Integrating Natural and Computer Sciences to Explore the Structure and Dynamics of Complex Ecological Networks

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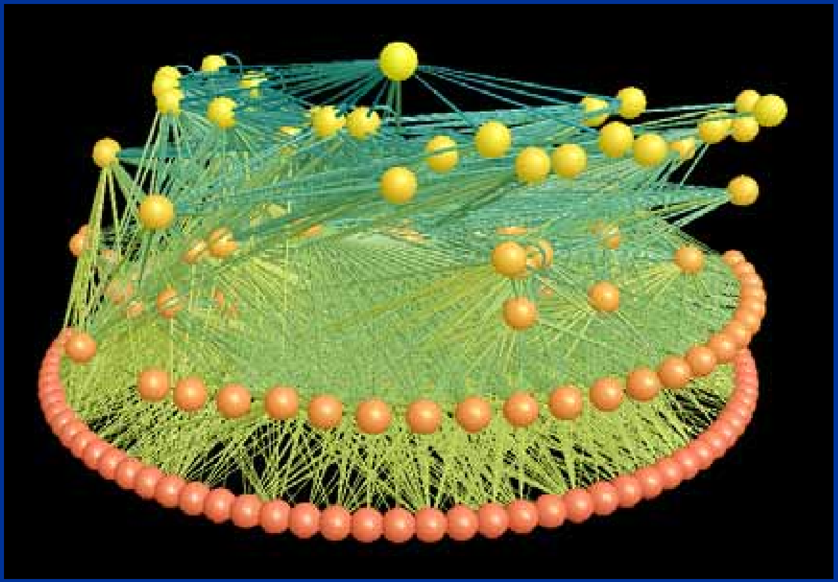

Lake Tahoe food web

Food web graphics by Web3D © Rich Williams

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Dalhousie Univ.

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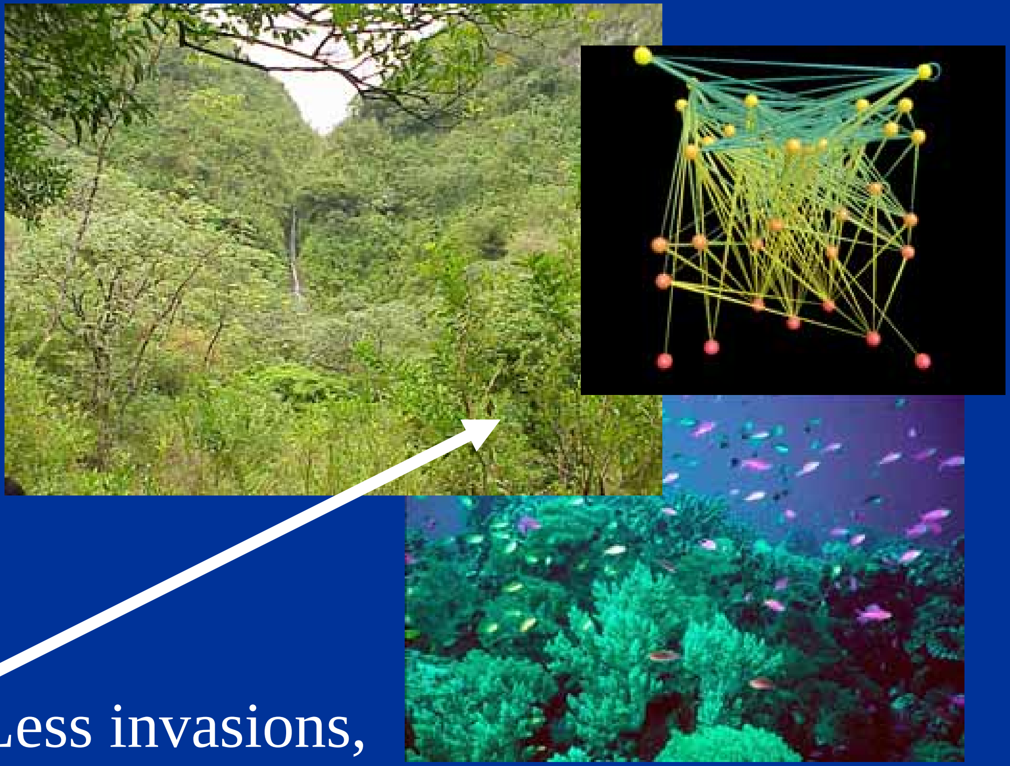
San Francisco State U.

Early paradigm: complex communities are more stable than simple ones (Odum 1953, MacArthur 1955, Elton 1958)



Less invasions,

less species turnover,

less calamities,...

Change of paradigm: Unstable complex systems

Mathematically, stability decreases with system diversity (species) and complexity (interactions)

Gardner & Ashby 1970 Nature;

May 1972 Nature

NATURE VOL. 228 NOVEMBER 21 1970

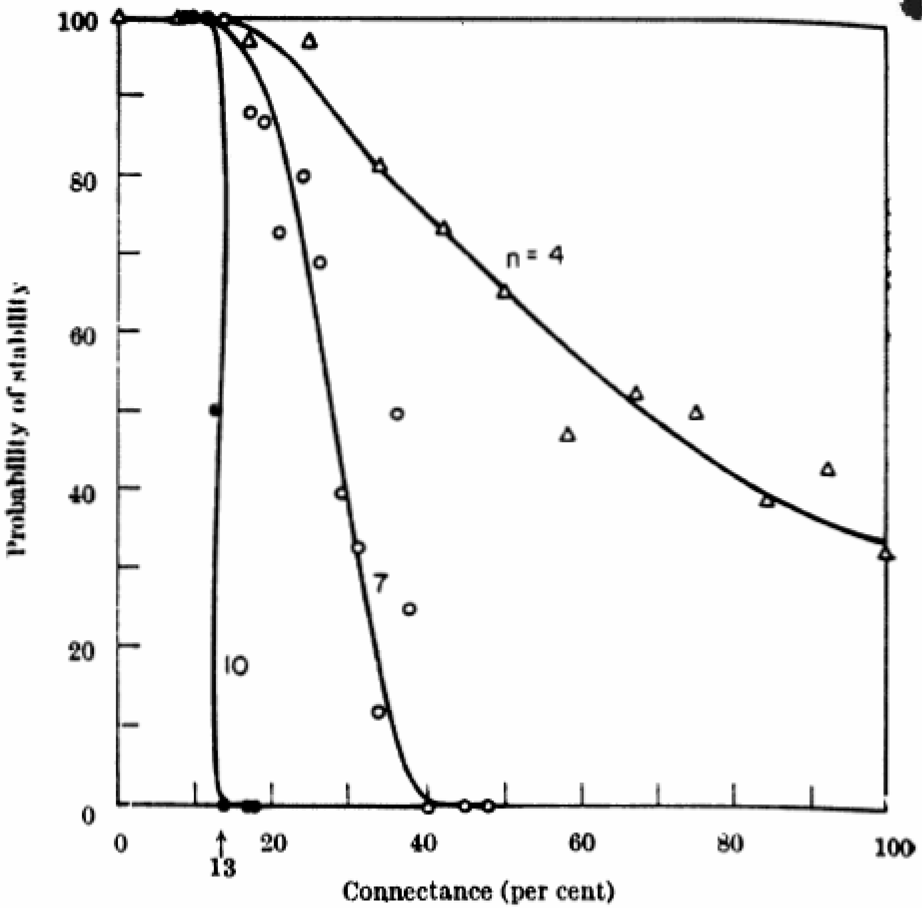
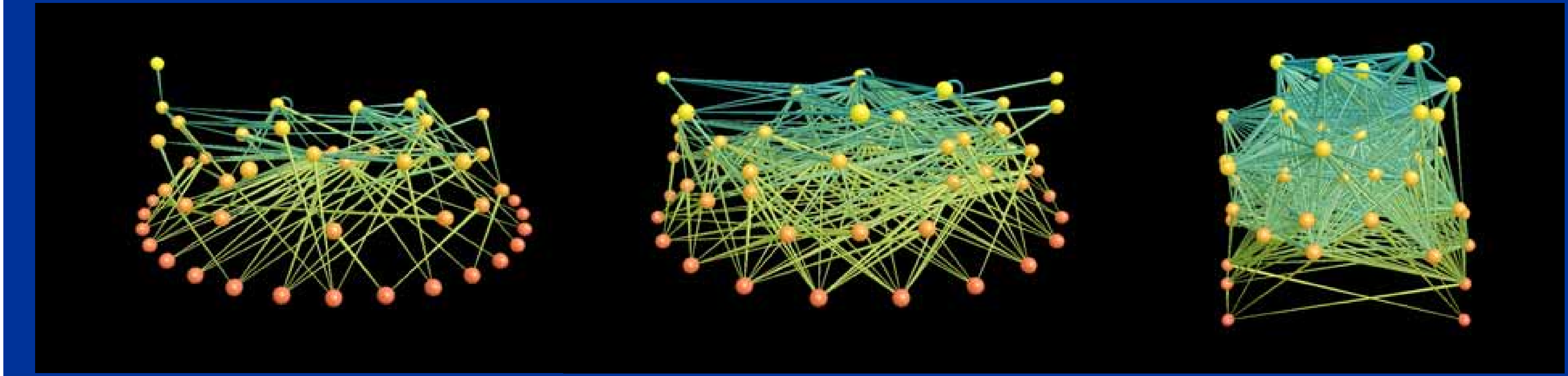


Fig. 1. Variation of stability with connectance.

3 “niche model” food webs with *S* = 50 and empirically observed range of connectance (*C* = Links/Species^2)

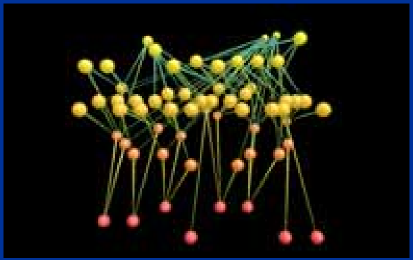
C = 0.03 *C* = 0.10 *C* = 0.30



75 links 250 links 750 links

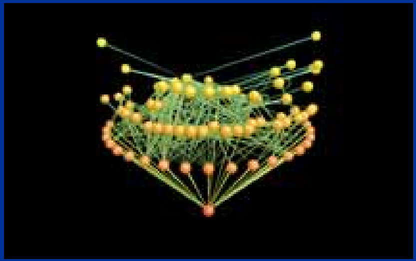
Low Connectance Webs, $C < 0.10$

UK Grassland



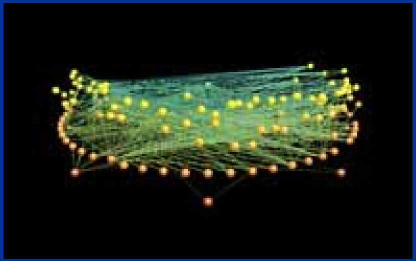
$C = 0.03$, $S = 61$, $L/S = 1.6$
Martinez et al. 1999

Scotch Broom



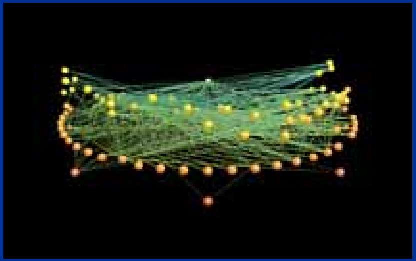
$C = 0.03$, $S = 85$, $L/S = 2.6$
Memmott et al. 2000

Ythan Estuary



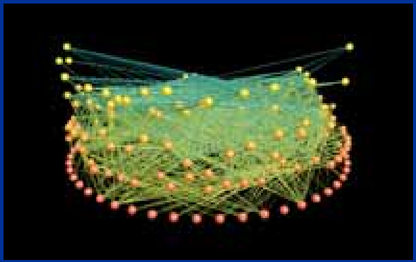
$C = 0.04$, $S = 124$, $L/S = 4.7$
Huxham et al. 1996

Ythan Estuary, no parasites



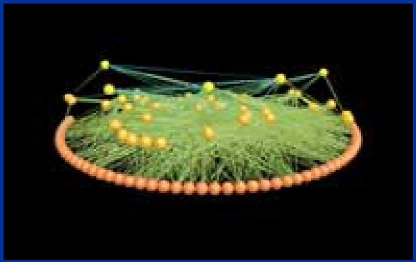
$C = 0.06$, $S = 83$, $L/S = 4.8$
Hall & Raffaelli 1991

El Verde Rainforest



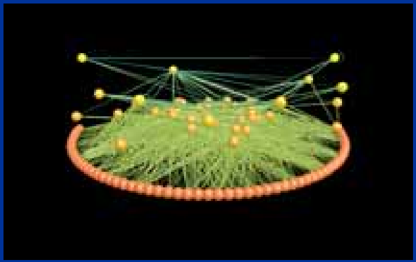
$C = 0.06$, $S = 155$, $L/S = 9.7$
Waide & Reagan 1996

Canton Creek



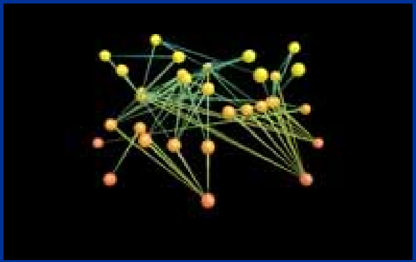
$C = 0.07$, $S = 102$, $L/S = 6.8$
Townsend et al. 1998

Stony Stream



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

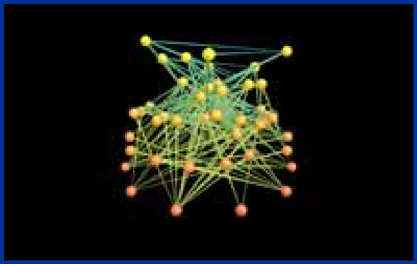
Chesapeake Bay



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

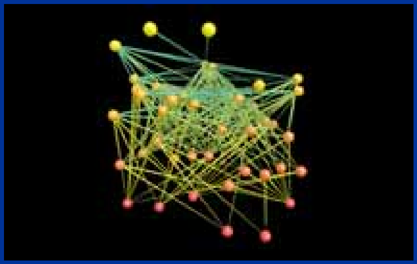
Middle and High Connectance Webs, $C < 0.10$

St. Marks Seagrass



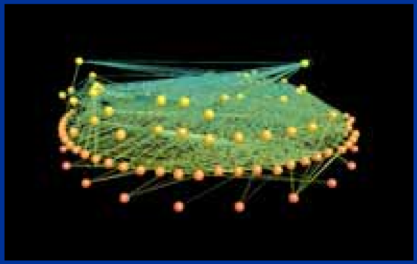
$C = 0.10$, $S = 48$, $L/S = 4.6$
Christian & Luczkovich 1999

St. Martin Island



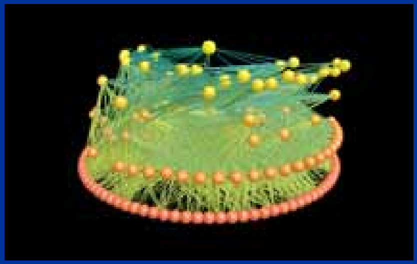
$C = 0.12$, $S = 42$, $L/S = 4.9$
Goldwasser & Roughgarden 1993

Little Rock Lake



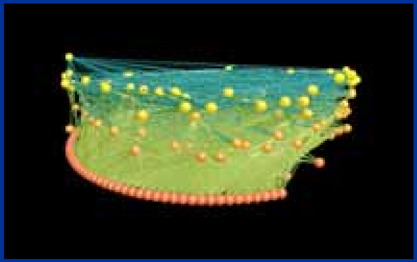
$C = 0.12$, $S = 92$, $L/S = 10.8$
Martinez 1991

Lake Tahoe



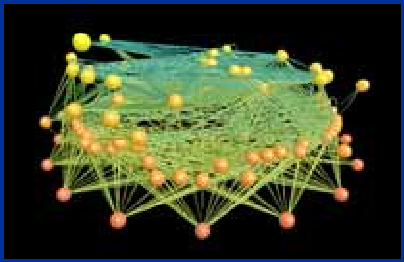
$C = 0.13$, $S = 172$, $L/S = 22.6$
Vaccaro and Martinez unpbl.

Mirror Lake



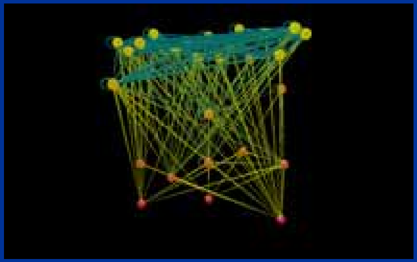
$C = 0.15$, $S = 172$, $L/S = 25.1$
Puleston and Martinez unpbl.

East River



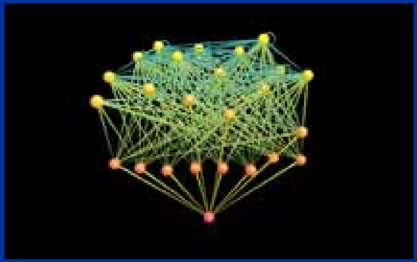
$C = 0.15$, $S = 104$, $L/S = 15$
Harvey and Martinez unpbl.

Coachella Valley



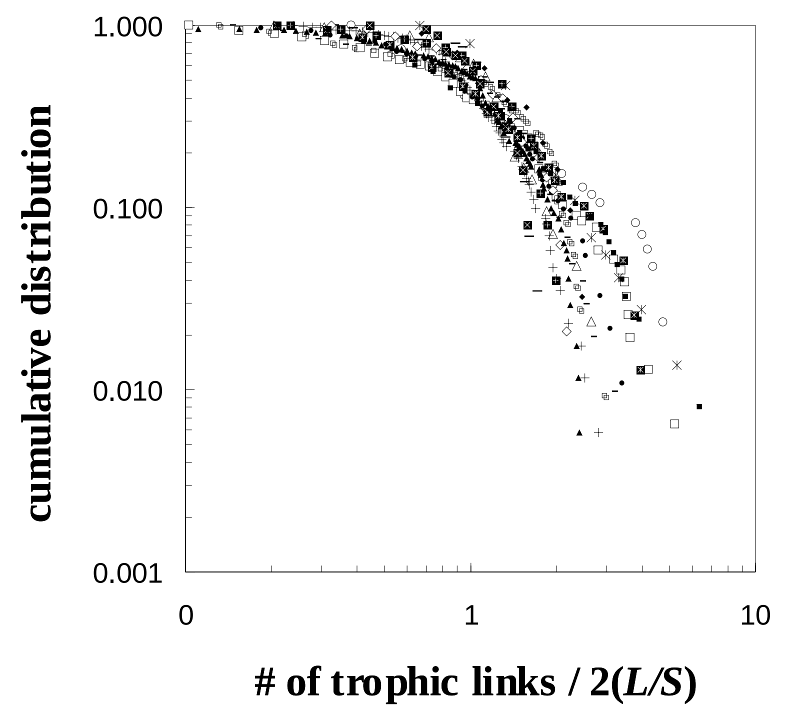
$C = 0.31$, $S = 29$, $L/S = 9.0$
Polis 1991

Skipwith Pond



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

Are food webs scale-free? Not really…



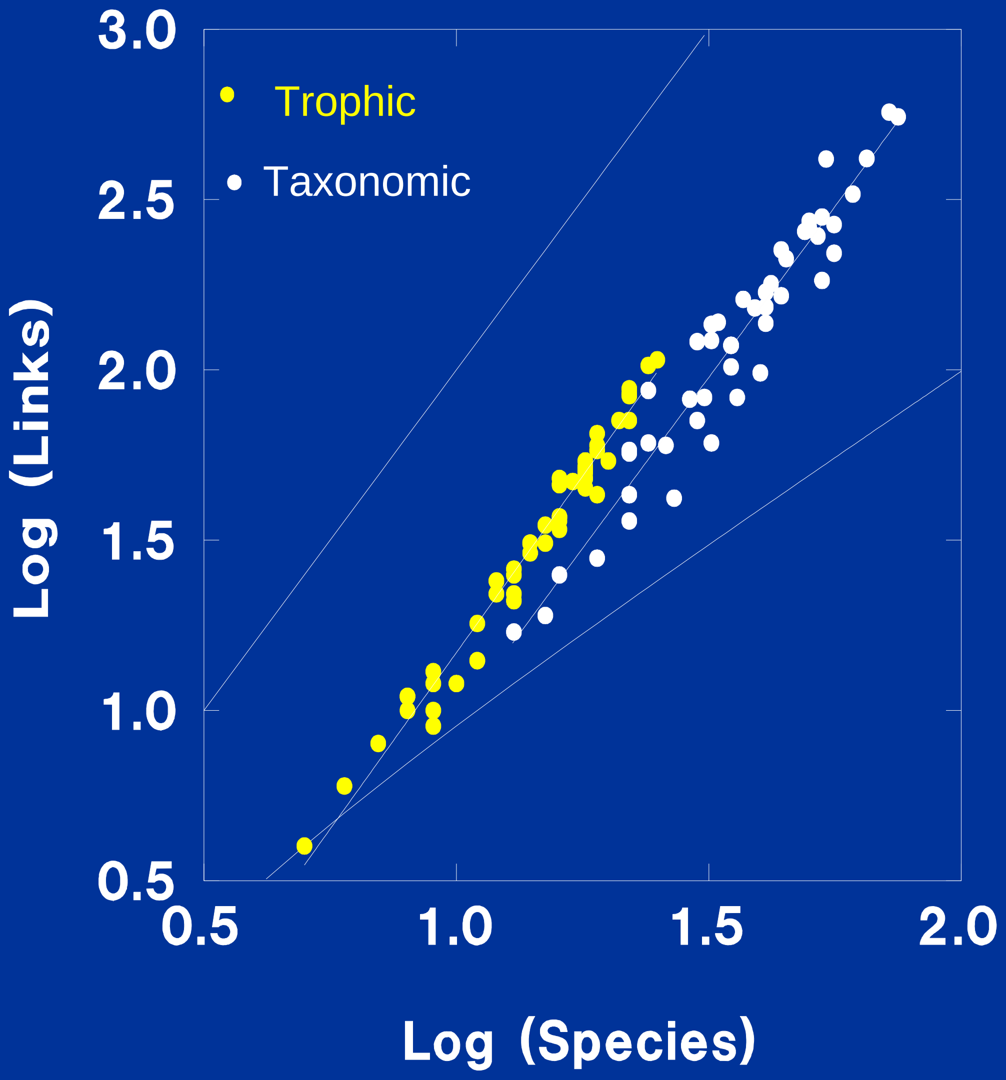
- Most food webs display single-scale (exponential or uniform) distributions.
  -i.e., no structurally ‘over-dominant’ taxa in food webs.
- The relatively high *C* and low *S* of food webs limits potential heterogeneity of feeding link distribution.

Dunne, Williams and Martinez

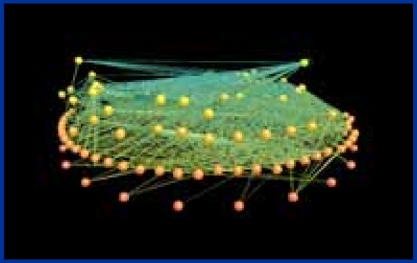
2002 *PNAS* 99:12917

Constant Connectance (L/S^2): S is orthogonal to L/S^2

- Taxonomic webs
  - Slope = 2.01
  - R^2 = 93%
- Trophic webs
  - Slope = 2.07
  - R^2 = 97%

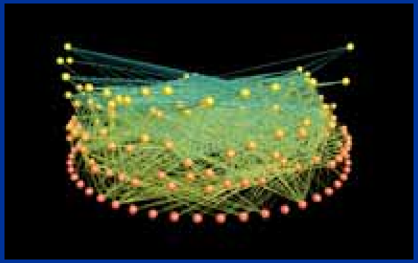


2 Versions of Havens'
50 Pelagic Food Webs
Martinez *Science* 1993



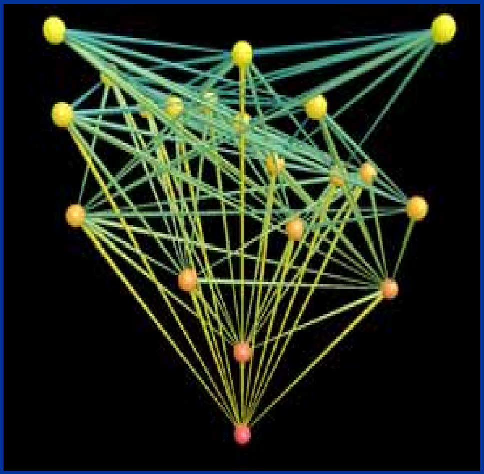
Challenge

Which structural properties
enable network persistence



Analyses by an ecoinformatics approach that synthesizes
(1) structural models of food webs and
(2) allometrically scaling population dynamics

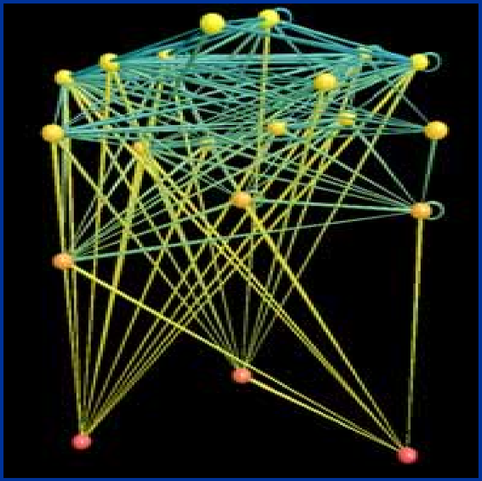
Structural models of complex food webs



Cascade model

Cohen et al. 1990

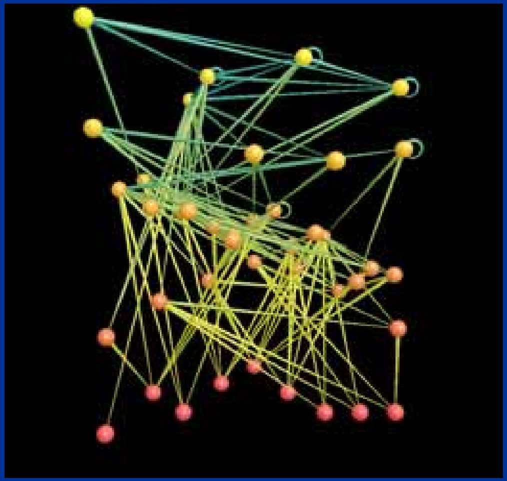
Strong trophic hierarchy



Niche model

Williams & Martinez 2000 *Nature*

Looping allowed, contiguity required



Nested-hierarchy model

Cattin et al. 2004 *Nature*

Phylogenetic grouping and adaptation

Niche Model: Simple Rules

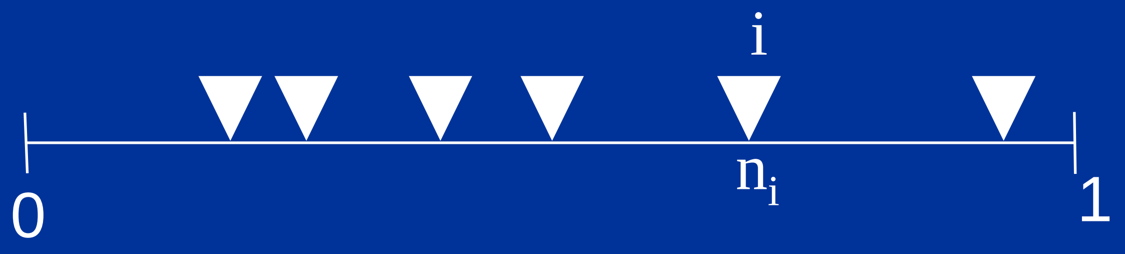
- Inputs: Diversity and Complexity (S & C)
    - Ecological contingency

- 3 Simple Rules

Niche Model Rule 1

- Fixed one-dimensional community niche space
- Each species given a fixed location or “niche value”

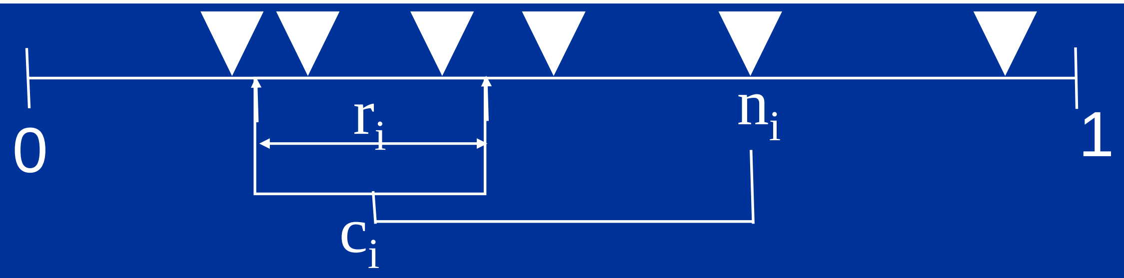
- **Rule 1: Assign each of *S* species a uniformly random number [0, 1] so that the “niche value” of S_i is n_i**



Niche Model
Rule 2

- Rule 1: Each species gets uniform random n_i
- **Rule 2: Each species gets assigned a random “feeding range” (r_i) $0 \leq r_i \leq 1$**
    - **chosen from a beta function (mean of 2C) multiplied by the species niche value (n_i).**
- Stochastically distributes generality among species while ensuring web has comparable C

Niche Model
Final Step 3

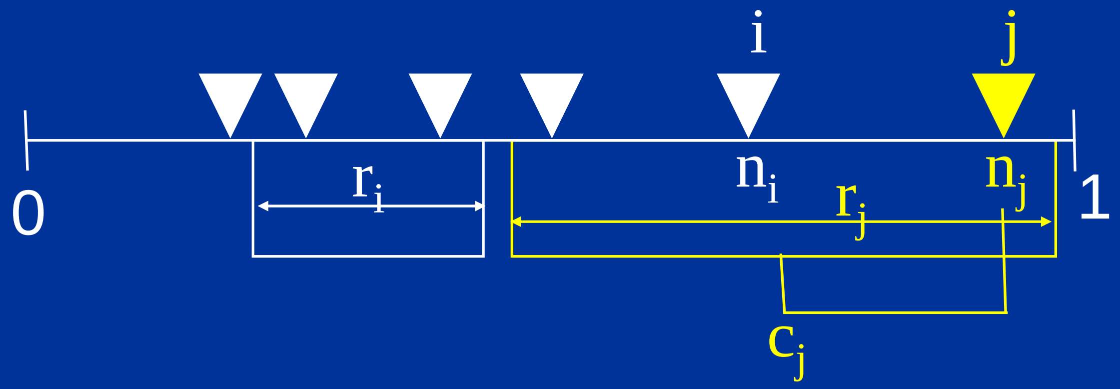


- Step 1: Each species gets uniform random n_i
- Step 2: Each species gets beta random r_i

- **Step 3: Each niche range is placed by uniformly choosing a random range center (c_i) so that $r_i/2 < c_i < n_i$**

- Establishes relaxed trophic hierarchy while allowing cannibalism and looping

Niche Model: Mechanics



- Randomly assign “j” species a niche value (n_j)
- Randomly assign species a niche range (r_j)
- Randomly assign the center of the range (c_j)

- Repeat 1000 times with observed S and C

Nested Hierarchy Model

- Inputs: Diversity and Complexity (S & C)
  - Ecological contingency

- Phylogenetic Adaptation
  - Species get beta-distributed diets
  - Starting with lowest ranked species, Species join feeding guilds that consume lower ranked species
  - If needed, more prey are randomly added

Bioenergetic Nonlinear Population Dynamics

Biomass change ~ growth – metabolism + consumption – being consumed

$$B_i'(t) = r_i G_i(\vec{B}) - \overbrace{x_i B_i(t)} + \sum_{j=1}^{n} \left(\overbrace{x_i y_{ij} F_{ij}(\vec{B}) B_i(t)} - \overbrace{x_j y_{ji} F_{ji}(\vec{B}) B_j(t) / e_{ji}} \right)$$

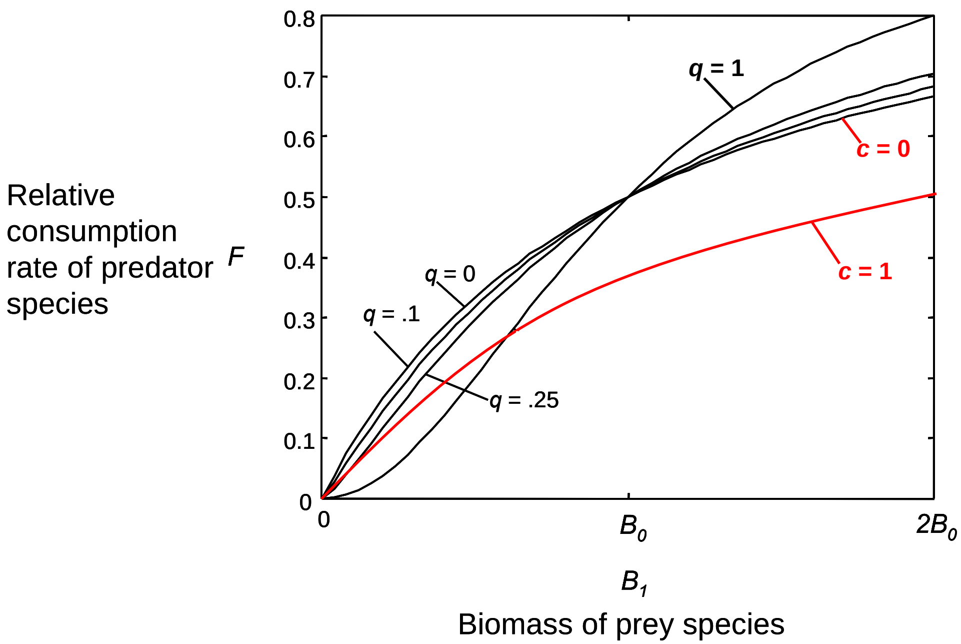
Growth rate

Metabolic rate

Maximum consumption rate

Functional response

Gradation from Type II to Type III Functional Response



$$F_{ij}(B) = \frac{B_j(t)^{1+q_{ij}}}{\sum_{k=1}^{n} \alpha_{ik} B_k(t)^{1+q_{ij}} + B_{0\,ji}^{\;1+q_{ij}}}$$

α: relative prey preference of predator species

B: biomass

B_o: half saturation density of prey species when consumed by predator species

q: controls form of functional response

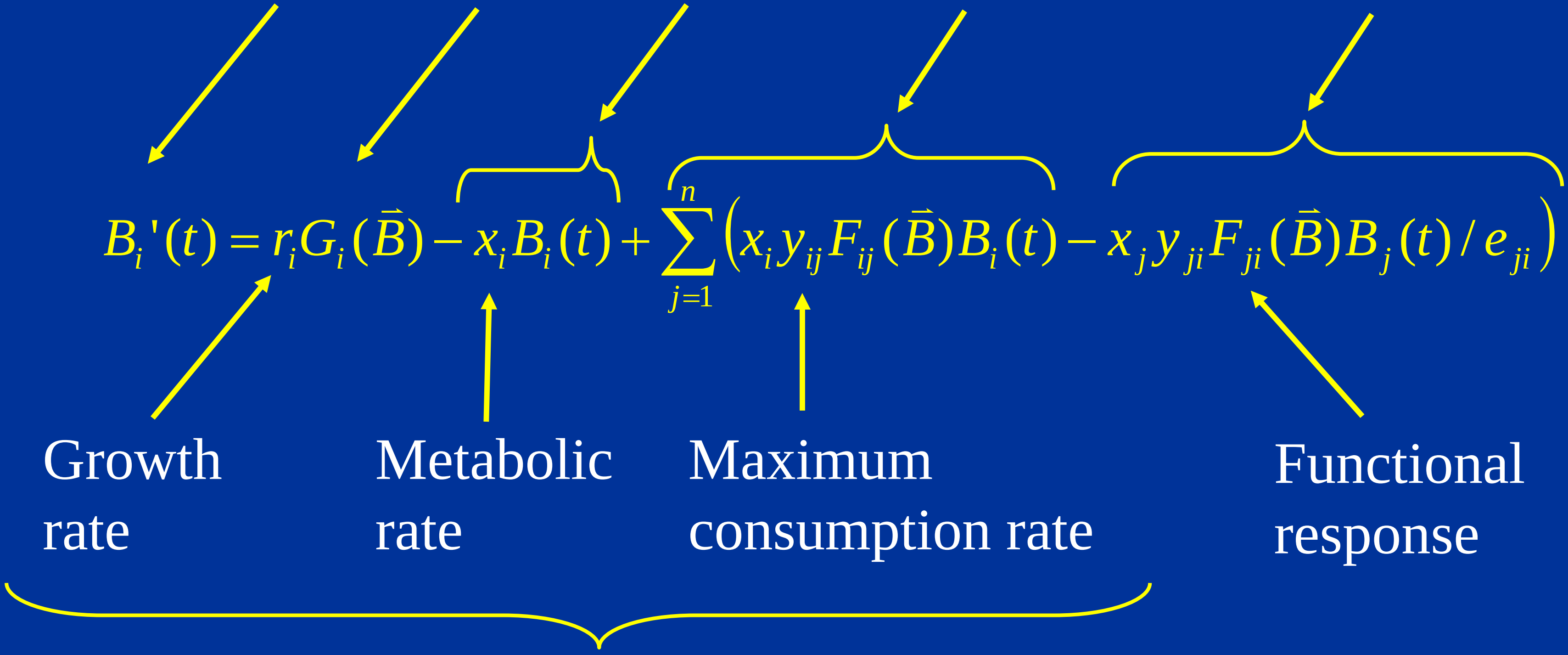
- *q* = 0 (Type II)
- *q* = 1 (Type III)

Addition of Predator Interference to Type II Functional Response:

$$F_{ij}(B) = \frac{B_j(t)}{\sum_{k=1}^{n} \alpha_{ik} B_k(t) + (1 + c_{ij} B_i(t)) B_{0\,ji}}$$

Bioenergetic Nonlinear Population Dynamics

Biomass change ~ growth – metabolism + consumption – being consumed



$$B_i'(t) = r_i G_i(\vec{B}) - x_i B_i(t) + \sum_{j=1}^{n} \left(x_i y_{ij} F_{ij}(\vec{B}) B_i(t) - x_j y_{ji} F_{ji}(\vec{B}) B_j(t) / e_{ji} \right)$$

Growth rate

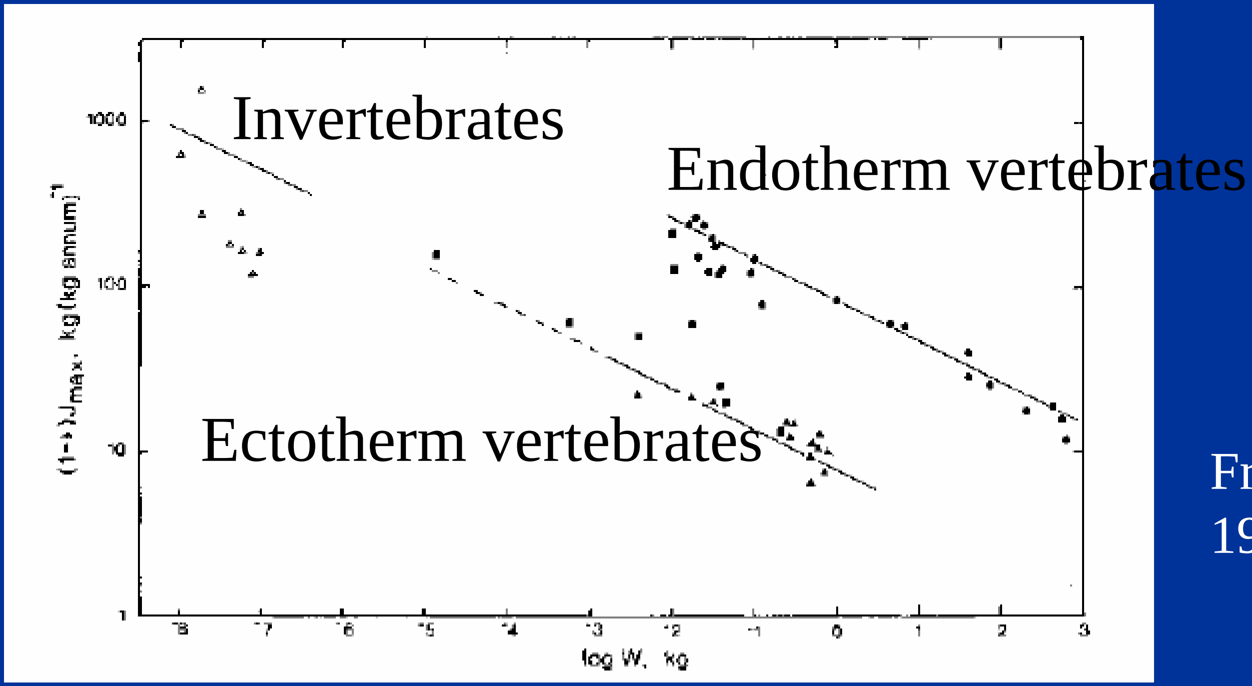
Metabolic rate

Maximum consumption rate

Functional response

Biological rates scale with a negative quarter power-law with species’ body masses (West et al. 1997 *Science*, Enquist et al. 1999 *Nature*, West et al 1999 *Nature*)

Power law allometric scaling relationships



From: Yodzis & Innes
1992 Am. Nat.

Different metabolic types of species:

- same negative quarter exponent
- different allometric constants

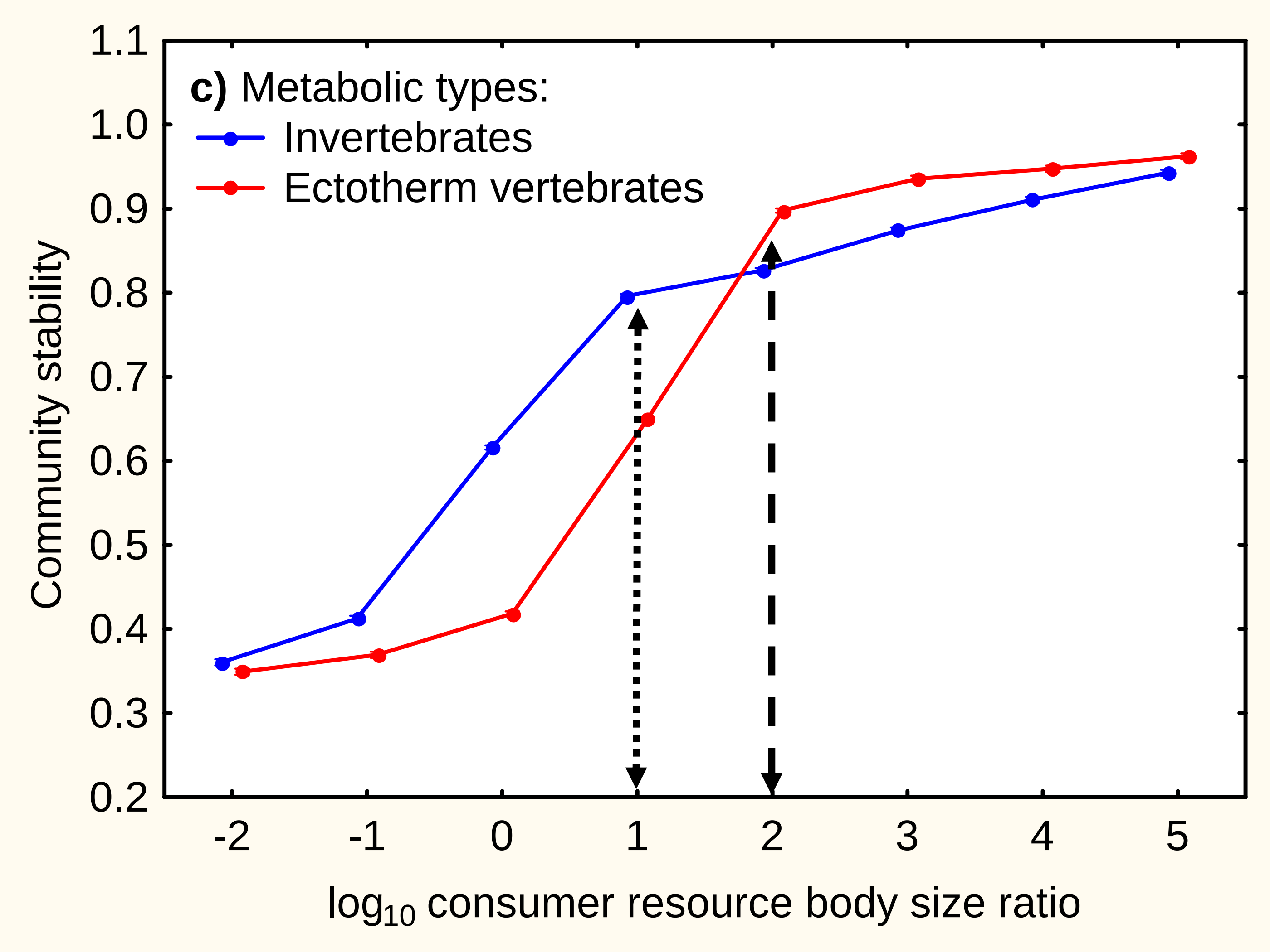
Generate binary network with structural network model

Scale biological rates with negative quarter power-law

Parameterize network model of population dynamics

Simulate nonlinear population dynamics

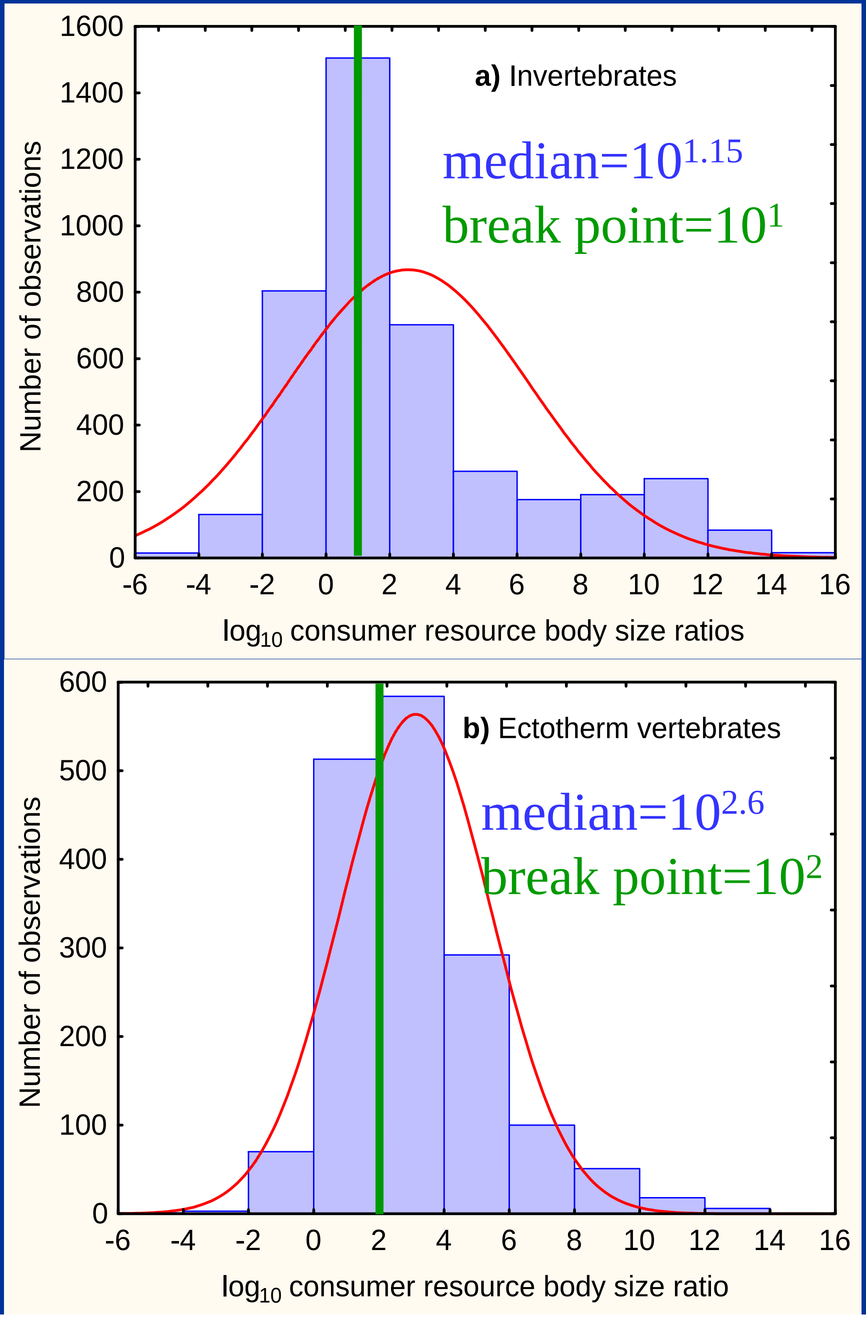
Measure stability as probability of species persistence

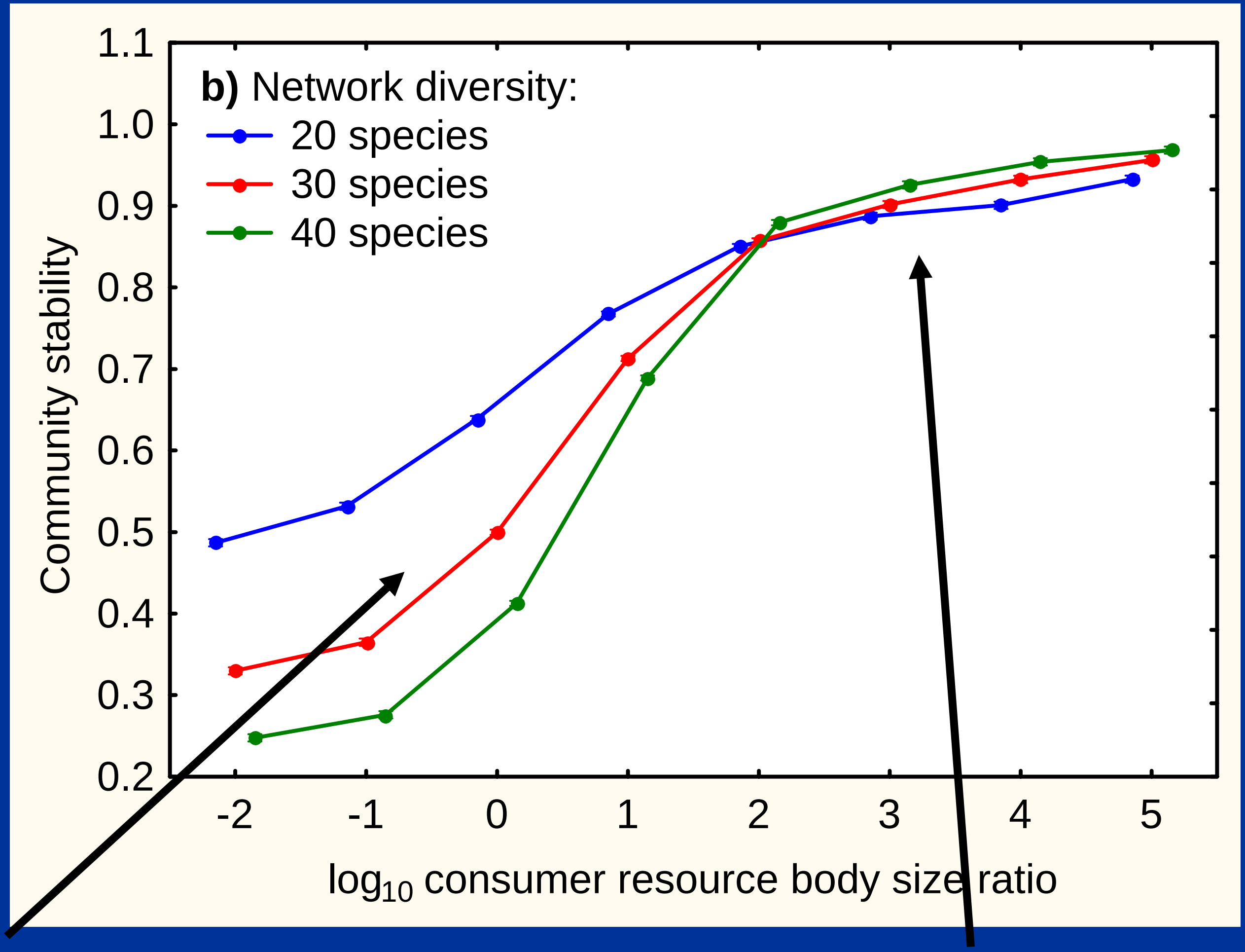

c) Metabolic types:
Invertebrates
Ectotherm vertebrates
Community stability
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
-2
-1
0
1
2
3
4
5
$\log_{10}$ consumer resource body size ratio

Global data base on natural body size ratios

Data for 3887 invertebrate predators and 1501 ectotherm vertebrate predators

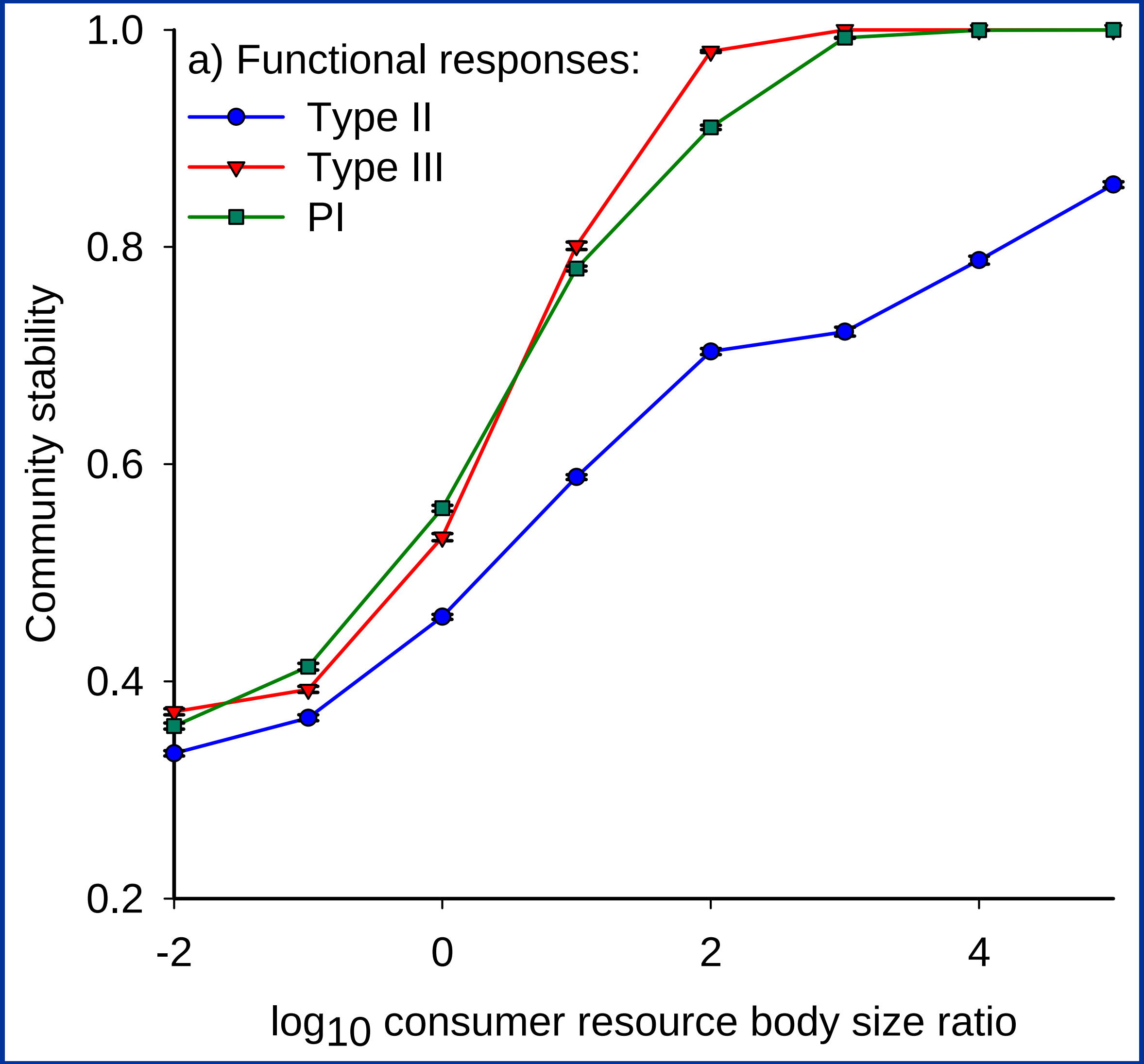
Geometric mean body size ratios are above break points



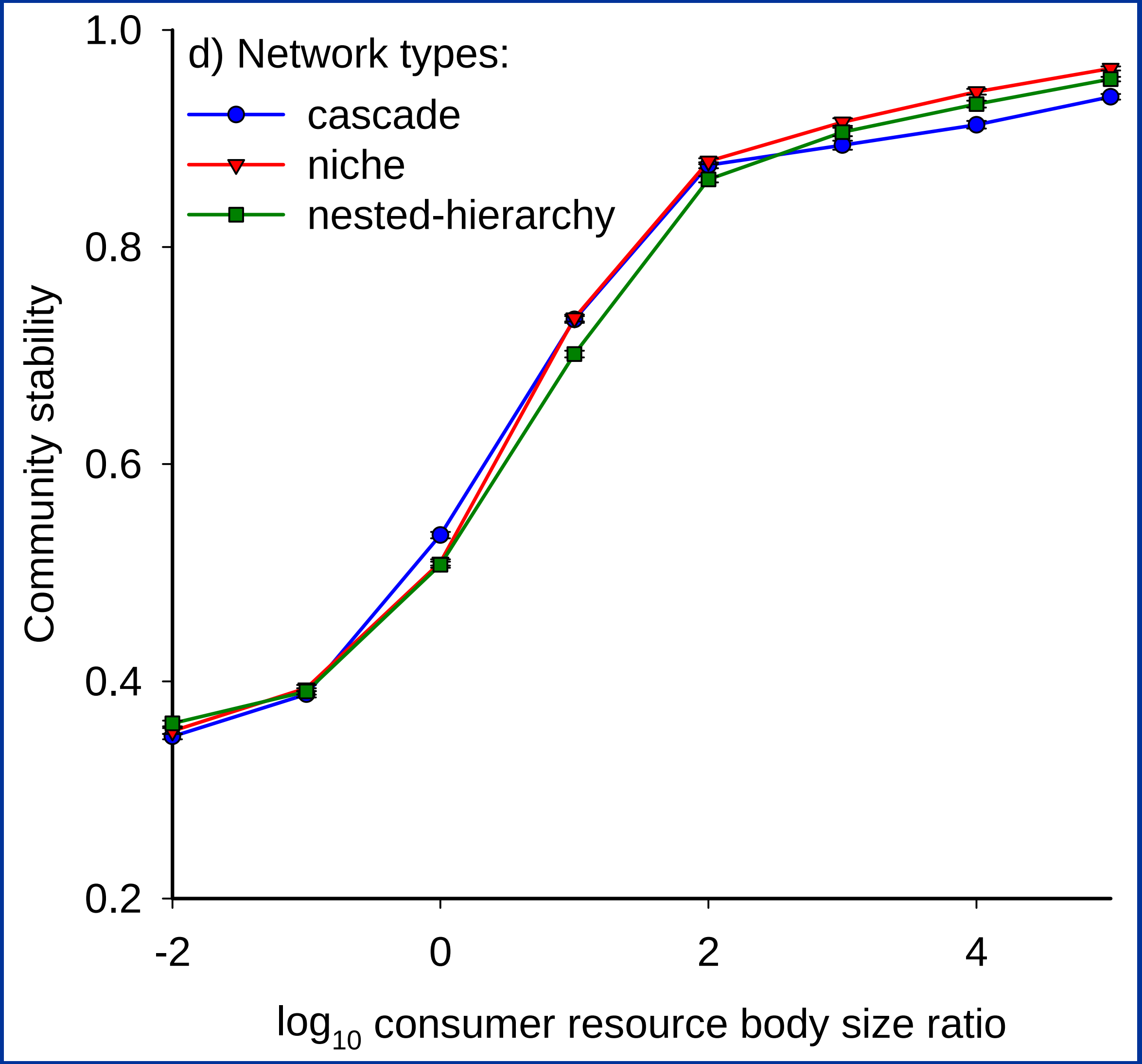


Negative diversity stability relationships under uniform body size distributions

Positive diversity stability relationships under natural body size distributions



Results qualitatively robust to variation in Functional Responses



Results generally robust to limited variation in Network Structure

Conclusions - Part I

- Instability under abstract (random) dynamics on abstract (random) networks

- Stability under realistic (allometrically scaled) dynamics on realistic (non-random) networks

- Natural ecosystems are stabilized by their body size structure

- Including empirical realism allows simulation of complex ecological network dynamics – So where do we get the data? How can more scientists contribute to and conduct such simulations?

  - INFORMATICS!

Conclusions Part II & Future Directions

- Ecoinformatics are Key to Computational and Basic Ecology

- Improve empirical estimates of maximum consumption rates, especially for invertebrates

- Empirically explore functional responses, especially variability within food webs

- *In Silico* explorations of network structure
- Improve and implement “data forever” ecoinformatics

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→ **Scaling of Network Complexity with Diversity in Food Webs**
→ **Webs on the Web: Internet Database, Analysis and Visualization of Ecological Networks**
→ **Science on the Semantic Web: Prototypes in Bioinformatics**

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Unified spatial scaling of species and their trophic interactions. ***Nature*** 428:167-171

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American Naturalist 163: 458-468

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