

Part 2: Models of Food-Web Structure

Stochastic models of food-web structure

-Two Parameters: S (species number) and C (connectance) -Randomly assign each species a niche value from 0 to 1 -Use simple rules to distribute links among species:

1) Random Model (Erdös & Rényi 1960, modified)

links assigned randomly

Goal: Create a minimal model

2) Cascade Model (Cohen et al. 1990, modified)

• species have a particular probability of feeding on species with lower rankings

Goal: Creates hierarchy of feeding that seems ecologically sensible

Stochastic models of food-web structure

-Two Parameters: S (species number) and C (connectance) -Randomly assign each species a niche value (n_i) from 0 to 1 -Use simple rules to distribute links among species:

3) Niche Model (Williams & Martinez 2000)

- each species assigned a feeding range r_i (drawn from a beta distribution)
- feeding range is assigned a center c_i (drawn from the interval $[r_i/2, n_i]$)
- species eat all taxa in their feeding range

Goals: Relaxes cascade feeding hierarchy to allow looping and cannibalism, creates "interval" feeding patterns



Species i feeds on 4 taxa including itself



More on the beta distribution





r_i is chosen from a beta
distribution parameterized*
by 2C then multiplied by n_i

Mean $n_i = 0.5$ Mean $n_i(2C) = C$

Species' generality proportional to n_i

Beta distribution is a type of exponential distribution

Testing the models against data

Data: 10 Food Webs

Original Test 2 Estuary 2 Lake 1 Pond 2 Terrestrial

Recent Test 3 Marine

Analysis: 15 Topological Food Web Properties

Types of Taxa % Top % Intermediate % Basal % Cannibals % Omnivores % Herbivores % Looping Overall Network Structure Generality SD (links to prey) Vulnerability SD (links from predators) Mean Chain Length Chain Length SD Log Chain Number Mean Maximum Trophic Similarity Mean Shortest Path Length Clustering Coefficient

Generate 1000 model webs with same S and C for each empirical web

For each property for each web & its 3 corresponding models:

- \rightarrow Calculate empirical value, model mean, and model SD
- → Normalized error = (empirical value model mean) / model SD
- \rightarrow If normalized error is ± 2, model mean is considered a good fit to data
- (i.e., if empirical values are within 2 standard deviations of the model mean)

Do any of the models generate observed topology?

7 Non-Marine Food Webs Distribution of Normalized Errors (across all webs & 12 properties)



NE > 2 : model significantly overestimated property NE < -2 : model significantly underestimated property

Properties predicted within ± 2 SD:			
Random model:	~15% (yuck)		
Cascade model:	~30% (blah)		
Niche model:	~80% (good!)		

Similar results for 3 marine webs and 15 properties





The niche model is surprisingly accurate: Simple rules yield complex food-web structure

- **Ecology:** Each community has different levels of species diversity and trophic complexity. **(S & C)**
- Energetics: Heterotrophs must eat to survive. Autotrophs introduce trophic energy into a dissipative system. (hierarchical feeding)
- Evolution: Each species may be eaten and is constrained to eat evolutionarily related species. (niche dimension & contiguity)

BENCHMARK: Allows comparison of broad and fine-scale structure of food webs.

Recent niche model variants

-Two Parameters: S (species number) and C (connectance) -Randomly assign each species a niche value from 0 to 1 -Use simple rules to distribute links among species:

4) Nested Hierarchy (Cattin et al. Nature 2004)

- assign a link to a species with a lower niche value n_i
- if that prey species is fed on by other species, next links are assigned to species in the following set: those consumed by the set of species that share at least one prey species, and at least one of them feeds on the original prey species
- when that set is exhausted, assign links to species that lack predators with lower n_i
- when that set is exhausted, assign links to species with equal or greater n_i.
- \rightarrow Link assignment constrained by a beta function parameterized by C, as in the niche model.
- → Introduces new property dDiet (diet discontinuity), the proportion of triplets of consumers whose prey cannot be ordered so that the three diets are fully contiguous (the niche model returns dDiet of 0).

Goals: Reflect "phylogenetic" constraints, allow non-contiguous feeding along niche axis

Recent niche model variants

-Two Parameters: S (species number) and C (connectance) -Randomly assign each species a niche value from 0 to 1 -Use simple rules to distribute links among species:

5) Generalized Cascade (Stouffer et al. *Ecology* 2005)

- Each species has a specific probability of consuming species with lower niche values, where probability is drawn from an exponential distribution
- → They suggest that the assignment of N_i along a single dimension and an exponential link distribution is enough to capture the central tendencies of the data.

Goal: Create a stripped down exponential model

Recent niche model variants

-Two Parameters: S (species number) and C (connectance) -Randomly assign each species a niche value from 0 to 1 -Use simple rules to distribute links among species:

6) Relaxed Niche (Williams & Martinez, in review)

- Adds niche contiguity parameter g that allows for non-interval feeding
- → For tests of the model, g is estimated so the mean model value of dDiet is close to the empirical value. Mean g across empirical webs is 0.715 (1 = complete diet contiguity).

Goal: Address non-intervality critique without complicated feeding rules

St. Marks Seagrass









Empirical data

Generalized cascade

Nested hierarchy

Niche



Original niche model outperforms other models

Mean Normalized Errors (across 11 webs)



Mean Normalized Errors (across 11 webs & 15 properties)

Model	Mean NE	NE SD	Fraction $>\pm 2$
Generalized Cascade	-2.01	5.41	0.50
Relaxed Niche	-0.94	3.66	0.28
Nested Hierarchy	-1.10	2.85	0.27
Niche	-0.22	2.66	0.27

Niche model NEs don't change as quickly with S



S

Models Summary

- Simple rules yield complex food-web structure.
- The niche model and its spin-offs (nested hierarchy, generalized cascade, relaxed niche) do a good job of predicting the fine-grained structure of empirical food webs, with a few exceptions (e.g., % Herbivores).
- Food webs for the whole range of habitat types display a fundamentally similar network structure that varies systematically with S and C, suggesting strong constraints on how species interactions are organized in communities, independent of the identity of the species.
- The niche model more closely predicts most aspects of network structure drastically better than random or cascade models and slightly better than the more recent models. It's predictions are also more robust to changes in species richness than other recent models.