The Architecture of Ecological Interactions: Patterns and Principles
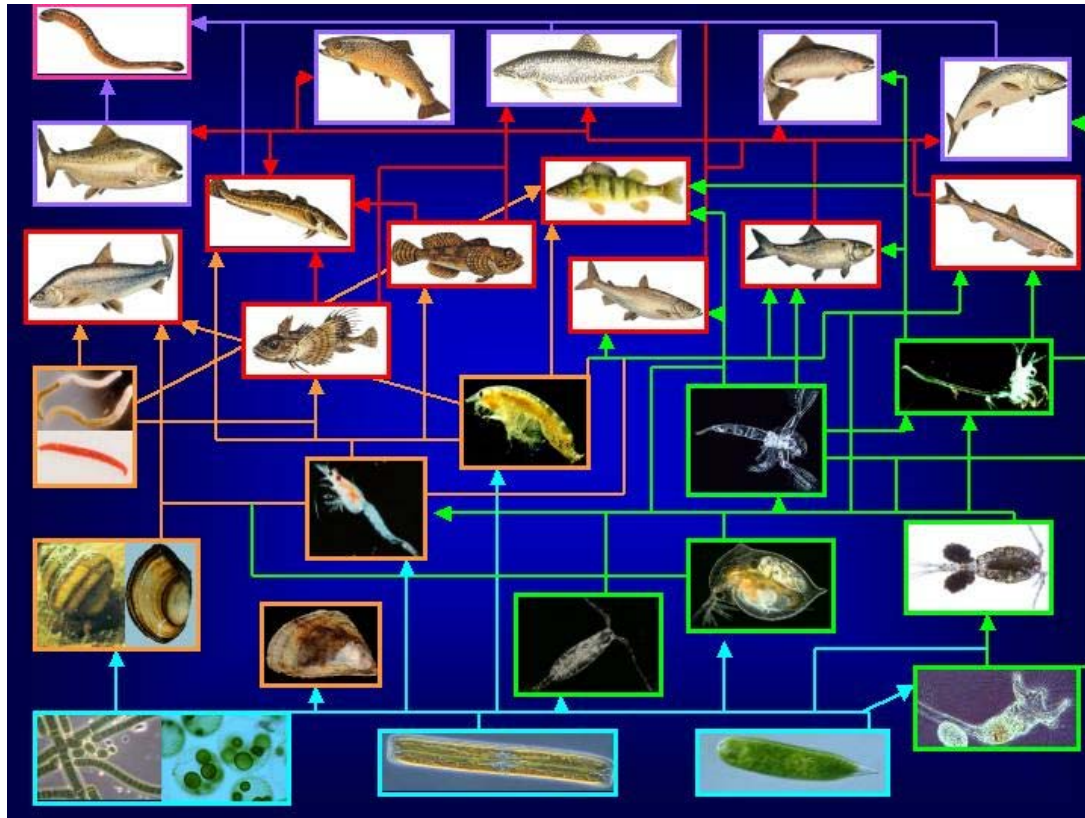
Jennifer A. Dunne

Santa Fe Institute
Pacific Ecoinformatics & Computational Ecology Lab
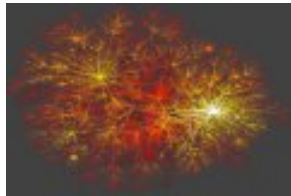
www.foodwebs.org

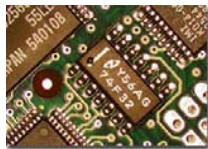"Why is network anatomy so important to characterize? Because structure always affects function."

Technological Networks
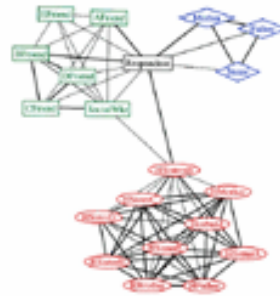

Road Maps

Internet Connectivity

Circuit Boards
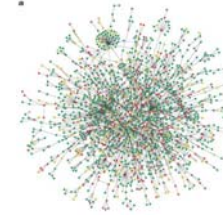
Social Networks

The Kevin Bacon Game

Support Network for a Homeless Woman

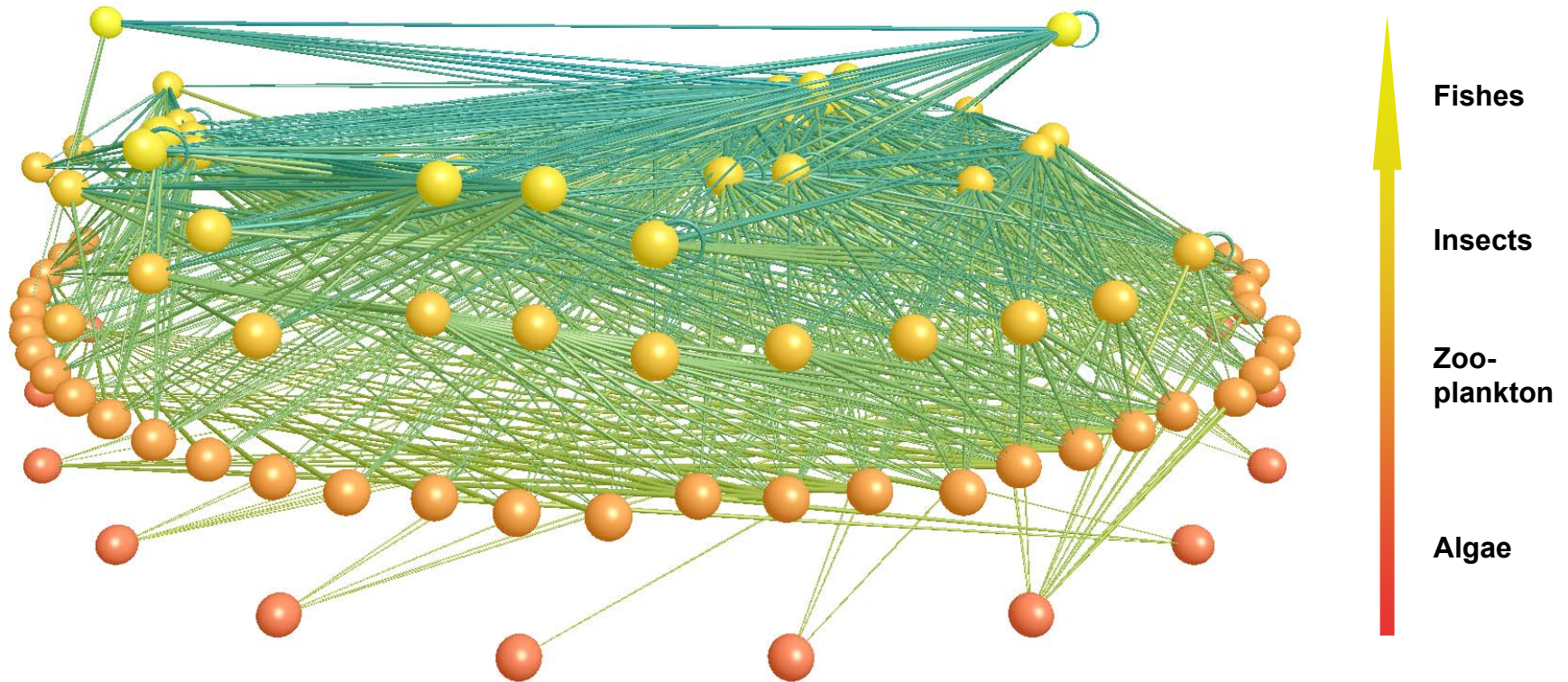# Biological Networks

Protein Networks
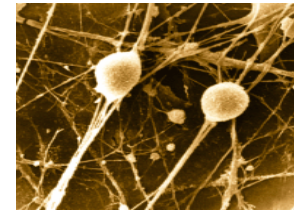
Neural Networks

Ecosystems
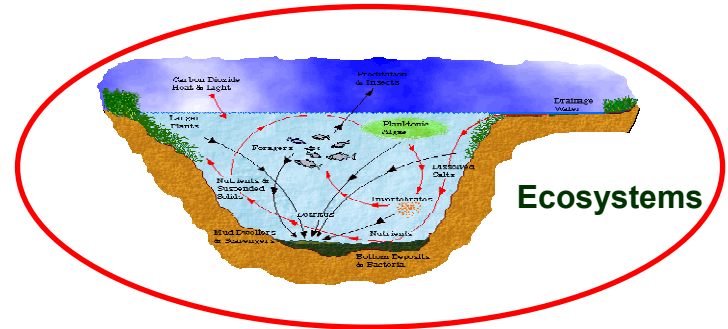
Food Web of Little Rock Lake, Wisconsin

997 Feeding Links among 92 Taxa: 10 Basal, 72 Invertebrates, 10 Fishes

Fishes

Insects

Zoo-plankton

Algae

S (# species)	= 92
L (# trophic links)	= 997
L/S (links per species)	= 10.8
C (connectance, L/S^2)	= 0.12

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, 1959

1950's Paradigm:

Complex communities MORE stable than simple communities

1970's Challenge:

Complex communities LESS stable than simple communities

Current & Future Research:

Food webs used to understand nature's "devious strategies" that promote stability

Marine

Estuary

Lake

Rain-forest

Desert
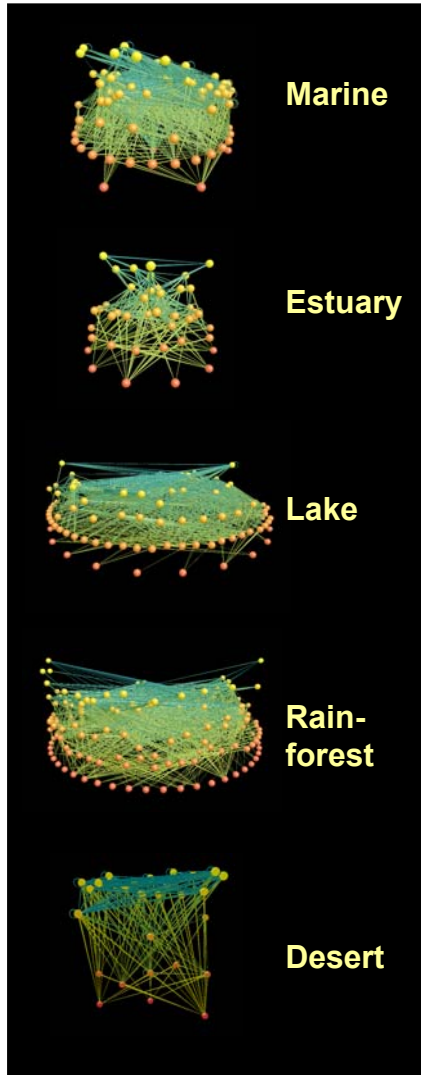
Apparent Complexity

Link distributions

Apparent complexity

Raw data for 16 webs

Link distributions

Apparent complexity $\longrightarrow$ Underlying simplicity?

Raw data for 16 webs
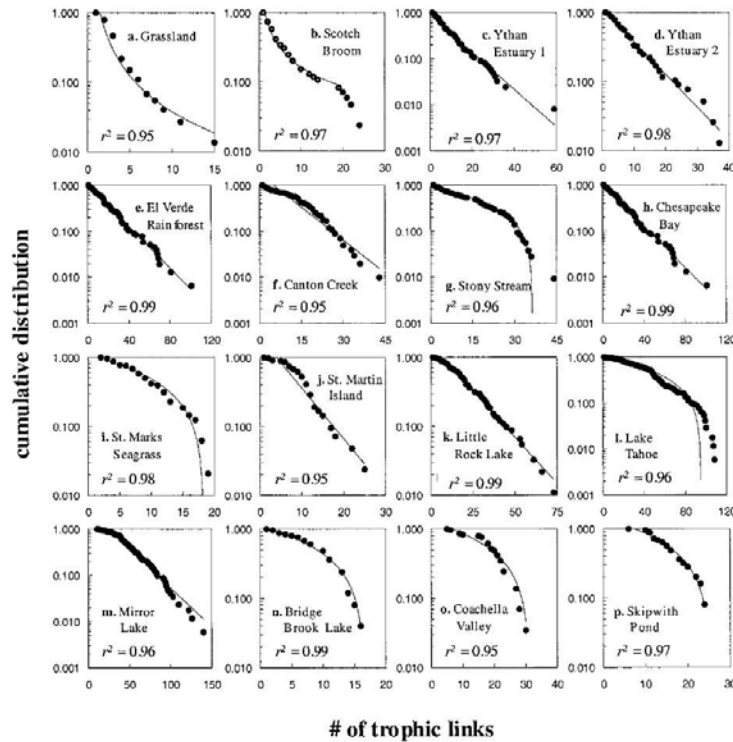
Normalized data for 16 webs

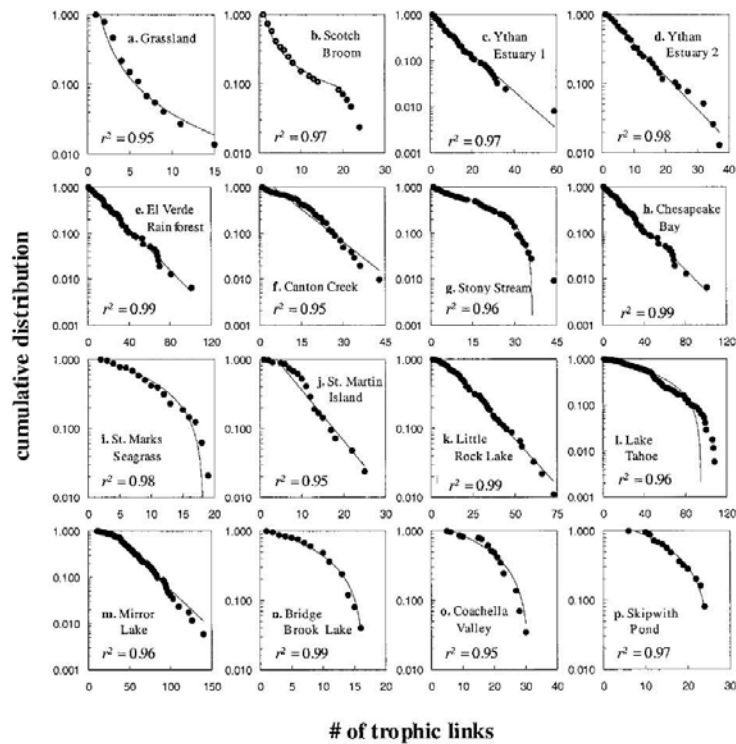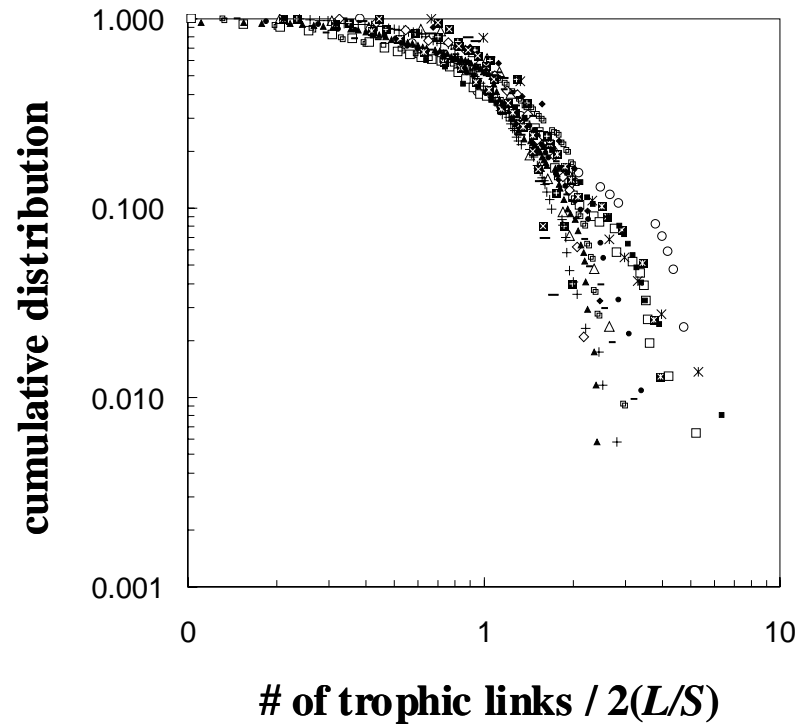# Modeling food-web structure

The niche model: a simple, stochastic model 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
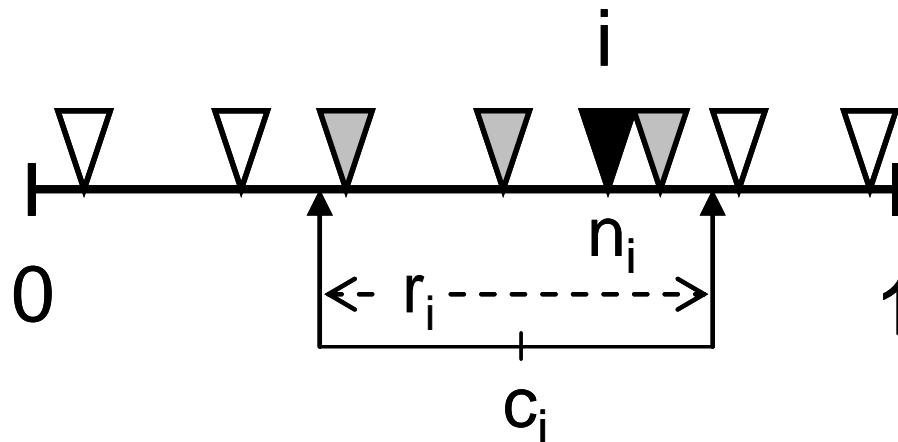
Feeding rules:

1) each species assigned a feeding range r_i
2) feeding range is assigned a center $c_i < n_i$
3) species eat all taxa in their feeding range

Summary of model constraints

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	$n_j \geq n_i$*

Assessing model fit

$$?$$
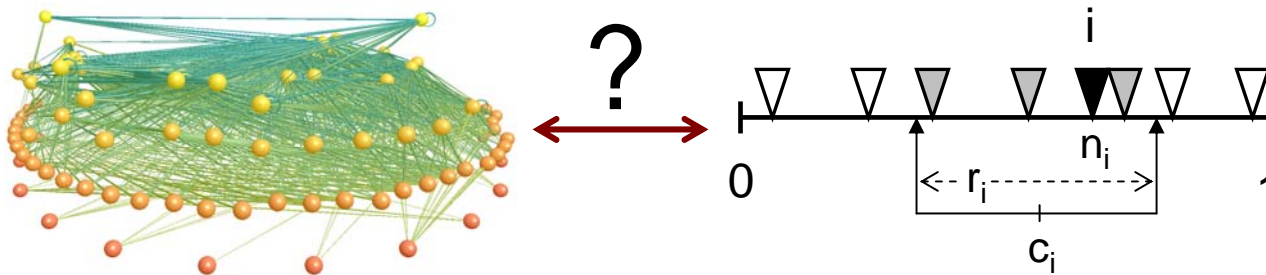
1. Degree distributions
2. Statistical approach
3. Likelihood approach

Assessing model fit: degree distributions

Niche Model Simulation Results
(generality: links to prey)

Assessing model fit: degree distributions

Niche Model Analytical Results
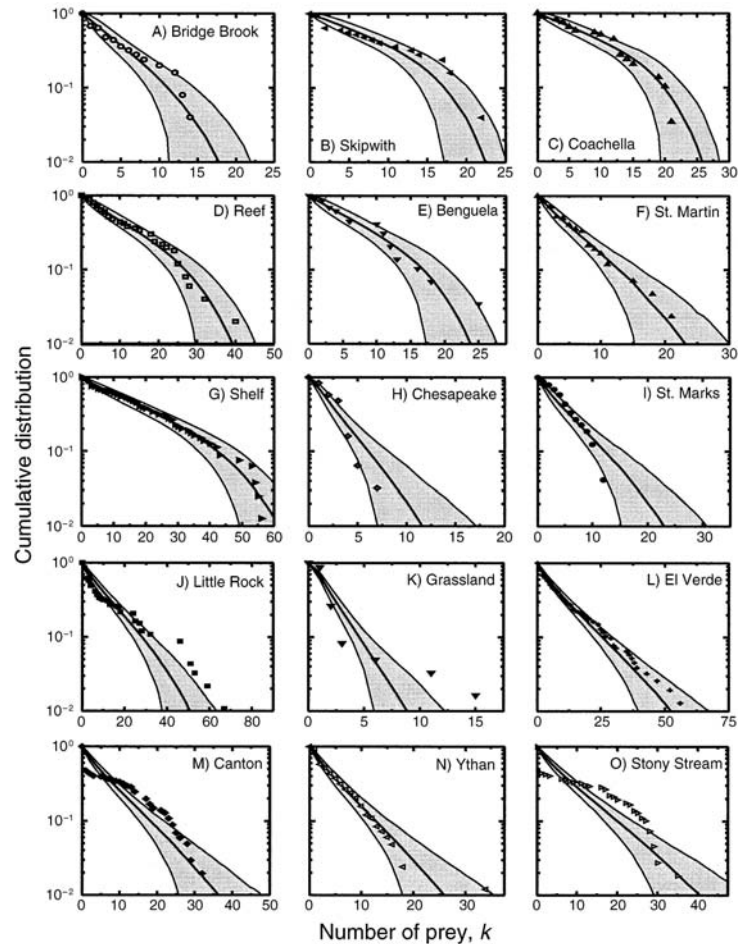
Property	Expression
Distribution of number of prey	$p_{prey}(k) = (1/2z)E_1(k/2z)$
Distribution of number of predators	$p_{pred}(m) = (1/2z)\gamma(m + 1, 2z)$
Distribution of number of links	$p_{links}(r) = \int_0^r p_{prey}(t)p_{pred}(r - t)dt$
	$= 1/(2z)^2\int_0^r E_1(t/2z)\gamma(r - t + 1, 2z)dt$
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	$\sigma_G = \sqrt{8/(3 + 6C)} - 1$
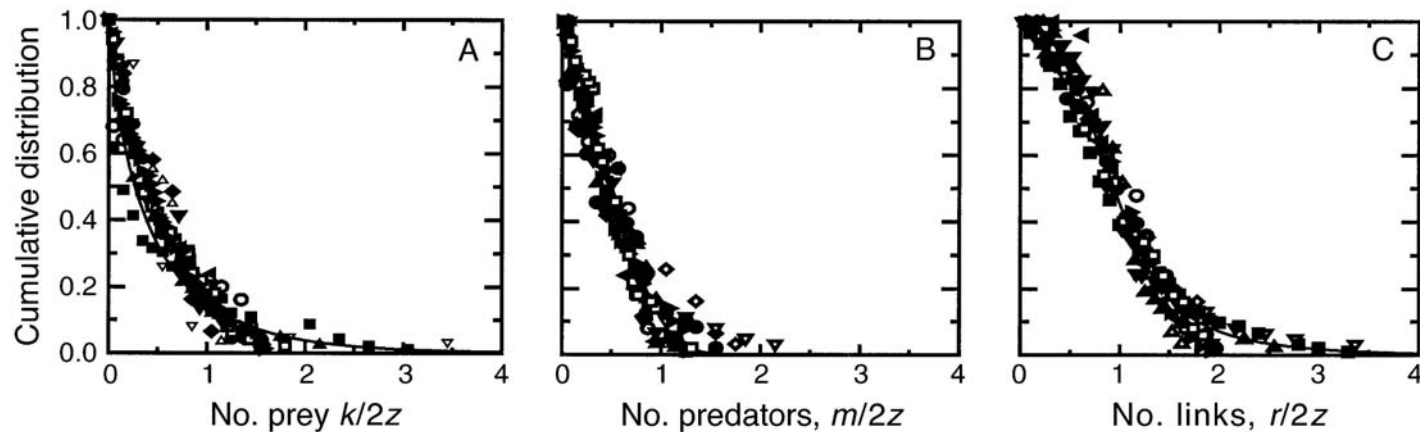
Assessing model fit: statistical approach

beyond degree distribution…

- **Test:** model against the structure of empirical food webs

- **Assess:** 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 distribution)

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

Single-number properties
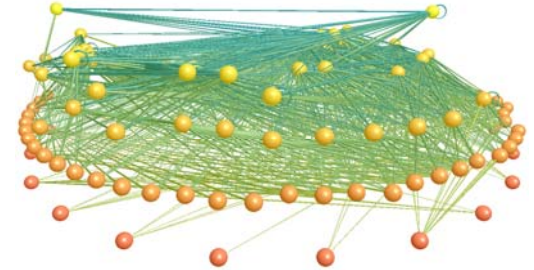
Types of Organisms:

% 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

Test of 10 webs, 5 models, 15 properties

Model	Mean of model error	SD of model error	Fraction outside ± 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
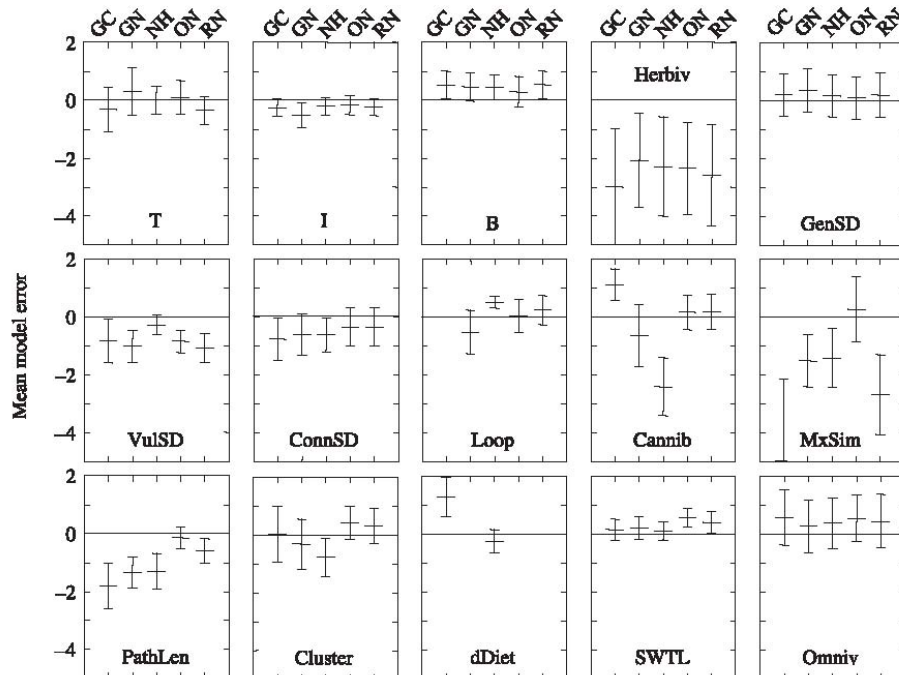
→ **Mean ME ≤ |1| for all models: effect of shared hierarchy + beta distribution constraints**

→ **Niche generally performs best**
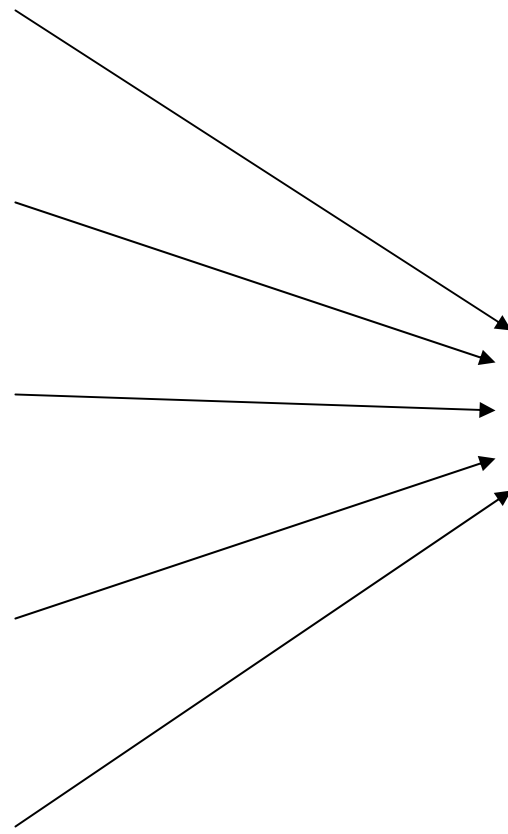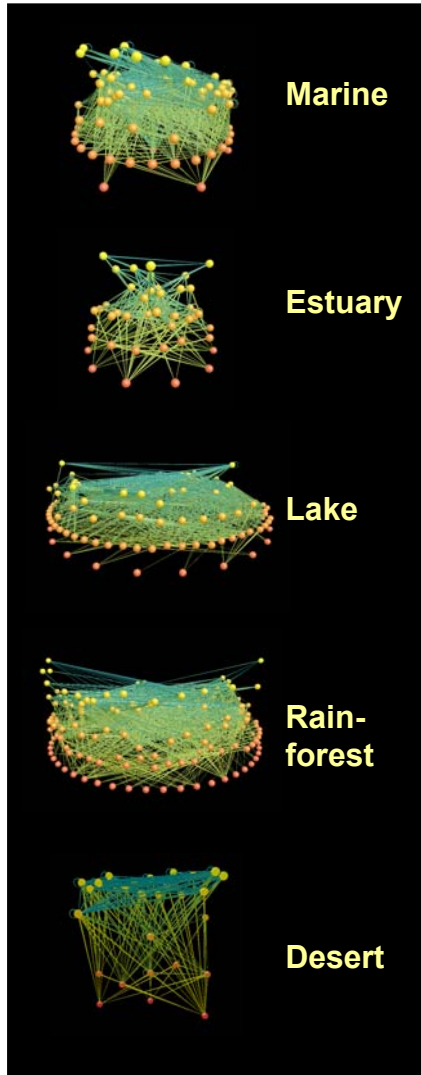
→ **All models drastically under-estimate herbivory.**

Assessing model fit: likelihood-based approach

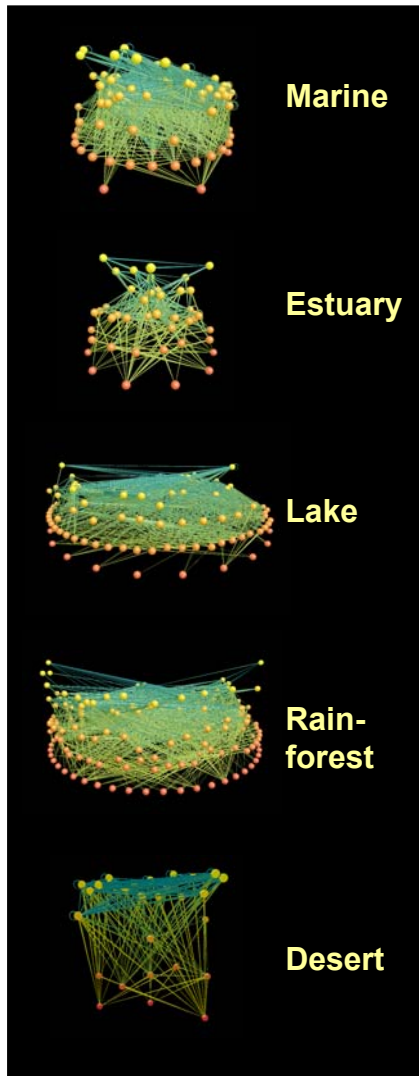## Assess topology of networks as a whole

Food web	S	L	Cascade			Niche			Nested hierarchy			Min. potential	
			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 niche model performs best:
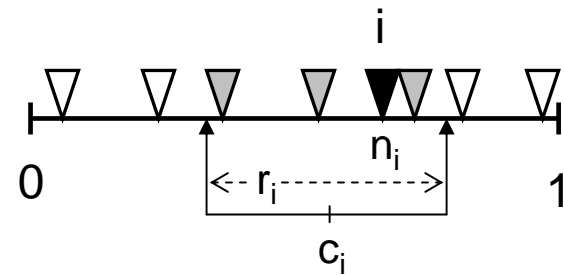
→ no irreproducible connections
→ marginally better likelihood than the niche model
→ much better likelihood than nested hierarchy or cascade.

Marine

Estuary

Lake

Rain-
forest

Desert

Apparent Complexity

Underlying Simplicity

Marine

Estuary

Lake

Rain-forest

Desert

i
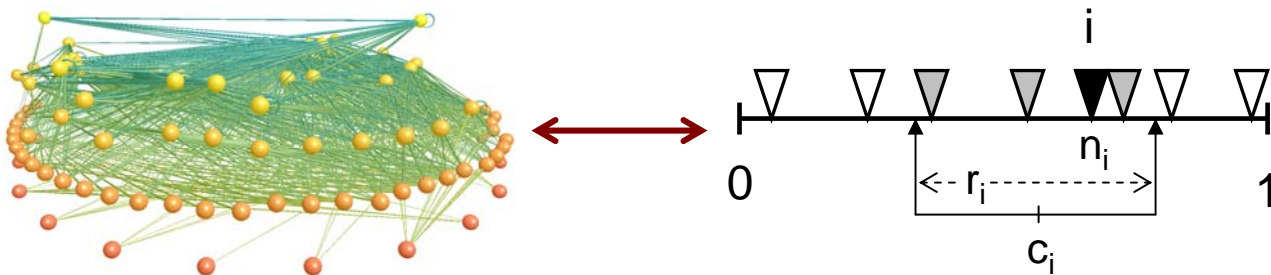
n_i

0 $\quad r_i \quad$ 1

c_i

Two Parameters (C, S)

Simple Link Distribution Rules

Successful Prediction of Structure

→ Food-web structure is systematically scale-dependent on S and L

→ Many aspects of structure are well-predicted by the niche model

→ Food webs from various habitats share many aspects of structure

Can these analyses be extended through deep time to ancient ecosystems?

Prior "deep-time" trophic structure research

Miocene (14 Ma) Seagrass Community
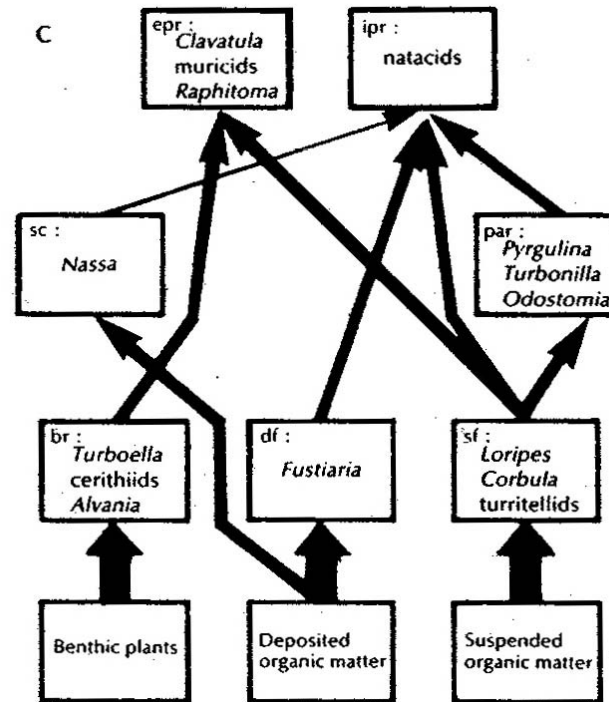
Methodological Issue: Low Resolution!

Geologic Time Scale

PHANEROZOIC	CENOZOIC		QUATERNARY	0
		TERTIARY	NEOGENE	1.65
			PALEOGENE	23.8
	MESOZOIC		CRETACEOUS	65
			JURASSIC	144.8
			TRIASSIC	200
	PALEOZOIC		PERMIAN	251
			CARBONIFEROUS	300
			DEVONIAN	355
			SILURIAN	418
			ORDOVICIAN	441
			CAMBRIAN	490
PRECAMBRIAN			EDIACARAN	544
				570
				4000+

CENOZOIC era subdivisions: HOLOCENE, PLEISTOCENE, PLIOCENE, MIOCENE, OLIGOCENE, EOCENE, PALEOCENE

Millions of years ago (ma)

Burgess Shale (505 Ma)

Chengjiang Shale (520 Ma)

Lagerstätten: Fossil assemblages with exceptional soft-tissue preservation

Burgess Shale Biota

Wiwaxia

Waptia

Marella

Anomalocaris

Hallucigenia

Opabinia

Ollenoides

Pikaia

Ottoia

Artist's Intuition

Anomalocaris canadensis **hunting trilobites Image by Ken Dowd (via NSF)**

Scientist's Intuition

We may perhaps therefore see in the process of evolution an increase in diversity at an increasing rate till the early Paleozoic, by which time the familiar types of community structure were established. -Hutchinson 1959
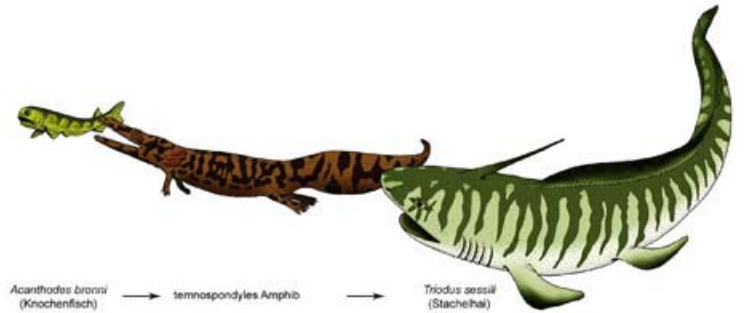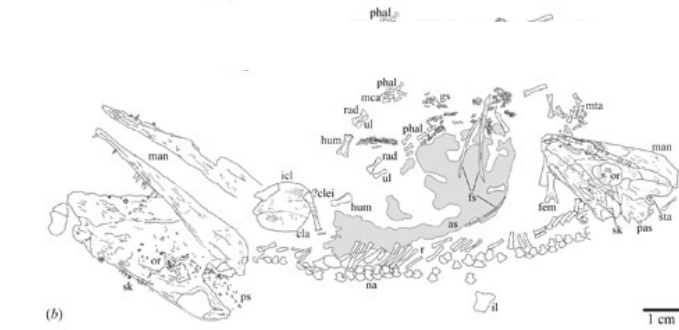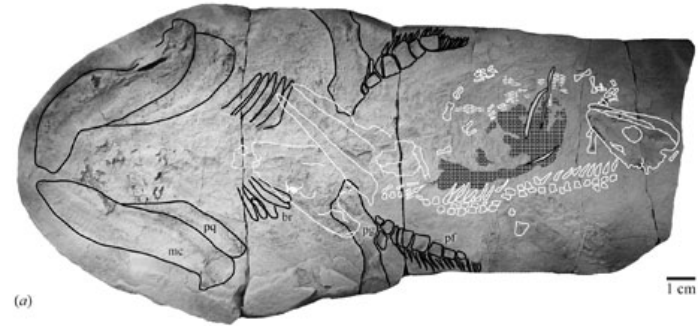
Who eats whom?

Fossil food chain (290 MA)

Caught in the act (49 MA)

predator   prey

Acanthodes bronni (Knochenfisch) → temnospondyles Amphib → Triodus sessii (Stachelhai)

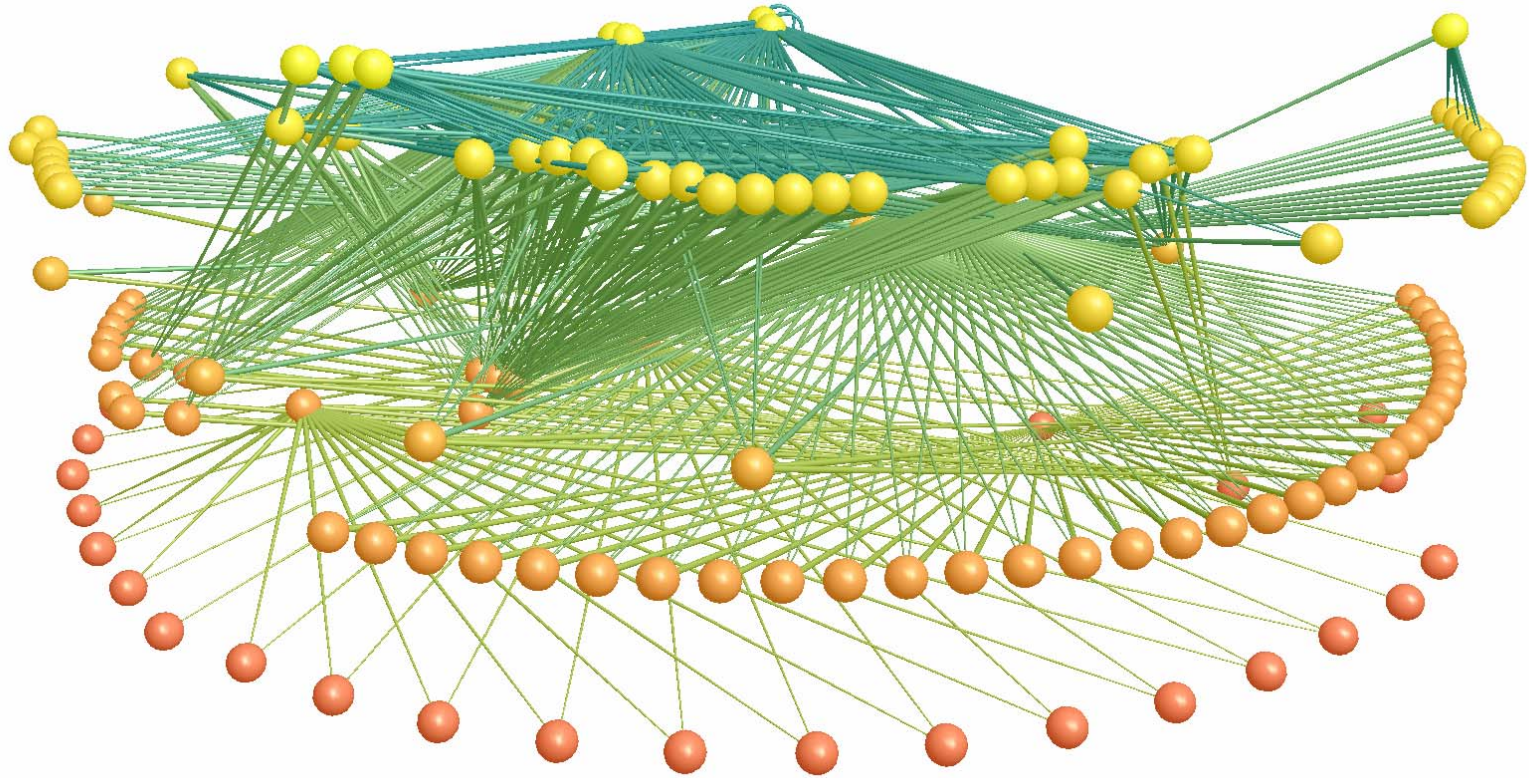# Lines of evidence for feeding links

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...
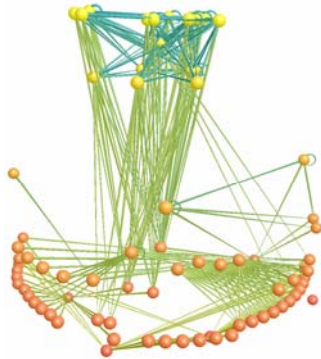
Certainty:
1 = possible
2 = probable
3 = certain

predator   prey
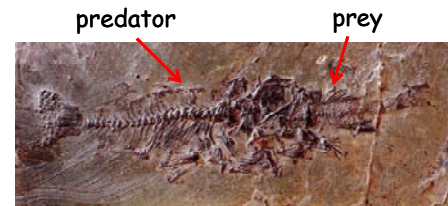
Burgess Shale Food Web

S = 85, L = 559, L/S = 6.6, C = 0.08, TL = 2.99
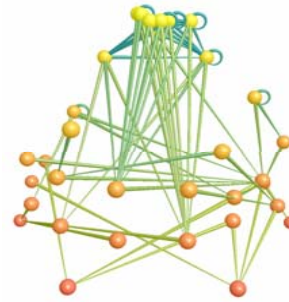
Original Species → **Trophic Species**

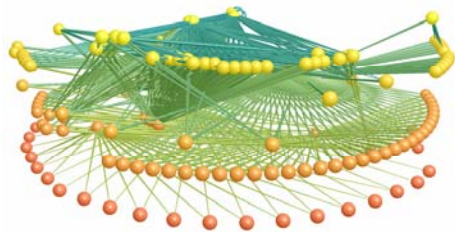**Chengjiang Shale**

$T = 85$, $L = 559$, $C = 0.077$
$TL = 2.99$, $MaxTL = 5.15$

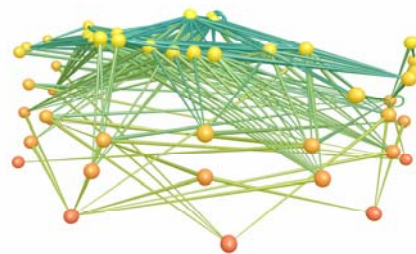$S = 33$, $L = 99$, $C = 0.091$
$TL = 2.84$, $MaxTL = 4.36$
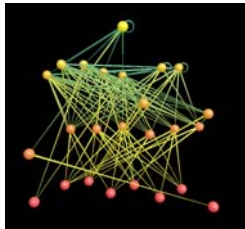
Burgess Shale

$T = 142$, $L = 771$, $C = 0.038$
$TL = 2.42$, $MaxTL = 3.67$

$S = 48$, $L = 249$, $C = 0.108$
$TL = 2.72$, $MaxTL = 3.78$

60%

Link Uncertainty
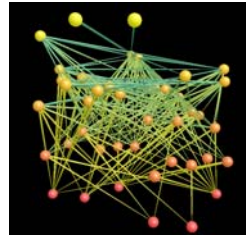
37%
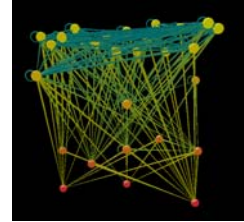
Bridge Brook (lake)
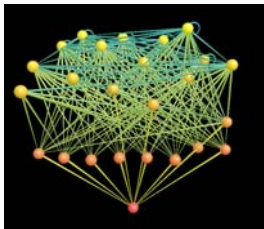
St. Martin (terrestrial)

Coachella Valley (terrestrial)

St. Marks (estuary)

Skipwith (pond)
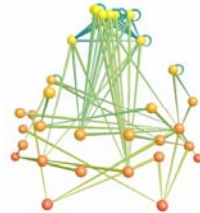
Chengjiang (marine)
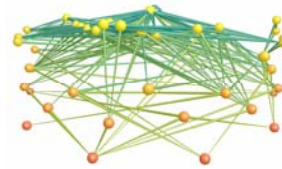
Burgess (marine)
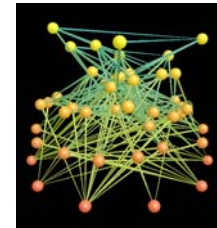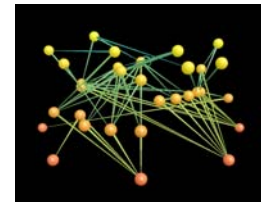
Chesapeake Bay (estuary)
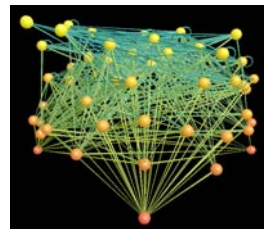
Caribbean Reef (marine)
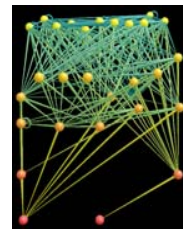
Benguela (marine)

?

Normalized link distributions
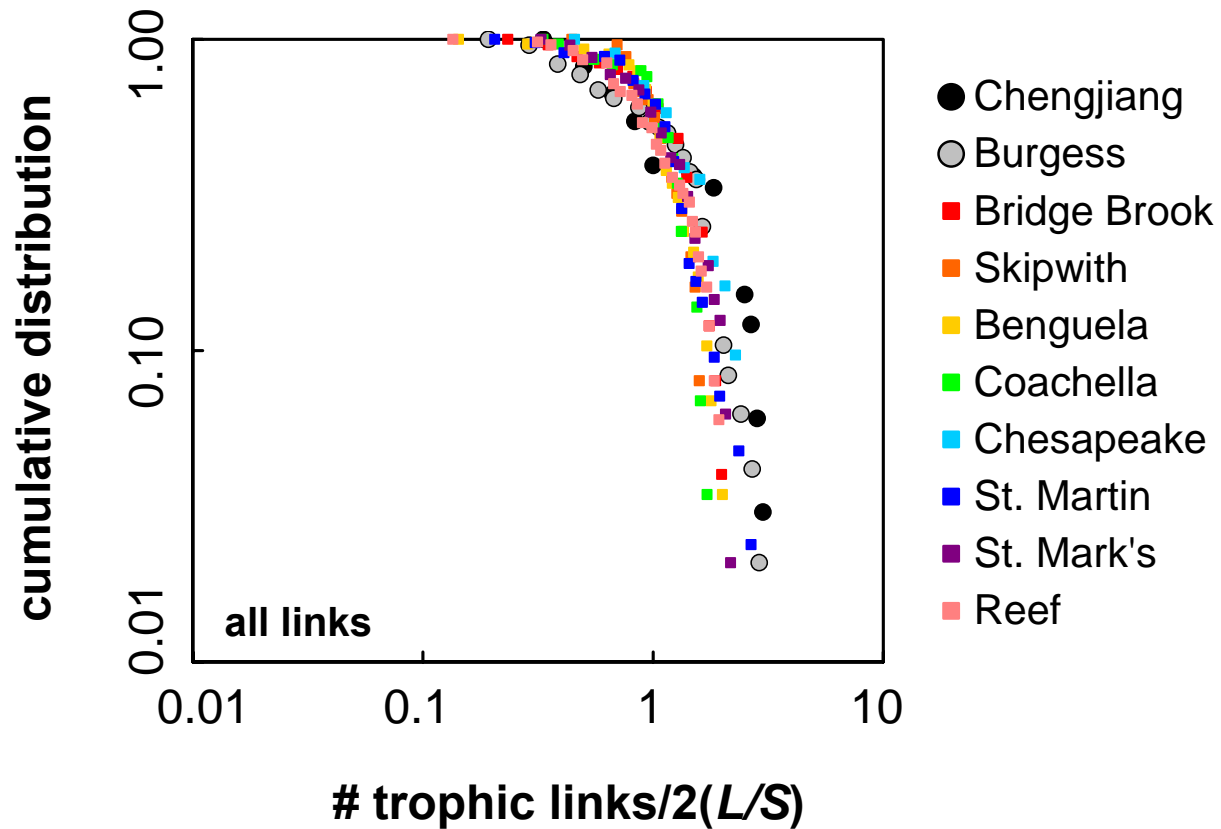
Niche model errors

Model Errors, 17 properties, 10 webs

Cambrian web MEs compared to modern web MEs

model error

Plots: Top, Int, Bas, Can, Herb, Omn, Loop, ChLen, ChSD, ChNum, TL, MaxSim, VulSD, GenSD, LinkSD, Path, Clust
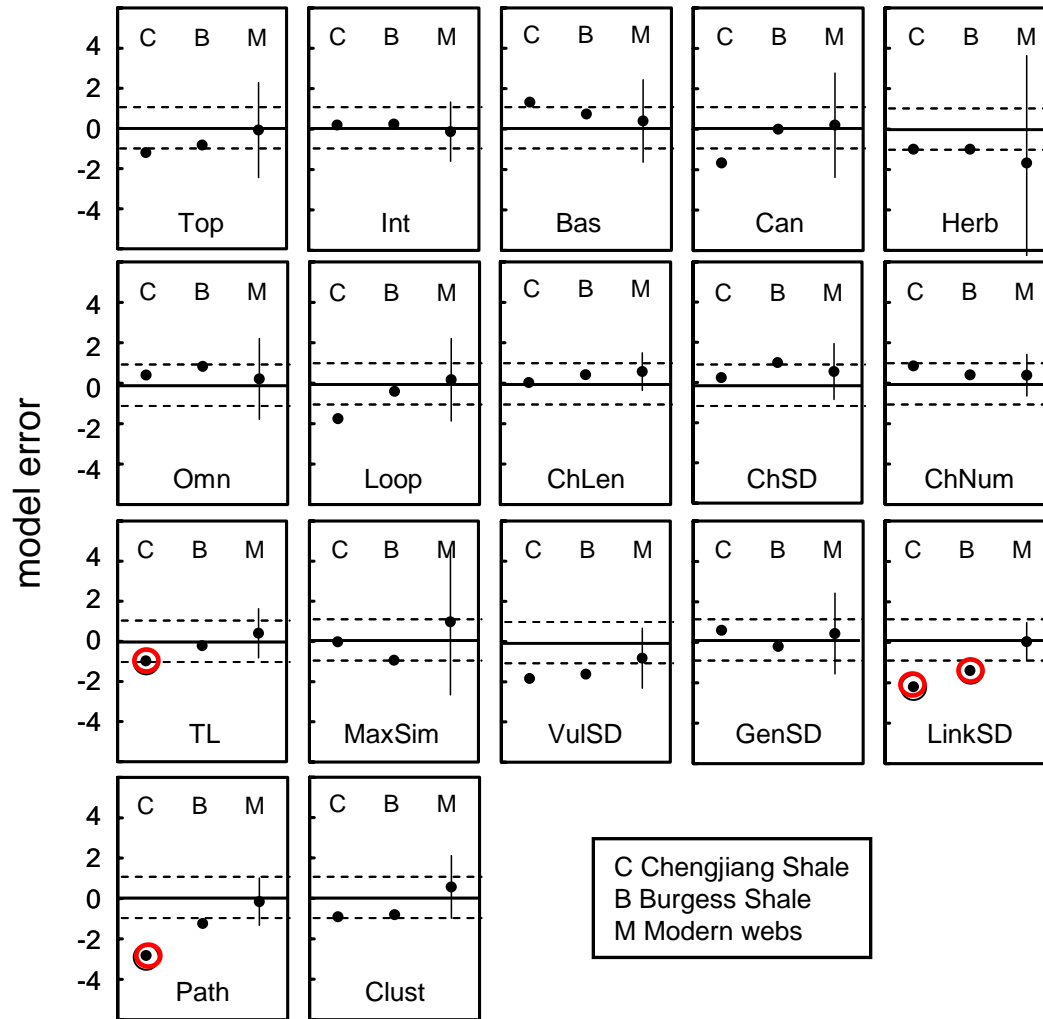
● Cambrian MEs outside 95% CI of modern web MEs

C Chengjiang Shale
B Burgess Shale
M Modern webs

What about uncertainty?

Removing links: effect on ME comparisons

Chengjiang Shale Web

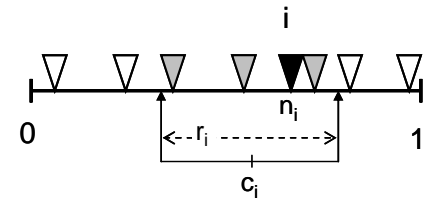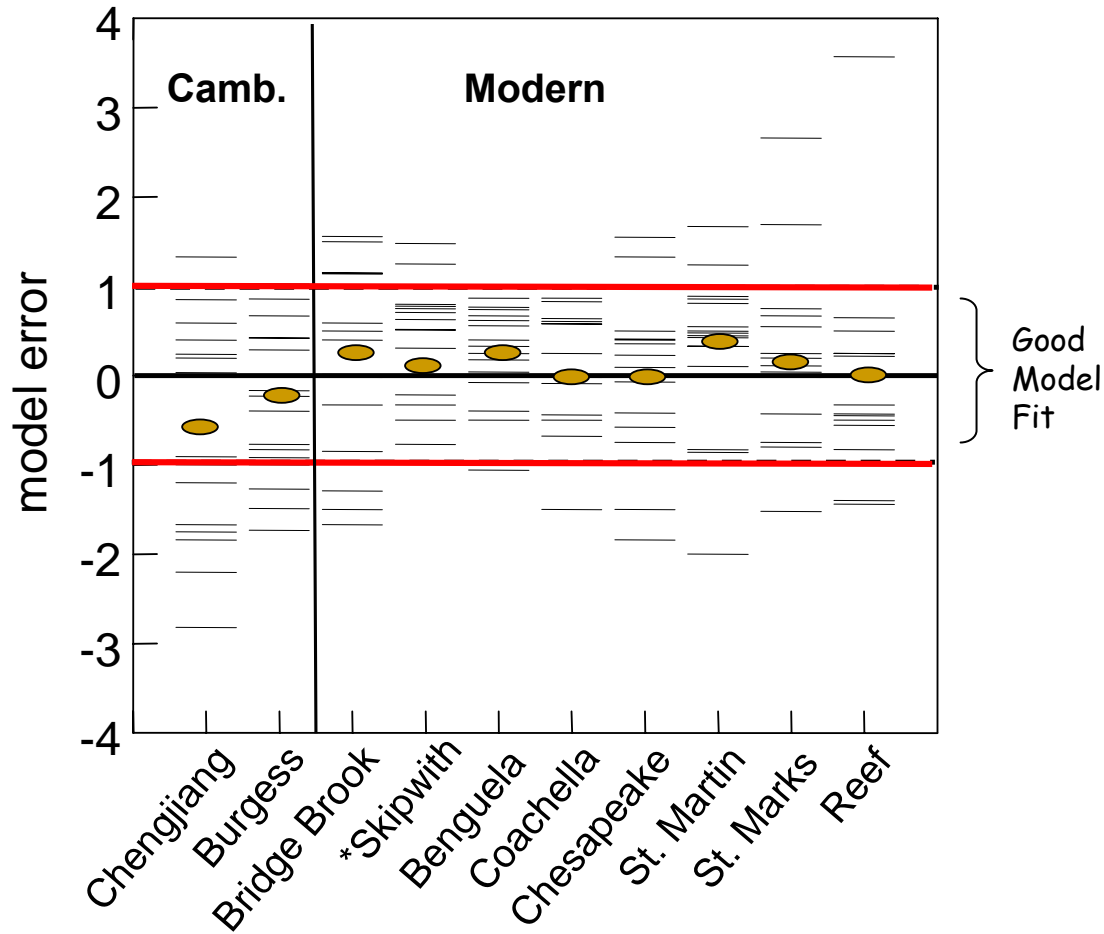|	Low-Certainty Link Removals					
# Links Removed:	0	6	15	30	44	59
Top	-1.20	-1.11	-1.18	-1.19	-1.21	-2.00
Int	0.20	0.28	0.34	0.31	0.29	1.00
Bas	1.33	1.28	0.98	1.05	1.08	1.00
Herb	-1.00	-0.80	-0.77	-0.76	-0.52	-0.50
Can	-1.67	-2.03	-1.73	-1.84	-1.65	-1.00
Omn	0.40	0.63	0.65	0.70	0.91	0.67
Loop	-1.75	**-2.15**	**-2.81**	**-2.99**	**-3.09**	**-2.50**
ChLen	0.03	0.02	-0.09	-0.25	-0.26	0.32
ChSD	0.24	0.21	0.08	-0.12	-0.06	0.73
ChNum	0.85	1.02	0.89	0.74	0.90	**1.81**
TL	**-0.98**	**-1.04**	**-0.98**	**-1.37**	**-2.24**	**-7.24**
MaxSim	-0.02	-0.04	0.11	0.33	-0.30	-2.65
VulSD	-1.84	-1.63	-1.53	-1.37	-1.68	-2.22
GenSD	0.59	0.47	0.43	0.48	0.54	0.78
LinkSD	**-2.20**	**-2.07**	**-2.20**	**-2.23**	**-2.22**	**-2.59**
Path	**-2.82**	**-3.50**	**-3.51**	**-2.85**	**-2.57**	**2.49**
Clust	-0.91	-0.94	-0.86	-0.88	-0.93	-1.27

Burgess Shale Web

	Low-Certainty Link Removals					
# Links Removed:	0	9	23	47	70	93
Top	-0.83	-0.85	-0.85	-0.81	-0.63	-0.43
Int	0.25	0.45	0.49	0.63	0.72	1.50
Bas	0.75	0.58	0.30	-0.04	-0.53	**-3.00**
Herb	-1.00	-0.96	-0.68	-0.48	-0.18	0.40
Can	0.00	0.04	0.06	-0.11	-0.06	-0.25
Omn	0.83	1.08	0.98	1.06	1.25	1.91
Loop	-0.40	-0.34	-0.36	-0.29	-0.43	-0.50
ChLen	0.42	0.36	0.40	0.40	0.49	0.98
ChSD	0.99	0.92	0.79	0.51	0.35	0.54
ChNum	0.41	0.42	0.45	0.53	0.68	0.77
TL	-0.22	-0.11	0.05	0.21	0.33	1.34
MaxSim	-0.94	-0.57	-0.12	0.22	-0.07	-2.07
VulSD	-1.62	-1.68	-1.40	-1.17	-0.78	-0.38
GenSD	-0.20	-0.52	-0.51	-0.98	**-1.62**	**-2.22**
LinkSD	**-1.40**	**-1.83**	**-1.52**	**-1.66**	**-2.02**	**-2.83**
Path	-1.24	**-1.65**	**-1.55**	**-1.46**	**-1.39**	**-1.49**
Clust	-0.81	**-1.00**	**-0.99**	**-1.17**	**-1.62**	**-1.99**

→ Niche model results very robust to exclusion of links
→ Cambrian & modern web structure remarkably similar

A few intriguing differences…
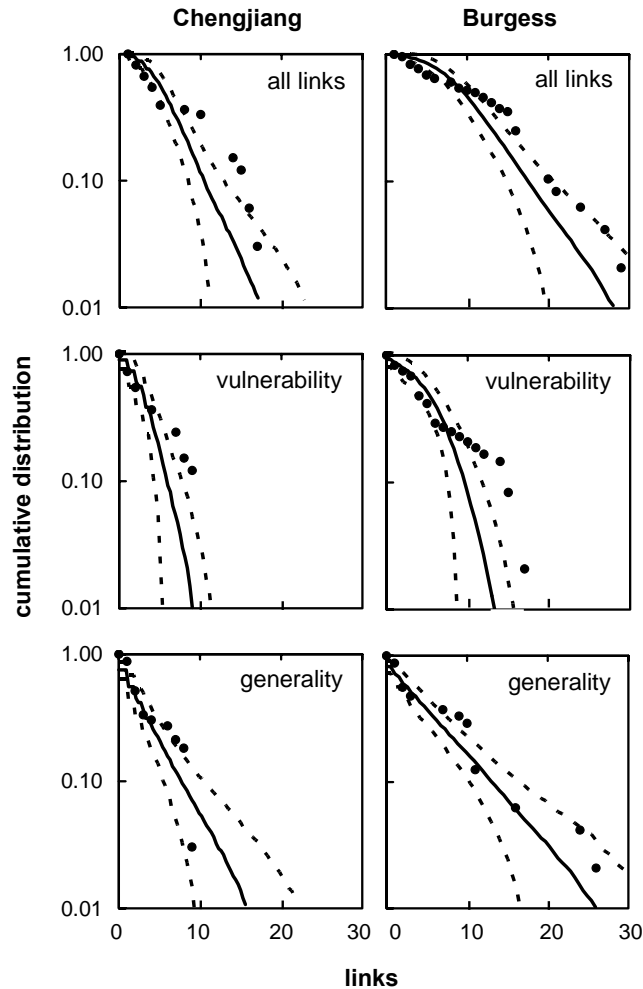
→ **Higher *LinkSD* in both Cambrian webs**
Reflects higher vulnerability to predation

→ **Longer *Path* lengths in Chengjiang web**
Reflects lower integration among taxa

→ **More taxa in *Loops* in Chengjiang web**
Reflects less hierarchical trophic organization

Patterns

- The structure of Cambrian & modern webs is very similar, with a few intriguing differences.

- The niche model predicts the structure of all the webs well.

- Results are robust to removal of uncertain or random links.

- Network structure is similar across habitats and across deep time, regardless of the identity of the species.
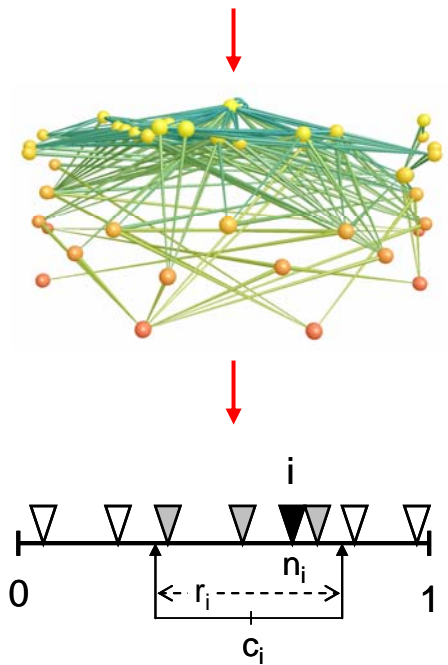
Principles?

- Shared architecture across **habitats** *and* **deep time** is suggestive of strong constraints on trophic organization.

- Differences in Cambrian structure may reflect a rapid transition during *de novo* ecosystem construction to more stable, constrained hierarchical, integrated trophic organization following the Cambrian "explosion" of diversity, body plans, and trophic roles.

- **Underlying principles (???):**

  → thermodynamics (MEP)
  → dynamical stability (structure ←→ dynamics)
  → natural selection (vulnerability constraints)

The Paleofoodweb Working Group

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Funding
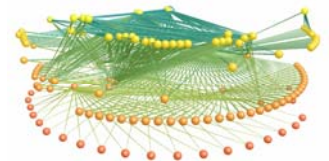
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