Nonlinear Dynamics of Complex Ecological Networks (aka food webs) I: Theory

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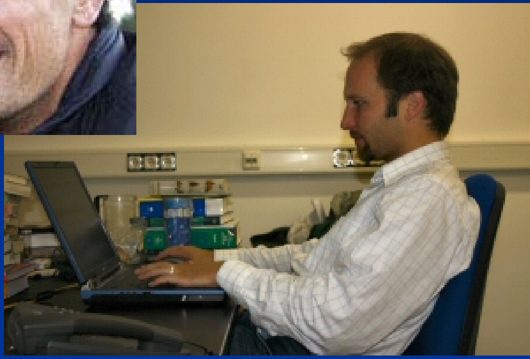
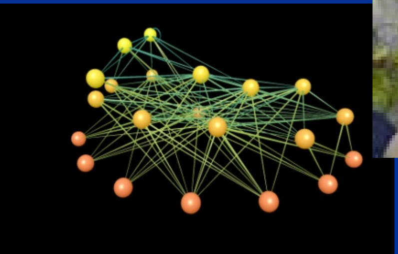




www.FoodWebs.org

Outline

- Introduction to food webs
- Why we study food webs
  - Relationships of diversity and complexity to stability
- What we have learned about their structure
  - Niche Model
- What we have learned about their dynamics
  - Structure function relationships
- How can such understanding be applied
  - Species loss

Food Webs: Why?

- Generality
  - Incorporates the vast majority of organisms
    - species and biomass
  - Includes the all habitats
    - aquatic, terrestrial, soil, endolythic, hyporeic.
    - substrate bound, free floating
- Basic ecological laws (assumptions):
  - During life, biomass is always created and destroyed.
  - continuous energy consumption and expenditure required
  - All heterotrophs need to eat to live
    - autotrophs are ultimately the only source of food.
- Species’ reproductive units share feeding potential
  - evolution

Darwin's *Origin of Species* (1859)

It is interesting to contemplate a tangled bank,

clothed with many plants of many kinds,

with birds singing on the bushes,

with various insects flitting about,

and with worms crawling through the damp earth,

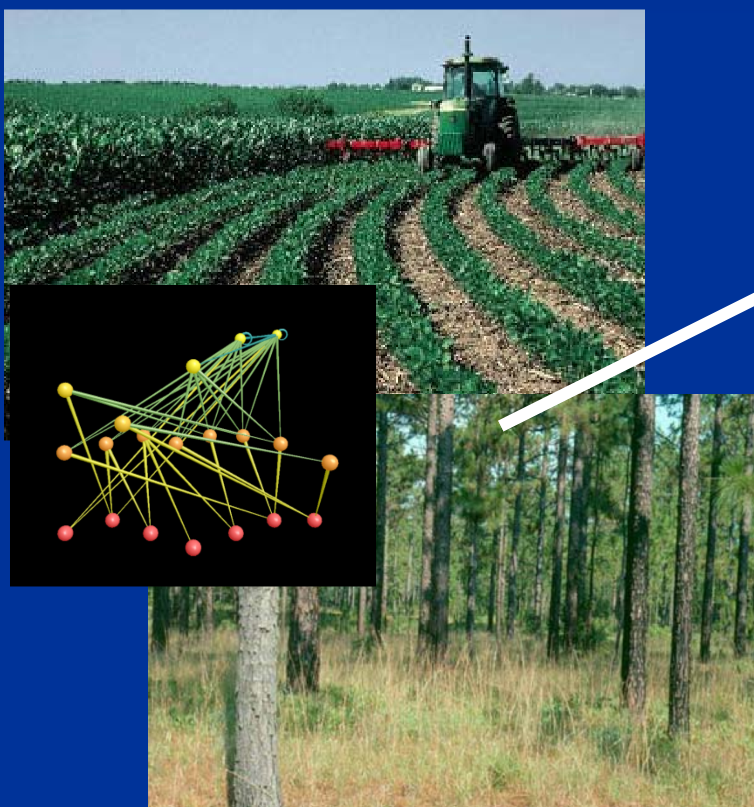
and to reflect that these elaborately constructed forms,

so different from each other,

and dependent upon each other in so complex a manner,

have all been produced by laws acting around us.

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*

Biological Computer Laboratory

University of Ilinois

May 1972 *Nature*: Will a Large Complex System be Stable

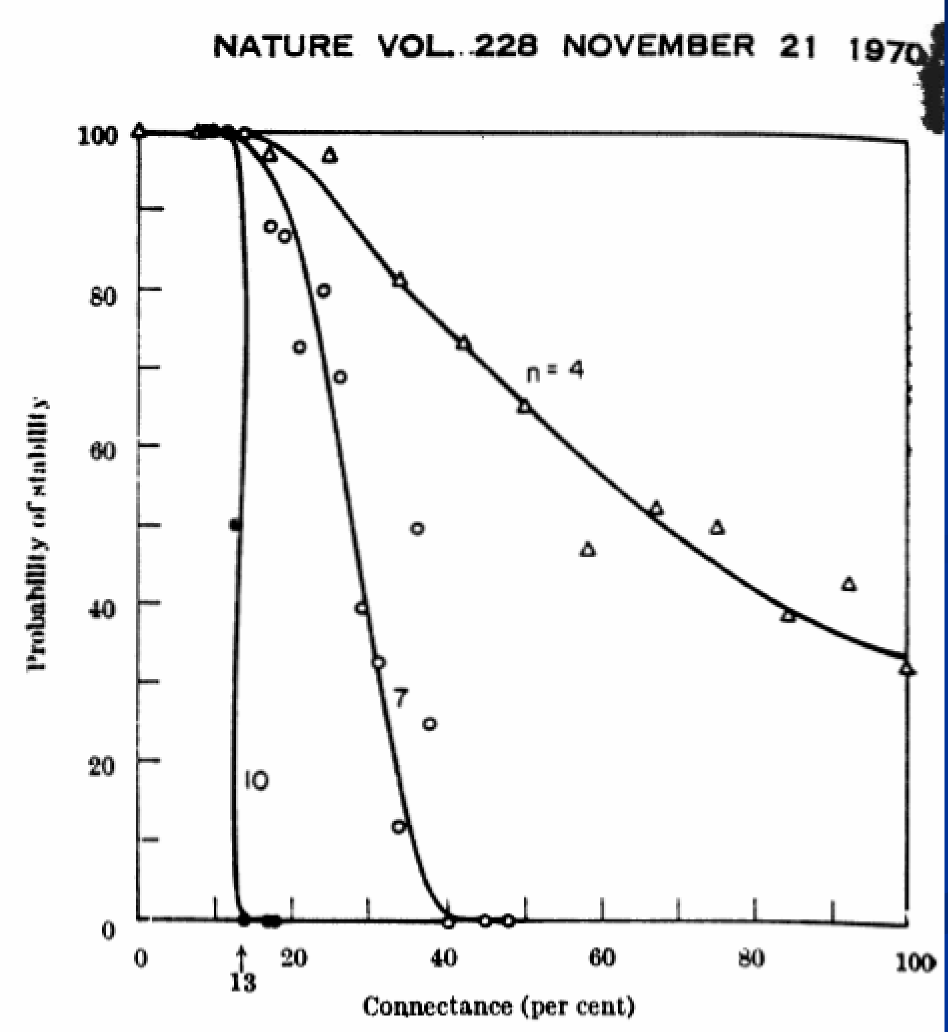


Fig. 1. Variation of stability with connectance.

Diversity-Stability & Connectance

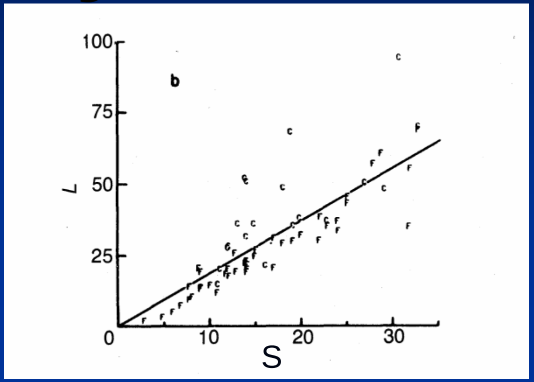
- MacArthur: Diversity enhances stability via increased complexity (Links per Species)

- May: Complexity inhibits stability: $i(SC)^{1/2}<1$
  - "elucidate the devious strategies which make for stability in enduring natural systems"

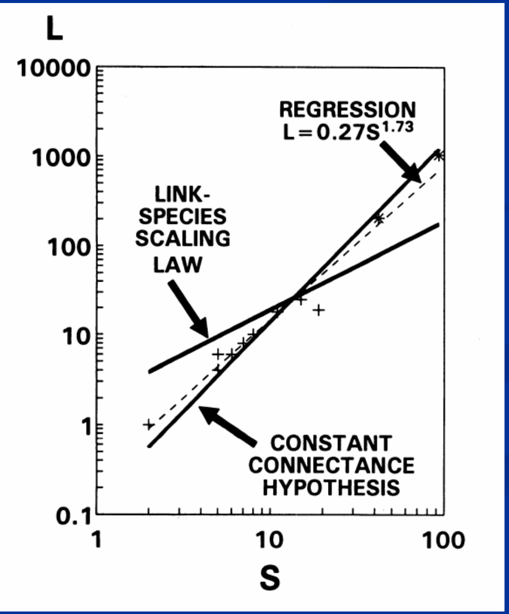
- $C=L/S^2$; $(SC)=L/S$, L=Directed Trophic Links

Diversity & Complexity

- Link-species Scaling Law L/S = 2
  - Cohen & Brian 1984 *PNAS*



- Constant Connectance Hypothesis $L/S^2=k$
  - Martinez 1992
  - *American Naturalist*



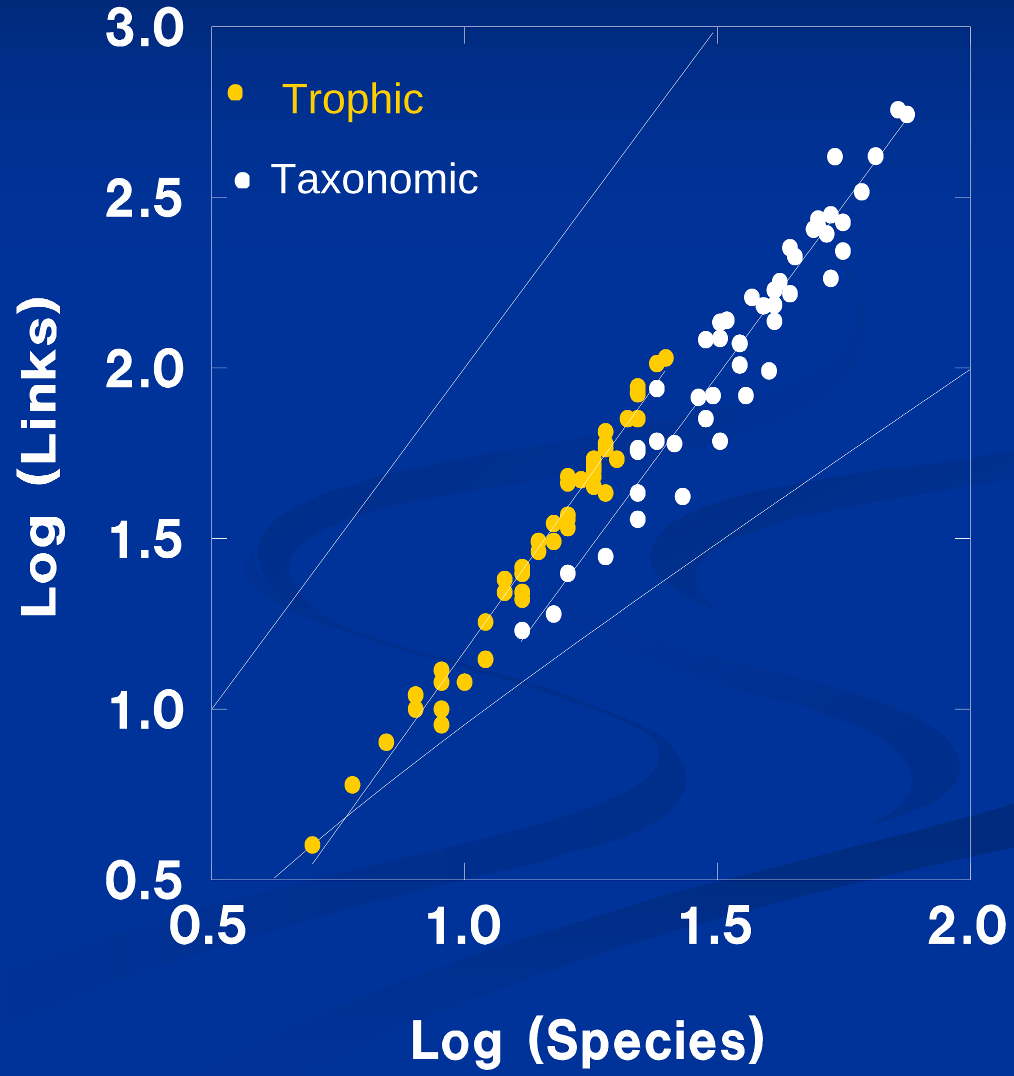
Constant Connectance (L/S^2): S is orthogonal to L/S^2

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

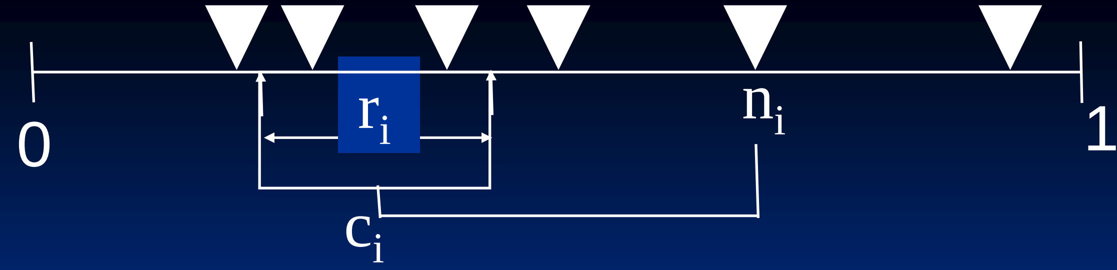
2 Versions of Havens'
50 Pelagic Food Webs

Martinez *Science* 1993.

Srinivasan, Dunne, Harte
& Martinez *Ecology* 2007



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 $r_i/2 < c_i < n_i$**

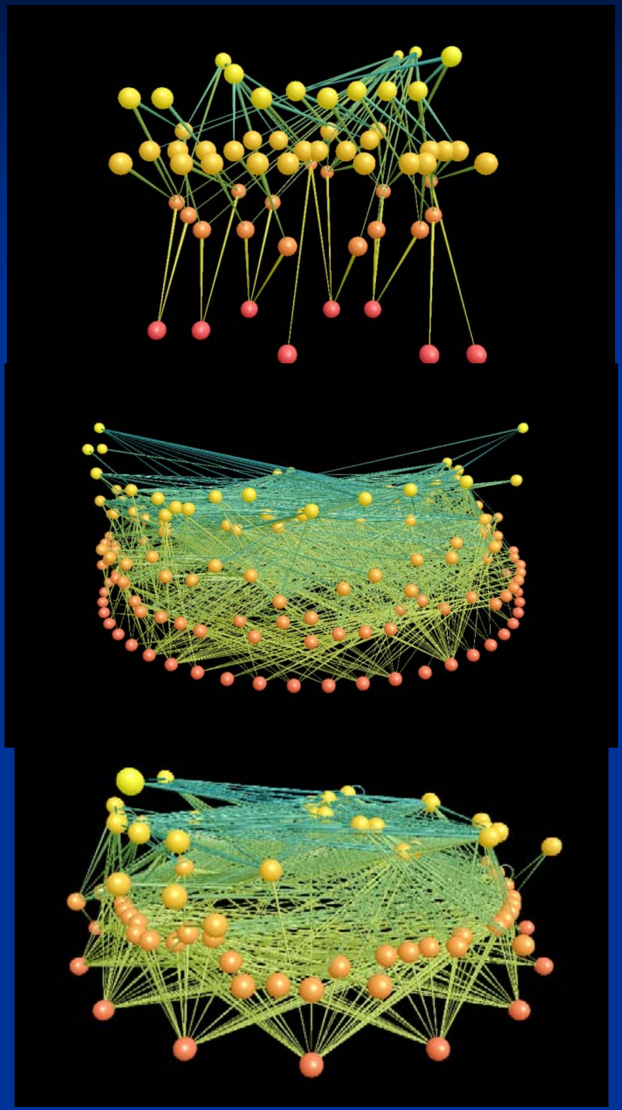
- Establishes relaxed trophic hierarchy while allowing cannibalism and looping

So what?

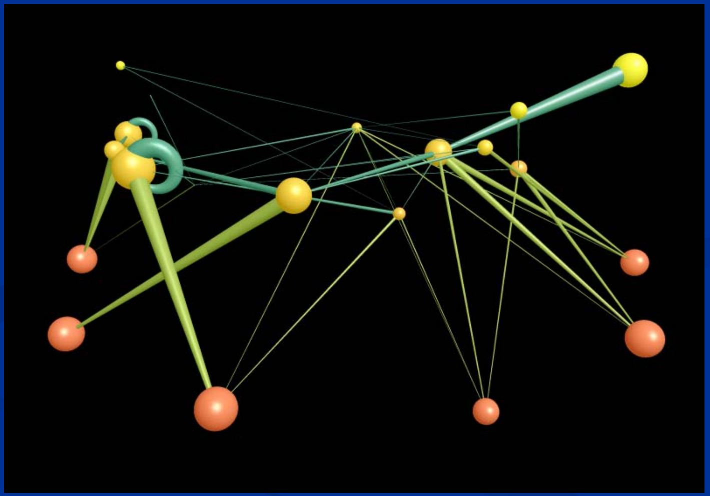
- Identified precisely predictable generalities in the trophic architecture among species.
  - virtually all ecosystems share remarkable regularities in how species divy up feeding within habitats

- Need to explore the functional consequences of these patterns.

- Exploration #1: interaction between network structure and dynamics.



How can
we model dynamics?



Nonlinear bioenergetic ecosystem model

The variation of B_i, the biomass of species i, is given by:

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

Rate of change in biomass = Production rate if species **i** is basal – Loss of biomass to metabolism + (Gain of biomass from resource spp. – Loss of biomass to consumer spp.)

What factors allow persistence of species in <u>dynamical models</u> of complex food webs?
(the “devious strategies”)

Rate of change in biomass = Production rate of basal spp. − Loss of biomass to metabolism + (Gain of biomass from resource spp. − Loss of biomass to consumer spp.)

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

3 species parameters:

$G_i(B)$: production rate of basal species i (Mass/Time)

For primary producers, $G_i(B) = r_i B_i(t) (1 - B_i(t) / K_i)$, where

r_i : intrinsic growth rate of species i (1/Time)

K_i : carrying capacity of species i (Mass)

---

x_i : mass-specific metabolic rate of species i (Mass/Time * 1/Mass)

4 species interaction parameters:

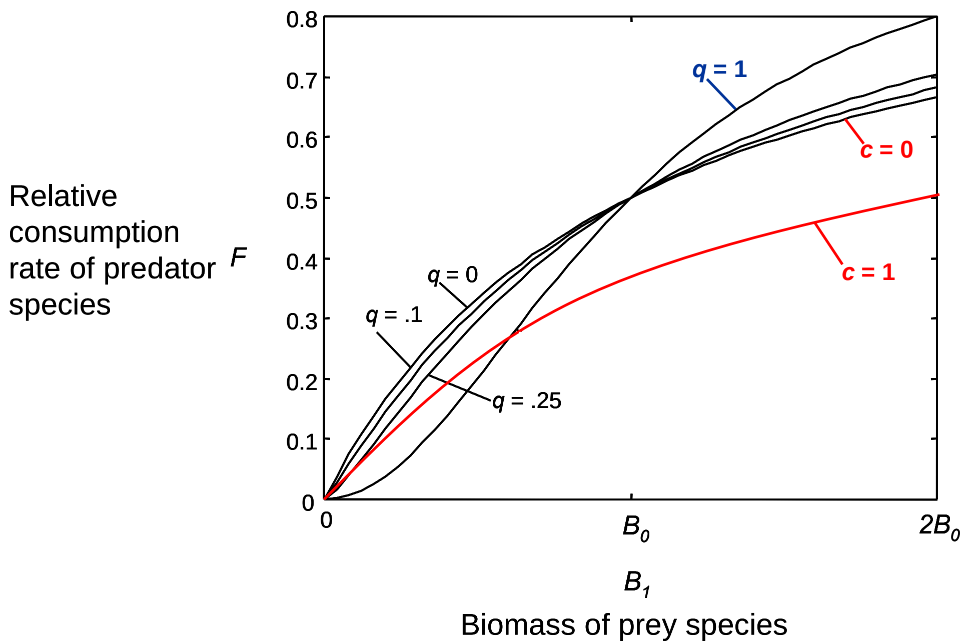
e_{ji} : assimilation efficiency of species j consuming species i (fraction of biomass)

y_{ij} : rate of maximum biomass gain by species i consuming j normalized by metabolic rate of species i (Mass/Time / Mass/Time)

α_{ij} : relative preference of species i for species j (fraction of diet)
(α_{ij} = 0 for producers and sums to 1 for consumers)

$F_{ij}(B)$: non-dimensional functional response (based on parameters q or c)
(relative consumption rate of predator species i consuming prey species j as a fraction of the maximum ingestion rate; function of species' biomass)

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

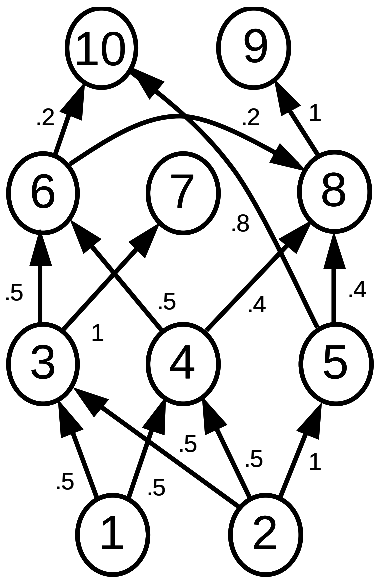
q: controls form of functional response

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

Addition of Predator Interference to Type II Functional Response:

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

10-species dynamics & functional response

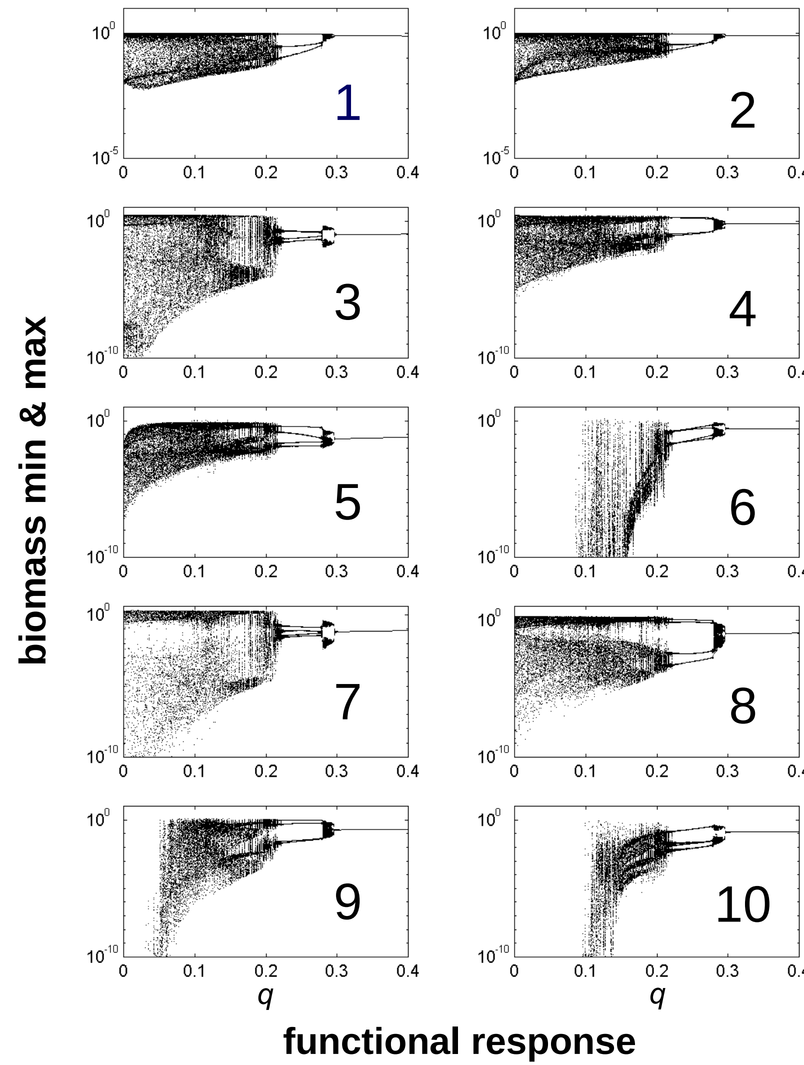


Strong Type II FR may stress dynamics by increasing feeding on rarer species while decreasing it on more abundant species.

At **q = 0** (conventional strong Type II response), only 4 taxa display persistent dynamics.

At **q > 0.15** (very weak Type III response), all 10 taxa are persistent.

At **q > 0.3** (weak Type III response), all 10 taxa are steady-state.



Generate binary network with structural network model

↓

Scale biological rates with negative quarter power-law

↓

Parameterize network model of population dynamics

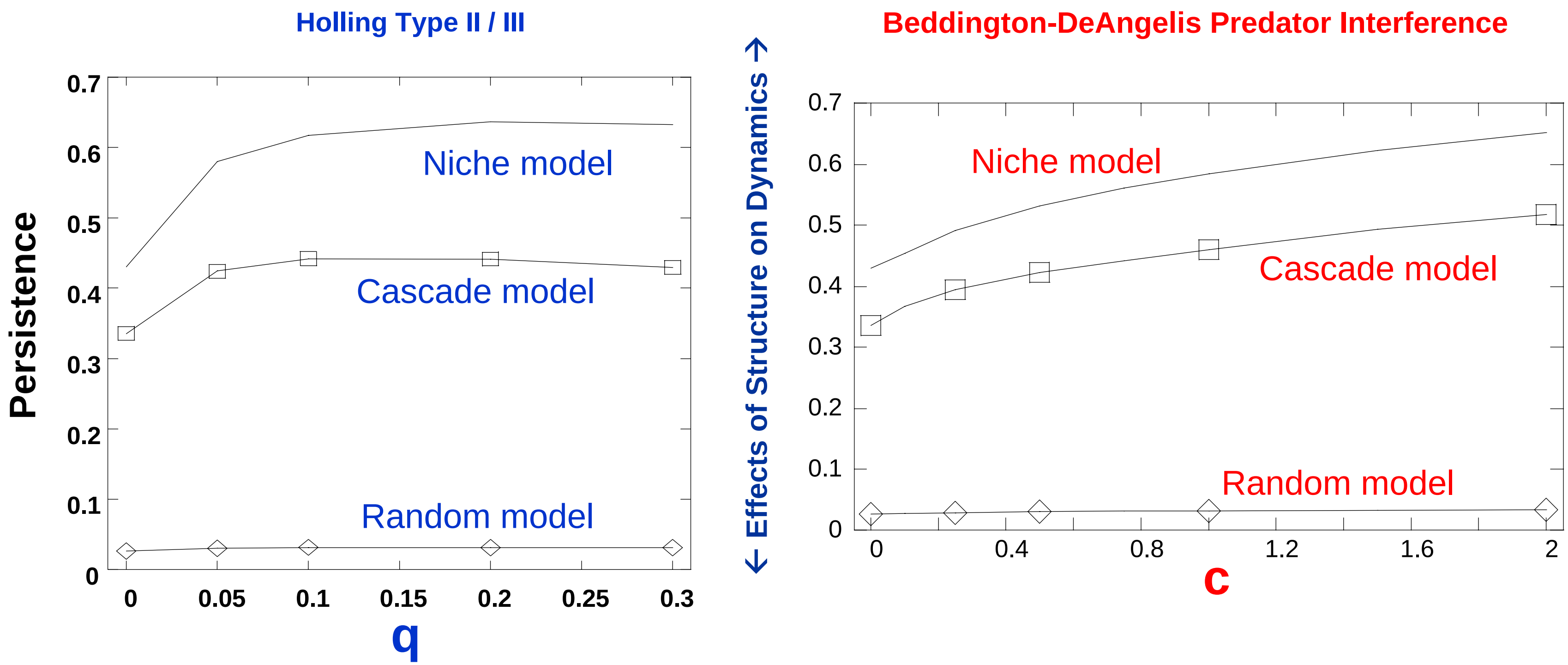
↓

Simulate nonlinear population dynamics

↓

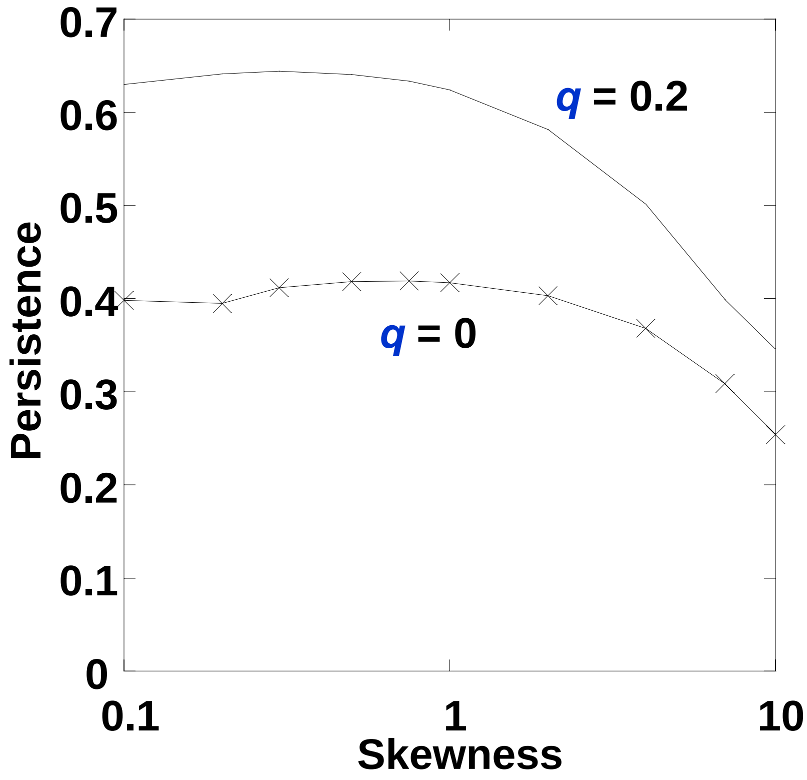
Measure stability as probability of species persistence

Stabilization of Dynamics of Ecological Networks (S=30, C=0.15) with Functional Responses



← Effects of Dynamics on Structure →

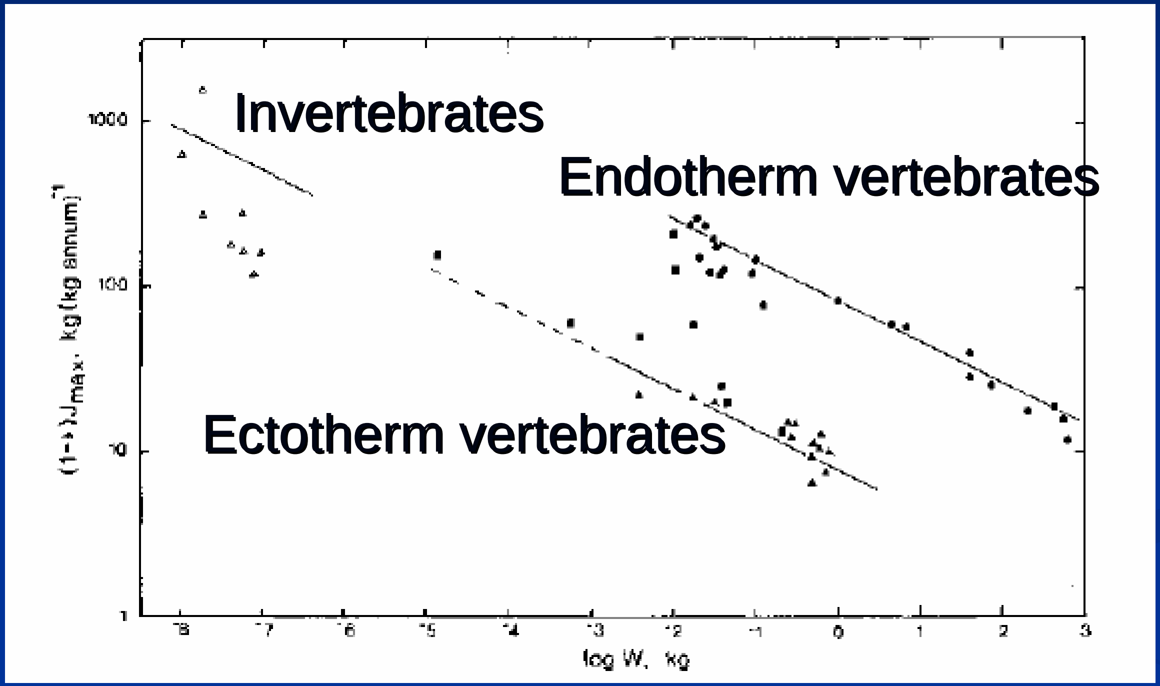
Effects of Omnivore Feeding Preference among Trophic Levels



Low Trophic-level Prey

High Trophic-level Prey

Power law allometric scaling relationships

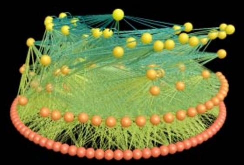


Different metabolic types of species:

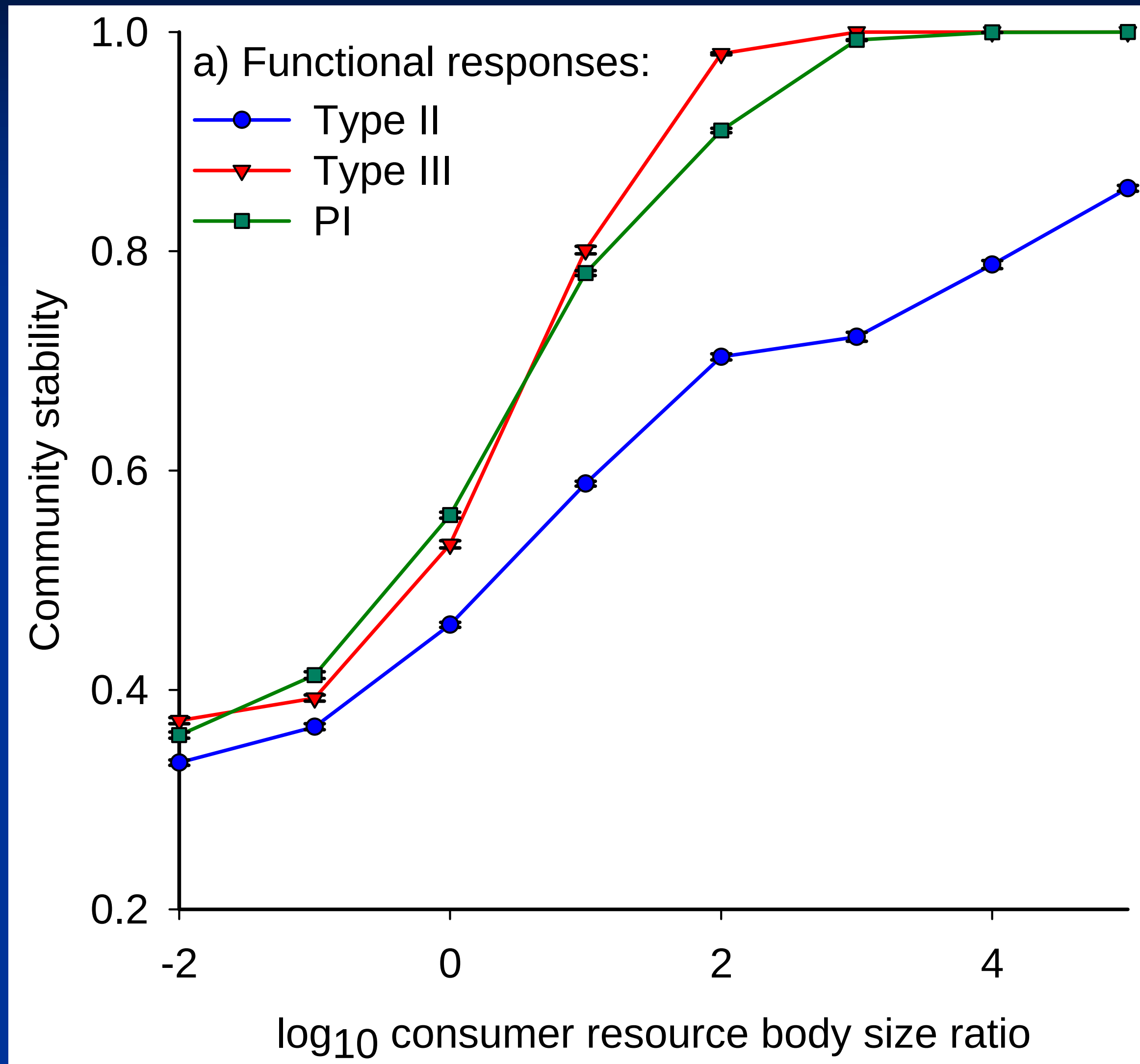
- same -0.25 exponent
- different constants

From: Yodzis & Innes 1992 *Am. Nat.*

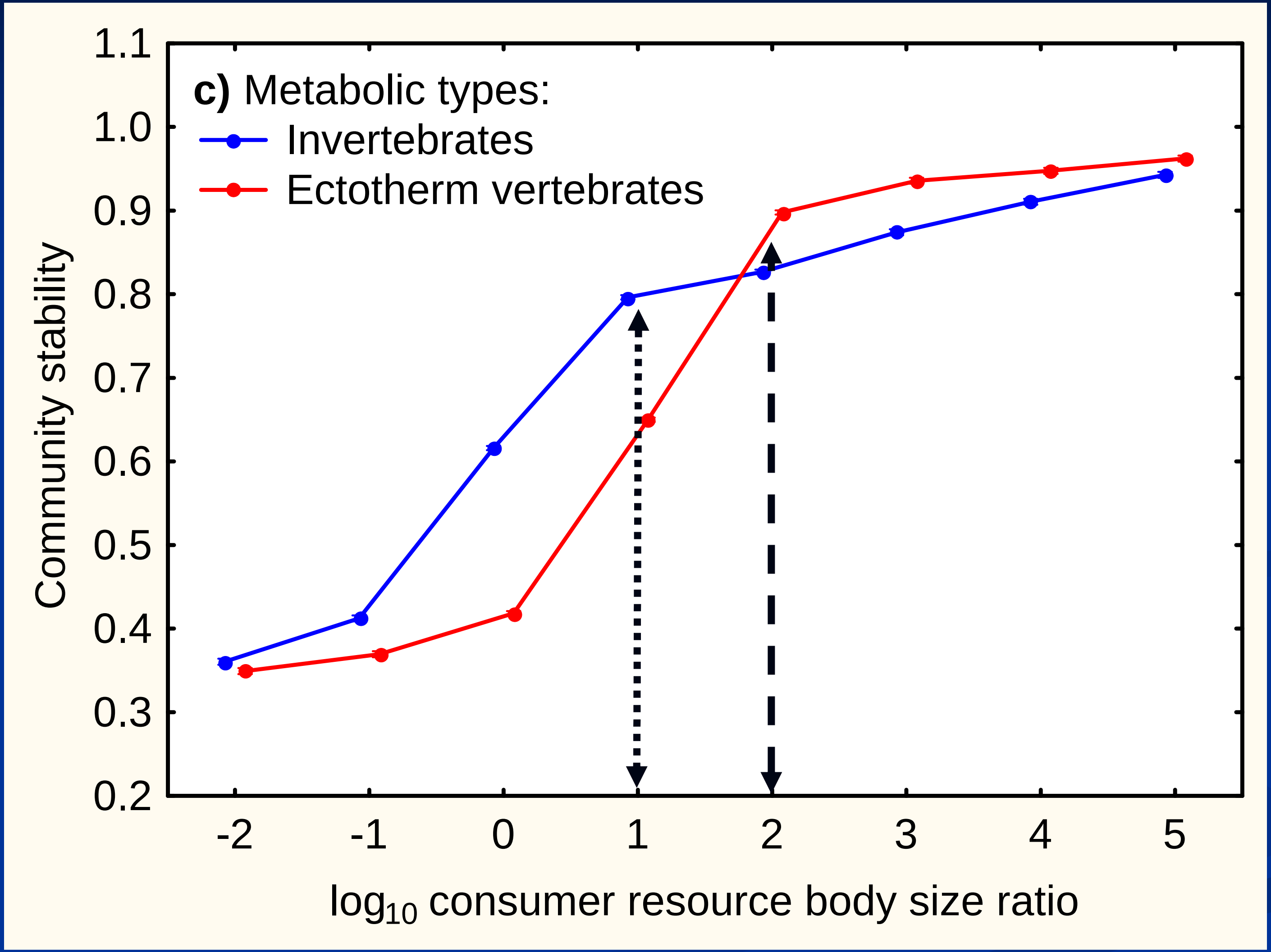
Biological rates scale with a negative quarter power-law with species' body masses (West et al. 1997 *Science*, Enquist et al. 1999 *Nature*, West et al 1999 *Nature*)



Complex ecological networks



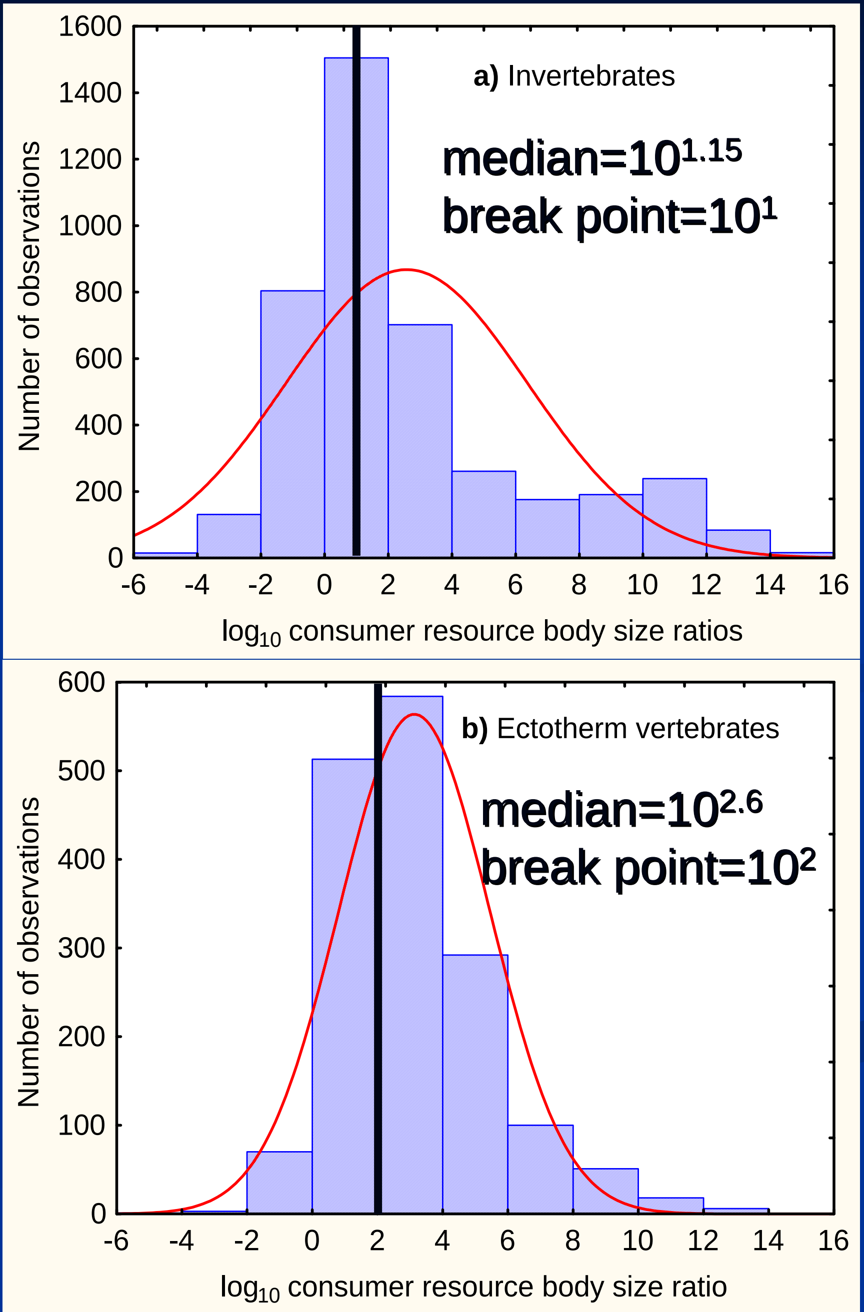
Results qualitatively robust to variation in Functional Responses

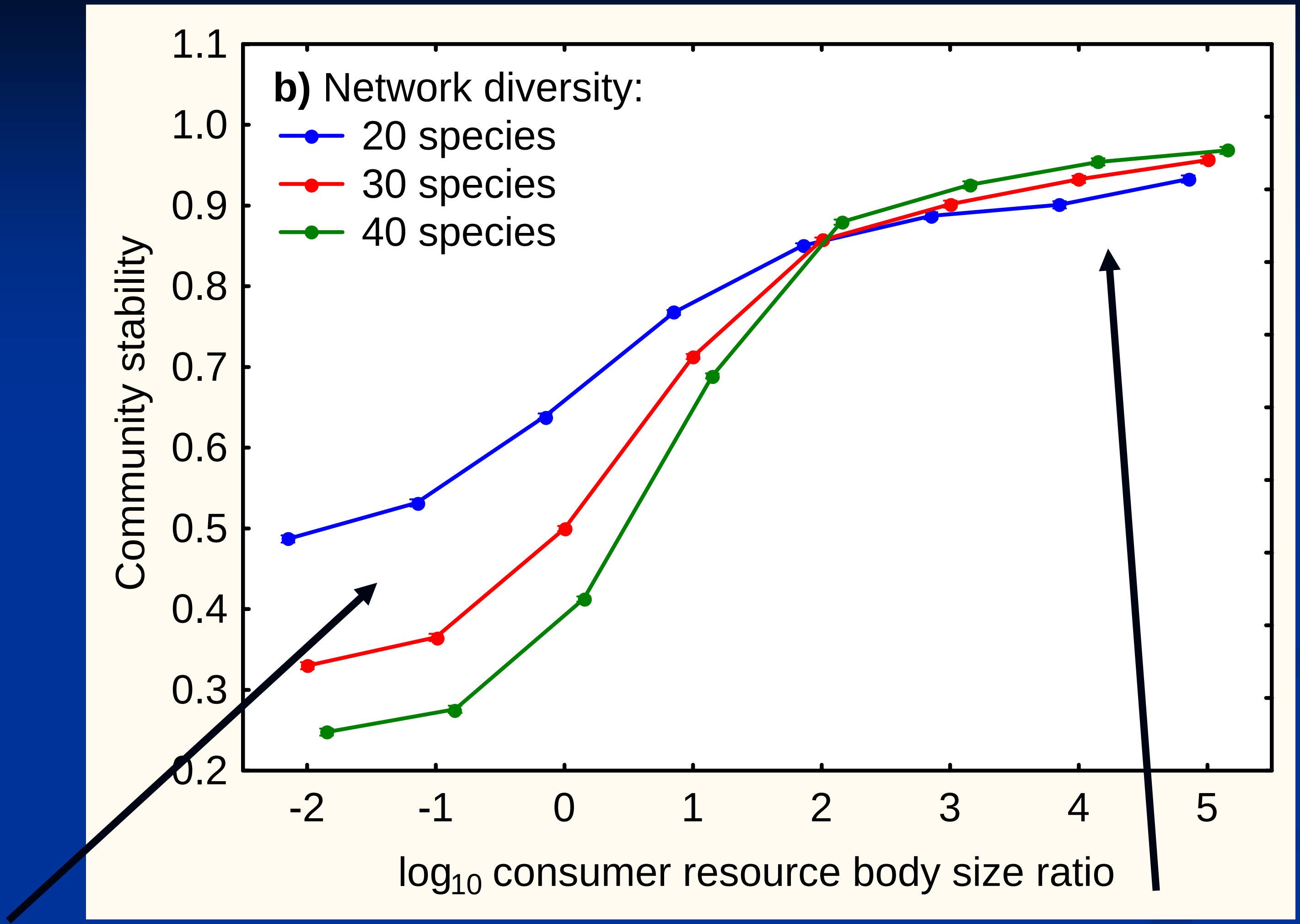

c) Metabolic types:
Invertebrates
Ectotherm vertebrates
Community stability
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
-2
-1
0
1
2
3
4
5
log10 consumer resource body size ratio

Global data base on natural body size ratios

Data for 3887 invertebrate predators and 1501 ectotherm vertebrate predators

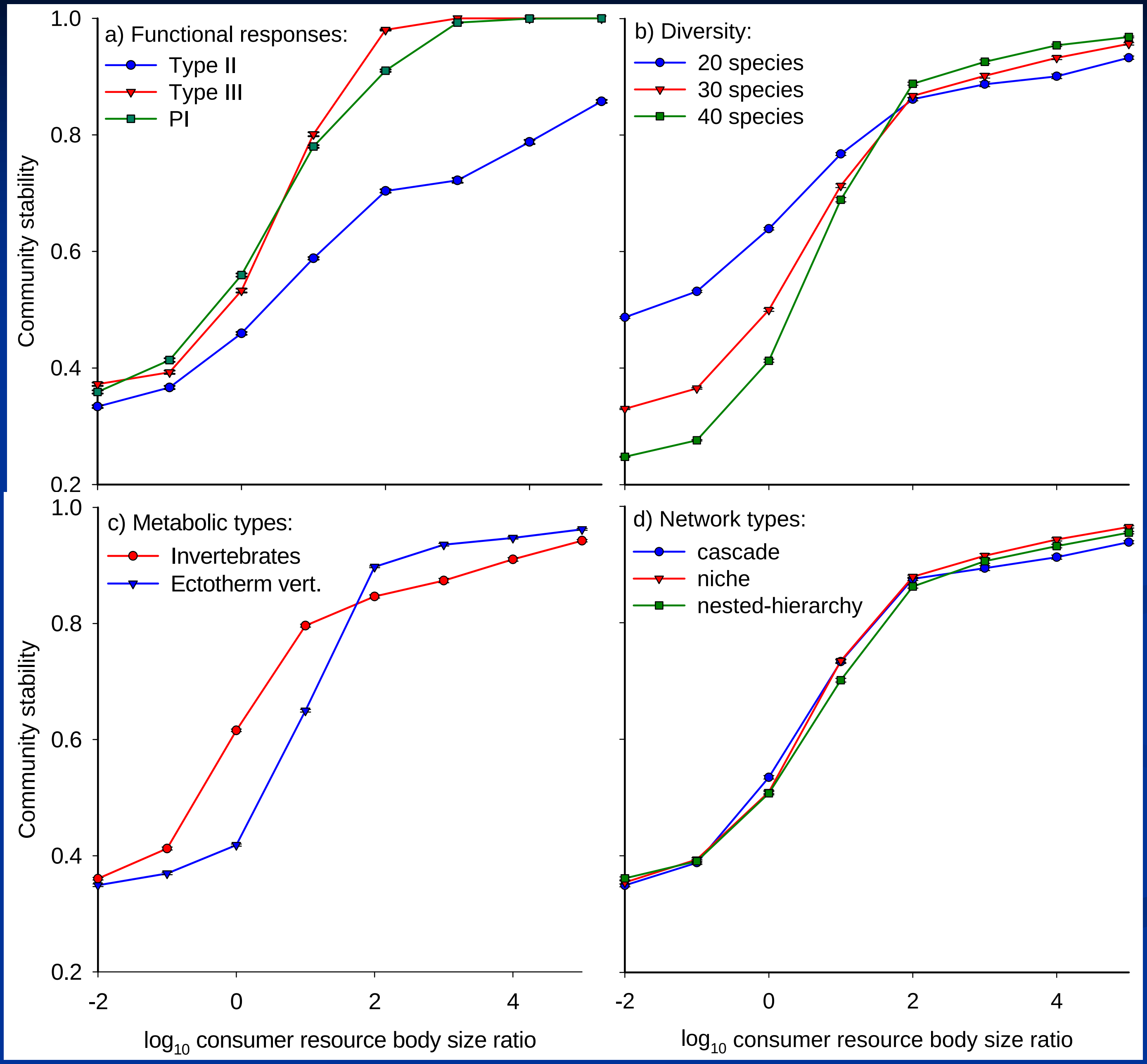
Geometric mean body size ratios are above break points



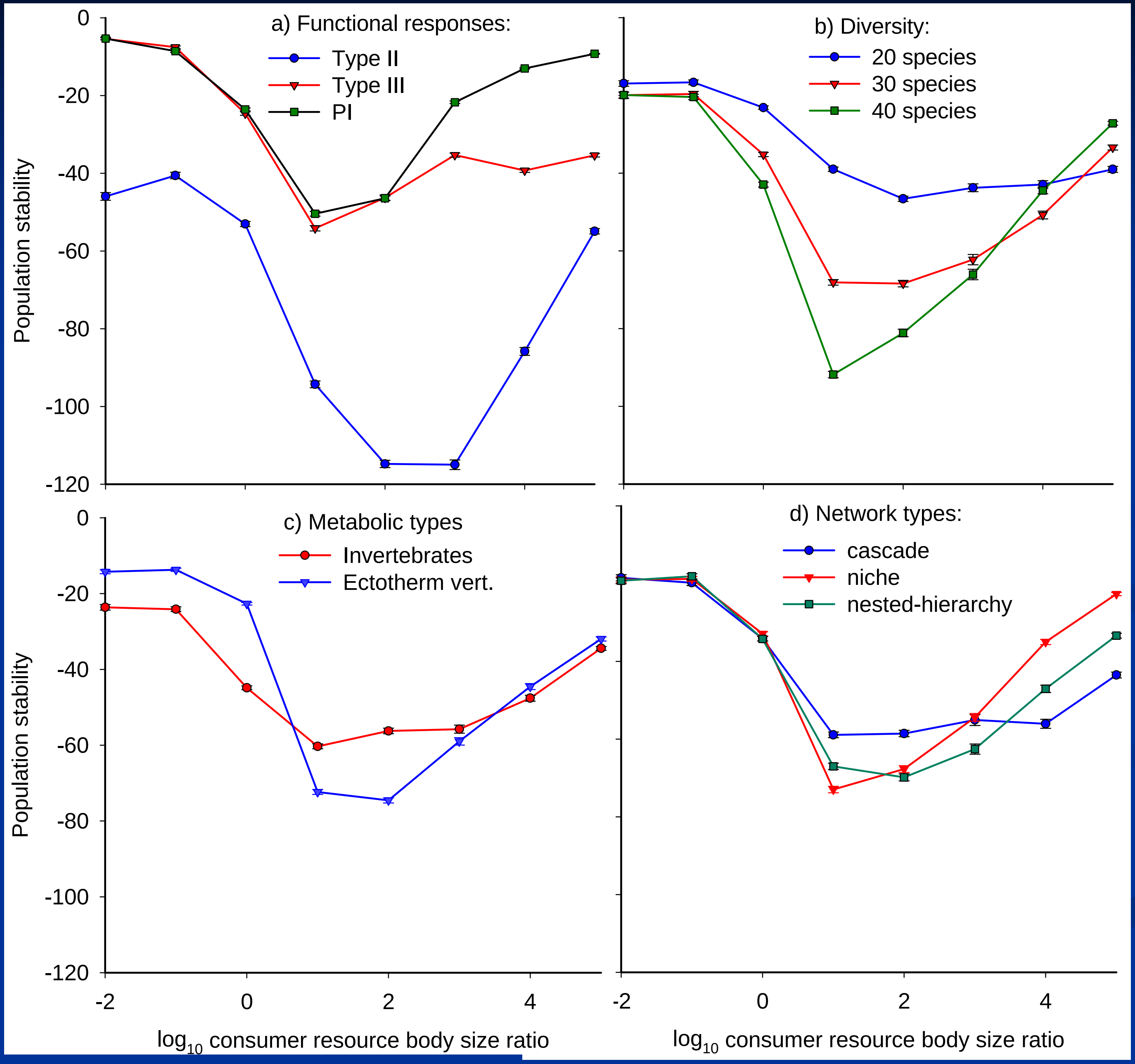


Negative diversity stability relationships under uniform body size distributions

Positive diversity stability relationships under natural body size distributions



a) Functional responses:
Type II
Type III
PI
b) Diversity:
20 species
30 species
40 species
c) Metabolic types:
Invertebrates
Ectotherm vert.
d) Network types:
cascade
niche
nested-hierarchy
Community stability
Community stability
1.0
0.8
0.6
0.4
0.2
-2
0
2
4
log10 consumer resource body size ratio
log10 consumer resource body size ratio


a) Functional responses:
Type II
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b) Diversity:
20 species
30 species
40 species
c) Metabolic types
Invertebrates
Ectotherm vert.
d) Network types:
cascade
niche
nested-hierarchy
Population stability
Population stability
0
-20
-40
-60
-80
-100
-120
-2
0
2
4
log10 consumer resource body size ratio
log10 consumer resource body size ratio

DEVIOUS STRATEGIES CONTINUED:

ALLOMETRIC DEGREE DISTRIBUTIONS

“Devious Strategies” that increase overall species persistence

- **Non-random network topology**
  - especially empirically well-corroborated niche model structure
- **Non-type II functional responses**
  - stabilizes chaotic & cyclic dynamics
  - more ecologically plausible & empirically supported
- **Consumption weighted to low trophic levels**
  - eat low on the food chain!
- **Predator/prey body-size ratios**
- **Allometric Degree Distributions**