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Article Overview
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Williams, R. J. and N. D. Martinez. 2000. Simple rules yield complex food webs. Nature. 404(6774): 180-183

Determining the causal mechanisms that generate food web topology (i.e. energetic interactions between species) has been generally unsuccessful. Here Williams and Martinez (2000) present a new model and compare its fit to actual data with that of two alternative models.

The "niche model" proposed by Williams and Martinez incorporates a "niche value" (***n***) for each individual trophic species (***S***) and a restriction on those species an individual consumes and random placement (***c***) of the niche range (Figure 1). These two conditions create biologically plausible behavior of species interaction.

The performance of the niche model was compared with a random model which created links between species probabilistically according to the directed connectance (***C***) of the actual food web being used for comparison. Performance of both the random and niche models was compared to that of a "cascade model". The "cascade model" shares the ***n*** parameter with the niche model (while termed differently it is effectively the same). The assignment of which species an individual consumes (of those with lower niche values) was determined probabilistically (p = [2***CS***/(***S***-1)]). The cascade model creates a hierarchical structure where individual trophic species only consume those with lower niche values than their own. The random placement of the niche range (***c***) in the niche model relaxes this constraint.

Empirically derived values for ***S*** and ***C*** from seven described food webs were used to generate model food webs using the random, cascade and niche models (1000 Monte Carlo replications of each set of parameters and of each model). Twelve properties of the model webs were calculated (Table 1) and compared to those of the food webs specific ***S*** and ***C's*** were drawn from. The normalized error (the sum of differences between a model's property estimate mean and the empirical value of the property divided by a model's standard deviation for that property) demonstrated that the niche model substantially outperformed the random and cascade models (Figure 2). Further, examining the niche model predictions by individual food web demonstrated the model's high overall predictive ability (Figure 3). Decomposing analysis to individual food web properties illustrated that the niche model faithfully reproduced web properties (Figure 4).

The ability of the niche model to accurately reproduce empirical food webs has three main implications for ecological research. First, it provides a robust mechanistic basis for food web topology. Second, it demonstrates that simple rules incorporating random assignment and breadth of niche (restricted solely to trophic species consumption) can accurately generate food webs. Third, it indicates those properties of food webs most sensitive to perturbation and indicates the species (in regards to trophic level) food webs are most sensitive to the loss of. These results also demonstrate the ability of simple ecological properties to generate complex patterns.

Tables and Figures

Table 1. Twelve quantified properties of model and empirical food webs. Asterisks indicate a property quantified only for model generated webs.

| Model Property | Description |
|---|---|
| *pT* | Proportion of species with no predator species |
| *pI* | Proportion of species with both predator and prey species |
| *pB* | Proportion of species with no prey species |
| *GenSD* | Standard deviation of generality (Schoener 1989) |
| *VulSD* | Standard deviation of vulnerability (Schoener 1989) |
| *MxSim* | Mean maximum niche similarity between species (Martinez 1991; Solow and Beet 1998) |
| *ChnLg* | Mean chain length from top to bottom trophic species |
| *ChnSD* | Standard deviation of chain length from top to bottom trophic species |
| *ChnNo* | Log of number of chains measured |
| *Cannib* | Proportion of species that are energetically cannibals |
| *Loop* | Proportion of species involved in loops within food webs |
| *Omniv* | Proportion of species with more than two prey species |

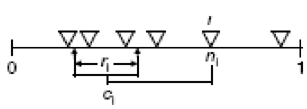


**Figure 1** Diagram of the niche model. Each of ***S*** species (for example, ***S*** = 6, each shown as an inverted triangle) is assigned a 'niche value' parameter ($n_i$) drawn uniformly from the interval [0,1]. Species ***i*** consumes all species falling in a range ($r_i$) that is placed by uniformly drawing the centre of the range ($c_i$) from [$r_i$/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 2***C*** and then multiplying that value by $n_i$ [expected $E(n) = 0.5$] 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 $\beta$ is chosen to obtain the desired expected value. We chose this form because of its simplicity and ease of calculation. The fundamental

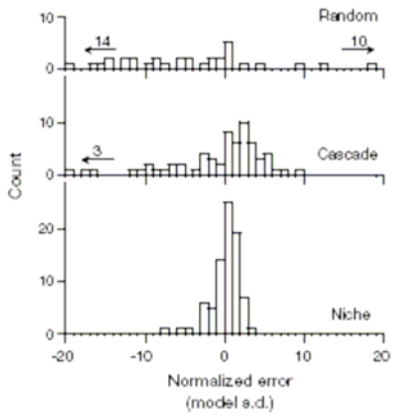


**Figure 2** Distribution of normalized errors between empirical data and model means for all properties of the random, cascade and niche models. Arrows show the number of errors beyond the *x*-axis. Of the 56 random-model means (8 properties of 7 webs), 16% are within 2 model s.d. of the empirical data. 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.

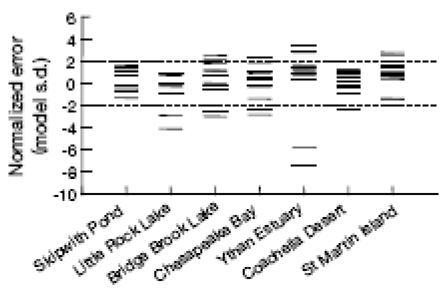


**Figure 3** The niche model's normalized errors for each property of each food web. Errors are < 2 model s.d. for all properties of the Skipwith Pond web and most properties of the other webs.

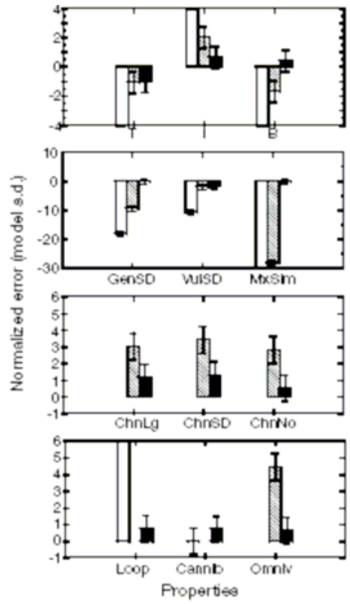


**Figure 4** Mean normalized error of each property for each model averaged across the seven food webs (Table 1). The three models are indicated by open bars (random model), hatched bars (cascade model) and filled bars (niche model). Properties are described in the text. Ideally, the across-web sample 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.

## Literature Cited


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