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Food Web Network Structure:
Data, Models & Inference

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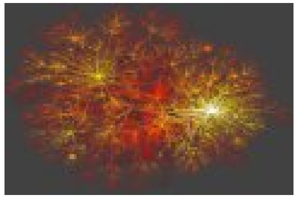
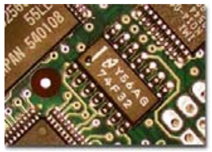
PEaCE Lab: www.foodwebs.org

Technological networks

Road maps



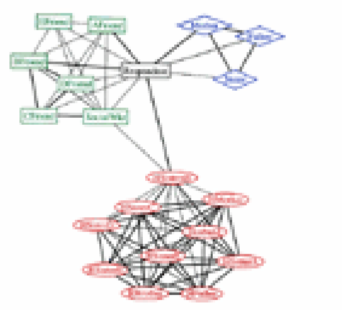
Internet connectivity



Circuit boards

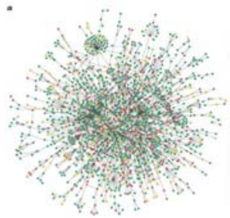
Social networks

The Kevin Bacon game

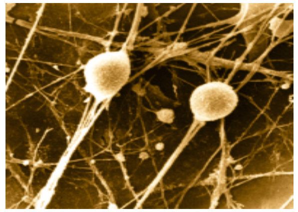


Support network for a homeless woman

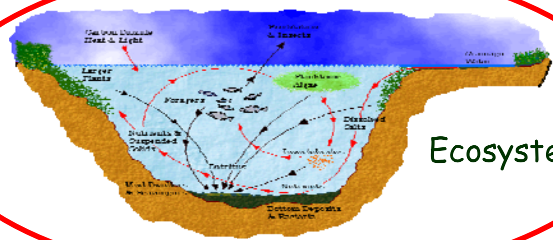
Biological networks



Protein networks

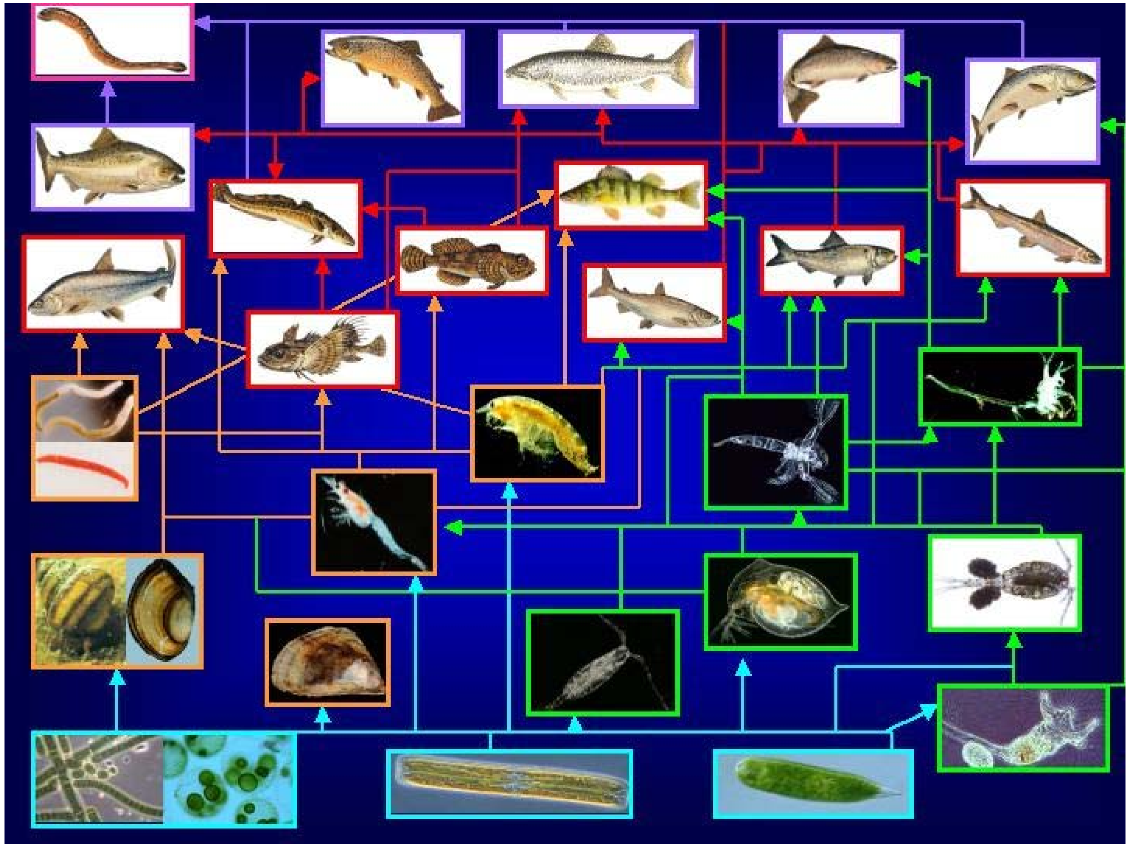


Neural networks



Ecosystems

Ecological networks: food webs



Nodes = Species/Taxa

Edges = Trophic links

→ Types of links
- -predation
- -herbivory
- -detritivory
- -parasitism
- -cannibalism

→ Directed & Undirected

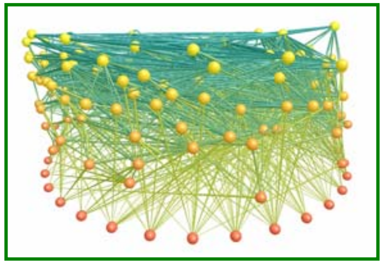
"Why is network anatomy so important to characterize? Because structure always affects function." (Strogatz 2001)

In any study of evolutionary ecology, food relations appear as one of the most important aspects of the system of animate nature. There is quite obviously much more to living communities than the raw dictum "eat or be eaten," but in order to understand the higher intricacies of any ecological system, it is most easy to start from this crudely simple point of view.

G. Evelyn Hutchinson: Address of the President to the American Society of Naturalists on Dec. 30, 1958. Published in 1959 as "Homage to Santa Rosalia, or Why are There so Many Kinds of Animal?" *The American Naturalist* 93: 145-159.

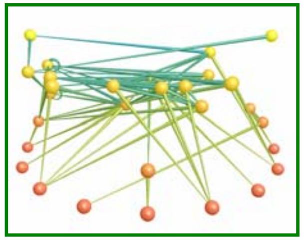
1950's Paradigm:

Complex communities MORE stable than simple communities



1970's Challenge:

Complex communities LESS stable than simple communities



Current & Future Research:

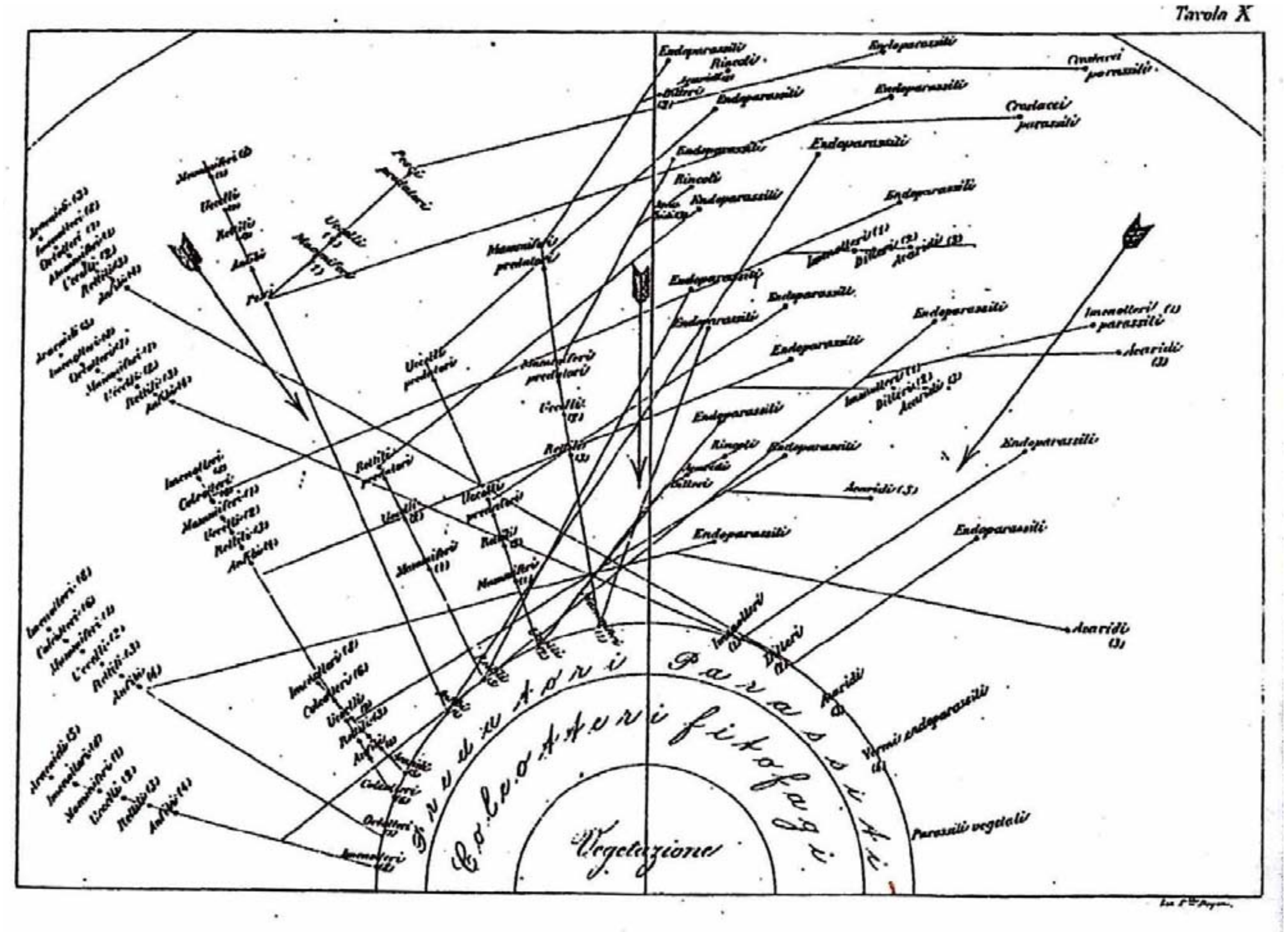
"Devious strategies" that promote stability and species coexistence

1. Food-Web Data
2. General Patterns Across Webs?
3. Network Structural Models
4. Confronting Models with Data
5. Case Study: Ancient Food Webs

1. Food-Web Data

Earliest known graph of feeding relations

Lorenzo Camerano, 1880

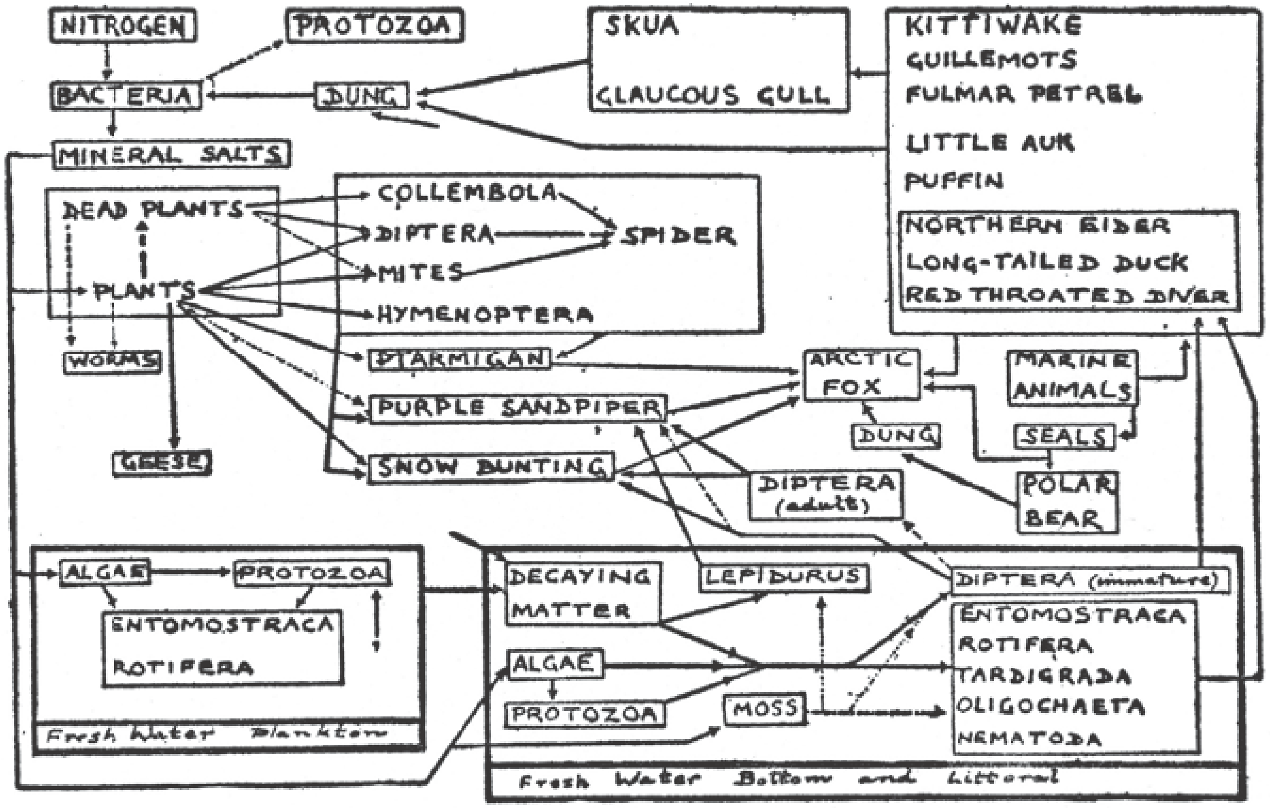


Network of 15 taxa:

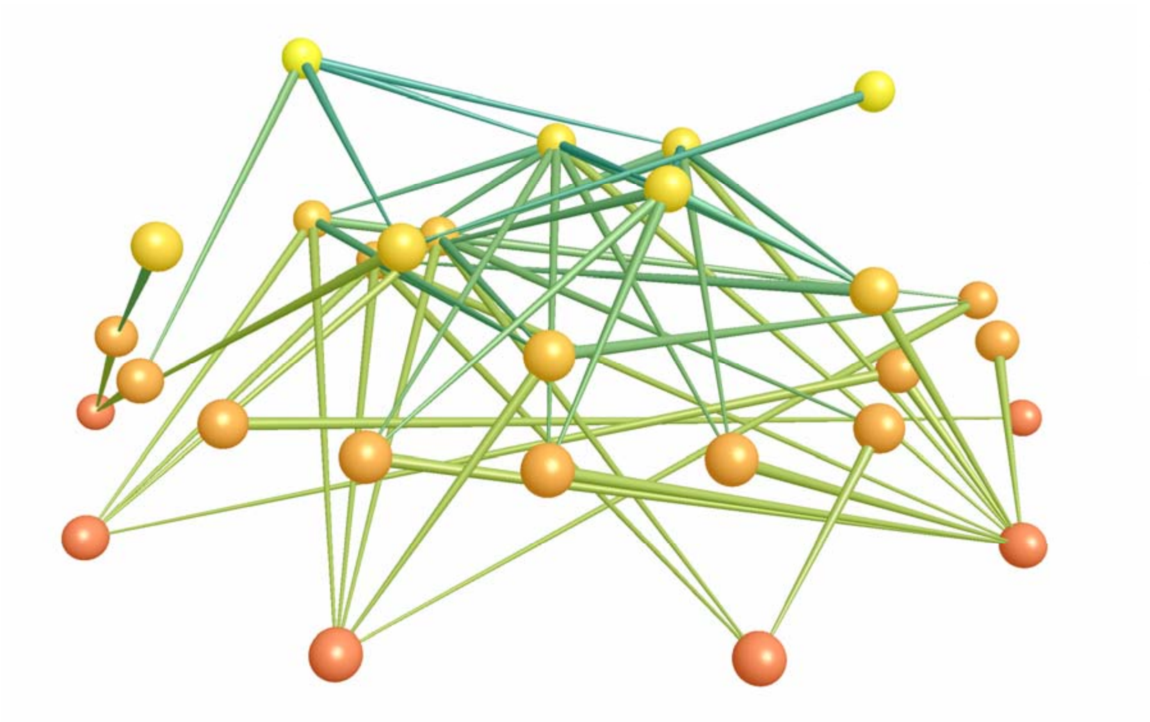
- Amphibians
- Reptiles
- Fish
- Birds
- Mammals
- Worms
- Crustaceans
- Spiders
- Various insects
- Plants
- Parasitic plants

1920s-1980s: "First Generation" food-web data

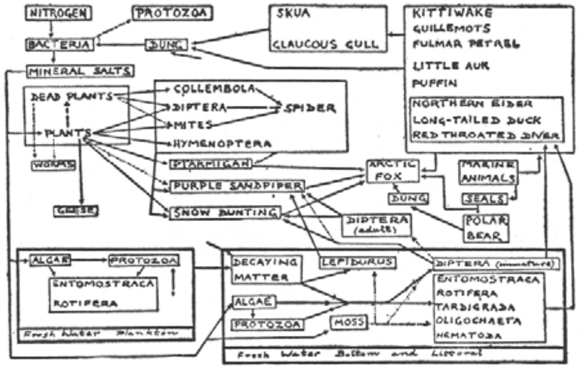
Summerhayes & Elton 1923: Food web of Bear Island



ECOWeB #22: Bear Island



1 bacteria, 4 autotrophs, 13 invertebrates, 6 birds, 4 mammals



S (# taxa) = 28
L (# links) = 59
L/S (links/species) = 2.1
C (connectance; L/S^2) = 0.075
TL (mean trophic level) = 2.07

Directed Connectance (C): Proportion of possible links (S^2) that are realized (L)

Upper Triangular Connectance: $C = L/[S(S-1)/2]$ *assumption of no cycles*

ECOWeB (1989): A collection of 200+ food webs, mostly mined from the literature, S < 50, mean S ~15

Data formats for binary webs

6 taxa with 12 links: 1 & 2 are basal; 3 eats 1,2,3; 4 eats 1,2; 5 eats 3,5,6; 6 eats 2,4,5,6

Partial Matrix

	3	4	5	6
1	1	1	0	0
2	1	1	0	1
3	1	0	1	0
4	0	0	0	1
5	0	0	1	1
6	0	0	1	1

Full Matrix

	1	2	3	4	5	6
1	0	0	1	1	0	0
2	0	0	1	1	0	1
3	0	0	1	0	1	0
4	0	0	0	0	0	1
5	0	0	0	0	1	1
6	0	0	0	0	1	1

2 Column

3	1
3	2
3	3
4	1
4	2
5	3
5	5
5	6
6	2
6	4
6	5
6	6

3 Column

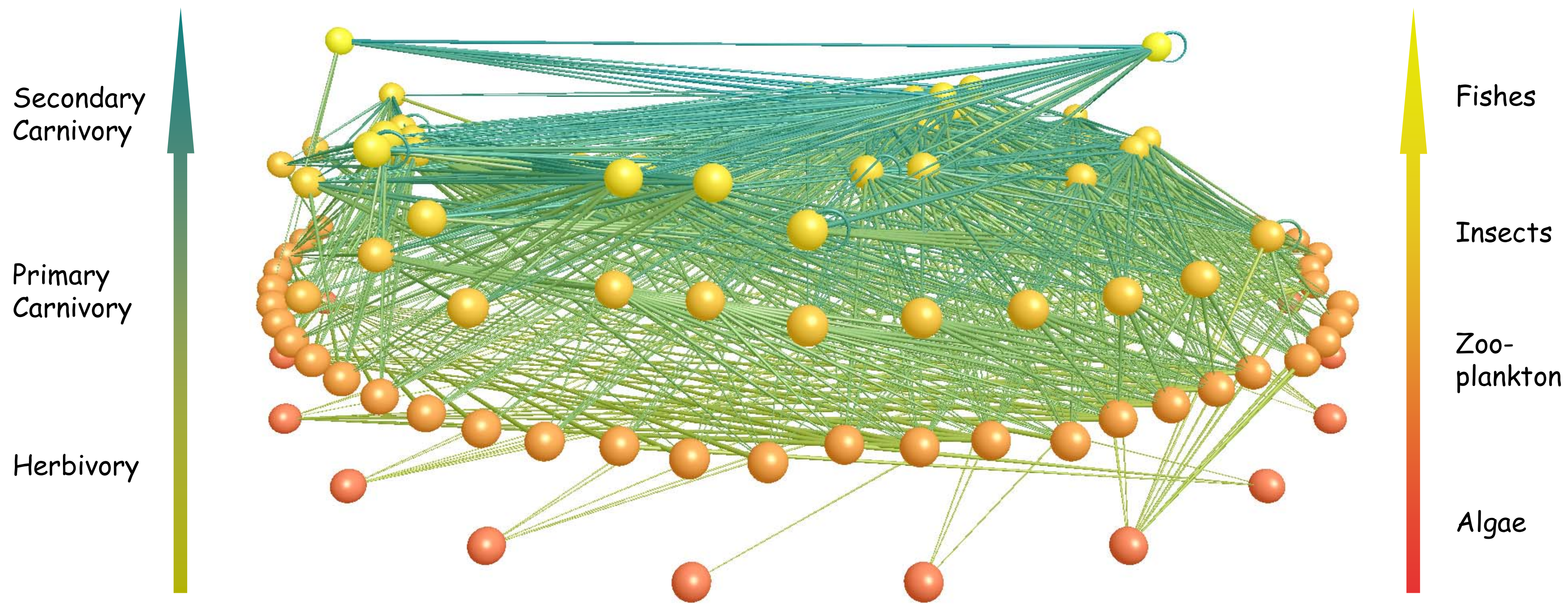
3	1	3
4	1	2
5	3	
5	5	6
6	2	
6	4	6

LOOPS/CYCLES:

- -3,4,5 have cannibalistic links (1 link cycles)
- -5 eats 6 and 6 eats 5 (2 link cycle)

1990s-present: “Second Generation” food-web data

Food Web of Little Rock Lake, Wisconsin



S = 92, L = 997, L/S = 11, C = 0.12, TL = 2.40

Original species = 181 (11 fishes, 110 invertebrates, 59 autotrophs, 1 detritus)

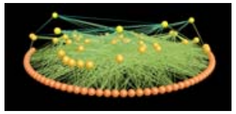
Martinez 1991

Examples of currently used datasets

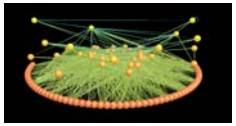
S ~ 25 to 180, C ~ 0.03 to 0.3

Stream Webs

Canton Creek

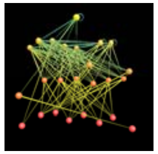


Stony Stream

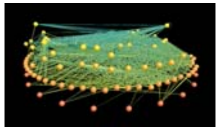


Lake & Pond Webs

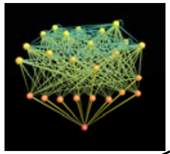
Bridge Brook Lake



Little Rock Lake

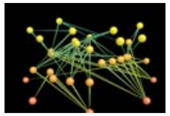


Skipwith Pond

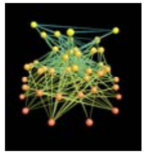


Estuary Webs

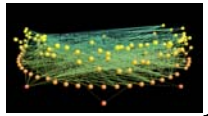
Chesapeake Bay



St. Marks Seagrass

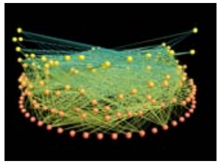


Ythan Estuary

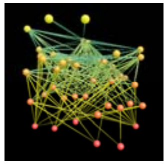


Terrestrial Webs

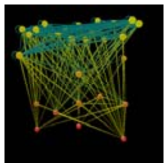
El Verde Rainforest



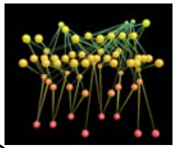
St. Martin Island



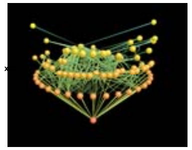
Coachella Valley



Grassland

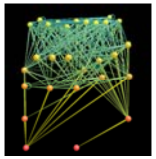


Scotch Broom

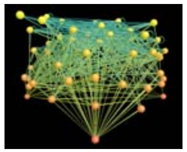


Marine Webs

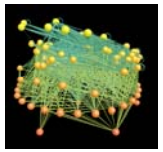
Benguela



Caribbean Reef

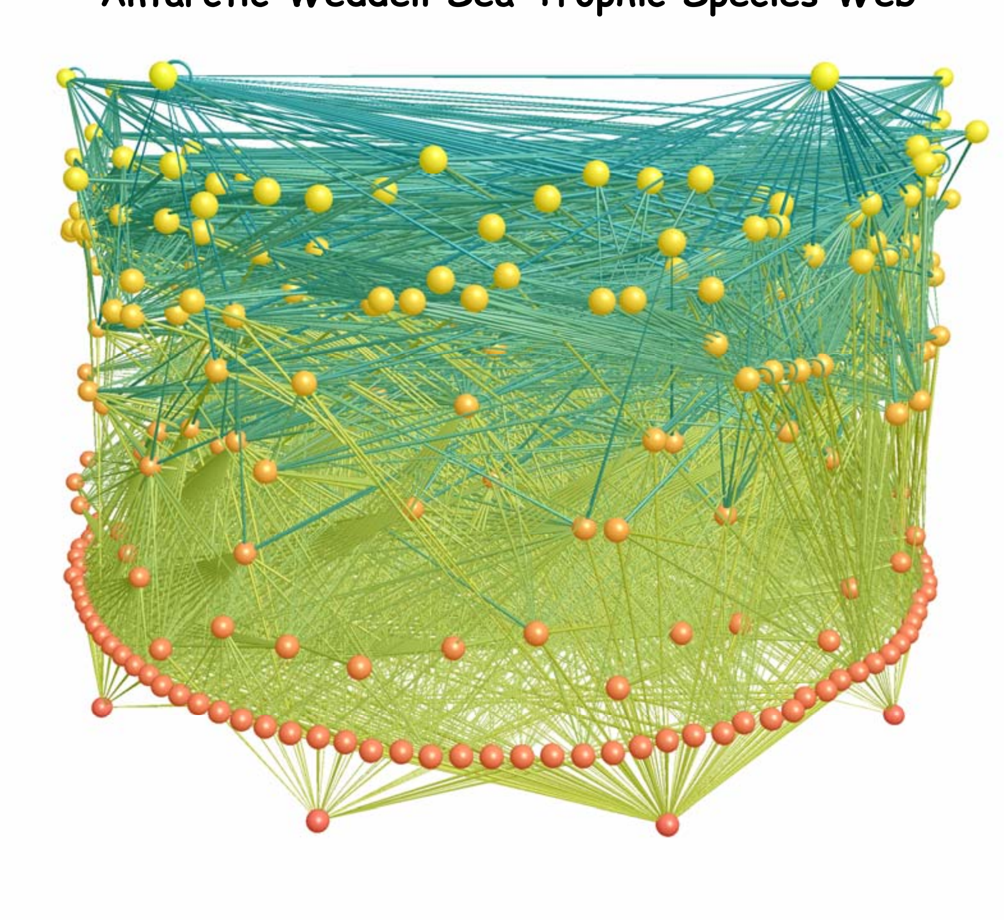


NE US Shelf



2008 and beyond: "Third Generation" food-web data

Antarctic Weddell Sea Trophic Species Web



Data compiled by Ute Jacob

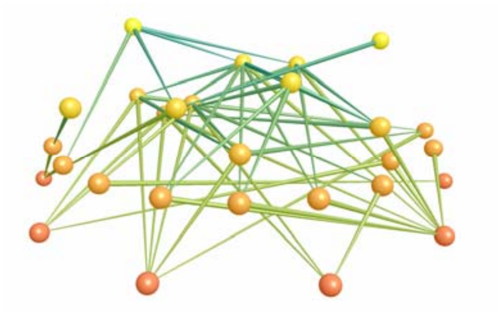
Highly & Evenly Resolved

Original species = 492

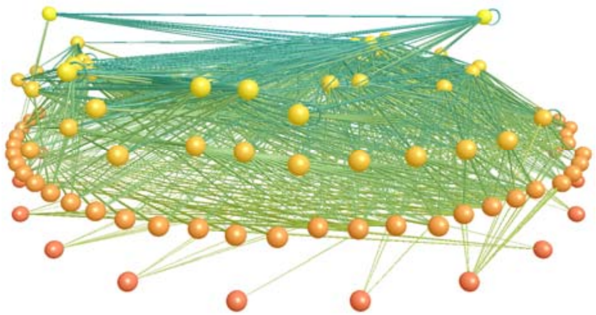
62 autotrophs
4 mixotrophs
345 invertebrates
48 ectotherm vertebrates
29 endotherm vertebrates
3 detritus
1 bacteria

S = 290
L = 7200
L/S = 24.8
C = 0.086
Mean TL = 3.79

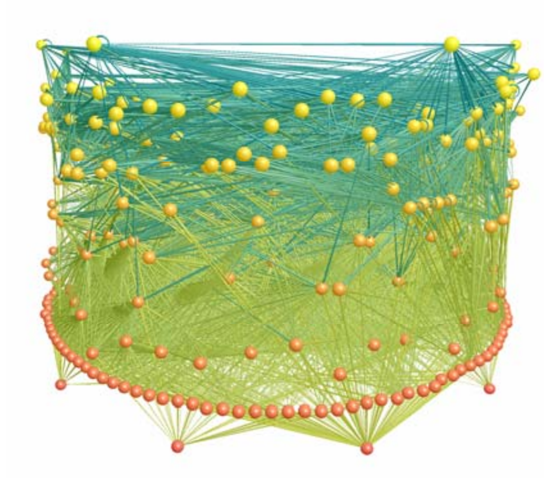
1923



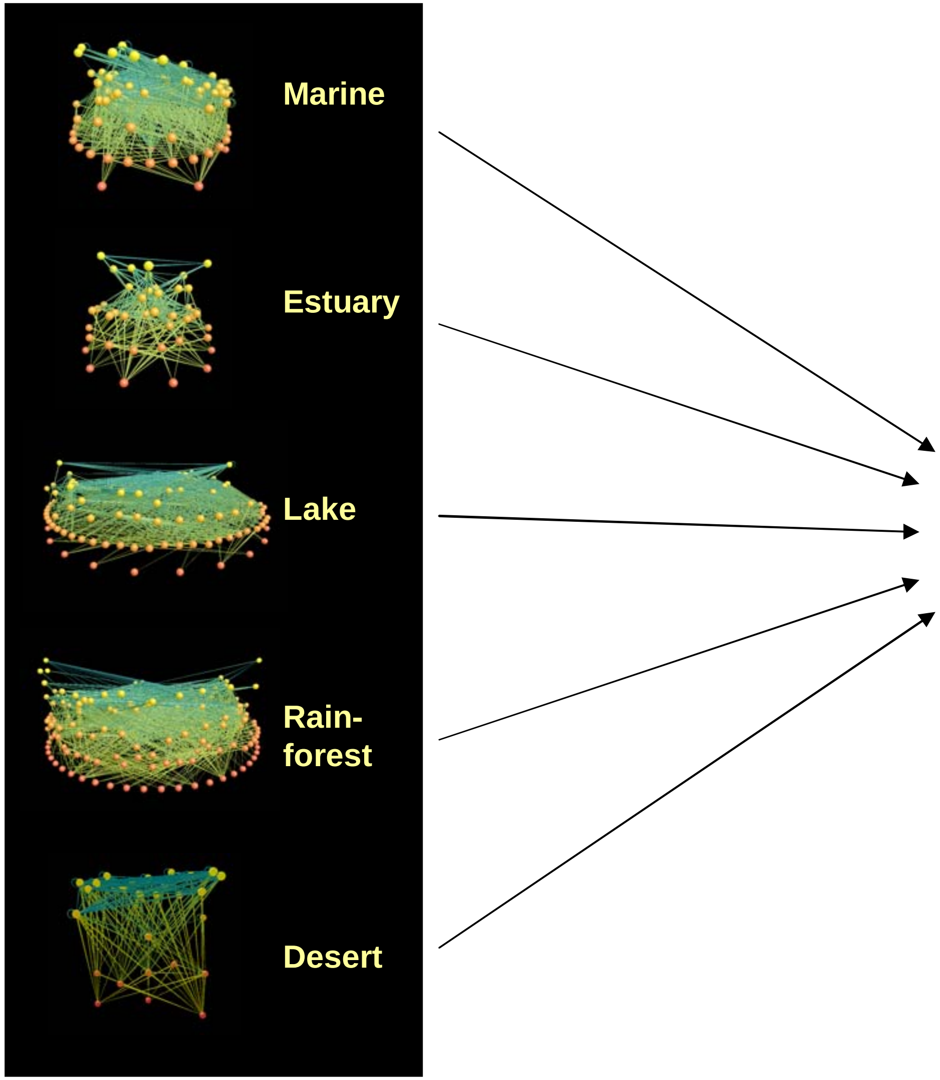
1991



2008

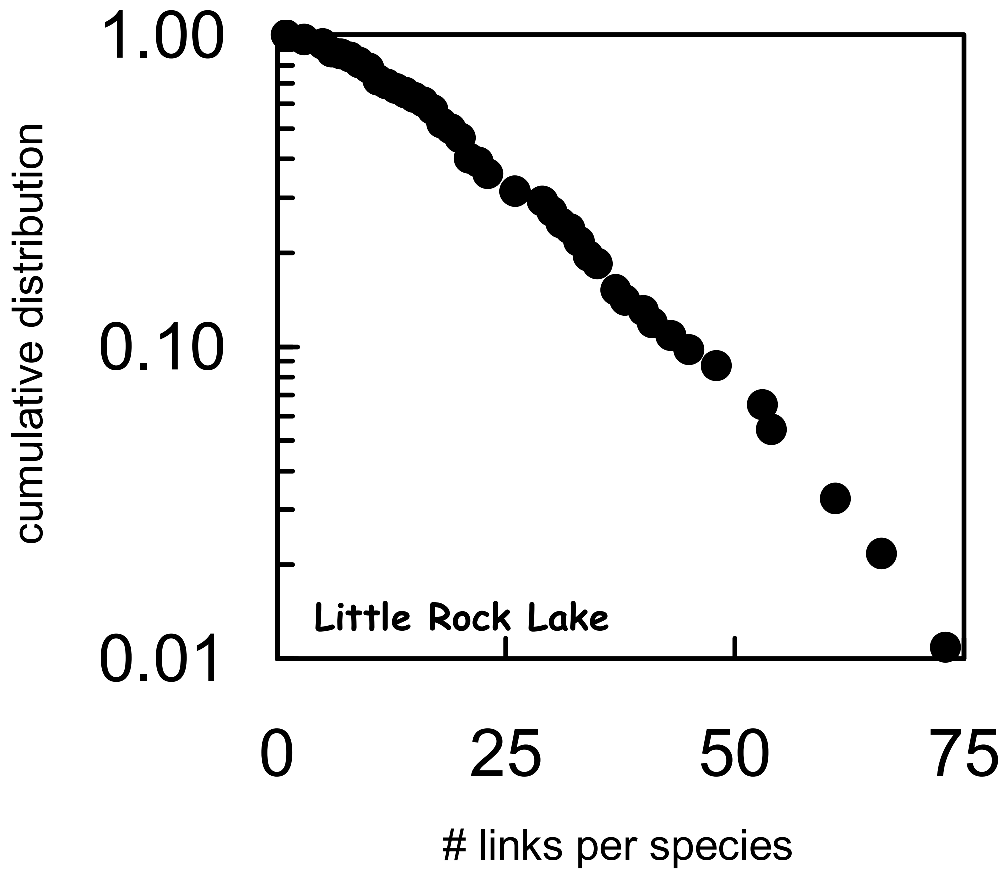


2. General Patterns Across Webs?

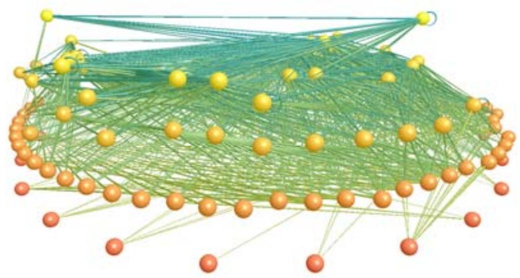


Apparent Complexity

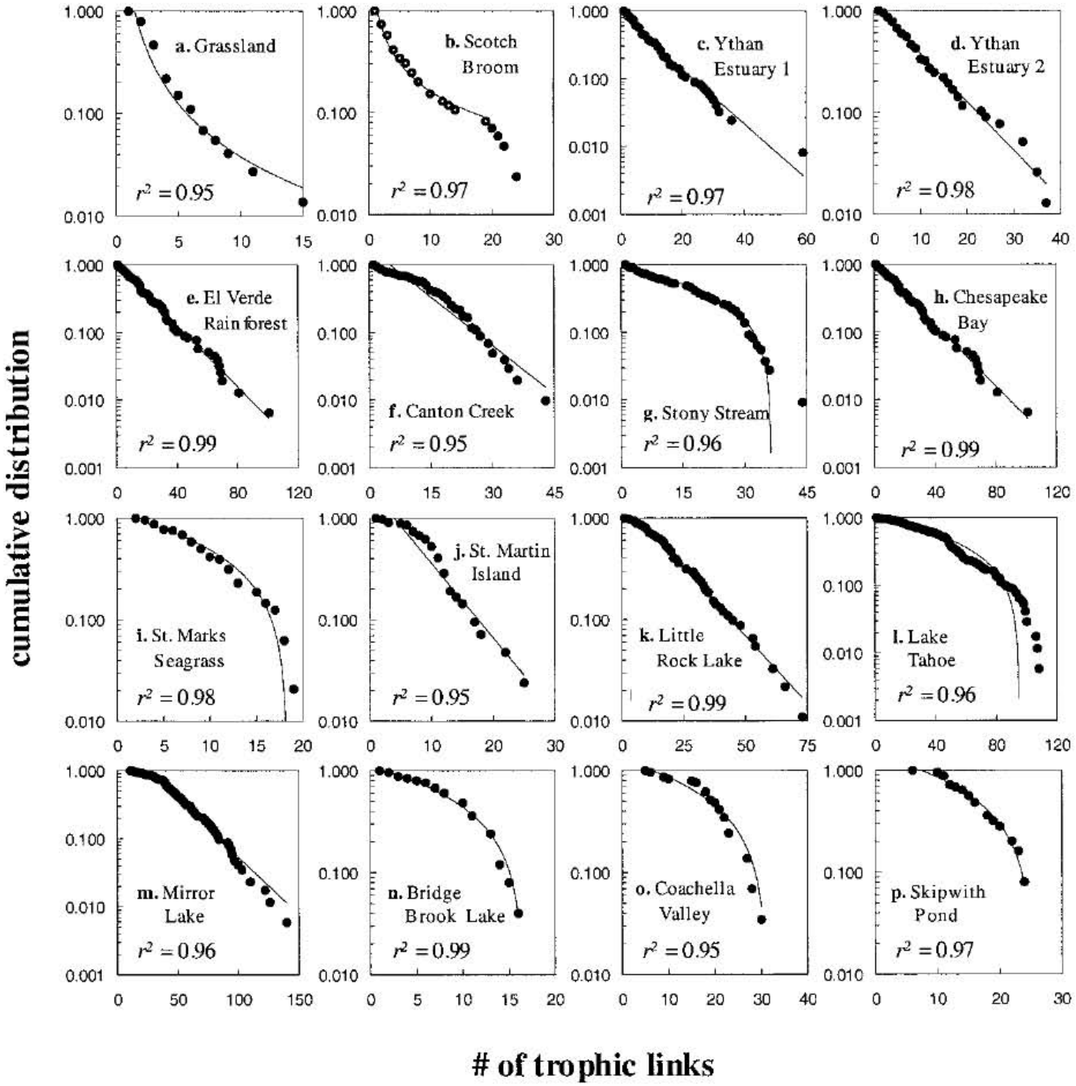
Beyond *S* and *C*: Link distributions



Exponential, not Power Law

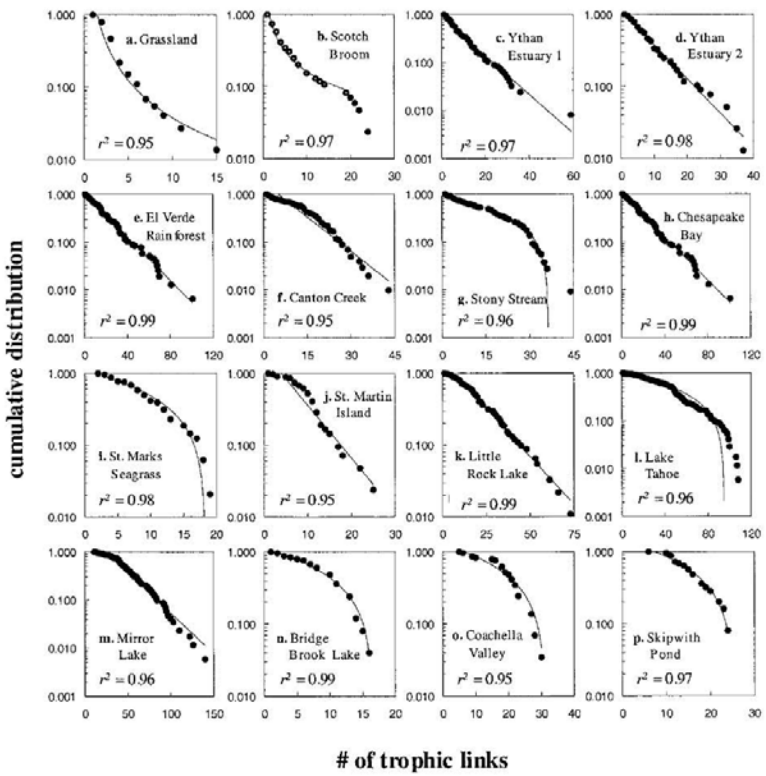


Raw data for 16 webs

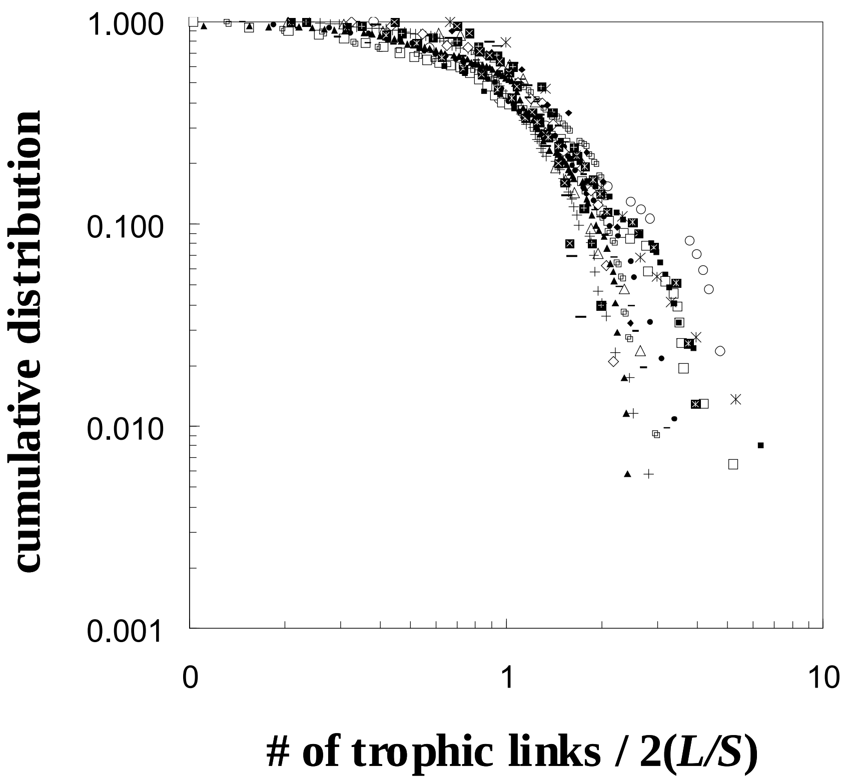


Apparent complexity → Underlying simplicity

Raw data for 16 webs



Normalized data for 16 webs



Dunne *et al.* 2002

Other properties?

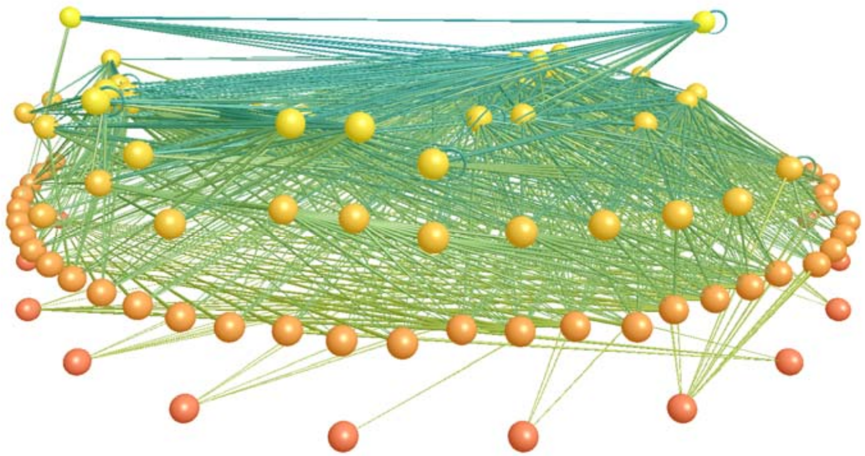
Types of Organisms:

% Top spp.	= 1.1
% Intermediate spp.	= 85.9
% Basal spp.	= 13.0
% Cannibal spp.	= 14.1
% Herbivore spp.	= 37.0
% Omnivore sp.	= 39.1
% Species in loops	= 26.1

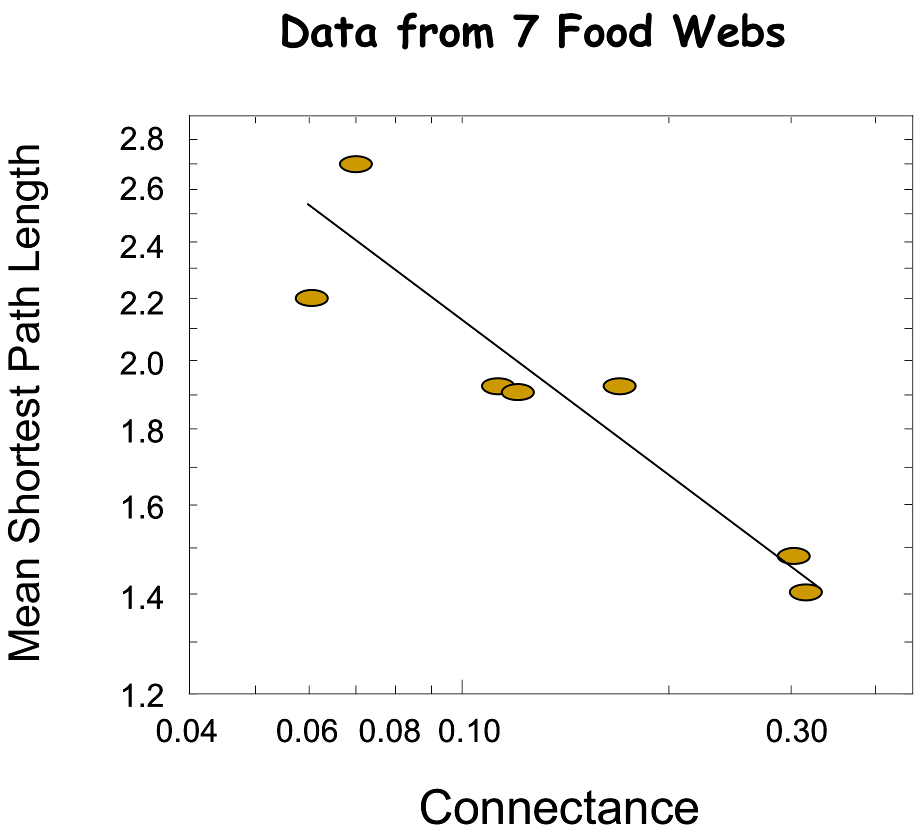
Linkage Metrics:

Mean food chain length	= 7.28
SD food chain length	= 1.31
Log number of chains	= 5.75
Mean trophic level	= 2.40
Mean max. trophic simil.	= 0.74
SD vulnerability (#pred.)	= 0.60
SD generality (#prey)	= 1.42
SD links (#total links)	= 0.71
Mean shortest path	= 1.91
Clustering coefficient	= 0.18

Little Rock Lake



Scale dependence with S & L



Williams *et al.* 2002

3. Network Structure Models

Empirical regularities provide modeling opportunities

Simple, stochastic, single-dimensional models of food-web structure

Explain "*the phenomenology of observed food web structure, using a minimum of hypotheses*" (Cohen & Newman 1985)

1) Two Parameters: ***S*** (species richness) and ***C*** (connectance)
2) Assign each species i a uniform random "niche value" n_i along a "niche dimension" of 0 to 1 (i.e., $0 \leq n_i \leq 1$)
3) Simple rules distribute links from consumers (predators) to resources (prey)

Cascade model (Cohen & Newman 1985)

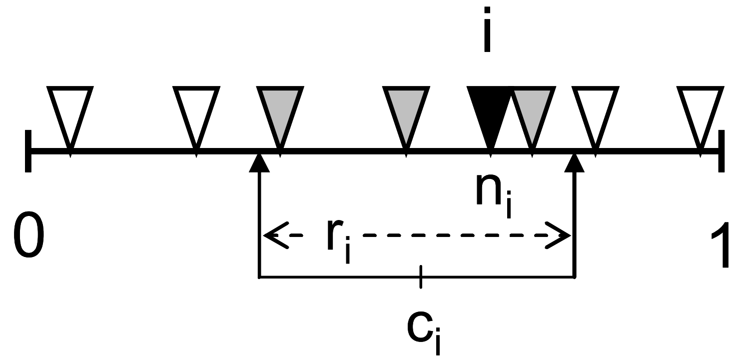
Link distribution rules:

→ Each species i has probability P = 2CS/(S-1) of consuming resource species j with lower niche values ($n_j < n_i$)

Effect of link distribution rules:

→ Creates strict hierarchy of feeding (cannibalism & longer cycles prohibited)

Niche model (Williams & Martinez 2000)



Link distribution rules:

→ Species i is assigned a feeding range r_i

- drawn from beta distribution

→ The center c_i of the feeding range r_i is a uniform random number between $r_i/2$ and min(n_i, $1-r_i/2$)

- $c_i < n_i$
- r_i placed entirely on the niche dimension
- consumers' diets biased towards resources with lower n_i

→ Species i feeds on all species that fall within the feeding range r_i

Effect of link distribution rules:

→ The feeding hierarchy is slightly relaxed (cycles can occur)

→ Food webs are "interval" (species feed on contiguous sets of species along a single dimension)

→ The beta distribution generates exponential-type degree distributions

Nested hierarchy model (Cattin *et al.* 2004)

Link distribution rules:

→ Each consumer i's number of resource species j assigned using beta distribution

→ Resources j chosen randomly from species with $n_j < n_i$ until all links are assigned or a j is obtained which already has at least one consumer

→ Species i links to j and joins j's "consumer group"

→ Subsequent j chosen randomly from the set of j of this group until all of i's links are assigned or all j of the consumer group have been chosen

→ Subsequent j chosen from remaining species with no consumers and $n_j < n_i$

→ Subsequent j chosen randomly from species with $n_j \geq n_i$

Effect of link distribution rules:

→ Rules meant to mimic phylogenetic effects

→ Food webs are not "interval"

→ Hierarchy relaxed in principle, in practice rarely violated

Generalized cascade model (Stouffer et al. 2005)

Link distribution rules:

→ Species i consumes resources species j with $n_j \leq n_i$ with a probability equal to a random number with mean ***2C*** drawn from a beta distribution

Effect of link distribution rules:

→ Create a simple, non-interval, beta-distributed hierarchical model that allows cannibalism

'Relaxed' niche models

Link distribution rules:

→ Same as niche model, but allow for gaps in a slightly expanded feeding range or for links external to feeding range

1. Generalized niche model (Stouffer et al. 2005)
2. Relaxed niche model (Williams & Martinez 2008)
3. Minimum potential niche model (Allesina et al. 2008)

Effect of link distribution rules:

→ Relax the intervality constraint of the niche model

Random models

Link distribution rules:

→ Distribute links randomly

1. Random model (Williams & Martinez 2000): $P = C$
2. Random beta model (Dunne *et al.* 2008): beta distribution

Effect of link distribution rules:

→ Minimal constraints

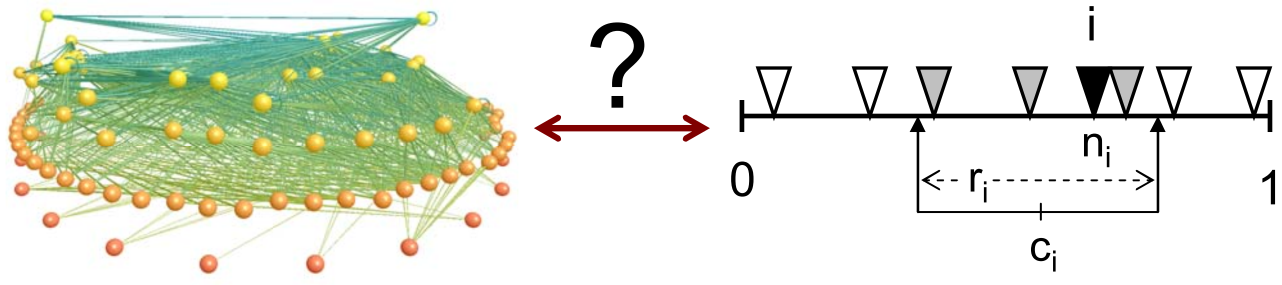
1. Random: no hierarchy, no intervality, no beta distribution
2. Random beta: no hierarchy, no intervality

Summary of model constraints

Model	beta distribution	intervality	hierarchical feeding: hierarchy	hierarchical feeding: exceptions
Random	no	no	no	—
Random beta	yes	no	no	—
Cascade	no	no	yes	no
Generalized cascade	yes	no	yes	$n_j = n_i$
Niche	yes	yes	yes	$n_j \geq n_i$
Relaxed niche	yes	no*	yes	$n_j \geq n_i$
Nested hierarchy	yes	no	yes	$n_j \geq n_i$*

4. Confronting Models with Data

Inference methods



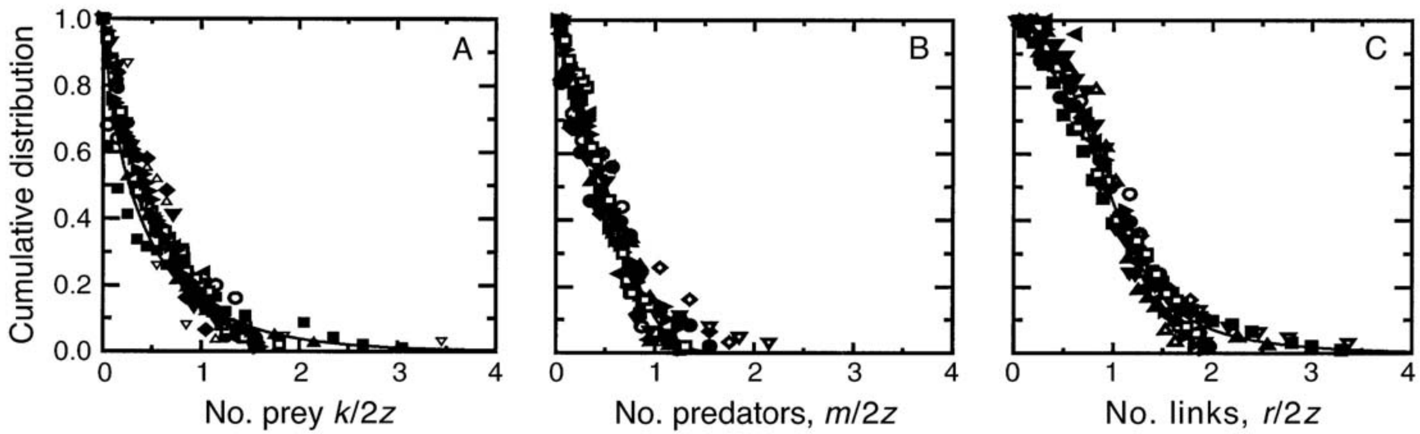
1. Degree distribution
2. Suite of properties
3. Likelihood

1) Degree distribution (Camacho *et al.* 2002, Stouffer *et al.* 2005)

Data Normalization & Analytical Analyses

TABLE 2. Summary of the analytical expressions obtained for the niche model in the limits $S \gg 1$ and $C \ll 1$. These properties also hold for the nested-hierarchy and generalized cascade models in the same limits.

Property	Expression
Distribution of number of prey	$p_{prey}(k) = (1/2z)E_1(k/2z)$
Distribution of number of predators	$p_{pred}(m) = (1/2z)\gamma(m+1, 2z)$
Distribution of number of links	$p_{links}(r) = \int_0^r p_{prey}(t)p_{pred}(r-t)dt$ $= 1/(2z)^2\int_0^r E_1(t/2z)\gamma(r-t+1, 2z)dt$
Fraction of top species	$T = (1-e^{-2z})/2z$
Fraction of basal species	$B = \ln(1+2z)/2z$
Standard deviation of the vulnerability	$\sigma_V = \sqrt{1/3 + 1/z}$
Standard deviation of the generality	$\sigma_G = \sqrt{8/(3+6C) - 1}$



'Degree distribution' summary

Model	beta distribution	intervality	hierarchical feeding	
			hierarchy	exceptions
~~Random~~	~~no~~	~~no~~	~~no~~	~~—~~
Random beta	yes	no	no	—
~~Cascade~~	~~no~~	~~no~~	~~yes~~	~~no~~
√ Generalized cascade	yes	no	yes	$n_j = n_i$
√ Niche	yes	yes	yes	$n_j \geq n_i$
Relaxed niche	yes	no*	yes	$n_j \geq n_i$
√ Nested hierarchy	yes	no	yes	$n_j \geq n_i$*

2) Suite of properties (Williams & Martinez 2000)

Beyond degree distribution…

- **Assess:** a suite of single-number structural properties
- **Generate:** sets of 1000 model webs with same ***S*** & ***C*** as empirical webs
- **Evaluate:** how well does the model perform?

→ normalized model error = (empirical value – model mean) / (model median value – value at upper or lower 95% boundary of model distr.)

→ MEs ≤ |1| show 'good' fit of model mean to empirical value

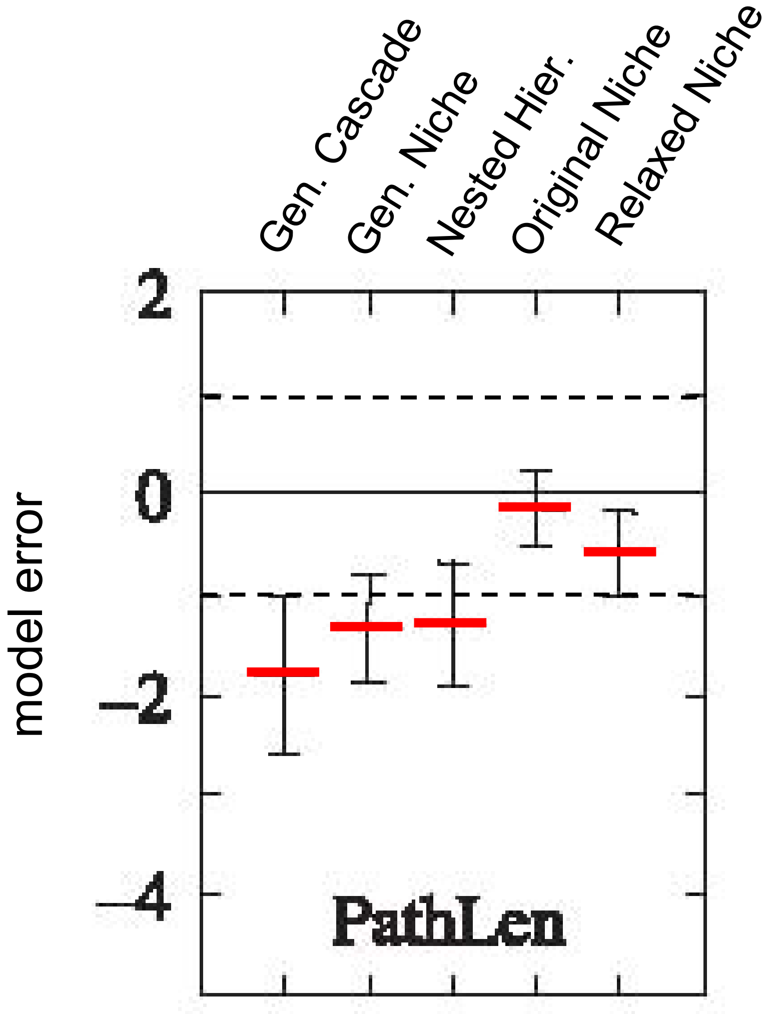
Types of Organisms:

% Top spp.
% Intermediate spp.
% Basal spp.
% Cannibal spp.
% Herbivore spp.
% Omnivore spp.
% Species in loops

Linkage Metrics:

Mean food chain length
SD food chain length
Log number of chains
Mean trophic level
Mean max. trophic sim.
SD vulnerability (#pred.)
SD generality (#prey)
SD links (#total links)
Mean shortest path
Clustering coefficient

Recent test (Williams & Martinez 2008: 10 webs, 5 models)

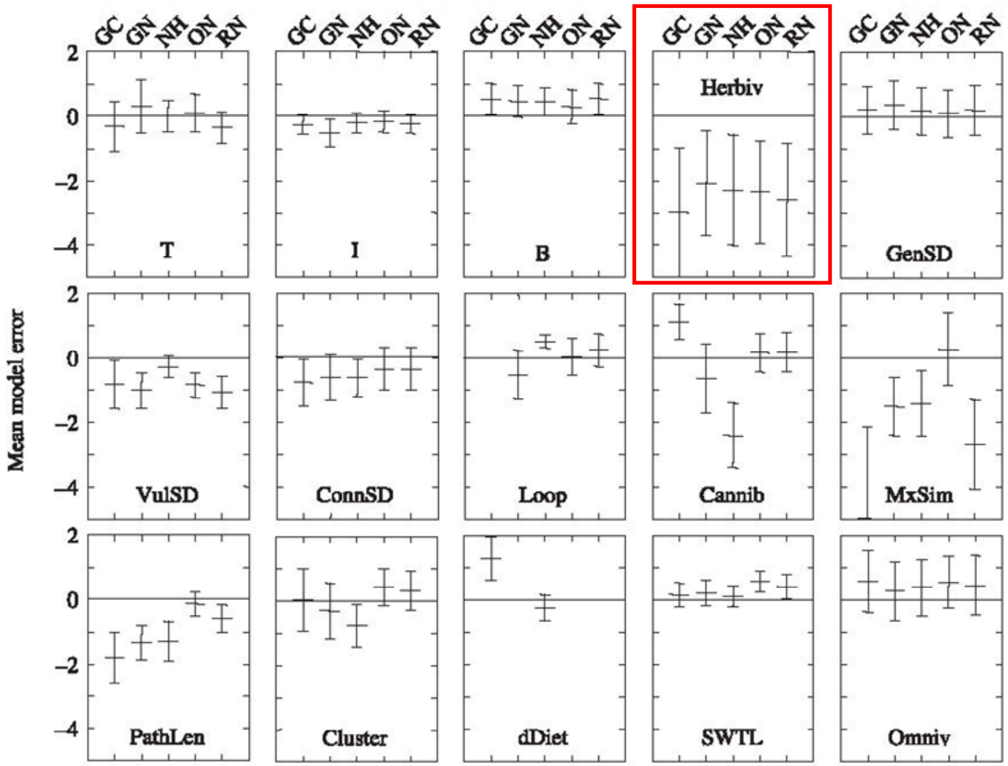


Path Length:

→ The average of the shortest chain of links between each pair of species.

→ Most models significantly underestimate path length.

10 webs, 5 models, 15 properties



Summary Stats

	ME mean	ME SD	% ME > |1|
Gen Cas	-0.57	2.37	46%
Gen Nic	-0.50	1.40	39%
Nes Hier	-0.53	1.45	26%
Niche	**-0.10**	**1.32**	**25%**
Rel Nic	-0.40	1.58	33%

1) Mean ME ≤ |1| for all models: effect of hierarchy + beta distribution constraints.

2) Niche: lowest ME mean & SD, most properties closest to 0, fewest properties >|1|.

3) All models drastically underestimate herbivory/detritivory.

'Suite of properties' summary

Model	beta distribution	intervality	hierarchical feeding: hierarchy	hierarchical feeding: exceptions
~~Random~~	~~no~~	~~no~~	~~no~~	~~—~~
~~Random beta~~	~~yes~~	~~no~~	~~no~~	~~—~~
~~Cascade~~	~~no~~	~~no~~	~~yes~~	~~no~~
Generalized cascade	yes	no	yes	$n_j = n_i$
Niche	yes	yes	yes	$n_j \geq n_i$
Relaxed niche	yes	no*	yes	$n_j \geq n_i$
Nested hierarchy	yes	no	yes	$n_j \geq n_i$*

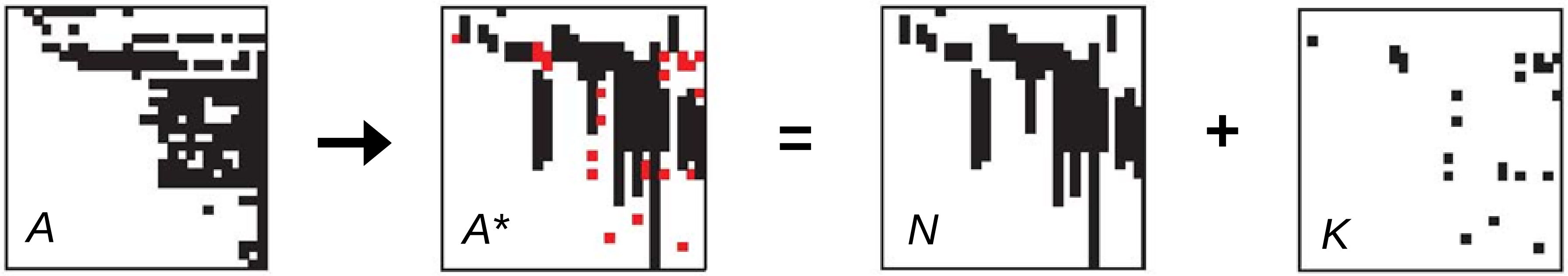
3) Likelihood: topology as a whole (Allesina *et al.* 2008)

1) 3 models (Cascade, Niche, Nested hierarchy) and 10 datasets considered.

2) All empirical webs have links that violate assumptions of each model.

3) Use a genetic algorithm to order species in datasets to minimize violating links for each model (Matrix *A*→ *A**).

4) Split datasets into links compatible with the model of interest (Matrix *N*), and links incompatible with the model (Matrix *K*).



5) Calculate probability of obtaining Matrix *N* with the model and Matrix *K* with a random graph (this introduces a 3rd parameter to models beyond *S* and *C*).

6) Product of those probabilities gives a "total likelihood" (Tot *L*) of that model for that dataset.

Alternate model: The minimum potential niche model

Link distribution rules:

→ Same as niche model, but define a feeding range where the consumer has a probability of <1 of feeding on species in that range.

Effect of link distribution rules:

→ Relax the intervality constraint of the niche model

→ No empirical links are incompatible with the models

→ Introduces an extra model parameter. However, its total likelihood is still comparable to other models, which now also include a 3rd parameter to reflect the random graph component.

S = # taxa; *L* = # links; *I* = # irreproducible links

$\mathcal{L}(K)$ = log-likelihood of obtaining *I* with random graph

Tot $\mathcal{L}$ = total log-likelihood for the model

			Cascade			Niche			Nested hierarchy			Min. potential	
Food web	*S*	*L*	*I*	$\mathcal{L}(K)$	Tot $\mathcal{L}$	*I*	$\mathcal{L}(K)$	Tot $\mathcal{L}$	*I*	$\mathcal{L}(K)$	Tot $\mathcal{L}$	Tot $\mathcal{L}$	*f*
Benguela	29	203	12	−62.91	−343.62	23	−105.46	−234.22	1	−7.73	−349.39	−213.52	0.170
Bridge	25	107	4	−24.19	−217.16	1	−7.44	−94.42	1	−7.44	−162.32	−92.18	0.013
Broom	85	223	4	−33.99	−857.42	36	−226.77	−737.56				−626.54	0.336
Chesapeake	31	68	1	−7.87	−199.59	10	−55.60	−166.84	3	−20.30	−200.15	−145.11	0.314
Coach	29	262	41	−163.85	−443.67	37	−151.75	−296.76	7	−40.49	−381.57	−296.10	0.240
Grass	61	97	0	0	−379.31	10	−69.18	−327.08	13	−86.52	−437.81	−294.94	0.243
Reef	50	556	59	−279.34	−1106.54	196	−687.11	−970.28	22	−126.03	−1053.50	−934.71	0.416
Skip	25	197	12	−59.32	−259.02	22	−95.24	−191.11	5	−29.12	−254.74	−169.67	0.142
St. Marks	48	221	3	−22.93	−576.69	72	−320.40	−546.48	18	−105.27	−634.04	−504.49	0.554
St. Martin	42	205	0	0	−472.58	52	−234.48	−421.53	10	−61.70	−531.55	−388.06	0.443

Minimum potential (relaxed) niche model performs best:

→ no irreproducible links (Niche model has most)

→ slightly better Tot *L* than the Niche model on every dataset

→ much better Tot *L* than Nested hierarchy or Cascade models

'Likelihood' summary

Model	beta distribution	intervality	hierarchical feeding	
			hierarchy	exceptions
Random	no	no	no	—
Random beta	yes	no	no	—
~~Cascade~~	~~no~~	~~no~~	~~yes~~	~~no~~
Generalized cascade	yes	no	yes	$n_j = n_i$
√ Niche	yes	yes	yes	$n_j \geq n_i$
√ Relaxed niche	yes	no*	yes	$n_j \geq n_i$
~~Nested hierarchy~~	~~yes~~	~~no~~	~~yes~~	~~$n_j \geq n_i$*~~

Pros and cons of inference approaches

1) Degree Distributions

Pros: Characterizes a central tendency of structure
Cons: Very minimal notion of “structure”

2) Suite of Properties

Pros: Allows assessment of details of how/why structure differs
Cons: Properties are not independent, making overall evaluation problematic

3) Likelihood

Pros: Based on full structure of network
Cons: How to understand details of how/why structure differs?
How to interpret magnitude of differences in Tot L?

Together, the 3 approaches suggest the following:

→ The Niche and Relaxed niche models fit data much better than Random or Cascade models, somewhat better than other beta-distributed models.

→ The combination of beta distribution, hierarchical feeding, and intervality or near-intervality constraints performs best.

Summary

- 'Complex' food webs aren't so complex: underlying common scale-dependent structure.
- The Niche model and its recent spin-offs (but not Random or Cascade models) do a good job of predicting many aspects of fine-grained structure of empirical food webs.

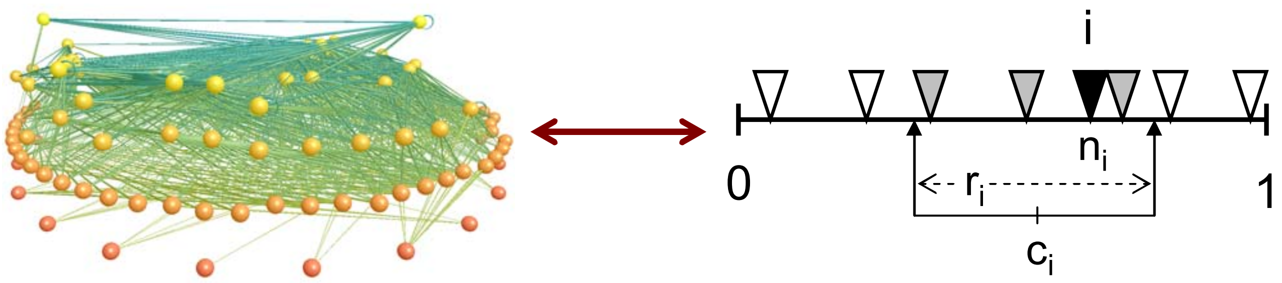
  → **Hierarchical Feeding + Beta Distribution**

- The Niche and Relaxed niche models fit data slightly better than non-interval variants (Nested hierarchy, Generalized cascade).

  → **Intervality + Cycles**

- Common structure across habitat and deep time suggests strong constraints on the organization of species interactions in communities.

  → **Ecology, Evolution, Energetics**



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Jim Lavrakas / Anchorage Daily News

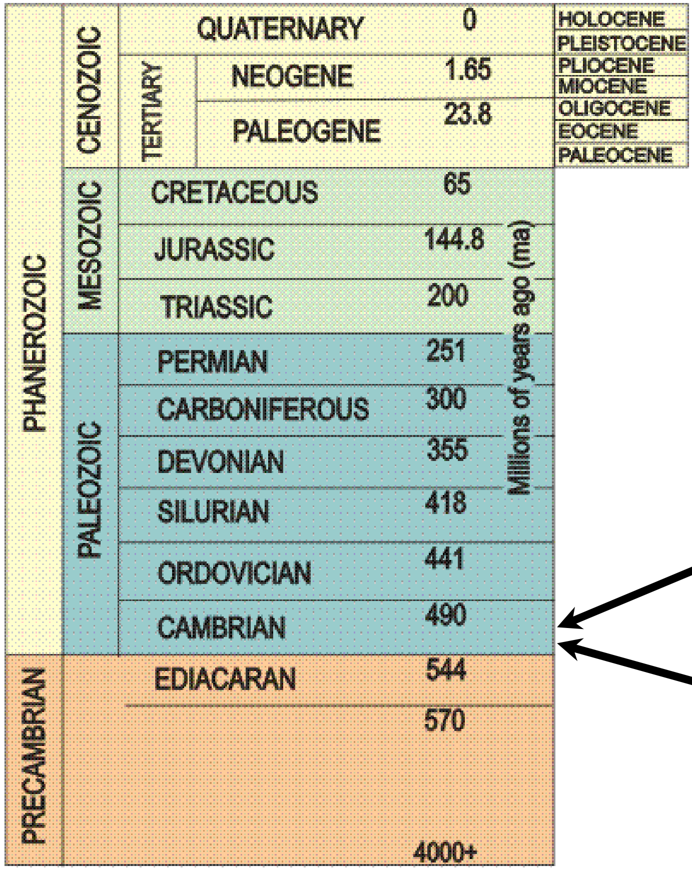
5. Case Study: Ancient Food Webs

Are species interactions structured differently in ancient versus modern ecosystems?

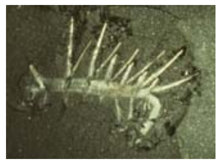
(can we even put convincing data together?)

- Have food webs become more complex since the beginning of the Phanerozoic?
- What do differences/similarities in ecological network structure suggest about fundamental constraints on species interactions?
- Does food-web complexity or structure change across extinction boundaries?
- Do major evolutionary innovations ramify throughout food webs?
- How does community structure respond to major environmental perturbations?

Geologic Time Scale



Burgess Shale (505 Ma)



Chengjiang Shale (520 Ma)

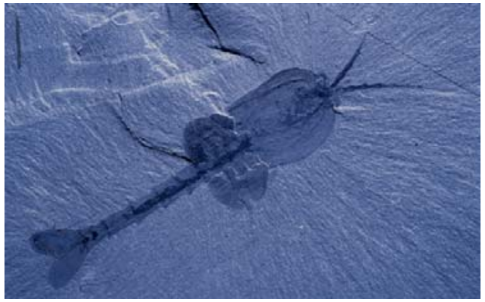
Lagerstätten: Fossil assemblages with exceptional soft-tissue preservation

Burgess Shale Biota

Anomalocaris

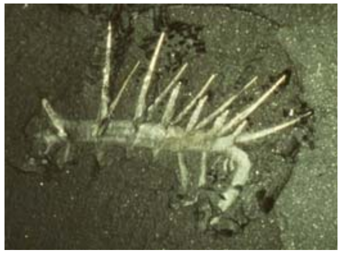
Wiwaxia

Waptia

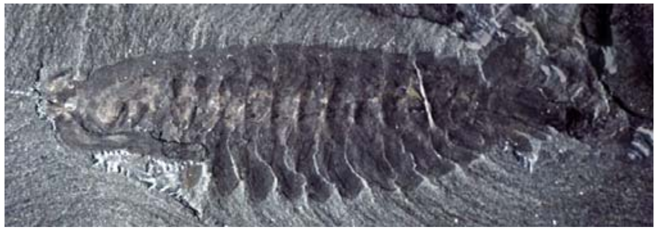


Marella

Hallucigenia



Opabinia



Ollenoides

Pikaia

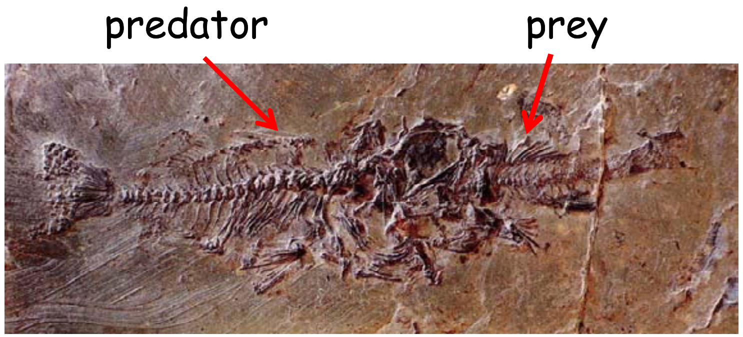
Ottoia

Lines of evidence for feeding links

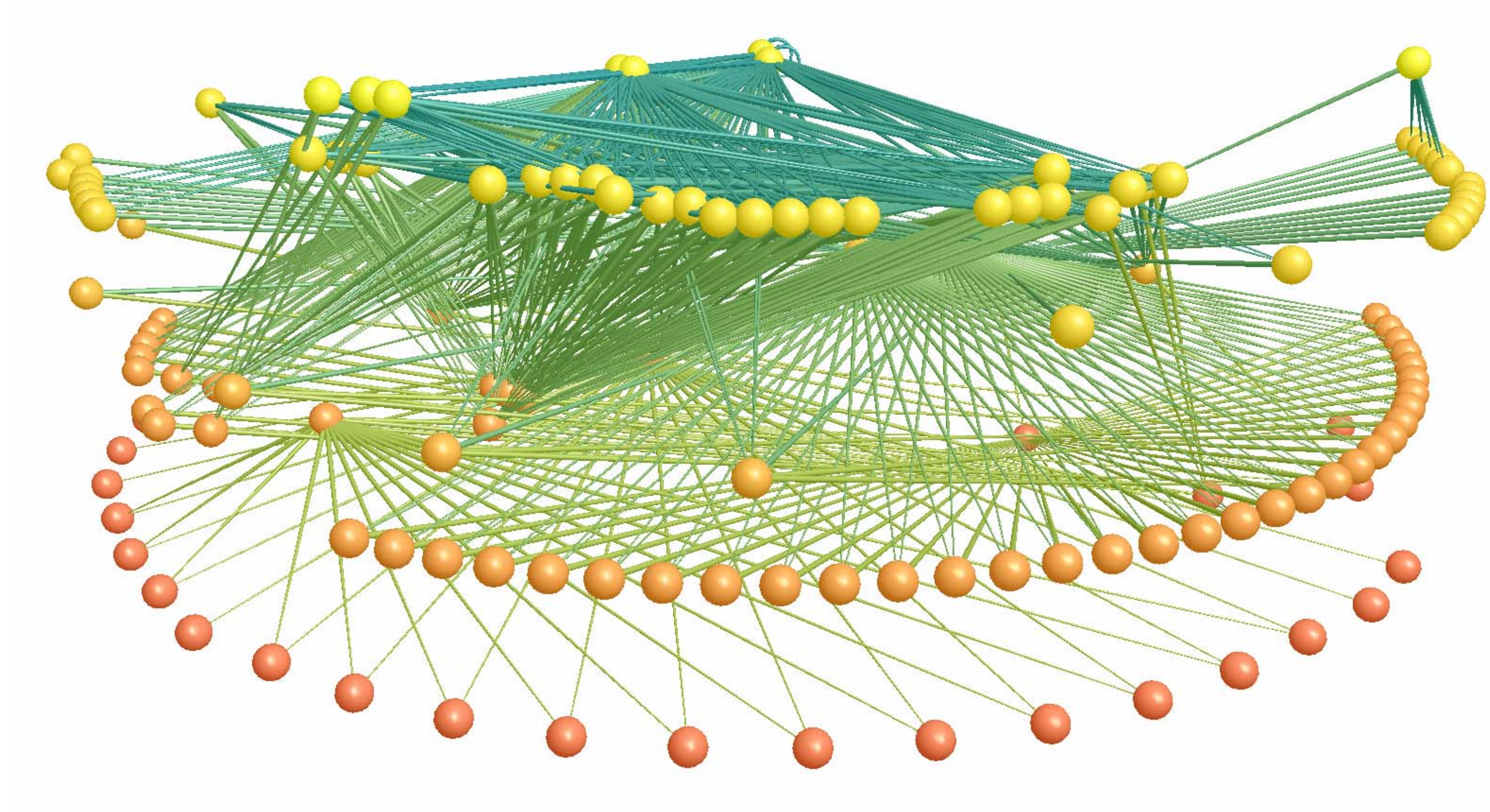
Every link is a hypothesis based on inferences

- Gut contents
- Body size
- By analogy with associated taxa
- Damage patterns
- Environmental deposition
- Functional morphology
- Stable isotopes
- Trace fossils
- Coprolites
- The occasional smoking gun…

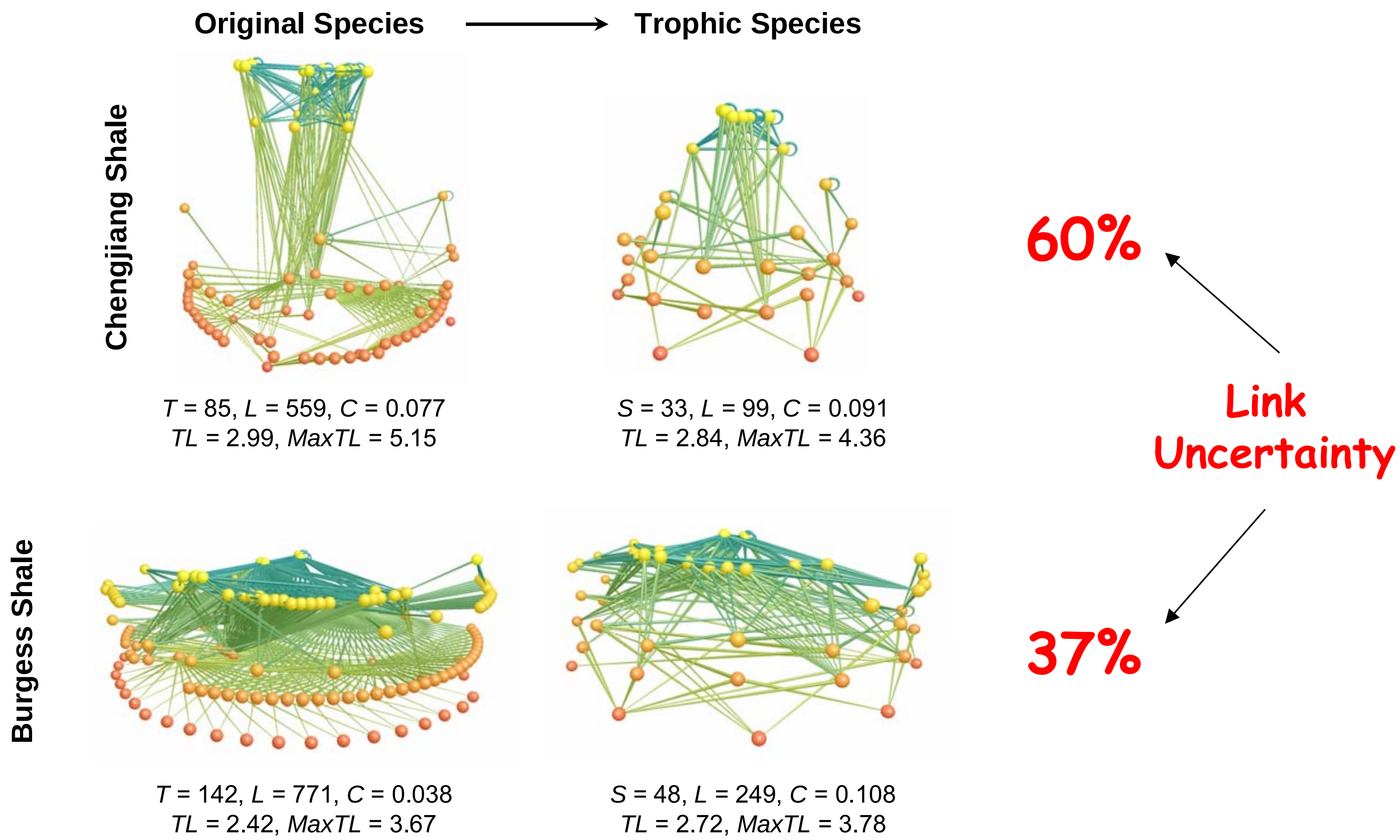
Certainty:
1 = possible
2 = probable
3 = certain



Burgess Shale Food Web



S = 85, ***L*** = 559, ***L/S*** = 6.6, ***C*** = 0.08, ***TL*** = 2.99



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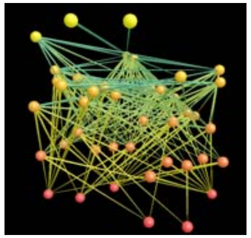
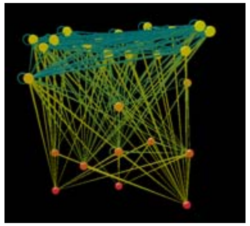
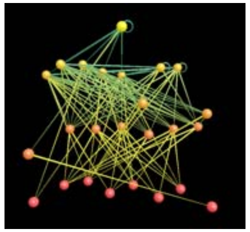


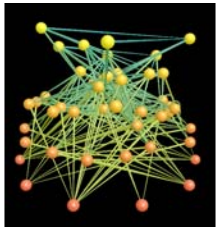
St. Martin (terrestrial)



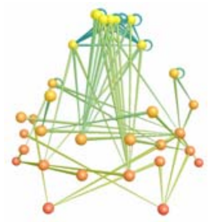
Coachella Valley (terrestrial)



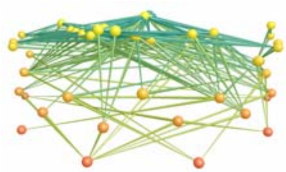
Bridge Brook (lake)



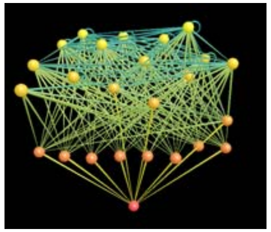
St. Marks (estuary)



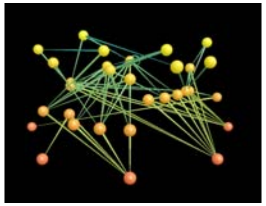
Chengjiang (marine)



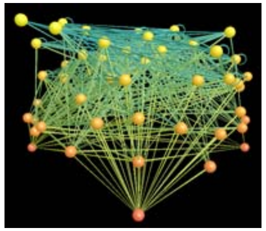
Burgess (marine)



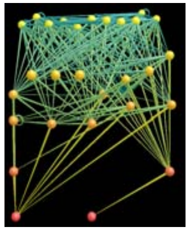
Skipwith (pond)



Chesapeake Bay (estuary)



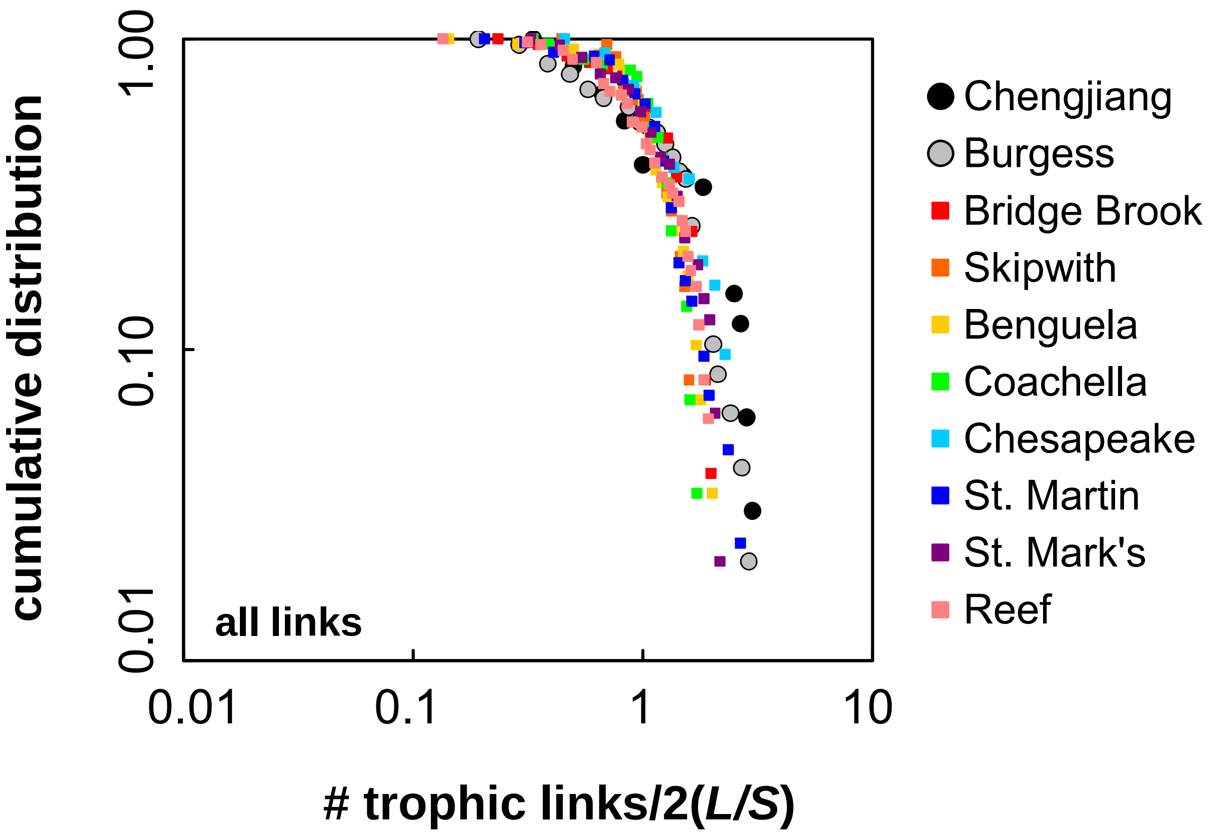
Caribbean Reef (marine)



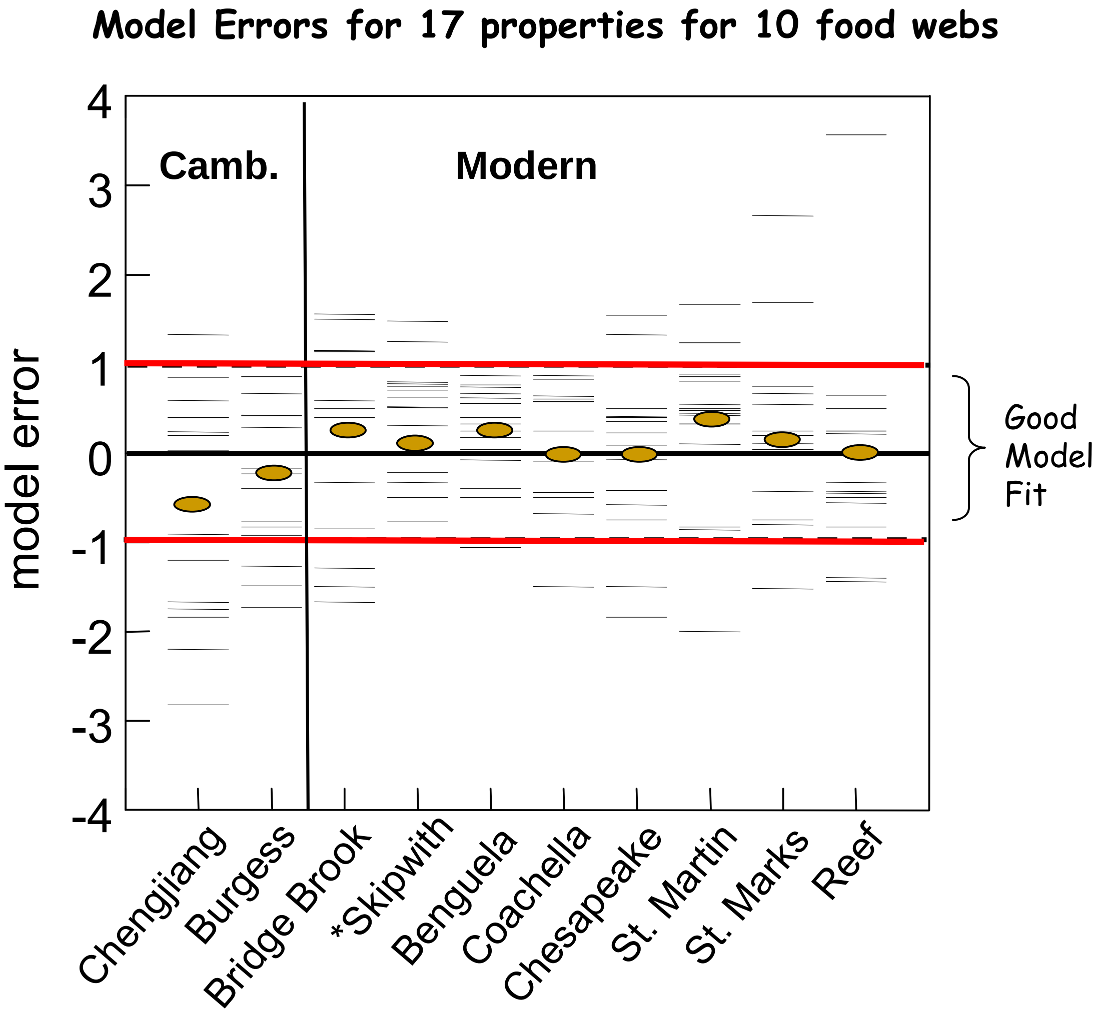
Benguela (marine)

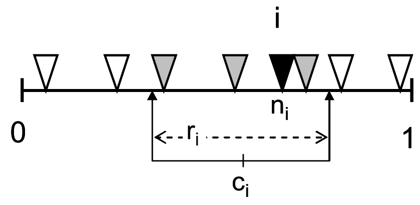
?

Normalized link distributions



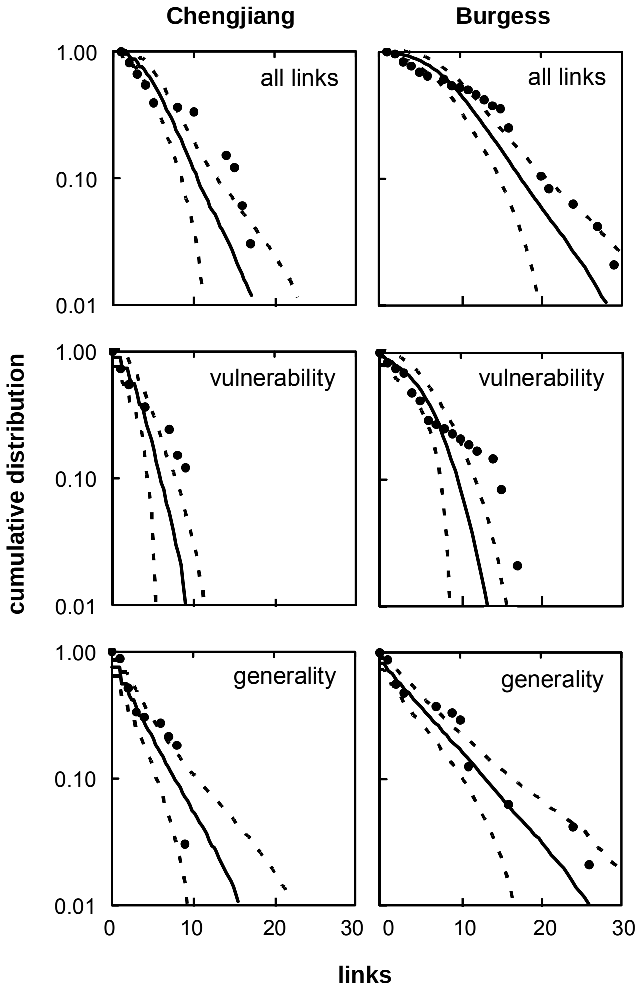
Niche model errors





Results generally robust to removal of uncertain links

A few potentially meaningful differences?



→ **Higher *LinkSD* in both Cambrian webs**

Reflects higher vulnerability of most vulnerable taxa to predation in early Paleozoic webs

→ **Longer *Path* lengths in Chengjiang web**

Reflects lower integration among taxa in earliest web

→ **More taxa in *Loops* in Chengjiang web**

Reflects less hierarchical trophic organization in earliest web

Summary (Dunne *et al.* 2008)

- Detailed species interaction data compiled for ancient ecosystems from the early Phanerozoic (> 500 MA).
- The structure of Cambrian & modern webs is very similar.
- The niche model predicts the structure of all the webs well.
- Results are robust to removal of uncertain or random links.
- The few differences in Cambrian structure may reflect a rapid transition to more stable, constrained, hierarchical, integrated, trophic organization following the Cambrian "explosion" of diversity, body plans, and trophic roles.
- Shared architecture across **habitats** *and* **deep time** is suggestive of strong constraints on trophic organization. (thermodynamic, dynamical stability, evolutionary?)