

# Success and its limits among structural models of complex food webs

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## Summary

1. Following the development of the relatively successful niche model, several other simple structural food web models have been proposed. These models predict the detailed structure of complex food webs given only two input parameters, the numbers of species and the number of feeding links among them.

2. The models claim different degrees of success but have not been compared consistently with each other or with the empirical data. We compared the performance of five structural models rigorously against 10 empirical food webs from a variety of aquatic and terrestrial habitats containing 25–92 species and 68–997 links.

3. All models include near-hierarchical ordering of species' consumption and have identical distributions of the number of prey of each consumer species, but differ in the extent to which species' diets are required to be contiguous and the rules used to assign feeding links.

4. The models perform similarly on a range of food-web properties, including the fraction of top, intermediate and basal species, the standard deviations of generality and connectivity and the fraction of herbivores and omnivores.

5. For other properties, including the standard deviation of vulnerability, the fraction of cannibals and species in loops, mean trophic level, path length, clustering coefficient, maximum similarity and diet discontinuity, there are significant differences in the performance of the different models.

6. While the empirical data do not support the niche model's assumption of diet contiguity, models which relax this assumption all have worse overall performance than the niche model. All the models under-estimate severely the fraction of species that are herbivores and exhibit other important failures that need to be addressed in future research.

**Key-words:** ecological networks, intervality, network structure, predator–prey network

## Introduction

Food webs describe who eats whom among species within ecosystems and have long been a central topic of ecological research (Hutchinson 1959; Dunne 2006; May, 2006; Montoya *et al.* 2006). Structure affects the function of all networks (Strogatz 2001) and it is no surprise that the structure of food webs provides valuable insight into the functioning of ecosystems (Belgrano *et al.* 2005; deRuiter *et al.* 2006; Pascual & Dunne 2006; May, 2006), as well as insight into responses of ecosystems to species loss (Dunne *et al.* 2002a; Srivasan *et al.* in press) and invasions (Mitchell & Power 2003; Torchin *et al.* 2003). Among the best-known of such insights are effects of diversity, complexity and other aspects of network structure

on population stability (May 1972), trophic cascades (Strong 1992; Pace *et al.* 1999) and biodiversity maintenance by keystone species (Paine 1980). Structural food-web models are used increasingly to investigate such insights by exploring population variability and persistence (Martinez *et al.* 2006), trophic cascades and keystone effects (Brose *et al.* 2005), as well as the consequences of prey switching among predators (Kondoh 2003) and species' body masses (Brose *et al.* 2006). These models' close fit to the structure of natural food webs helps to ensure that insights from such explorations apply to realistically complex ecosystems.

Structural models of food webs are also needed for comparative purposes because food-web properties are variable and systematically sensitive to diversity (Schoener 1989; Martinez 1994) and complexity (Williams *et al.* 2002). Without such models, direct comparisons of food-web

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**Table 1.** Source and basic properties of the empirical food webs analysed here.  $S$  is the number of trophic species,  $C$  is the connectance,  $c$  is the contiguity of the generalized niche model webs and  $g$  is the contiguity of relaxed niche model webs that, on average, have the same  $dDiet$  as the empirical web. \*The generalized niche model could not produce webs with mean  $dDiet$  equal to the empirical value for the Skipwith Pond food web

Web	Reference	$S$	$C$	$c$	$g$
Benguela	(Yodzis 1998)	29	0.241	0.866	0.816
Chesapeake	(Baird & Ulanowicz 1989)	31	0.071	0.784	0.835
Coachella	(Polis 1991)	29	0.312	0.587	0.681
Bridge Brook Lake	(Havens 1992)	25	0.171	0.995	0.994
Little Rock Lake	(Martinez 1991)	92	0.118	0.903	0.890
Reef	(Opitz 1996)	50	0.222	0.686	0.606
Shelf	(Link 2002)	79	0.225	0.836	0.694
Skipwith Pond	(Warren 1989)	25	0.315	*	0.446
St Marks	(Christian & Luczkovich 1999)	48	0.096	0.743	0.722
St Martin	(Goldwasser & Roughgarden 1993)	42	0.116	0.739	0.695

properties require observed distributions of such properties from large sets of empirical food webs with similar diversity and complexity. Given the absence of such data, scientists developed structural models to understand more clearly different types of food webs (Dunne *et al.* 2004) and to discover fundamental rules organizing trophic interactions in all ecological systems (Dunne 2006; Stouffer *et al.* 2006).

The first widely accepted model of food-web structure was the cascade model (Cohen *et al.* 1990). Its success motivated compilation of a new generation of empirical data which helped overturn the cascade model in favour of the more empirically successful niche model (Williams & Martinez 2000). Recently, three important models have attempted to improve on the niche model. First, the more complex nested hierarchy model (Cattin *et al.* 2004) tries to retain the accuracy of the niche model while also producing non-interval networks (Cohen 1978). Large complex food webs are rarely interval (Cohen & Palka 1990; Williams & Martinez 2000), which means that consumers' diets cannot be represented as an unbroken segment along an ordered sequence of all resource species in the food web. The niche model creates only interval webs, and while the nested hierarchy model corrects this important empirical deficiency, its more general success is in dispute (Bersier *et al.* 2006; Martinez & Cushing 2006; Stouffer *et al.* 2006). Secondly, the simpler generalized cascade model (Stouffer *et al.* 2005) combines the hierarchical ordering of species found in the cascade model (Cohen *et al.* 1990) with a distribution of the number of prey consumed by each predator similar to that found in the original niche model. This model reproduced successfully some features of empirical networks but has not been tested against many other network properties. The third model, the generalized niche model (Stouffer *et al.* 2006), has been developed to address the issue of intervality in the niche model but it, too, has not been tested against many other network properties. This leaves open considerable uncertainty as to which models best fit the data and therefore should be relied upon for further interpretation and exploration.

Here, we compare closely recent food-web models with the highest quality data currently available. To facilitate this comparison, we introduce a simple modification of the niche

model, the 'relaxed niche model', which allows the construction of non-interval networks within a niche model framework. Our new model is similar to the generalized niche model (Stouffer *et al.* 2006), but deviates less from the original niche model when generating non-interval webs. We then compare the original niche, nested hierarchy, generalized cascade, generalized niche and relaxed niche models using 10 high-quality empirical food webs (Table 1) by evaluating the models' performance at predicting 15 different structural properties of food webs (see Methods). All five models have as input parameters the empirical number of species  $S$  and the directed connectance (Martinez 1991)  $C = L/S^2$ , where  $L$  is the number of links in the food web. The generalized and relaxed niche models also require niche contiguity parameters  $c$  and  $g$ , respectively. We show that both the simpler generalized cascade model and the more complex nested hierarchy, generalized niche and relaxed niche models have decreased performance compared to that of the original niche model while confirming that food webs are close to interval (Williams & Martinez 2000; Stouffer *et al.* 2006). Finally, we find several deficiencies shared by all five models that suggest directions for future research.

## Methods

### STRUCTURAL MODELS

The **original niche model (ONM)** (Williams & Martinez 2000) orders all  $S$  species according to a uniformly random 'niche value' ( $n_i$ ) assigned to each species. This value places the species randomly somewhere along a 'niche dimension' from 0 to 1 ( $0 \leq n_i \leq 1$ ). A consumer eats all species whose niche values fall within a range ( $r_i$ ) whose centre ( $c_i$ ) is a uniformly random number between  $r_i/2$  and  $\min(n_i, 1 - r_i/2)$ . This ensures that  $c_i < n_i$ , that  $r_i$  fits entirely on the niche dimension and that consumers' diets are biased strongly towards resource species with niche values  $< n_i$ . The niche range  $r_i = xn_i$ , where  $0 \leq x \leq 1$  is a random variable with beta-distributed probability density function  $p(x) = \beta(1-x)^{\beta-1}$  with  $\beta = (1/2C) - 1$ . This causes species with higher  $n_i$  to tend to eat more species and ensures that the average of all species'  $r_i$  equals  $C$ , so the model creates food webs with connectance close to the  $C$  put into the model.

The **nested hierarchy model (NHM)** (Cattin *et al.* 2004) assigns each consumer's number of resource species using the same rules as the ONM, but introduces a multistage process that attempts to incorporate phylogenetic constraints and adaptation into the assignment of links between predator and prey. The first stage chooses randomly resource species  $j$  of consumer species  $i$  from among species with  $n_j < n_i$  until either consumer  $i$  obtains all its resource species or obtains a resource species  $j$ , which already has at least one consumer. When the latter occurs,  $i$  joins the group of  $j$ 's consumers. This group is defined as all consumers sharing at least one prey, with at least one consumer of that group feeding on  $j$ . Subsequent prey of  $i$  are chosen randomly from the prey of this group until either all of  $i$ 's prey have been assigned or all prey of the group have been chosen. If  $i$  still requires more prey, they are chosen randomly from all prey with no consumers and  $n_j < n_i$ . Finally, if there are not enough prey with  $n_j < n_i$  to complete  $i$ 's diet, more prey are chosen randomly from species with  $n_j > n_i$ .

The **relaxed niche model (RNM)** modifies the ONM by adding a third input called 'contiguity' ( $g$ ) that can vary from 0 to 1 and controls the niche widths relative to their maximum possible widths. When  $g = 1$ , the niche widths are at their narrowest and the model is identical to the ONM. As  $g$  is reduced towards zero, feeding ranges are widened while species that fall within the niches have lower probability of being consumed, so that non-interval networks can occur. When  $g = 0$ , niches are as wide as possible and the RNM is equivalent to the generalized cascade model described below. Formally, the maximum possible width of the feeding range is  $r_{\max} = \min(n_i + g r_i/2, 1)$ . The 'relaxed' feeding range  $r_{\text{rel}} = r_{\max} - g(r_{\max} - r_i)$  is a linear function of  $g$ , the original  $r_i$ , and  $r_{\max}$ . The probability of species  $i$  consuming species within  $r_{\text{rel}}$  is  $r_i/r_{\text{rel}}$ . The centre of the feeding range ( $c_{\text{rel}}$ ) is adjusted so that the new broader range falls in the interval  $(0, r_{\max})$ :  $c_{\text{rel}} = \max[r_{\text{rel}}/2, \min(c_i, r_{\max} - r_{\text{rel}}/2)]$ . The amount that a resource species' niche values can exceed  $n_i$  is reduced as  $r_{\text{rel}}$  increases, which prevents excessive levels of looping.

Like the RNM, the **generalized niche model (GNM)** (Stouffer *et al.* 2006) introduces a contiguity parameter  $c$  that enables the ONM's intervality to be broken. The GNM narrows species' contiguous feeding ranges by multiplying  $r_i$  by  $c$  ( $0 \leq c \leq 1$ ) and compensates by forcing additional consumption of an integer number of species closest to  $[(1 - c)r_i/S]$  outside the narrowed range but with  $n_j \leq n_i$ . This allows a species to feed further outside its feeding range than does our RNM and also creates subtle differences in how feeding ranges are located on the niche axis. In both the GNM and RNM, setting the contiguity parameters  $c$  and  $g$  to 0 and 1 make both models equivalent to the GCM and ONM, respectively.

Recent work (Stouffer *et al.* 2005) identified two features of the ONM and NHM that are crucial to the models' success: first, species' niche values form a completely ordered set; and secondly, each species has a probability of preying on species with lower niche values drawn from an approximately exponential distribution. The **generalized cascade model (GCM)** (Stouffer *et al.* 2005) is identical to the original cascade model (Cohen *et al.* 1990) modified to accept  $S$  and  $C$  as independent input parameters (Williams & Martinez 2000) except that the prey distribution has a different form and allows cannibalism. The GCM maintains the hierarchical ordering of the original cascade model between consumer  $i$  and resource  $j$ , with the exception that species can be cannibalistic i.e.  $n_j \leq n_i$ . The resources of each consumer are not required to be adjacent on the niche dimension. The modified cascade model (Williams & Martinez 2000) replaced the original cascade model's constraint of  $L/S = 2$  (Cohen *et al.* 1990) by adding  $C$  as an input parameter and using it to assign the probability ( $p$ ) of consumers feeding on any species

with lower niche value values to be  $2CS/S-1$ . This probability is  $p_i = r_i/n_i$ , which can be derived from the RNM and GNM when  $g = 0$  and  $c = 0$ , respectively. Here, we explore the properties of the GCM with beta distributed diets as was performed recently for intervality (Stouffer *et al.* 2006). The use of the beta distribution to determine the prey distribution in the GCM means that all five models compared here have the same prey distribution.

## STRUCTURAL PROPERTIES

Fifteen properties of the empirical networks are compared with the same properties in large set of networks created with each model. These properties are:  $B$ ,  $I$  and  $T$ , the proportions of basal (without prey), intermediate (with both predators and prey) and top (without predators) species, respectively; *Herbiv*, the fraction of species that consume only basal species (Dunne *et al.* 2004); *GenSD*, *VulSD* and *ConnSD*, the standard deviations of generality, vulnerability and connectivity, which measure the variation in the number of prey, predator and all links of each species, respectively. *ConnSD* extends the previously described *GenSD* and *VulSD* (Williams & Martinez 2000) to quantify in one number the 'degree distributions' analysed in detail elsewhere (Dunne *et al.* 2002b; Stouffer *et al.* 2005); *MxSim*, the mean of the maximum trophic similarity of each species (Martinez 1991); *Cannib*, the fraction of species that are cannibalistic; *Loop*, the fraction of species involved in loops other than cannibalism; *PathLen*, the mean characteristic path length between species (Watts & Strogatz 1998; Williams *et al.* 2002); *Cluster*, the mean clustering coefficient (Watts & Strogatz 1998; Williams *et al.* 2002); *dDiet*, the diet discontinuity, the proportion of triplets of consumers whose prey cannot be ordered so that the three diets are fully contiguous (Cattin *et al.* 2004); *SWTL*, the mean 'short-weighted' trophic level (Dunne *et al.* 2004; Williams & Martinez 2004a); and *Omniv*, the fraction of species that are omnivores, species that have non-integer trophic level and consume more than one species.

We use a recent measure of trophic level instead of the more conventional measure of mean food chain length (Martinez 1991; Williams & Martinez 2000) because the new measure is both more accurate (Williams & Martinez 2004a) and more computationally efficient. This allows *SWTL* and *Omniv* to be computed for even the largest empirical food webs studied here, unlike earlier studies (Williams & Martinez 2000; Cattin *et al.* 2004). This algorithm works only on energetically feasible food webs in which all species have food chains that connect to a basal species. Unfeasible networks, for example those with cannibals that have no other prey or with mutual predators that lack other prey, are eliminated from further analysis.

Each food-web property is evaluated for 1000 energetically feasible food webs generated by each particular model parameterized with the same  $S$  and  $C$  as the empirical food web. When a network is constructed with disconnected species, with trophically identical species (species with identical predators and prey) or with  $C$  more than 3% different from the empirical web's connectance, the network is rejected and the model is run again. Based on the distribution of 1000 values computed for the model, a 'model error' for a property is calculated as the normalized difference between the median model value and the empirical value. If the distribution is two-tailed, the difference is normalized by the difference between the median model value and the upper or lower bound of the central 95% of the 1000 model values of the property for empirical values higher or lower than the model's median, respectively. For one-tailed distributions, the difference is normalized by the difference between the model median and the upper or lower 95% of the distribution, depending on the direction of the distribution tail. A model error whose

absolute value is greater than one indicates that the empirical property value is not within the most likely 95% model property values and so is significantly different from the range of property values produced by the model. This procedure does not assume anything about the shape of the model property distribution and so is more accurate than the procedure based on standard errors used in earlier work that assumed normally distributed properties (Williams & Martinez 2000; Dunne *et al.* 2004; Mio *et al.* 2002).

The number of properties evaluated differs for each model. All properties are evaluated for the NHM. The error in *dDiet* is not measured for the ONM because the model produces interval webs in which *dDiet* is always zero, which lacks any variation and prevents computation of the model error for *dDiet*. Similarly, the GCM has no looping beyond cannibalism, so the model error for *Loop* cannot be computed for this model. The value of *dDiet* of the empirical food web is used to choose the value of the niche contiguity parameters *g* and *c* for the RNM and GNM, so *dDiet* is an additional input parameter for these models. The model errors of input parameters are not evaluated, and so the model error of *dDiet* is not computed for the RNM and GNM.

The overall performance of the models is sometimes evaluated by averaging errors either across all properties and all webs or across all properties in a single web. This procedure is a useful way to collapse a large amount of data and assess each model roughly, even though the properties are not statistically independent. Further work is needed to study the correlations between properties and develop a more statistically rigorous method of evaluating these models.

#### EMPIRICAL DATA

A recent study of the degree distributions of 15 empirical food webs and found that 11 of the 15 had degree distributions that matched closely the degree distributions of the structural models we are considering (Stouffer *et al.* 2005). Because our primary interest is to examine the variation across different structural models, we chose to use only the 11 empirical webs that have this degree distribution and so are reasonably well described by these models. Earlier work has argued that the four excluded data sets are not well described by the models, largely because of the methods used to assemble the food webs (Williams & Martinez 2000; Stouffer *et al.* 2005). Including these four webs would cause the large errors from these data sets to dominate the results and mask the interesting differences between the models. We selected 10 of the 11 webs for our detailed tests against the structural models described above. The eleventh web identified as being well described by the models, the UK Grassland web (Martinez *et al.* 1999), was not considered in this study because its low link density meant that the stochastic models being tested here failed consistently to produce networks without disconnected species or trophically identical species and with reasonably similar

connectance to the empirical data set. As in earlier studies, we use the trophic-species (Briand & Cohen 1984) versions of the empirical food webs. A trophic species is comprised of one or more taxa in a particular food web with exactly the same set of consumer and resource species. The webs studied here are listed in Table 1.

## Results

#### CONTIGUITY OF EMPIRICAL DATA

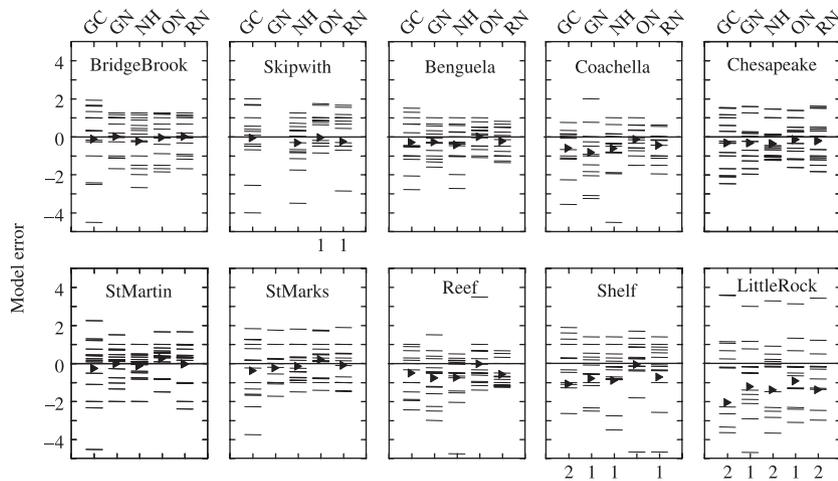
For each empirical food web, mean properties of the RNM and GNM were computed for model webs with the same *S* and *C* as the empirical web and for a range of values of the niche contiguity parameters *g* and *c*. We then estimated the values of *g* and *c* that gives model webs with the same diet discontinuity (*dDiet*) as the empirical web by interpolating between values of *g* and *c* that bracketed the empirically observed *dDiet*. The values of *g* and *c* found using this procedure are listed in Table 1. These values were assigned to their respective models to generate the 1000 webs used to test the models against the empirical webs. The mean values of *g* and *c* across the 10 webs studied here are 0.738 and 0.793, which corroborates earlier findings that, while empirical data sets are often non-interval (Cohen & Palka 1990), the ONM's assumption of intervality is surprisingly useful, due apparently to the relatively high contiguity of feeding niches (Williams & Martinez 2000; Stouffer *et al.* 2006).

#### OVERALL FIT OF THE STRUCTURAL MODELS

Given the overall statistics computed across all 10 food webs and up to 15 properties for each web (Table 2), both the mean magnitude of the errors and the range of errors, as measured by the standard deviation, are least for the ONM and greatest for the GCM. The GNM and RNM performance tends to be similar to the GCM and ONM, respectively. For all models, the fraction of errors whose magnitudes are greater than 1 is much larger than the expected value of 0.05. The number of outlying error values is least for the ONM and NHM, while the GCM has far more outlying error values than the other models. The relatively high variability in the normalized errors indicates that the empirical data have more variability than the models despite the various stochastic components of the models. This relatively low model variability was noted previously for the ONM (Williams & Martinez 2000), and model variability is even lower in all the other models explored here.

**Table 2.** Average performance of each model. Model error is the normalized difference (see text) between the empirical property value and the median value of that property in 1000 model iterations evaluated for all properties and all food webs

Model	Mean of model error	SD of model error	Fraction outside $\pm 1$ model error
Generalized Cascade (GCM)	-0.57	2.37	0.46
Generalized Niche (GNM)	-0.50	1.40	0.39
Relaxed Niche (RNM)	-0.40	1.58	0.33
Nested Hierarchy (NHM)	-0.53	1.45	0.26
Original Niche (ONM)	-0.10	1.32	0.25



**Fig. 1.** Each panel shows the model errors for each property and each model for a particular food web. Angled labels designate the models as follows: GC, generalized cascade; GN, generalized niche; NH, nested hierarchy; ON, original niche; RN, relaxed niche. The horizontal triangles show the mean model error, averaged across all properties. Numbers at the bottom of some panels show how many of a model's properties have model errors  $< -5$ .

#### FIT OF INDIVIDUAL WEBS

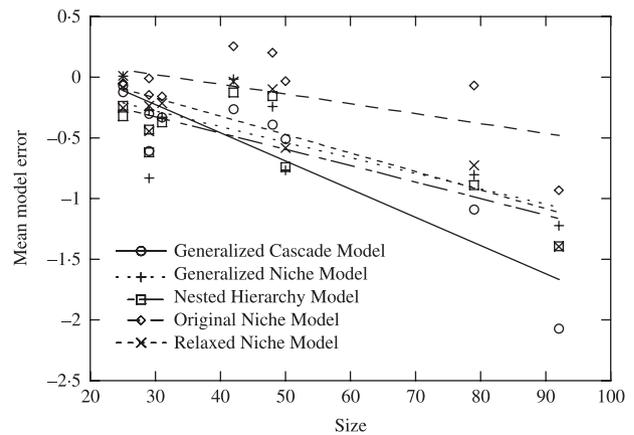
The model error of each property, along with the mean of the model errors across all properties, is shown for each model and each web in Fig. 1. The behaviour of the five models is fairly consistent across the 10 food webs. The ONM typically performs as well or better than any other model, with mean error closest to zero. The GCM or NHM usually has the mean error furthest from zero. The models always have negative mean errors with the exception of the ONM on the StMartin and StMarks webs, and many more property errors fall below  $-1$  than above  $1$ . This bias towards negative values is greatest for the GCM and least for the ONM.

The food webs in Fig. 1 are ordered from smallest at the top left to largest at the bottom right. This arrangement makes it clear that two largest food webs (Shelf and LittleRock) have more large property errors (magnitude greater than 1) than the other food webs. For most properties, larger error magnitudes occur in larger webs because the widths of the distributions of model property values shrink with increasing  $S$ .

The tendency of all the models to perform worse on larger food webs is seen again in Fig. 2, which shows that there is systematic variation in the mean normalized property error for each web as a function of food-web size. All models tend to have larger negative mean errors as the number of species in the food web grows. This scale-dependent bias is small and only marginally significant ( $P = 0.075$ ) in the ONM, larger but still marginally significant ( $P = 0.031$ ) in the GNM and more severe and more significant ( $P \leq 0.005$ ) in the other models, particularly in the GCM.

#### FIT OF INDIVIDUAL PROPERTIES

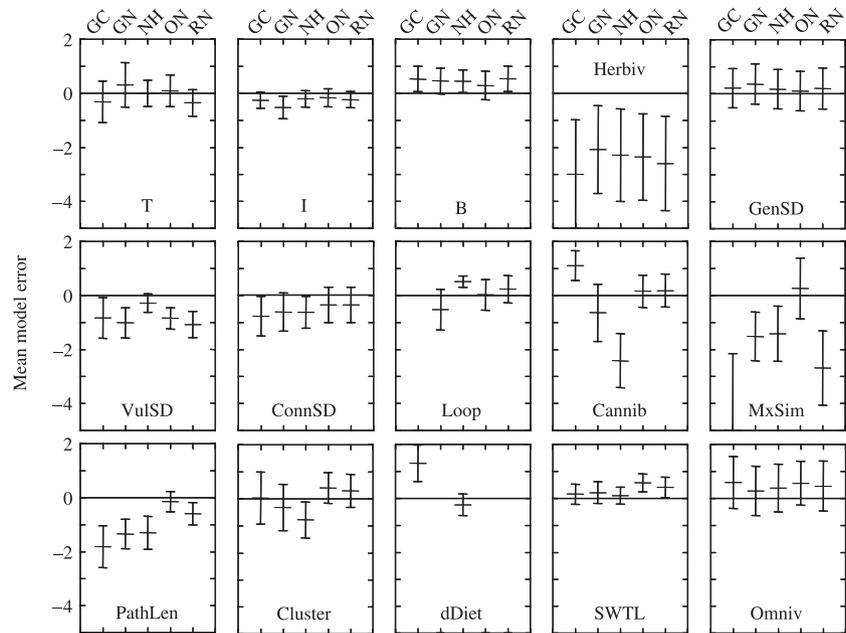
The mean model error for each property and each model, averaged across all webs, is shown in Fig. 3. Ideally, the mean model error averaged across the webs should not differ significantly from zero, although one significant difference is expected by chance among 14 or 15 properties each evaluated separately at the 95% confidence level. Significant errors occur on three of 14 properties for the ONM, six of 15



**Fig. 2.** For each model, the mean model error for each food web, averaged across all properties, plotted vs. food web size ( $S$ ). The lines show a linear regression. Original niche model ( $\diamond$ )  $r^2 = 0.26$ ,  $P = 0.075$ ; nested hierarchy model ( $\square$ )  $r^2 = 0.60$ ,  $P = 0.005$ ; relaxed niche model ( $\times$ )  $r^2 = 0.67$ ,  $P = 0.002$ ; generalized niche model ( $+$ )  $r^2 = 0.44$ ,  $P = 0.031$ ; generalized cascade model ( $\circ$ )  $r^2 = 0.80$ ,  $P < 0.001$ .

properties for the NHM, five and six of 14 properties for the GNM and RNM, respectively, and eight of 14 properties for the GCM.

For some properties (i.e.  $T$ ,  $I$ ,  $B$ ,  $GenSD$ ,  $ConnSD$ ,  $Herbiv$  and  $Omniv$ ), there is little difference in the performance of the different structural models. Estimates of the values of other properties (most notably  $VulSD$ ,  $Loop$ ,  $Cannib$ ,  $MxSim$ ,  $PathLen$ ,  $Cluster$ ,  $dDiet$  and  $SWTL$ ) display large variations among the structural models. The ONM is generally the best-performing model, the GCM is generally the worst-performing, and the NHM and RNM usually fall in between (Fig. 3). We note three exceptions to this pattern. First, the NHM is the only model with two input parameters to fit  $dDiet$ . Secondly, the short-weighted trophic level ( $SWTL$ ) is over-estimated by the ONM while the GCM and NHM are fairly accurate. Finally, the variability in the number of predators that prey on a particular species ( $VulSD$ ) is underestimated by all models, but the error of the NHM is less than for the three other models.



**Fig. 3.** Each panel shows the mean model error of a particular property, averaged across all empirical food webs, for each model. Angled labels designate the model as in Fig. 1. The error bars show  $\pm 2$  standard errors of the mean.

The poor fit of species at the second trophic level (*Herbiv*) is particularly interesting, as this ecologically important property is under-estimated seriously by all five models. The models are roughly equally inaccurate, and the under-estimation appears related to other inaccuracies. For example, increasing the fraction of species at the second trophic level (*Herbiv*) could reduce fractions at higher trophic levels and lower the mean trophic level of the food web, which could help models to avoid over-estimating *SWTL*. Similarly, as omnivores have trophic levels above 2, reducing the number of higher trophic level species could reduce the fraction of species that are omnivores and lessen the models' slight over-estimation of omnivorous species (*Omniv*). Alternatively, increasing *Herbiv* could reduce species at trophic level 1 (*B*), which the models tend to over-estimate. Overall, the under-estimation of *Herbiv* helps to drive the tendency for all five models to under-estimate properties both averaged across all webs (Table 2) and across individual food webs (Fig. 1). The strong under-estimation of species' trophic similarity (*MxSim*) by all models except the ONM (Fig. 3) exacerbates further this general under-estimation.

## Discussion

While all the models discussed here perform well compared to earlier models such as the cascade model, there are clear systematic differences in the performance of the five models. Both the simplification of the generalized cascade model and the additional complexity of the nested hierarchy model and the relaxed and generalized niche models produce models that generally perform worse than the original niche model. Our analysis also shows that, despite the relative success of all these models, they all have consistent problems when predicting the structure of empirical food webs.

Neither the additional complexity of the NHM, GNM or RNM nor the simplification of the GCM succeeds in producing a model with better overall predictive ability than the ONM. Our results also show that while the five models perform roughly equivalently when predicting some food web properties, they differ significantly when predicting other ecologically interesting features of food webs. It has been claimed (Stouffer *et al.* 2005) that any model that orders all species hierarchically, as in the cascade model, and distributes prey among consumers, as in the ONM, can predict successfully some properties of empirical food webs. Our results generally verify this claim for some properties while illuminating wide differences when predicting other ecologically interesting food-web properties. As also found recently by Stouffer *et al.* (2007), there are relatively more and less successful models among those that satisfy these two criteria. Overall, the GCM, which implements the two criteria but impose no further constraints on prey assignment, performs worse than the other models considered here. This general conclusion is also supported by analyses of network motifs depicting all possible ways in which three species can interact trophically within the food webs analysed here (Stouffer *et al.* 2007). In particular, only the ONM predicts correctly the prevalence of the eight three-species motifs that include mutual predation which supports very strongly the niche model's assumption of contiguity (Stouffer *et al.* 2007). While this very much increases the evidence favouring the niche model over alternative models, we note that none of the available models are successful in reproducing all the ecologically interesting features of the empirical data.

There are several reasons for the variability of models containing the two criteria discussed above (Stouffer *et al.* 2005), relating primarily to the rules used to assign resources to consumers. A recent study (Camacho *et al.* 2002) derived

analytical forms in the limit of  $C \ll 1$ ,  $S \gg 1$  for  $T$ ,  $I$ ,  $B$ ,  $GenSD$  and  $VulSD$  based only on the prey distribution, which is identical in the models considered here. It has also been argued that comparing degree distributions of different food webs is more informative than comparing food-web properties (Stouffer *et al.* 2005). The problem with this approach is that most other properties show considerable variation across models with identical prey distributions (Fig. 3). In other words, ecologically interesting properties such as  $MxSim$ ,  $PathLen$ ,  $Cluster$ ,  $Loop$ ,  $Cannib$ ,  $SWTL$  and  $dDiet$  depend upon details of food-web structure that are not captured by the prey distribution alone. While not explored here, one may reasonably expect varying the ordering criterion to also affect the performance of the niche model variants. For example, biasing  $n_i$  towards particular locations on the niche dimension rather than the uniformly random locations used here could reasonably be expected to systematically alter the network structures produced by these models.

The NHM introduces more complex prey-assignment rules than those used in the ONM in an attempt to simulate phylogenetic constraints and adaptation. Like the empirical food webs, the resulting model food webs break the strict interval ordering of the diets established by the ONM. The additional model complexity, while introducing a realistic level of diet discontinuity, also worsens significantly the model's performance compared to the ONM on most other properties, as noted previously (Martinez & Cushing 2006) using less sophisticated analyses. A notable exception is that the NHM better predicts  $VulSD$ . However, this is balanced somewhat by the ONM's better performance for  $ConnSD$ , thus making overall performance on connectivity distributions very similar between the two models. A more noteworthy distinction may be the NHM's improved performance for  $SWTL$  over that of the ONM. While the RNM and GNM produce broadly similar results to the NHM (see Table 2), e.g. better performance on  $SWTL$  than the ONM, the RNM and GNM have neither the NHM's improved performance on  $VulSD$  nor its poorer performance on  $Loop$ ,  $Cannib$  and  $Cluster$ . However, even adding another parameter quantifying diet contiguity and associated rules that deliberately reproduce empirical aspects of intervality further demonstrates that strategic attempts to remedy problems of the ONM create generally less empirically successful models.

The NHM is based on the observation that phylogenetically similar consumers tend to have similar diets (Ives & Godfray 2006). This causes taxonomic and trophic similarities to be correlated strongly and underlies the NHM's rules forcing consumers to have similar diets. High trophic similarity is an important property of empirical webs (Solow & Beet 1998) and may be related to the phylogenetic similarity of organisms in food webs. However, the NHM predicts poorly the occurrence of species pairs with high trophic similarity by under-estimating  $MxSim$ , whereas the ONM performs well for  $MxSim$ . This suggests that the complex rules by which the NHM simulates phylogenetic effects actually reduce the model's ability to predict phylogenetic aspects of food webs compared to the ONM. Instead of complex rules, the simpler contiguity and

placement of the ONM's feeding ranges appears to simulate more accurately phylogenetic aspects by increasing the prey shared between species and also increasing the probability that species adjacent on the niche dimension share predators, leading to higher trophic similarities.

All five models tested here consistently under-estimate empirically observed fractions of second-trophic-level species exclusively feeding on plants and detritus. Species that specialize on living or dead plant material are morphologically and physiologically distinct from omnivores and carnivores who feed on heterotrophs. Herbivores and detritivores transform plant biomass and transfer energy to the upper trophic levels of food webs. Because these critical ecological phenomena may well be tied to other failures such as the ONMs' over-estimation of trophic level, the inability of existing models to predict these numbers accurately in empirical food webs is a highly significant failure that needs to be addressed in future models. Distinguishing herbivores from detritivores may be an important first step in such explorations. Our informal observations suggest that the herbivores will be more difficult to predict than the detritivores, perhaps because consuming live plant biomass requires herbivores to cope with very potent and widespread antiherbivory adaptations and responses (Felton 2005) largely absent in detritus.

In summary, these models, and especially the original niche model, perform surprisingly well given their simple inputs and the huge variability seen among ecosystems, but all the current network models have a number of important deficiencies. Ideally, future models should perform better on larger food webs, predict herbivory more accurately, produce non-interval food webs and retain or improve upon the accuracy of the original niche model for other food-web properties. More successful new models may incorporate currently neglected ecological processes in order to address these deficiencies and improve significantly the model's performance. For example, non-linear bioenergetic models have been added recently to the structural network frameworks discussed above (Drossel *et al.* 2001, 2004; Williams & Martinez 2004b; Brose *et al.* 2005; Martinez *et al.* 2006). Adding these dynamics to niche model networks finds that the subset of niche webs with relatively large fractions of herbivores and short mean trophic levels allow unusually large numbers of species to persist dynamically (Martinez *et al.* 2006). This suggests that a combination of dynamic and structural modelling may yield more ecologically realistic networks than structural models are able to achieve alone.

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