Ecological Network Structure

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Life emerged from the burrow and fissures. Soon, the desert was filled with the buzz and click and screech of creatures which, lacking mankind's superior brainpower, did not concern themselves with finding someone to blame and instead tried to find someone to eat.

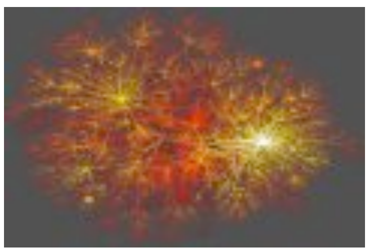
Jingo, Terry Pratchett, p.372

Part 1: Ecological Network Structure Intro
Part 2: Models of Food-Web Structure
Part 3: Food-Web Robustness
Part 4: Ancient Food Webs

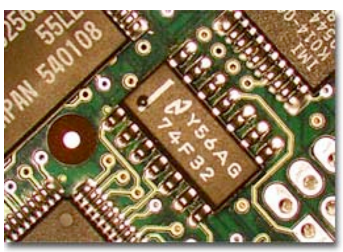
Part 1: Ecological Network Structure Intro

Technological networks

Road Maps



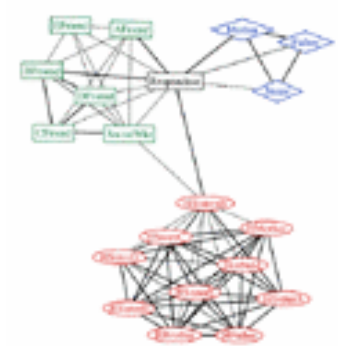
Internet Connectivity



Circuit Boards

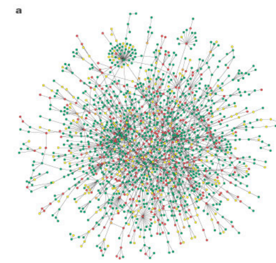
Social networks

The Kevin Bacon Game

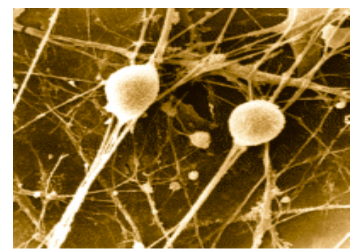


Support Network for a Homeless Woman

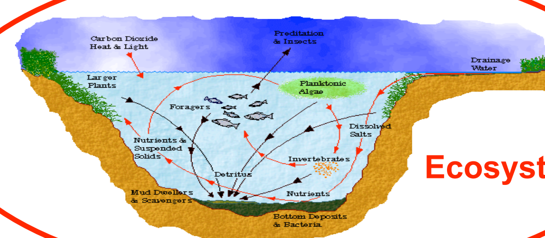
Biological networks



Protein Networks



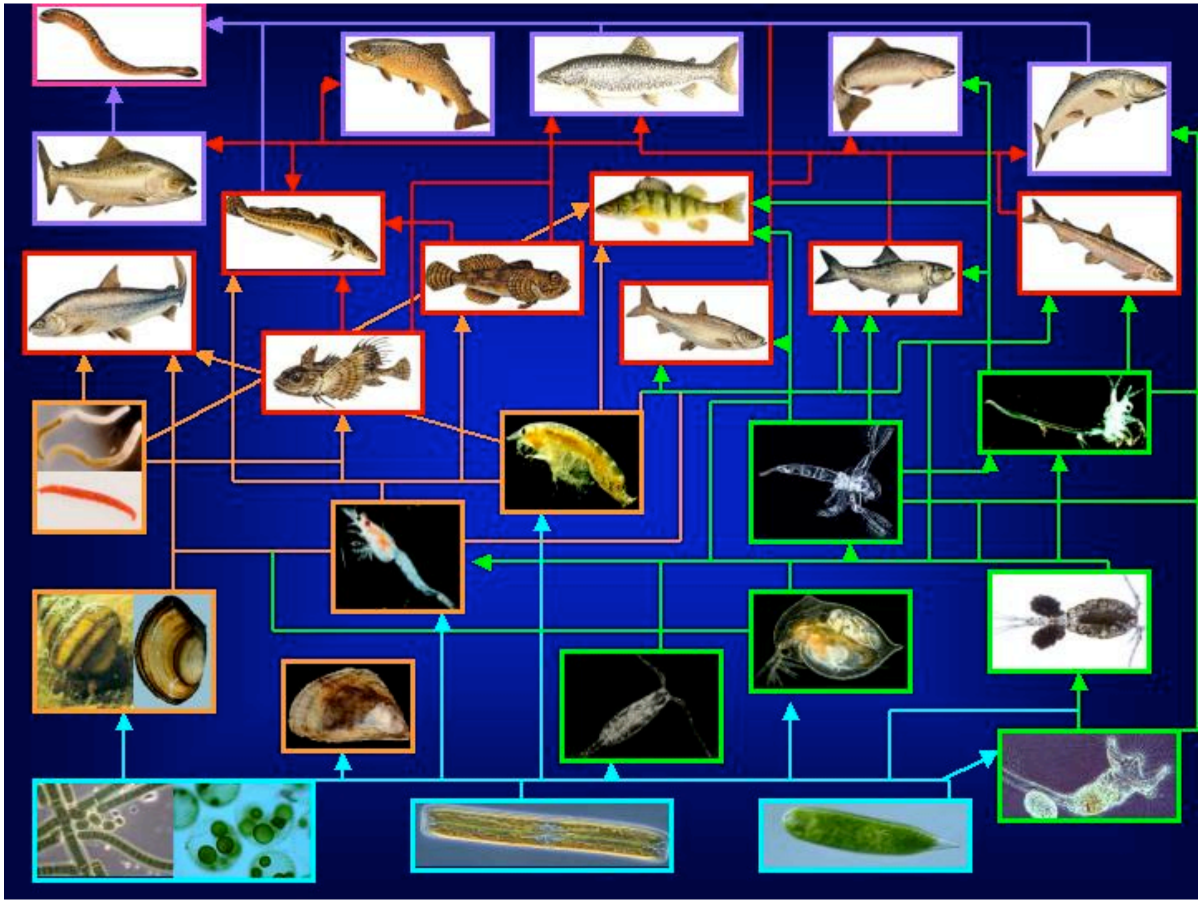
Neural Networks



Ecosystems

Nodes/Vertices = Species (usually)

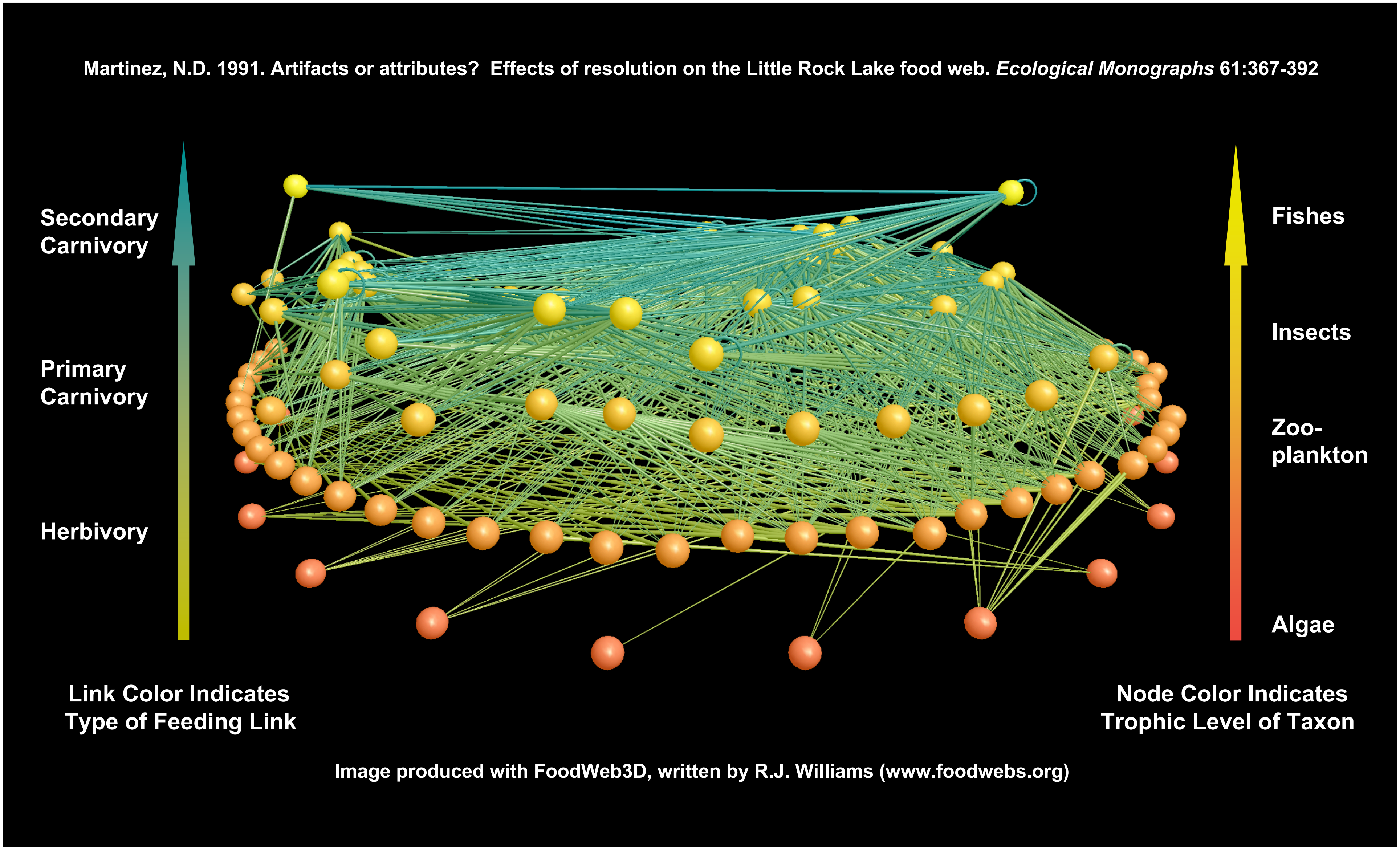
Edges = Trophic (Feeding) Links/Interactions
Types of links: herbivory, predation, parasitism, cannibalism
Links are directed in terms of feeding relationships (Consumer → Resource)
Links are undirected in terms of changes to population and evolutionary dynamics



“Original Species Webs” versus “Trophic Species Webs”

Little Rock Lake Food Web

92 Trophic Species with 997 Feeding Links



Diversity & complexity in food webs

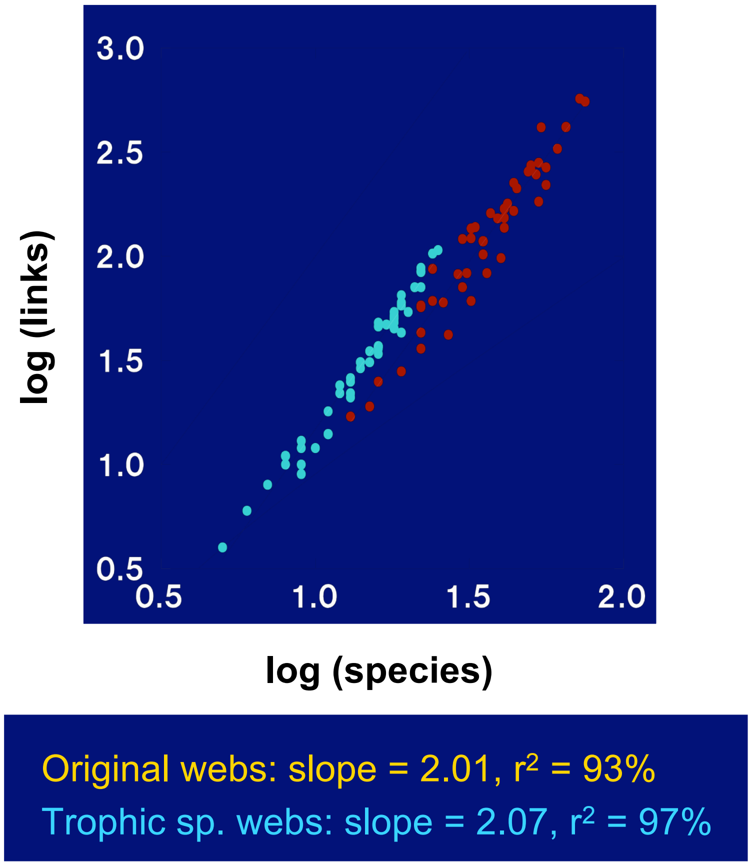
Trophic Species Richness (*S*)

- Functionally distinct taxa
- Share the same set of predators & prey
- Reduces methodological bias
- Largest *S* thus far: 346

Connectance (*Links/Species*^{2})

- Potential feeding links that are realized
- Theoretically varies from 0 to 1
- Empirically varies from ~0.01 to 0.3
- *C* varies independently of *S*
- Power-law relationship: $L = 0.1S^2$

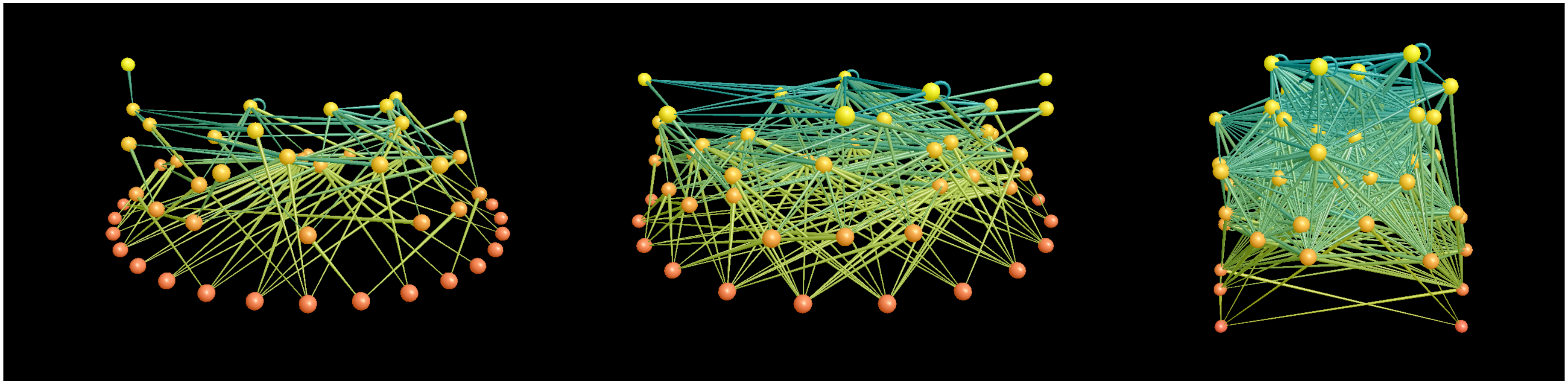
50 pelagic lake food webs



Data: Havens 1992 Science, analysis: Martinez 1993 Science

3 model food webs with S = 50

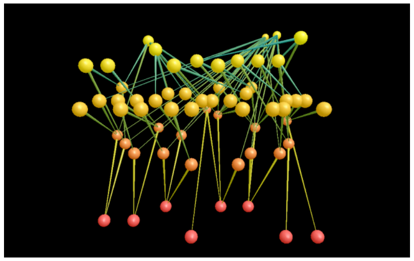
C = 0.03 | C = 0.10 | C = 0.30



75 links | 250 links | 750 links

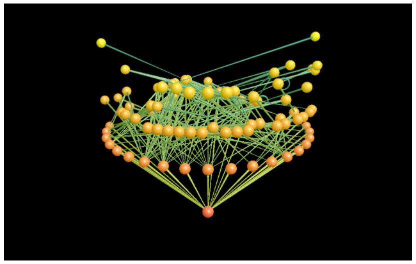
Low connectance webs, *C* < 0.10

Grassland



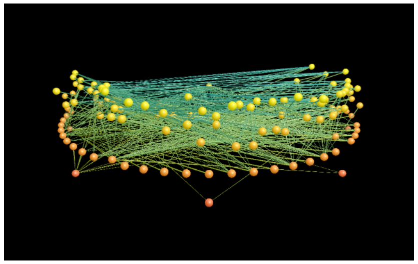
C = 0.03, *S* = 61, *L/S* = 1.6
Martinez et al. 1999

Scotch Broom



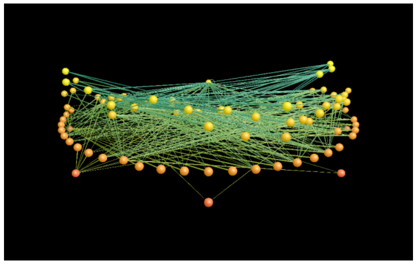
C = 0.03, *S* = 85, *L/S* = 2.6
Memmott et al. 2000

Ythan Estuary



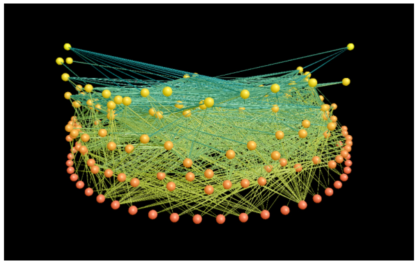
C = 0.04, *S* = 124, *L/S* = 4.7
Huxham et al. 1996

Ythan Estuary, no parasites



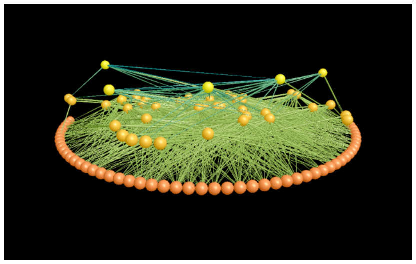
C = 0.06, *S* = 83, *L/S* = 4.8
Hall & Raffaelli 1991

El Verde Rainforest



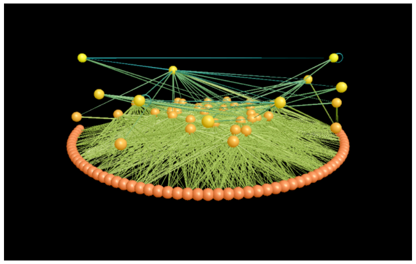
C = 0.06, *S* = 155, *L/S* = 9.7
Waide & Reagan 1996

Canton Creek



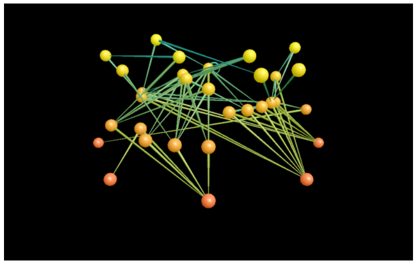
C = 0.07, *S* = 102, *L/S* = 6.8
Townsend et al. 1998

Stony Stream



C = 0.07, *S* = 109, *L/S* = 7.6
Townsend et al. 1998

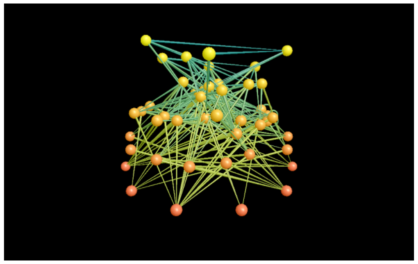
Chesapeake Bay



C = 0.07, *S* = 31, *L/S* = 2.2
Baird & Ulanowicz 1989

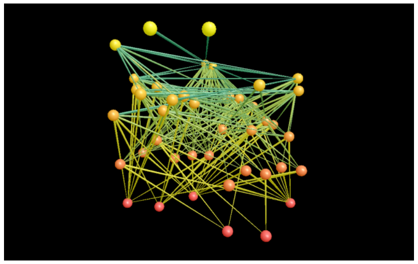
Middle & high connectance webs, $C \geq 0.10$

St. Marks Seagrass



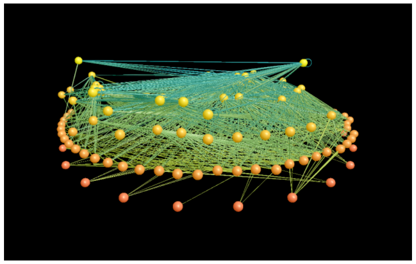
$C = 0.10$, $S = 48$, $L/S = 4.6$
Christian & Luczkovich 1999

St. Martin Island



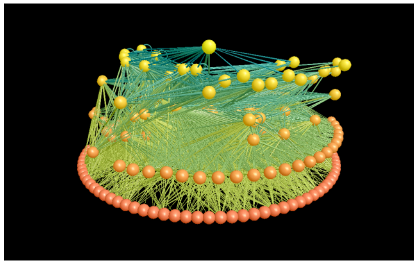
$C = 0.12$, $S = 42$, $L/S = 4.9$
Goldwasser & Roughgarden 1993

Little Rock Lake



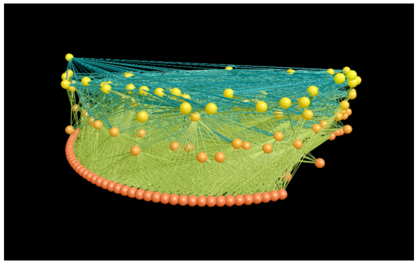
$C = 0.12$, $S = 92$, $L/S = 10.8$
Martinez 1991

Lake Tahoe



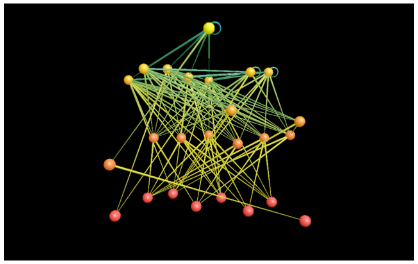
$C = 0.13$, $S = 172$, $L/S = 22.6$
Martinez unpublished data

Mirror Lake



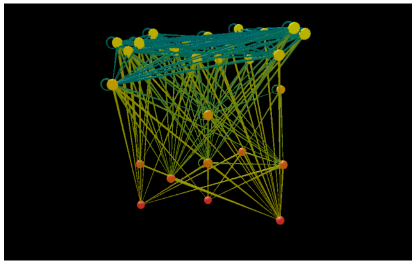
$C = 0.15$, $S = 172$, $L/S = 25.1$
Martinez unpublished data

Bridge Brook Lake



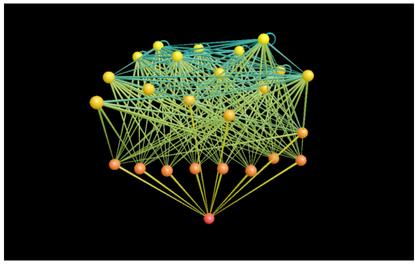
$C = 0.17$, $S = 25$, $L/S = 4.3$
Havens 1992

Coachella Valley



$C = 0.31$, $S = 29$, $L/S = 9.0$
Polis 1991

Skipwith Pond



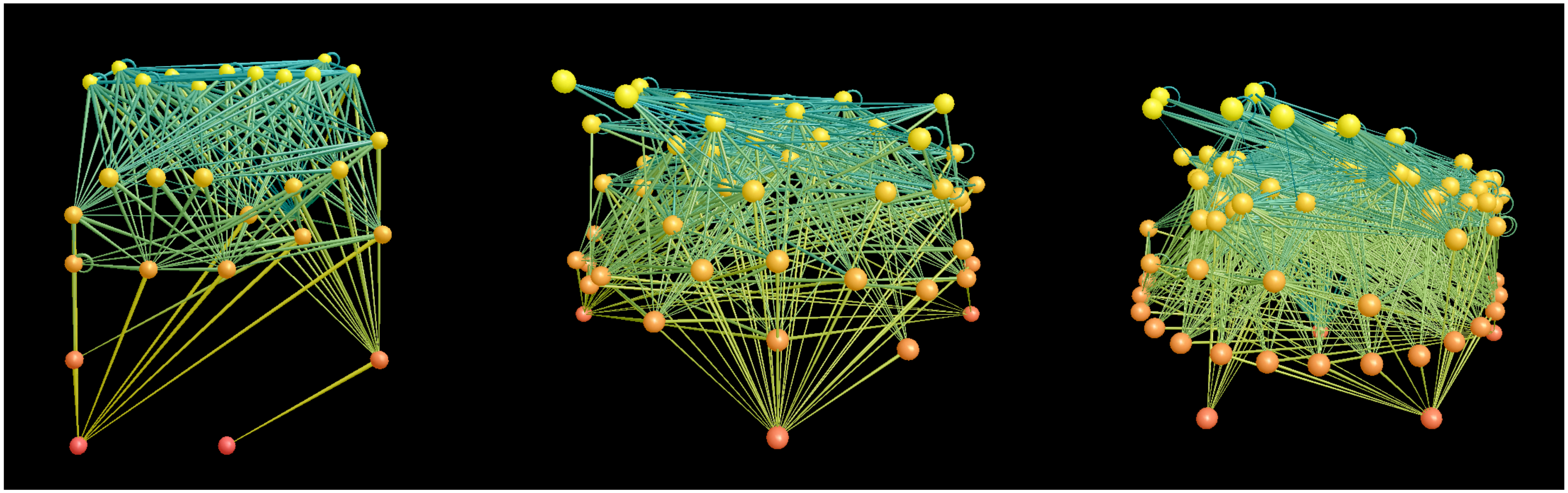
$C = 0.32$, $S = 25$, $L/S = 7.9$
Warren 1989

Three recent marine food webs (C = 0.22 to 0.24)

Benguela , S. Africa
(Yodzis 1998 JAE)

Caribbean Reef
(Opitz 1996 ICLARM)

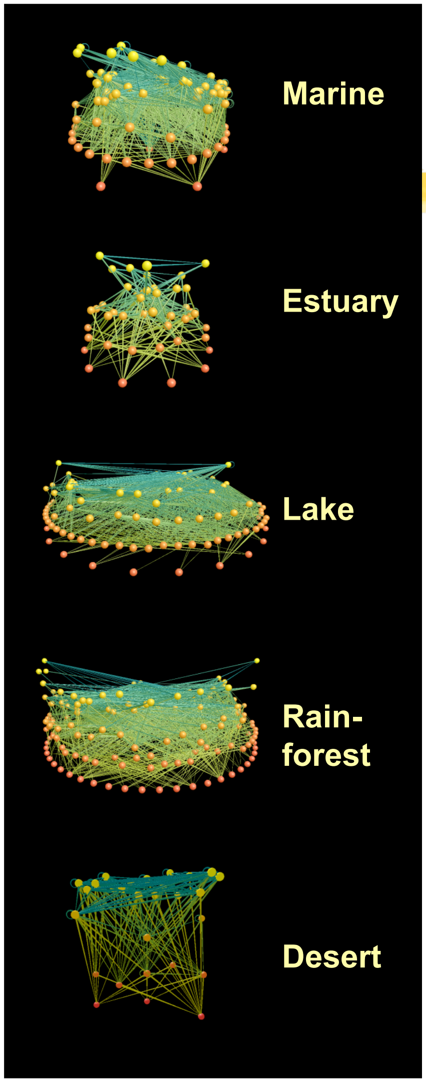
NE US Shelf
(Link 2002 MEPS)



***S* = 29, *C* = 0.24**

***S* = 50, *C* = 0.22**

***S* = 79, *C* = 0.22**



Apparent Complexity?

Structure of ‘real-world’ networks

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

Small-world topology

Watts, D.J. and Strogatz, S.H. 1998. Collective dynamics of ‘small-world’ networks. *Nature* 393:440-442.

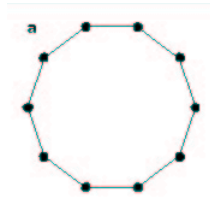
- Short path lengths
  - average shortest distance between pairs of nodes
  - short compared to regular network
- High clustering
  - proportion of nodes linked to a node that are also linked
  - high compared to random network

Scale-free degree distribution

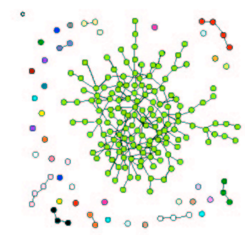
Albert, R., Jeong, H., and Barabási, A.-L. 1999 The diameter of the world-wide web. *Nature* 401:130-131.

- Power-law link distribution
  - most most nodes have few links
  - a few nodes have many links (‘hubs’)

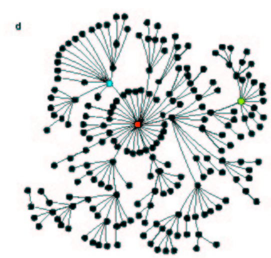
Regular Network



Random Network



Small-World, Scale-Free Network



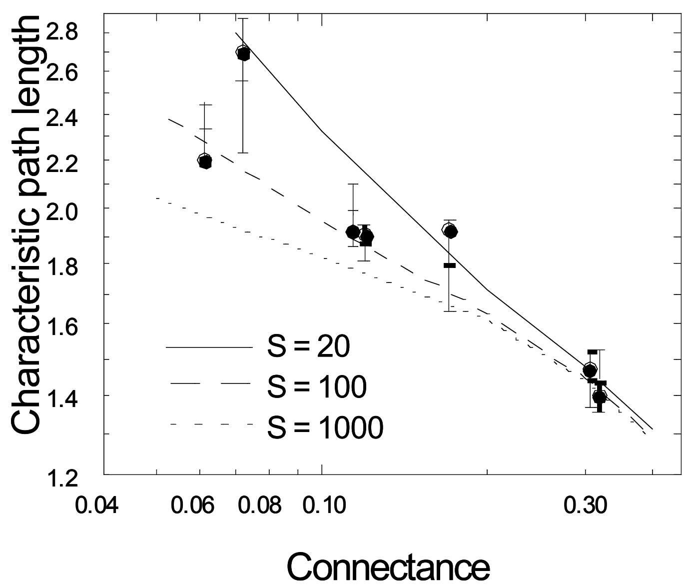
Are food webs small worlds? Nope.

Path lengths are small
(~2 degrees of separation)

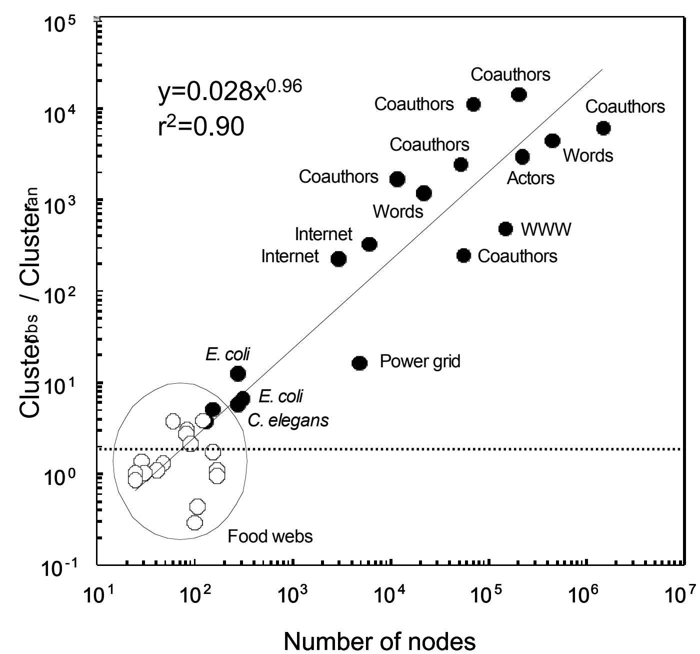
BUT

Clustering is low
(few food webs have high clustering)

Path lengths of 7 empirical food webs



Clustering of many empirical networks



Networks above dashed line have at least 2X random clustering

Are food webs scale-free? Nope.

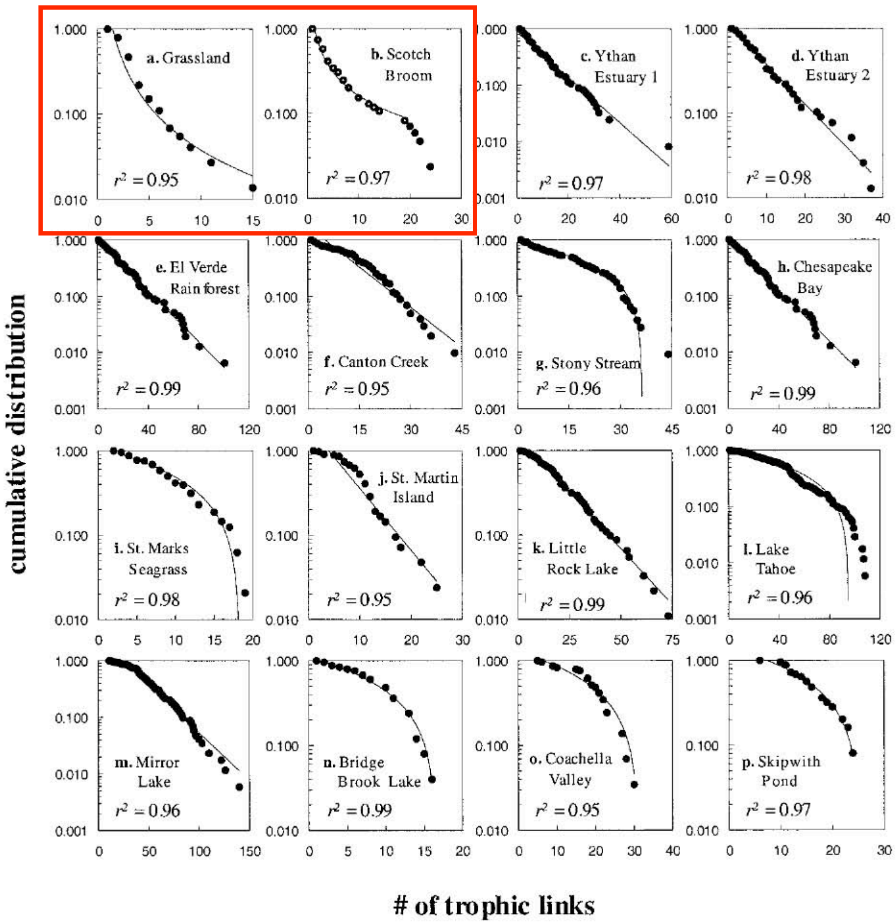


Fig. 2. Linear-log plots of the cumulative distributions of links per species (both predator and prey links) in 16 food webs. Webs are ordered by increasing connectance (see Table 1). Lines and r^2 values show the fit to the data of the best of three simple models: power–law distribution (upward curved line), exponential decay (straight line), or uniform distribution (downward curved line). No food web is well fit by a Poissonian or Gaussian distribution.

Webs shown in order of increasing connectance.

Exponential distribution indicated by straight line on log-linear graph.

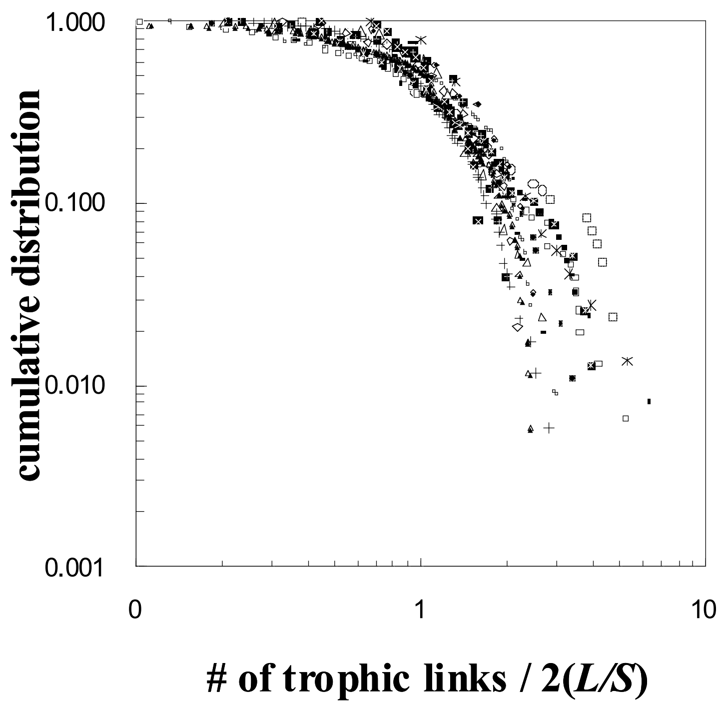
Most food webs display single-scale distributions (exponential or uniform).

Only two very low C webs display power-law distributions.

Are food webs scale-free? Nope.

Overlay of Link Distribution Data from 16 Food Webs

(power law would display straight line on log-log plot)



- Evidence for a unified functional form for food-web link distributions?
- The relatively high *C* and low *S* of food webs limits potential heterogeneity of feeding link distribution.
- When might power-laws occur?
  - -Cross habitat boundaries
  - -Systems dominated by specialists
  - -Snapshot vs. integrative data

Limitations of small-world, scale-free analyses

Only 3 aspects of topology typically considered:

1) Characteristic Path Length
2) Clustering Coefficient
3) Link Distribution

These properties give a sense of coarse structure.
What about more system-specific, fine-grain structure?

Other aspects of network structure

Compartmentalization

Densely connected subgroups

(Girvan & Newman *PNAS* 2002, Krause et al. *Nature* 2003, Melián & Bascompte *Ecology* 2005)

Disassortative Mixing

Low degree species tend to link to high degree species

(Newman *Phys. Rev. E* 2003)

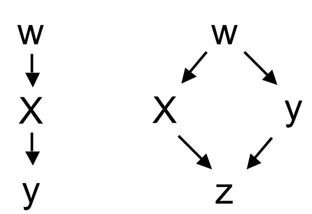
Simple Patterns

Universal scaling of minimum structure

(Garlaschelli et al. *Nature* 2003, but see Camacho & Arenas *Nature* 2005)

Repeating simple motifs

(Milo et al. *Science* 2002)



Possible configurations: 13 3-node, 199 4-node

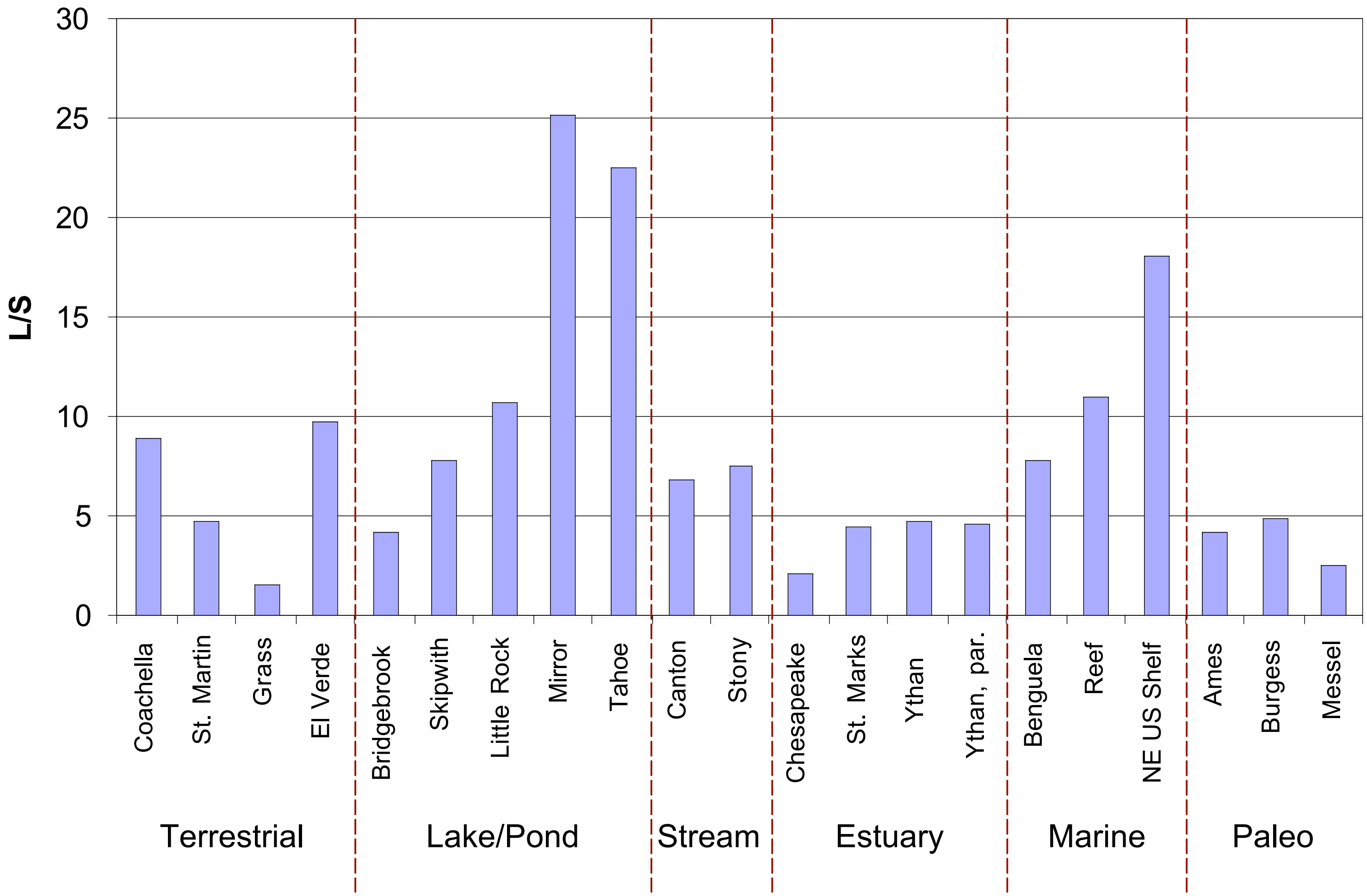
Gene Regulation (2)
Neurons (3, 1 shared w/ food webs)
Food Webs (2)
Electronic Circuits 1 (3, 1 shared w/ food webs)
Electronic Circuits 2 (3)
World Wide Web (3)

Properties Specific to Food-Webs

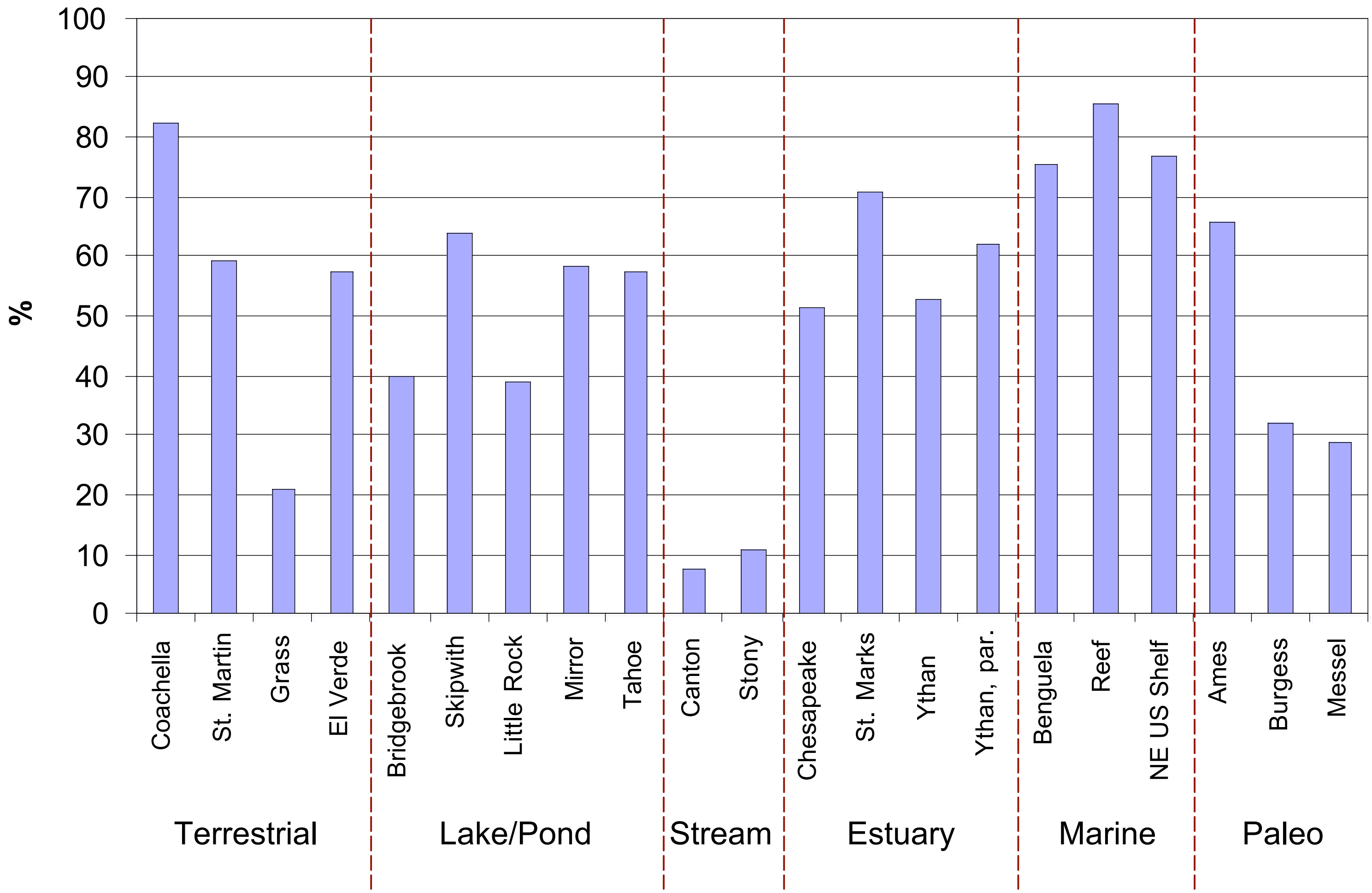
Basic Properties: *S* (# species), *L* (# links), *L/S* (links per species), *C* (connectance = L/S^2)

<u>**Types of Taxa**</u>	<u>**Overall Network Structure**</u>
% Top	Generality SD (var. of links to resources) (out degree)
% Intermediate	Vulnerability SD (var. of # links from consumers) (in degree)
% Basal	Link SD (var. of total links) (degree)
% Cannibals	Maximum Trophic Similarity Mean (max. diet overlap)
% Omnivores	Chain Length Mean
% Herbivores	Chain Length SD
% Spp. in Loops	Log Chain Number
(A→B→C→A)	Mean Trophic Level

Links per Species



Percent Omnivores



Red = Lowest Value
Green = Highest Value

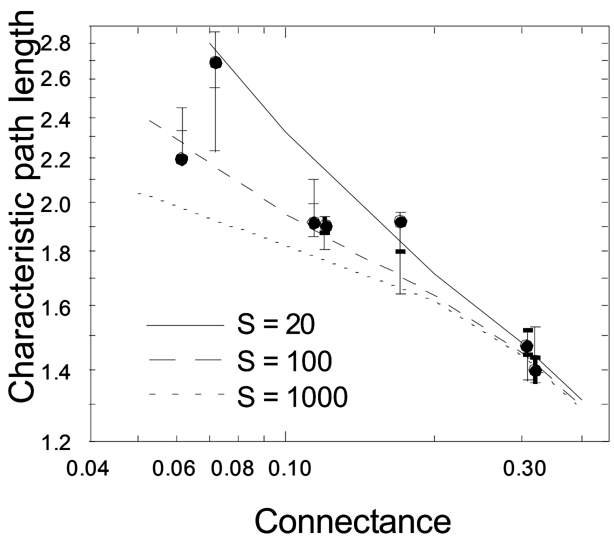
Some properties of diverse food webs

		Taxa	*S*	*C*	*L/S*	Ch len	Path len	%T	%I	%B	%Can	%Omn
Terrestrial	Coachella Valley	**30**	29	0.31	9.0	6.7	1.4	**0**	90	10	**66**	76
	St. Martin Island	44	42	0.12	4.9	5.2	1.9	17	69	14	**0**	60
	UK Grassland	75	61	**0.03**	**1.6**	3.2	**3.7**	31	56	13	**0**	21
Pond/Lake	Skipwith Pond	35	**25**	**0.32**	7.9	6.2	**1.3**	4	92	**4**	32	60
	Bridge Brook Lake	75	**25**	0.17	4.3	4.0	1.9	**0**	68	32	12	40
	Little Rock Lake	**182**	92	0.12	4.9	7.3	1.9	1	86	13	14	38
Stream	Canton Creek	108	102	0.07	6.8	3.2	2.3	25	**22**	53	1	**8**
	Stony Stream	112	**109**	0.07	7.6	**3.1**	2.3	17	27	**56**	2	10
Estuary	Chesapeake Bay	33	31	0.07	2.2	4.0	2.7	32	52	16	3	52
	St. Marks Estuary	48	48	0.10	4.6	6.6	2.0	17	69	12	6	71
	Ythan Estuary	92	83	0.06	4.8	5.9	2.2	**37**	54	9	4	54
Marine	Benguela	29	29	0.24	7.0	6.4	1.6	**0**	93	7	24	76
	Caribbean Reef	50	50	0.22	11.1	9.8	1.6	**0**	**94**	6	42	**86**
	NE US Shelf	81	79	0.24	**17.8**	**15.3**	1.6	4	94	**3**	32	78

Food-web properties are highly variable

Many food-web properties are “scale-dependent” with S and/or C.

Path lengths of 7 empirical food webs



As a result, direct comparison of web properties is problematic.

Structure Summary

- Ecological communities can be characterized as networks of interacting species. Trophic interactions, compiled into food webs, are a central concept for empirical and theoretical ecological research.

- Trophic links scale as a power-law with number of species, such that $L = 0.1S^2$, or about 10% of possible trophic links in a community are actually realized (Connectance = $L/S^2 = 0.1$). Early studies suggested linear scaling (constant links/species), other studies suggest an exponent between 1 and 2.

- Most food webs are not small-world or scale-free, and thus have a different topology than most other types of real-world networks.

- Food-web structure analysis considers a wide range of topological properties. Those properties vary widely across food webs, and are typically scale-dependent on S and/or C.