in the primary reference. S refers to trophic species[3]. The seven food webs address (1) primarily invertebrates in Skipwith Pond[15]; (2) pelagic and benthic species in Little Rock Lake[17], the largest food web in the primary literature; (3) Bridge Brook Lake, the largest among a recent set of 50 Adirondak lake pelagic food webs[6,7]; (4) the pelagic portion of Chesapeake Bay emphasizing larger fishes[30]; (5) mostly birds and fishes among invertebrates and primary producers in the Ythan Estuary[16]; (6) a wide range of highly aggregated taxa in the Coachella desert[5]; and (7) trophic interactions emphasizing *Anolis* lizards on the Caribbean island of St Martin[18].

two are from habitats at freshwater–marine interfaces: Chesapeake Bay and Ythan Estuary; and two are from terrestrial habitats: Coachella Valley and the island of St Martin.

Throughout this work, 'species' refers to trophic species, which are functional groups of taxa that share the same predators and prey in a food web[3]. 'Trophic species' is a widely accepted[3,4,8,14,17,18] and sometimes criticized convention[5,14] within structural food-web studies that reduces methodological biases in the data[3,4,8]. A matrix with S rows and columns represents a food web with S species. Element a_{ij} is 1 if species j consumes species i and 0 if not. There are S^2 possible and L actual links. Directed connectance[17] (C) equals L/S^2.

In the random model[3,19], any link among S species occurs with the same probability (P) equal to C of the empirical web. This creates webs as free as possible from biological structuring while maintaining the observed S and C. The cascade model[3,19] assigns each species a random value drawn uniformly from the interval [0,1] and each species has probability $P = 2CS/(S-1)$ of consuming only species with values less than its own. This pecking order helps to explain species richness among trophic levels[3] but underestimates inter-specific trophic similarity[19] and overestimates food-chain length and number in larger webs[3,18]. The niche model (Fig. 1) similarly assigns each species a randomly drawn 'niche value'. The species are then constrained to consume all prey species within one range of values whose randomly chosen centre is less than the consumer's niche value. The single range adds a previously discussed[20] community-level contiguity of niche space to the cascade model by causing species with similar niche values to share consumers frequently within the community. The placement of the niche partially relaxes the cascade hierarchy by allowing up to half a consumer's range to include species with niche values higher than the consumer's value. All three models incorporate substantial stochastic variability along with dependence on S and C.

Twelve properties of each empirical and model web are measured (see Methods):

(i–iii) Species types[1–8,14–18,21]: the fractions of top (T, species with no predators), intermediate (I, species with both predators and prey) and basal (B, species with no prey) species.

(iv, v) The standard deviations (s.d.) of generality[14] (*GenSD*) and vulnerability[14] (*VulSD*) quantify the respective variabilities of species' normalized prey (G_i) and predator (V_i) counts:

$$G_i = \frac{1}{L/S} \sum_{j=1}^{s} a_{ji} \qquad V_i = \frac{1}{L/S} \sum_{j=1}^{s} a_{ij}$$

Normalizing with L/S makes s.d. comparable across different webs by forcing mean G_i and V_i to equal 1.
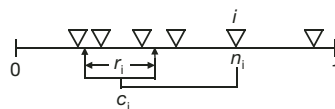
Figure 1 Diagram of the niche model. Each of S species (for example, $S = 6$, each shown as an inverted triangle) is assigned a 'niche value' parameter (n_i) drawn uniformly from the interval [0,1]. Species i consumes all species falling in a range (r_i) that is placed by uniformly drawing the centre of the range (c_i) from [$r/2$, n_i]. This permits looping and cannibalism by allowing up to half of r_i to include values $\geq n_i$. The size of r_i is assigned by using a beta function to randomly draw values from [0,1] whose expected value is 2C and then multiplying that value by n_i [expected E(n_i) = 0.5] to obtain the desired C. A beta distribution with $\alpha = 1$ has the form $f(x|1, \beta) = \beta(1-x)^{\beta-1}$, $0 < x < 1$, 0 otherwise, and $E(X) = 1/(1+\beta)$. In this case, $x = 1-(1-y)^{1/\beta}$ is a random variable from the beta distribution if y is a uniform random variable and β is chosen to obtain the desired expected value. We chose this form because of its simplicity and ease of calculation. The fundamental generality of species i is measured by r_i. The number of species falling within r_i measures realized generality. Occasionally, model-generated webs contain completely disconnected species or trophically identical species. Such species are eliminated and replaced until the web is free of such species. The species with the smallest n_i has $r_i = 0$ so that every web has at least one basal species.

(vi) Trophic similarity of a pair of species (s_{ij}) is the number of predators and prey shared in common divided by the pair's total number of predators and prey[17,19]. We average all species' largest similarity index to calculate mean maximum similarity (*MxSim*) of a web:
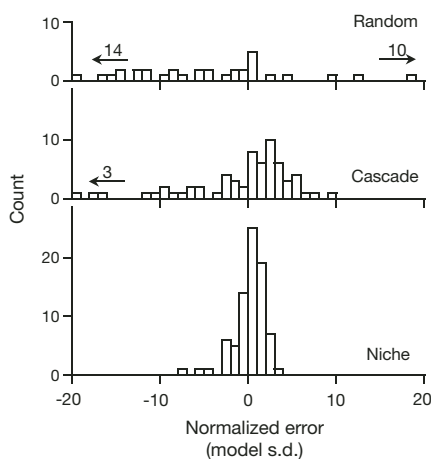
$$MxSim = \frac{1}{S} \sum_{i=1}^{s} \max_{i \neq j} s_{ij}.$$

(vii–ix) A food chain is a linked path from a species to a basal species[17]. The mean (*ChnLg*) and s.d. (*ChnSD*) of food chain lengths and the log of the number of food chains (*ChnNo*) are measured. Computational considerations require that chains with loops be ignored[17].
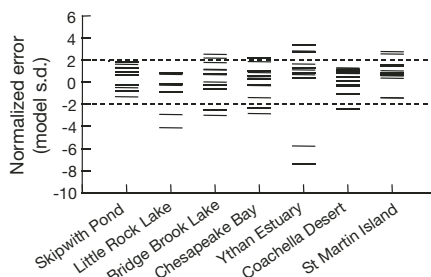
(x, xi) The fraction of species that are cannibals (*Cannib*) and the fraction of species involved in longer 'loops' (*Loop*), which are food chains that include the same species twice[5,17].

(xii) Omnivory[5] is the fraction of species that consume two or more species and have food chains of different lengths (*Omniv*).

Raw error is the difference between empirical properties and a model's mean predicted by Monte Carlo simulations (see Methods). We normalize raw errors by dividing them by the s.d. of the property's simulated distribution. As expected, an average of 95.8% (s.d. = 1.5, $n = 202$) of synthetic webs have properties within 2 model s.d. of the model's mean, which makes normalized errors between −2 and 2 a good fit because they are within the model's expected range.

Figure 2 shows the overall performance of the three models. Generally, the niche model estimates the central tendency of the empirical data remarkably well. The average normalized error is 0.22, although the s.d. of 1.8 (expected value 1) illustrates greater variability in the empirical data than in the niche model[21] despite three distinct stochastic model components. The cascade model is over an order of magnitude worse, with an average normalized error of −3.0 and s.d. of 14.1. The random model's average of 27.1 and s.d. of 202 indicates an even worse fit. The niche model performs similarly across the different webs (Fig. 3) and consistently predicts individual properties across the group of webs more accurately than the other models (Fig. 4).

The random model's large errors show that simply matching an empirical web's **S** and **C** does little to account for empirical food-web properties except *Cannib*, which is surprisingly close to our null expectation. The cascade model improves over the random model for all properties except *Cannib* and closely estimates **T**, **I** and **B**, as suggested earlier[3] but previously untested against all seven webs. It

Figure 2 Distribution of normalized errors between empirical data and model means for all properties of the random, cascade and niche models. Arrows show the number of errors beyond the *x*-axis. Of the 56 random-model means (8 properties of 7 webs), 16% are within 2 model s.d. of the empirical data. Of the 66 cascade-model means (10 properties of 6 webs and 6 properties of one web), 27% are within this range. In contrast, 79% of 80 niche-model means (12 properties of 6 webs and 8 properties of one web) are within 2 model s.d. of the empirical data. Although attention to normalized-error magnitudes tends to reward models for increased variability, this tendency is kept in check by normalized-error s.d. < 1 that indicates excessive variability.
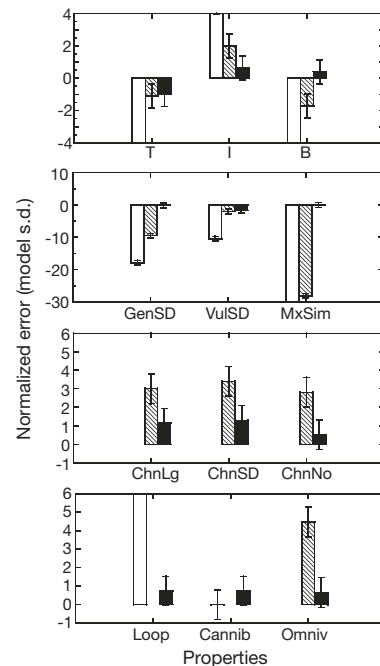

Figure 3 The niche model's normalized errors for each property of each food web. Errors are < 2 model s.d. for all properties of the Skipwith Pond web and most properties of the other webs.

Figure 4 Mean normalized error of each property for each model averaged across the seven food webs (Table 1). The three models are indicated by open bars (random model), hatched bars (cascade model) and filled bars (niche model). Properties are described in the text. Ideally, the across-web sample average should not significantly differ from the model average of zero. Significant positive and negative average errors indicate that on average the model over- and underestimates empirical properties, respectively. Error bars show 95% confidence limits on the value of the mean assuming the empirical data are drawn from the model distribution and therefore have known population mean 0 and s.d. 1. The expected average of zero falls within the 95% confidence limits for only one property of the random model (*Cannib*), no properties of the cascade model, and eight properties of the niche model. Normalized errors do not directly correspond to raw errors because niche-model s.d. is twice as large (mean, 2.0; s.d., 0.84; $n = 66$) as cascade-model s.d. However, even in absolute terms, the magnitudes of the niche model's raw errors (Table 2) are roughly one-fifth (median 0.19, $n = 77$) of the raw errors of the random model and about one-quarter (median 0.27, $n = 80$) of the raw errors of the cascade model. In addition, the niche model has smaller average raw errors than the cascade model for all properties except **T** and smaller s.d. of those averages for 9 of 12 properties (see Supplementary Information). These findings show that the much greater accuracy and precision of the niche model's predictive abilities are robust to the distinction between normalized and raw errors.

also closely estimates *VulSD* but has quite large errors for other properties. The niche model improves over the cascade model for all 12 properties including *Cannib* and *Loop*, which invariably equal zero in cascade webs. This improvement is most dramatic for *MxSim*, which determines how quickly species are initially lumped in aggregation studies[17,19] and is poorly predicted by the cascade model[19].

The niche model's most significant errors may indicate problems with the data. For example, the model's underestimation of empirical variability may well be due to methodological inconsistencies among studies[21]. Also, the niche model's small but consistent overestimation of *ChnLg* and *ChnSD* (Fig. 4, Table 2) could be reduced by overcoming the well known bias against including parasites in food webs[2,22,23]. Underestimating **T** in the Ythan Estuary web by 5.8 model s.d. (Table 2) appears to result from the web's bias towards many 'top' bird species whose consumers were excluded[22]. Consequently, **I** and **B** are overestimated by 3.4 and 2.8 model s.d., respectively. The other 18 empirical observations of **T**, **I** and **B** are within 1.9 model s.d. except for two at −2.3 and −2.5. Bias towards top species with zero vulnerability inflates *VulSD* and explains the niche model's underestimation of the Ythan web's *VulSD* by 7.4 model s.d.

By definition, constraining all consumers to eat one contiguous interval within a fixed sequence of species causes the niche model to generate 'interval' webs[20]. However, larger empirical webs are rarely interval[3]. This discrepancy may be due to the delicacy of the intervality property. Among niche model webs with the same **S** and **C** as the seven empirical webs, intervality is broken by losing any one of almost half (mean, 41%) of the links in the webs. This suggests that we should devise a measure of the degree of intervality rather than considering intervality solely as a yes or no condition. We hypothesize that this degree is very high in empirical food webs.

A classic formulation of niche space[24] is of an '*n*-dimensional hyperspace' with *n* corresponding to innumerable ecological or environmental characteristics. An often-considered space that inspired our model is a species' feeding niche that restricts feeding to resources whose characteristics fall within a contiguous region of niche space[20,24–26]. Our results show that, with respect to food-web structure, community niche space is usefully collapsible to one dimension[20]. Whereas niche theory often infers repulsion of overlapping niches owing to interspecies competition[24,26], our model lacks such repulsion. Adding it or other modifications might improve the model's fit. The success for a model as simple as ours is very unexpected given the wide variety of aquatic and terrestrial food webs examined and the recently recognized complexity of their structure[5,7–10,14–19,21,25]. The niche model merits further testing against webs from other habitats that avoid biases such as those in the Ythan web.

As it stands, the niche dimension is an empirically successful model component that facilitates a relaxed hierarchy of trophic interactions among species ordered in one dimension. Future exploration may determine the dimension's meaning and measur-

ability in the field. Such work should focus on the relationship between the mechanics of the niche model and one or more physical, evolutionary, behavioural or other mechanisms responsible for species' trophic activities. Mechanisms related to body size should be explored[27,28], as should algorithms that order species in empirical food webs in their 'most interval' sequence. If applying such algorithms yields strongly phylogenetic orders, evolutionary mechanisms as opposed to more conventionally invoked ecological dynamics would be suggested[8,9,14]. Ordering algorithms would also help test the niche model's predictions, including: (1) empirical webs are close to interval; (2) species with similar niche values tend to share more predators than prey because close proximity on the niche dimension greatly increases the probability of being eaten by the same consumers while still allowing substantial differences in diet; and (3) species' niche values positively correlate with generality because species' niche ranges are products of these values (Fig. 1).

The niche model provides a benchmark for evaluating food webs as well as a structural framework to extend studies of link-strength distributions to systems larger than those previously examined[11–13]. Link strength may be highest and lowest, respectively, for prey species near the centre and ends of a species' niche range. Although our model lacks this and many other biological mechanisms, its empirical success indicates that exploring more of the model's predictions is warranted. For example, the general effects of losing functionally distinct species on ecological systems with different levels of **S** and **C** could be predicted by simulating species losses and observing how many other species lose all their resource or consumer species. Such observations could predict extirpations due to starvation and population increases due to predation release. Effects due to species' functional traits such as omnivory could be distinguished from effects more generally due to the number of species[29] by simulating all possible combinations of fixed numbers of species lost. Such analyses could greatly advance scientific understanding of the potentially catastrophic consequences of species loss for the complex ecological systems on which all organisms depend.　□

Methods

Monte Carlo simulations generated 1,000 webs with the same **S** and within 3% of the same **C** as an empirical web. Three per cent represents a compromise between closely matching the **C** of the empirical web and inefficiently rejecting too many model webs to find one with the empirical **C**. Several properties of some webs could not be normalized or computed. The cascade model prohibits looping and cannibalism resulting in model s.d. = 0 and raw errors that cannot be normalized. When normalized errors are discussed, these properties of the cascade model are excluded. In many random webs, **B** = 0 eliminates meaningful food-chain and omnivory properties. High *ChnLg* and *Loop* in random webs with **B** >0 make their computation impracticable. Little Rock Lake has too many chains to compute *Omniv* or food-chain properties in a reasonable length of time for any of the models[17].

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Table 2 Comparison of empirically observed properties with niche-model means

Property	Skipwith Pond	Little Rock Lake	Bridge Brook Lake	Chesapeake Bay	Ythan Estuary	Coachella Desert	St Martin Island
T	0.040 (0.030)	0.011 (0.043)	0 (0.081)	0.32* (0.14)	0.37† (0.073)	0 (0.029)	0.17 (0.078)
I	0.92 (0.88)	0.86 (0.85)	0.68 (0.75)	0.52 (0.59)	0.54† (0.74)	0.90 (0.88)	0.69 (0.75)
B	0.040 (0.095)	0.13 (0.11)	0.32* (0.17)	0.16 (0.27)	0.090* (0.19)	0.10 (0.089)	0.14 (0.17)
GenSD	0.92 (0.81)	1.42† (1.08)	1.09 (1.02)	0.78* (1.13)	1.14 (1.18)	0.73 (0.82)	1.02 (1.09)
VulSD	0.54 (0.51)	0.61 (0.58)	0.61 (0.61)	1.12* (0.72)	1.41† (0.65)	0.60 (0.51)	0.78 (0.62)
MxSim	0.76 (0.75)	0.75* (0.69)	0.74* (0.62)	0.50 (0.49)	0.52* (0.59)	0.72 (0.76)	0.54* (0.62)
ChnLg	6.22 (7.30)		4.04 (5.75)	3.99 (4.23)	5.91 (7.37)	6.69 (7.92)	5.20 (6.73)
ChnSD	1.43 (1.56)		0.93* (1.48)	1.20 (1.34)	1.46 (1.87)	1.45 (1.63)	1.30 (1.67)
ChnNo	3.71 (4.09)		2.85 (3.10)	2.37 (2.31)	4.03 (4.36)	4.31 (4.60)	3.52 (3.86)
Loop	0.40 (0.69)	0.33 (0.47)	0.32 (0.27)	0 (0.030)	0 (0.098)	0.62 (0.73)	0 (0.21)
Cannib	0.32 (0.46)	0.14 (0.14)	0.12 (0.21)	0.032 (0.082)	0.038 (0.069)	0.66* (0.45)	0* (0.13)
Omniv	0.60 (0.75)		0.40* (0.60)	0.52 (0.41)	0.54 (0.60)	0.76 (0.77)	0.60 (0.62)

Niche-model means are in parentheses. See text for property descriptions. See Supplementary Information for complete results for all three models.
* Normalized errors between 2 and 3 model s.d.
† Normalized errors >3 model s.c.

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# Inhibitory threshold for critical-period activation in primary visual cortex

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Neuronal circuits across several systems display remarkable plasticity to sensory input during postnatal development[1–10]. Experience-dependent refinements are often restricted to well-defined critical periods in early life, but how these are established remains mostly unknown. A representative example is the loss of responsiveness in neocortex to an eye deprived of vision[2–6]. Here we show that the potential for plasticity is retained throughout life until an inhibitory threshold is attained. In mice of all ages lacking an isoform of GABA (γ-aminobutyric acid) synthetic enzyme (GAD65), as well as in immature wild-type animals before the onset of their natural critical period, benzodiazepines selectively reduced a prolonged discharge phenotype to unmask plasticity. Enhancing GABA-mediated transmission early in life rendered mutant animals insensitive to monocular deprivation as adults, similar to normal wild-type mice. Short-term presynaptic dynamics reflected a synaptic reorganization in GAD65 knockout mice after chronic diazepam treatment. A threshold level of inhibition within the visual cortex may thus trigger, once in life, an experience-dependent critical period for circuit consolidation, which may otherwise lie dormant.

The term 'critical period' refers to a cascade of functional and anatomical events in the brain, which ultimately consolidate synaptic connections into their final wiring patterns. Once activated within visual cortex, this machinery bestows a transient sensitivity to brief monocular deprivation, which is very low just after eye opening, peaks around four weeks, and rapidly declines over the next days (rats[4]; mice[5], Fig. 1b) or weeks (cat[2]; monkey[3]; human[6]). The critical period, however, is not a simple age-dependent maturational process, but is rather a series of events itself controlled in a
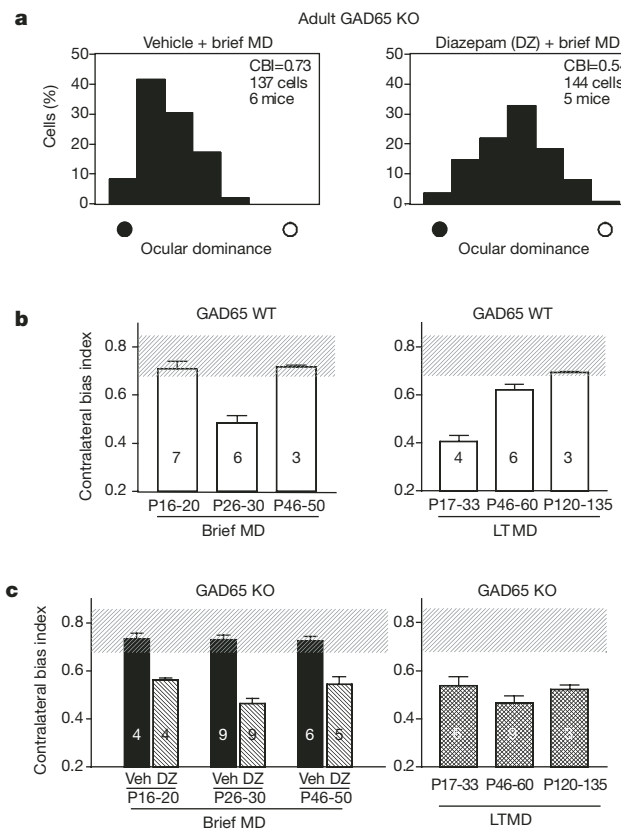
Figure 1 GAD65 knockout (KO) mice can express experience-dependent plasticity throughout life. **a**, Adult knockout mice exhibit ocular dominance shifts (diazepam versus vehicle, $P < 0.0001$, χ^2 test). **b**, Left, wild-type (WT) mice display a critical period. Brief monocular deprivation (MD) induces a significant CBI reduction only at ~P26. CBI indicates distribution bias in favour of contralateral eye (P26–30 versus non-deprived, CBI = 0.77 ± 0.02, 6 mice, $P < 0.0001$, t-test). Right, LTMD is strongly effective only early in life. Little or no effect is detected after P45 or P120 (P17–33 versus non-deprived, $P < 0.0001$, t-test). **c**, Left, brief monocular deprivation with diazepam (DZ) infusion induces plasticity of similar strength across ages in knockout mice ($P < 0.001$ within each group, t-test). Right, LTMD is similarly effective throughout life (each group versus non-deprived, CBI = 0.77 ± 0.03, 5 mice, $P < 0.0001$, t-test). Shaded region, range of non-deprived mice. The number of animals is indicated per group.

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