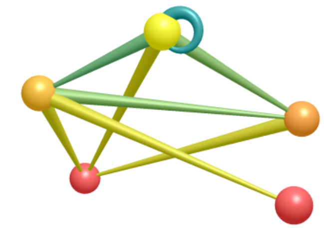

Sustaining Ecological Networks and their Services:

Network theory of biodiversity and ecosystem function

Neo D. Martinez
Pacific Ecoinformatics and Computational Ecology Lab
www.FoodWebs.org

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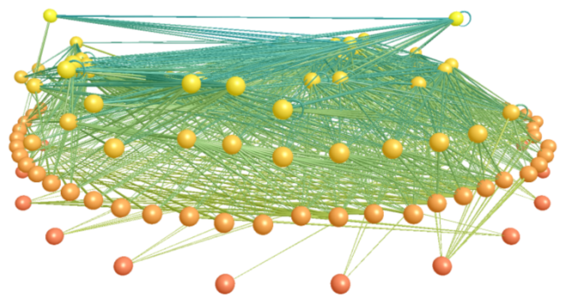


www.FoodWebs.org

Eric Berlow
Univ. of Cal., Merced

Ulrich Brose
Georg-August-U. Göttingen

Jennifer Dunne
Santa Fe Institute

Neo Martinez
Pacific Ecoinformatics &
Computational Ecology Lab

Tamara Romanuk
Dalhousie University

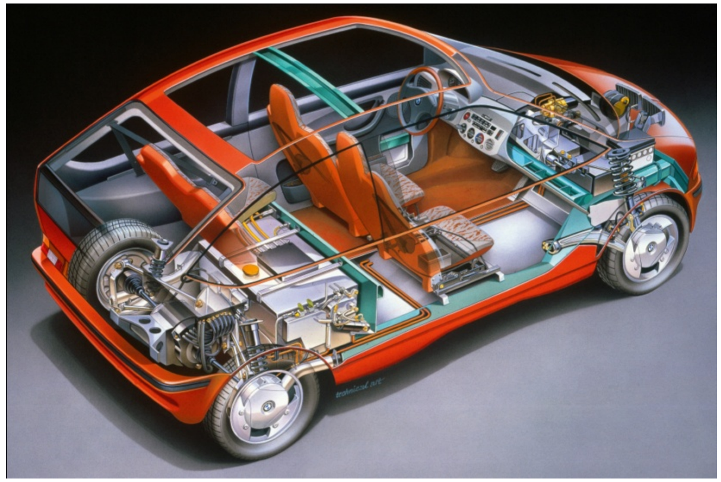
Rich Williams
Microsoft Research

Ilmi Yoon
San Francisco State U.

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.

Towards a theory of diversity and system function

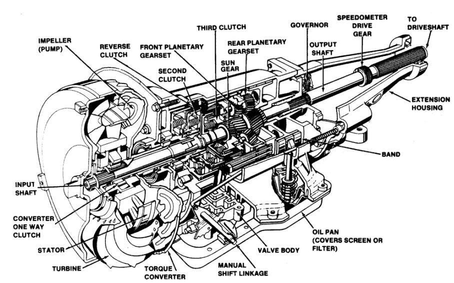


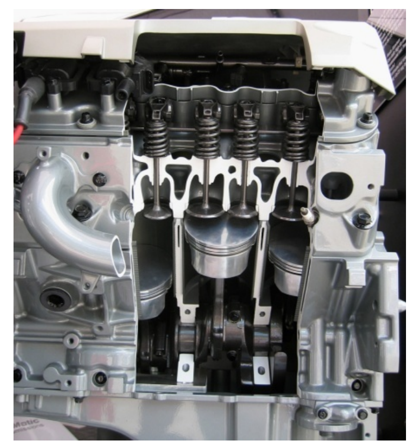
Knowledge:

- informs operator
- role of parts
- consequence of loss
- implications of change

Modules/communities

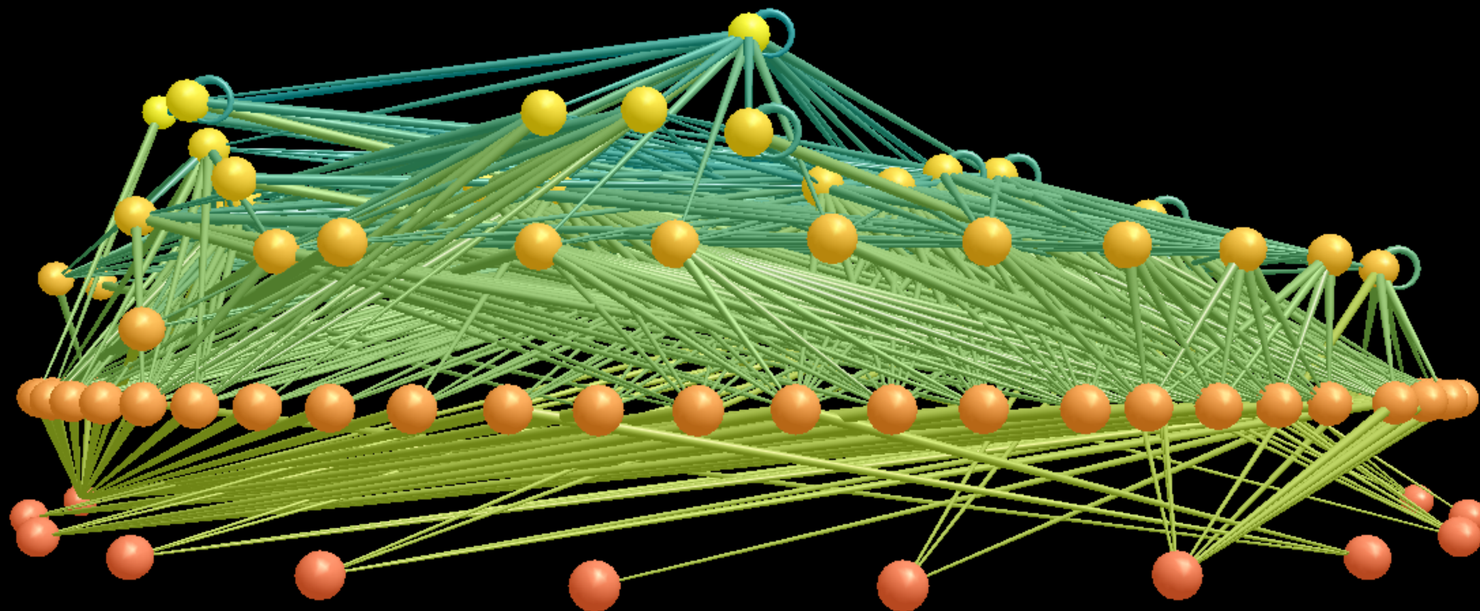
components





Food-web theory of
Biodiversity and Ecosystem function

"Dominant Processes governing biodiversity"
Consumer-resource interactions
Network Structure and Function



Martinez (1991) Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecol. Mon.* 61:367-392.

Talk Outline

1. complex ecological network theory
   structure
   function

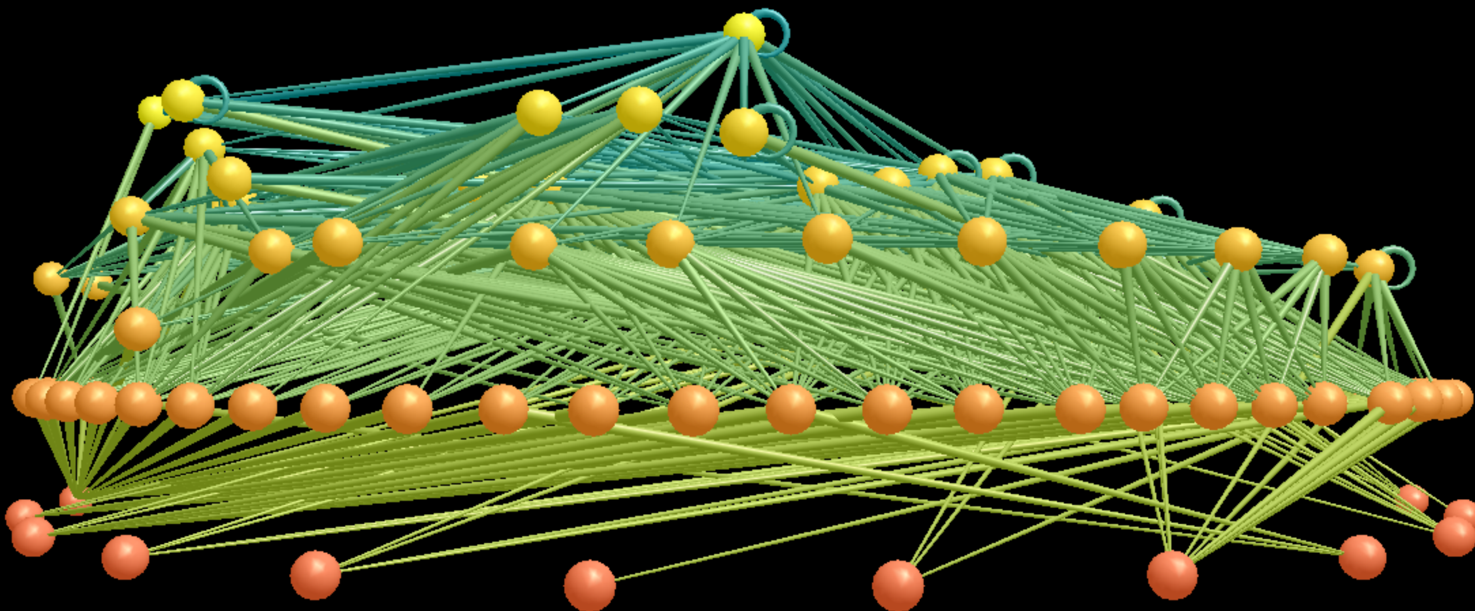
3. Empirical support among ecosystems

3. Responses of ecosystems & biodiversity to
   species loss and invasions

4. Major directions for theory to advance:
   fit specific systems
   include evolution and humans

Food-web Structure Theory

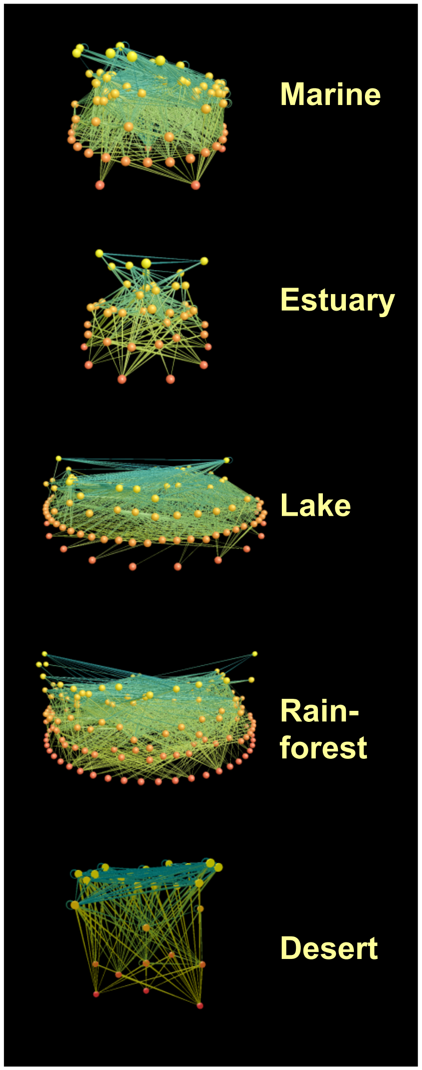
Inputs are Species Diversity and Network Complexity



Species Diversity (S) = 92, Connectance ($C=L/S^2$) = 0.12

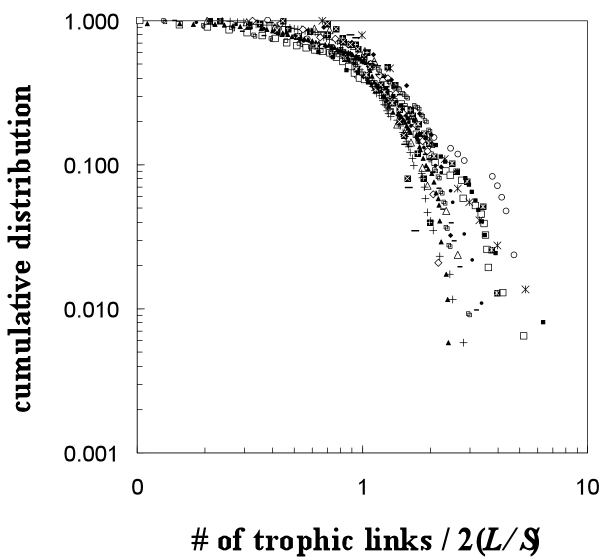
Martinez (1991) Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecol. Mon.* 61:367-392.

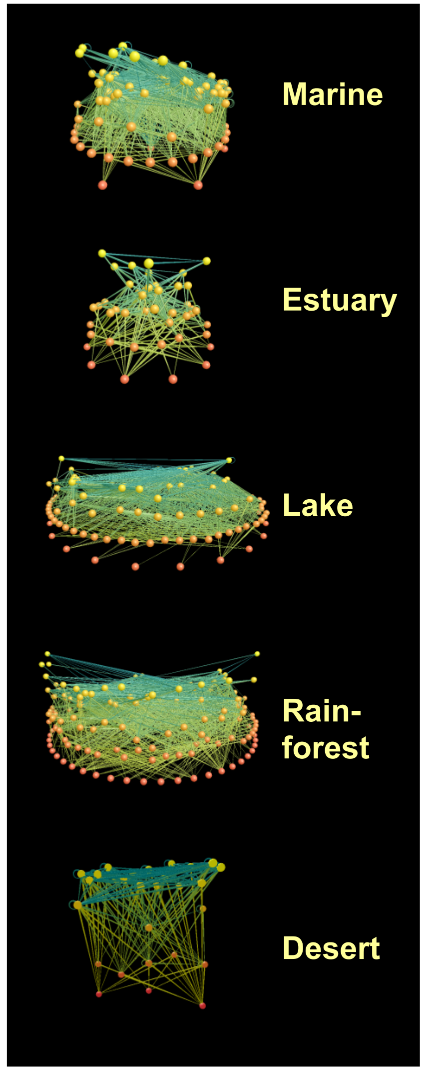
Apparent Complexity



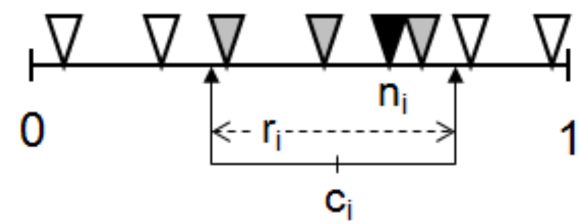
Underlying Simplicity

Normalized Data for 16Wwebs





The Niche Model

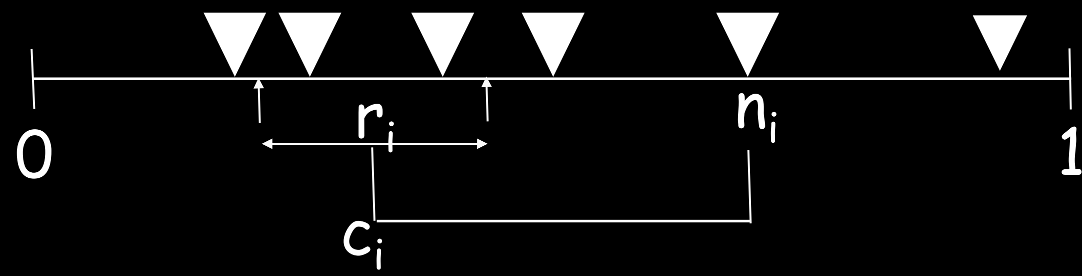


Two Parameters (*C*,*S*)

Simple Link Distribution Rules

Predicts Network Structure

Williams & Martinez (2000) Simple rules yield complex food webs. *Nature* 404:180–183.
Dunne, Williams & Martinez (2002) Food-web structure and network theory. *PNAS* 99:12917-12922.



Niche Model: Input S & C, 3 Rules

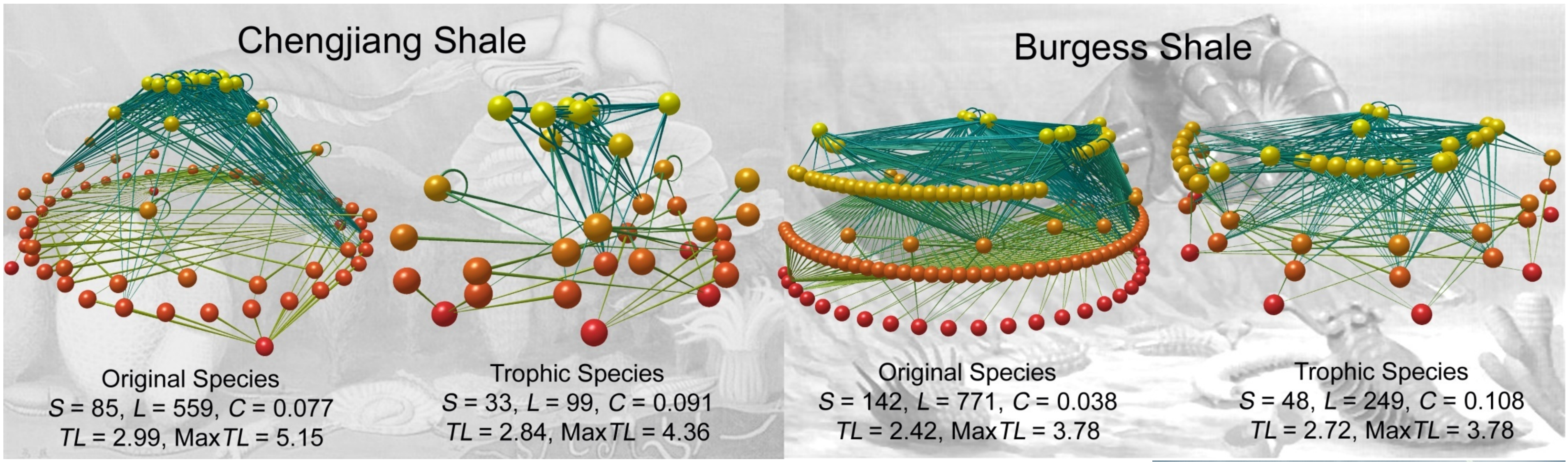
- Rule 1: Each of S species gets uniform random n_i
- Rule 2: Each species gets assigned a random "feeding range" (r_i) $0 \le r_i \le 1$
  - chosen from a beta function (mean of 2C) multiplied by the species niche value (n_i).
- Step 3: Range is placed by uniformly choosing a random range center (c_i) so that $r_i/2 < c_i < n_i$

Williams and Martinez 2000 *Nature*

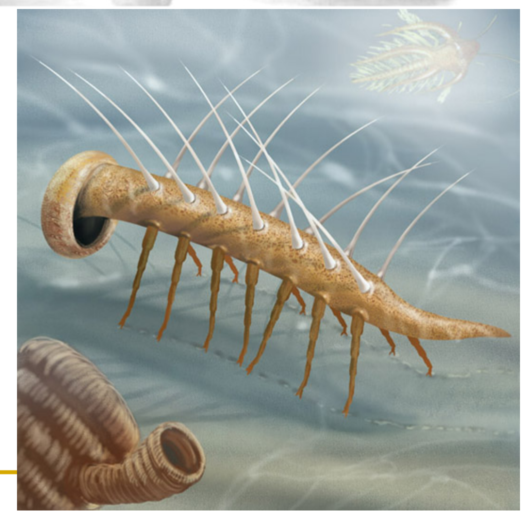
Empirical Support

- Niche model does very well
  - 19 webs, 16 network properties each (Dunne *et al.* 2004)
- Gets degree distributions right (Stouffer *et al.* 2005)
- New models limited (Williams & Martinez 2008, Allesina et al. 2008)
  - Fixing the intervality problem creates others…
  - Improved testing: Normality assumption replaced with model distributions, Max Likelihood
- Applies to Paleowebs (Dunne et al. 2008, *PLoS Biology*)
  - Number nodes that are: Herbivores, Carnivores, Omnivores, Cannibals, etc.
  - Network properties: mean length, variability and number of food chains

Paleofoodwebs

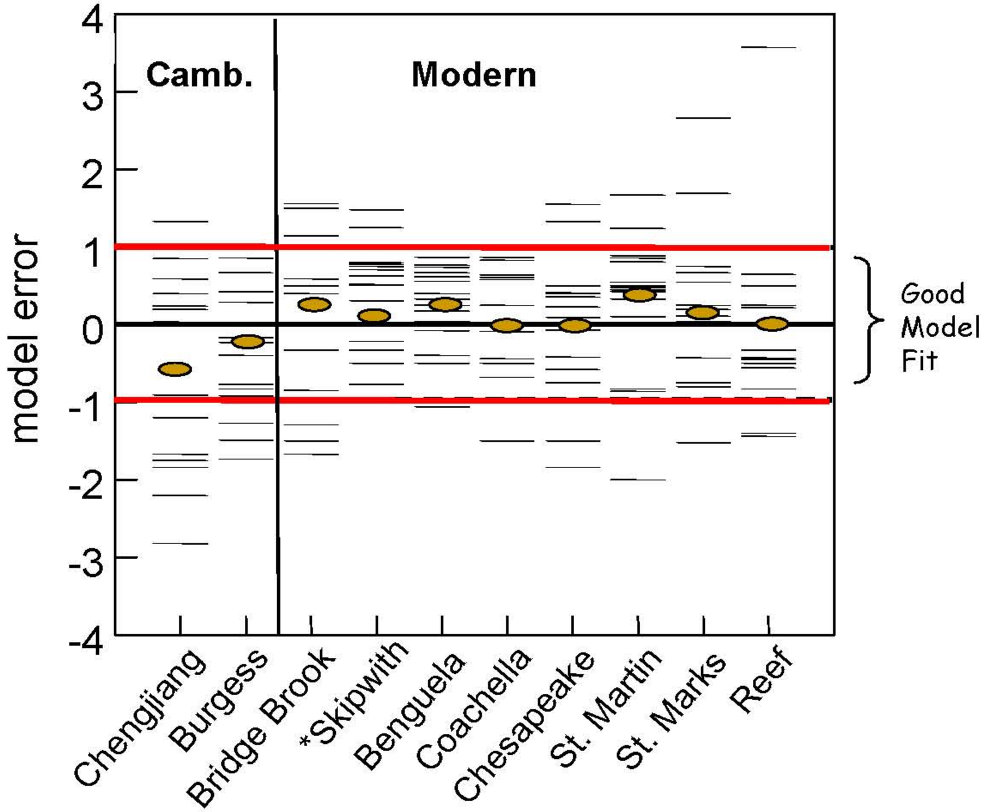


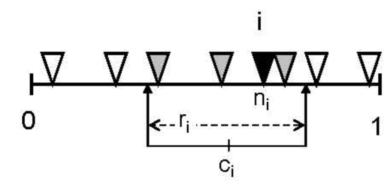
Compilation and Network Analyses of Cambrian Food Webs
Dunne, Williams, Martinez, Wood & Erwin et al. 2008
PLoS Biology



Niche model errors

Model Errors for 17 properties for 10 food webs



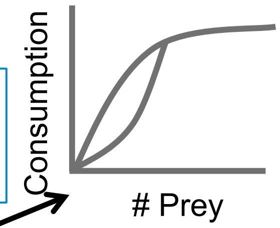


Results generally robust to removal of uncertain links

Bioenergetic model for complex food webs

Extending Yodzis & Innes 1992

Handling
Attack
Interference



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

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.)

Time evolution of species' biomasses in a food web result from:

- Basal species grow via a carrying capacity, resource competition, or Tilman/Huisman models
- Other species grow according to feeding rates and assimilation efficiencies (e_{ji})
- All species lose energy due to metabolism (x_i) and consumption
- Functional responses determine how consumption rates vary
- Rates of production and metabolism (x_i) scale with body size
- Metabolism specific maximum consumption rate (y_{ij}) scales with body type

Yodzis & Innes (1992) Body size and consumer-resource dynamics. *Amer. Nat.* 139:1151-1175.
Williams & Martinez (2004) Stabilization of chaotic and non-permanent food web dynamics. *Eur. Phys. J. B* 38:297-303.

Theory predicts Population Dynamics and Evolution: 2 species in the lab

REPORTS

Crossing the Hopf Bifurcation in a Live Predator-Prey System

Gregor F. Fussmann,[1*] Stephen P. Ellner,[1,2] Kyle W. Shertzer,[2] Nelson G. Hairston Jr.[1]

17 NOVEMBER 2000 VOL 290 SCIENCE

letters to nature

Rapid evolution drives ecological dynamics in a predator–prey system

Takehito Yoshida*, Laura E. Jones*, Stephen P. Ellner*, Gregor F. Fussmann*† & Nelson G. Hairston Jr*

* *Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA*

NATURE | VOL 424 | 17 JULY 2003 |

Journal of Animal Ecology 2002 **71**, 802–815

Predator–prey cycles in an aquatic microcosm: testing hypotheses of mechanism

KYLE W. SHERTZER*, STEPHEN P. ELLNER†, GREGOR F. FUSSMANN‡ and NELSON G. HAIRSTON JR†

OPEN ACCESS Freely available online PLoS BIOLOGY

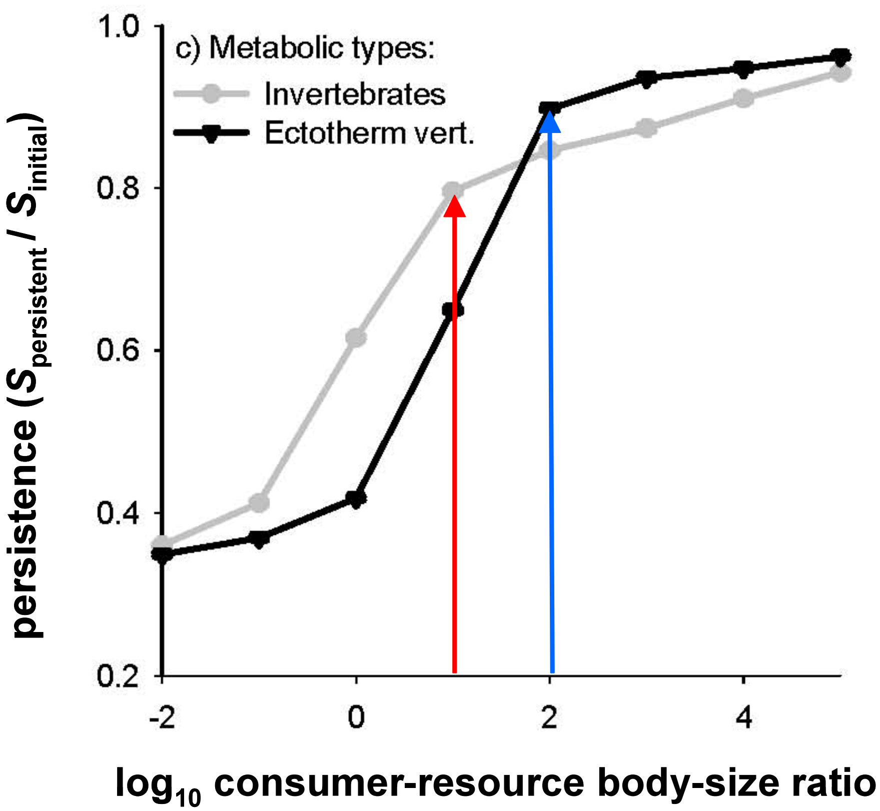
Cryptic Population Dynamics: Rapid Evolution Masks Trophic Interactions

Takehito Yoshida[1¤], Stephen P. Ellner[1], Laura E. Jones[1], Brendan J. M. Bohannan[2], Richard E. Lenski[3], Nelson G. Hairston Jr.[1*]

September 2007 | Volume 5 | Issue 9 | e235

Importance of body-size ratios

Model: Persistence as *f* (Body-Size Ratios)

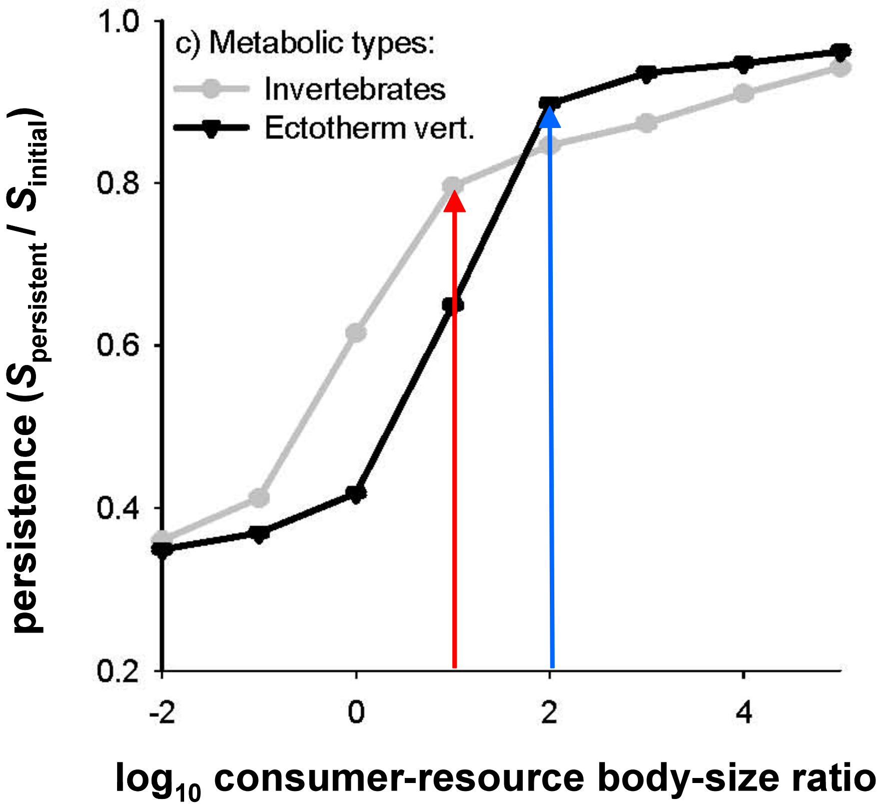


Each food web:
S = 30
C = 0.15
vary Body-size ratios

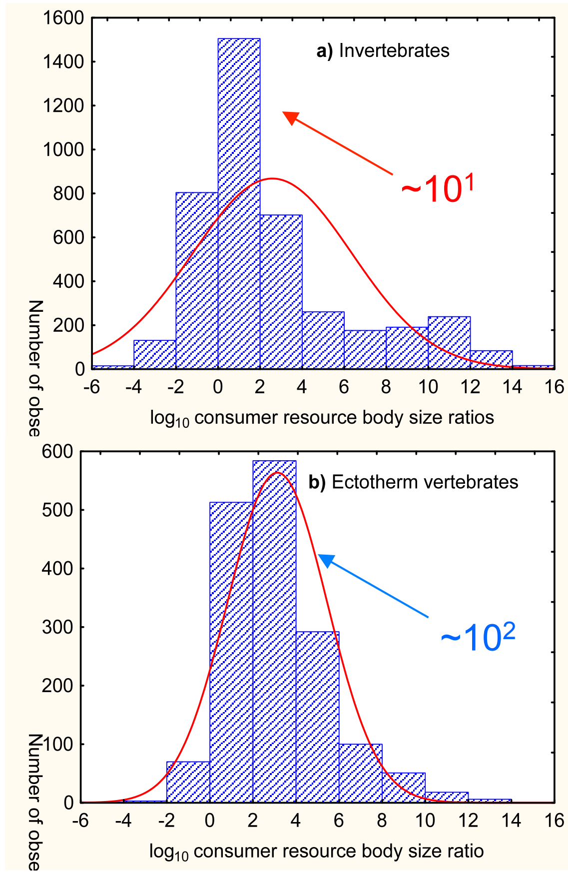
Brose, Williams & Martinez (2006) Allometric scaling enhances stability in complex food webs. *Ecol. Lett.* 9:1228-1236.

Importance of body-size ratios

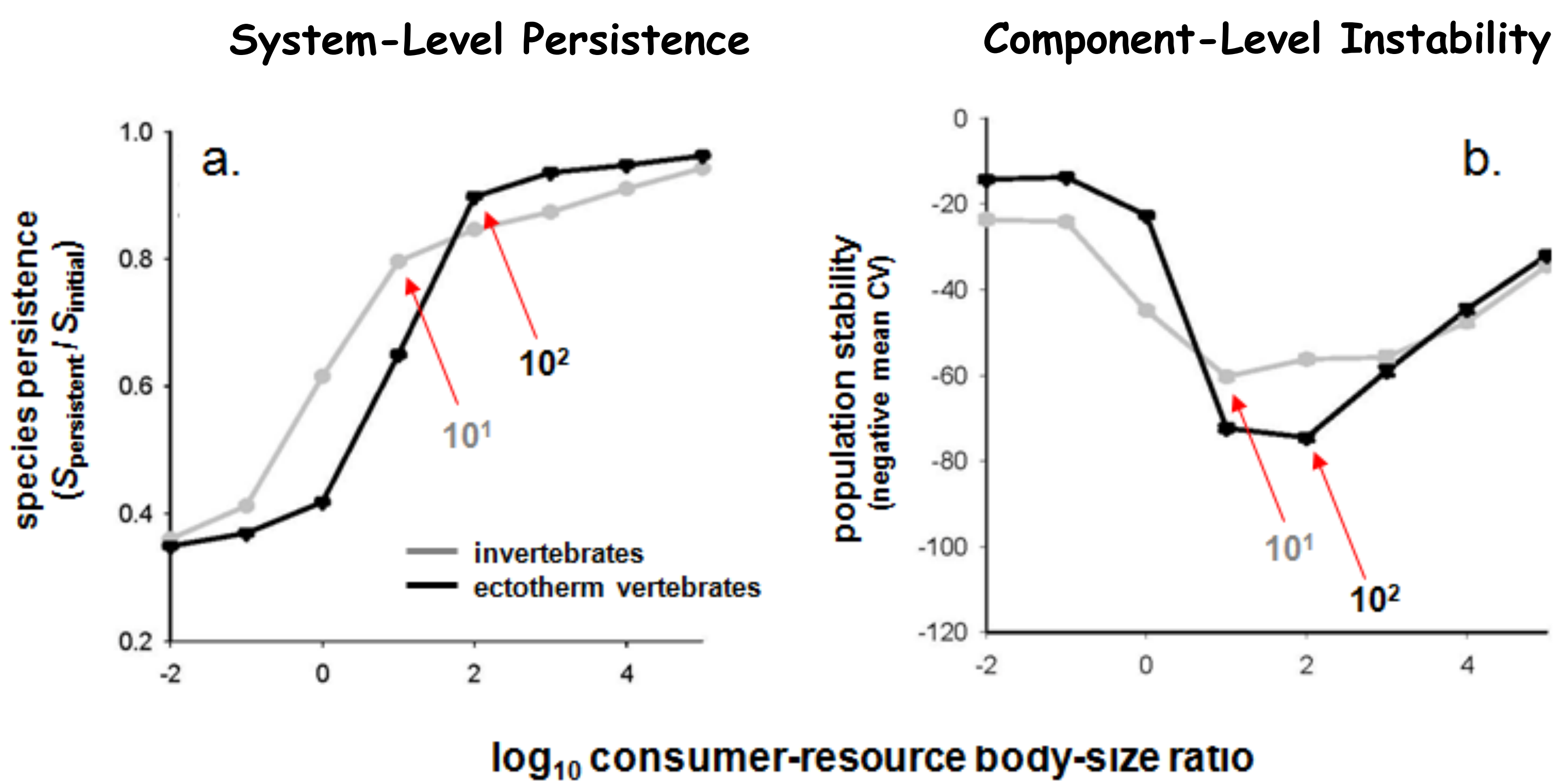
Model: Persistence as *f* (Body-Size Ratios)



Empirical Body-Size Ratios



Brose, Williams & Martinez (2006) Allometric scaling enhances stability in complex food webs. *Ecol. Lett.* 9:1228–1236.


System-Level Persistence
Component-Level Instability
a.
species persistence
(S_persistent / S_initial)
1.0
0.8
0.6
0.4
0.2
-2
0
2
4
10^2
10^1
invertebrates
ectotherm vertebrates
b.
population stability
(negative mean CV)
0
-20
-40
-60
-80
-100
-120
10^1
10^2
log10 consumer-resource body-size ratio

Otto, Rall & Brose (2007) Allometric degree distributions facilitate food web stability. *Nature* 450:1226-1229.

→ "Persistence domains" of body-size ratios: constrained by bottom-up energy availability when consumers << resources, and by enrichment dynamics when consumers >> resources

→ 97% of tri-trophic food chains exhibit ratios within this persistence domain

→ Generality increases and vulnerability decreases with body-mass of a species

Kartascheff, Heckman, Drossel & Guill (2010) Why allometric scaling enhances stability in food webs. *Theoretical Ecology* 3:195-208.

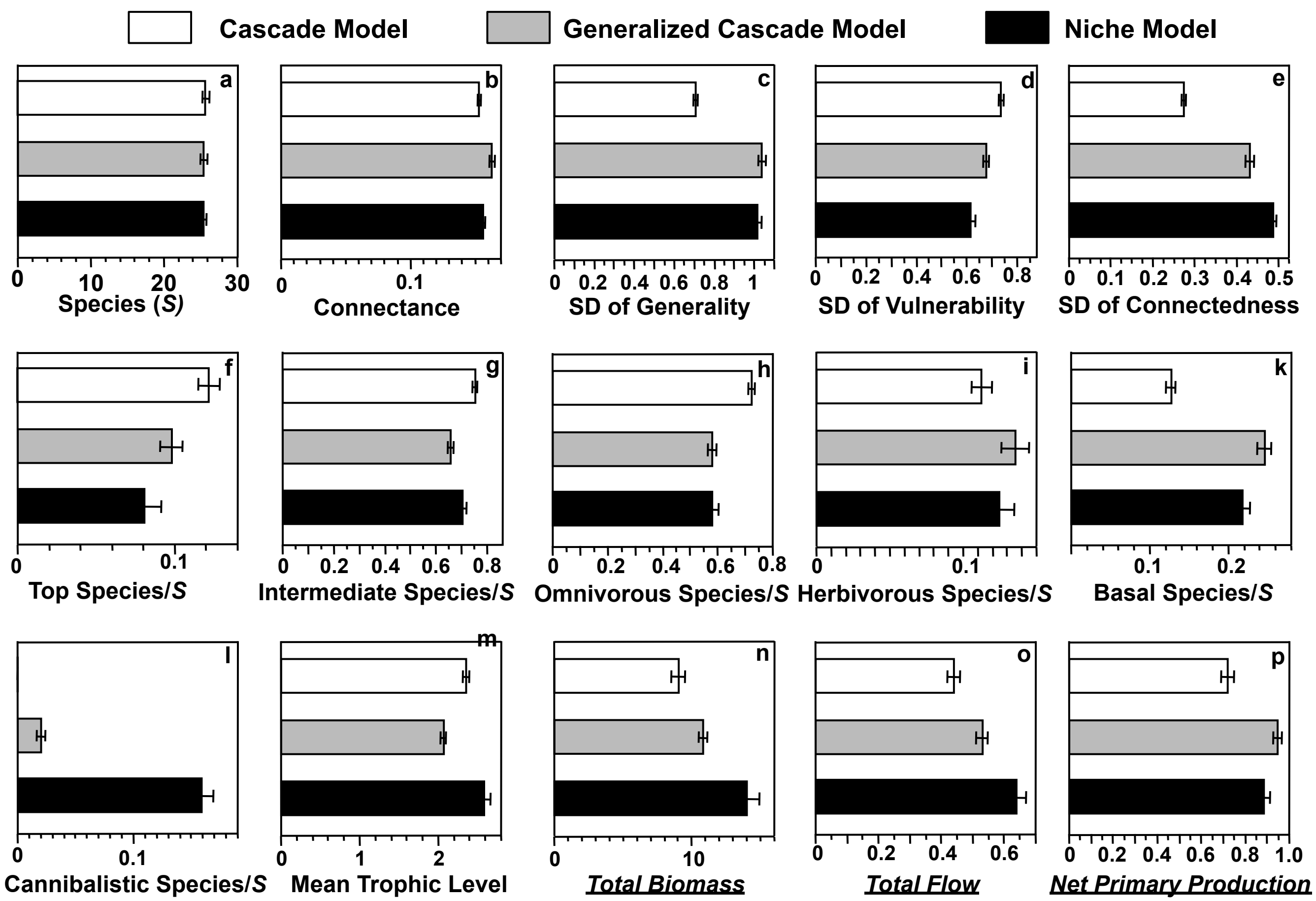
→ Allometric scaling increases intraspecific competition relative to metabolic rates for species with higher body mass

→ Allometric scaling leads to reduced biomass outflow from resource to consumer when the consumer is larger than the resource

Brose (2010) Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Functional Ecology* 24:28-34.

→ How to include such factors into functional response: attack rates, Hill exponents, (i.e., Type II → III), and predator interference coefficients

Network Structure and Ecosystem Function



Martinez and Williams in prep.

2009 *PNAS* 106:187-191

Simple prediction of interaction strengths in complex food webs

Eric L. Berlow[a,b,c,1,2], Jennifer A. Dunne[c,d], Neo D. Martinez[c], Philip B. Stark[e], Richard J. Williams[c,f], and Ulrich Brose[b,c,2]

[a]University of California, Merced, Sierra Nevada Research Institute, Wawona Station, Yosemite National Park, CA 95389; [b]Darmstadt University of Technology, Department of Biology, Schnittspahnstrasse 10, 64287 Darmstadt, Germany; [c]Pacific Ecoinformatics and Computational Ecology Lab, 1604 McGee Ave., Berkeley, CA 94703; [d]Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501; [e]University of California Berkeley, Department of Statistics, Berkeley, CA 94720-3860; and [f]Microsoft Research Ltd, 7 J. J. Thomson Avenue, Cambridge CB30FB United Kingdom

Edited by Simon A. Levin, Princeton University, Princeton, NJ, and approved November 10, 2008 (received for review July 15, 2008)

Allometric Trophic Network (ATN) Model

Food Web Structure: *Niche Model*
→ Williams & Martinez 2000

Predator-Prey Interactions: *Bioenergetic Model*
→ Yodzis & Innes 1992
→ Williams & Martinez 2004
→ Brose et al. 2006

Plant Population Dynamics: *Plant-Nutrient Model*
→ Tilman 1982
→ Huisman & Weissing 1999

Experimental Field System

1) Small intertidal habitats, S ~ **30**

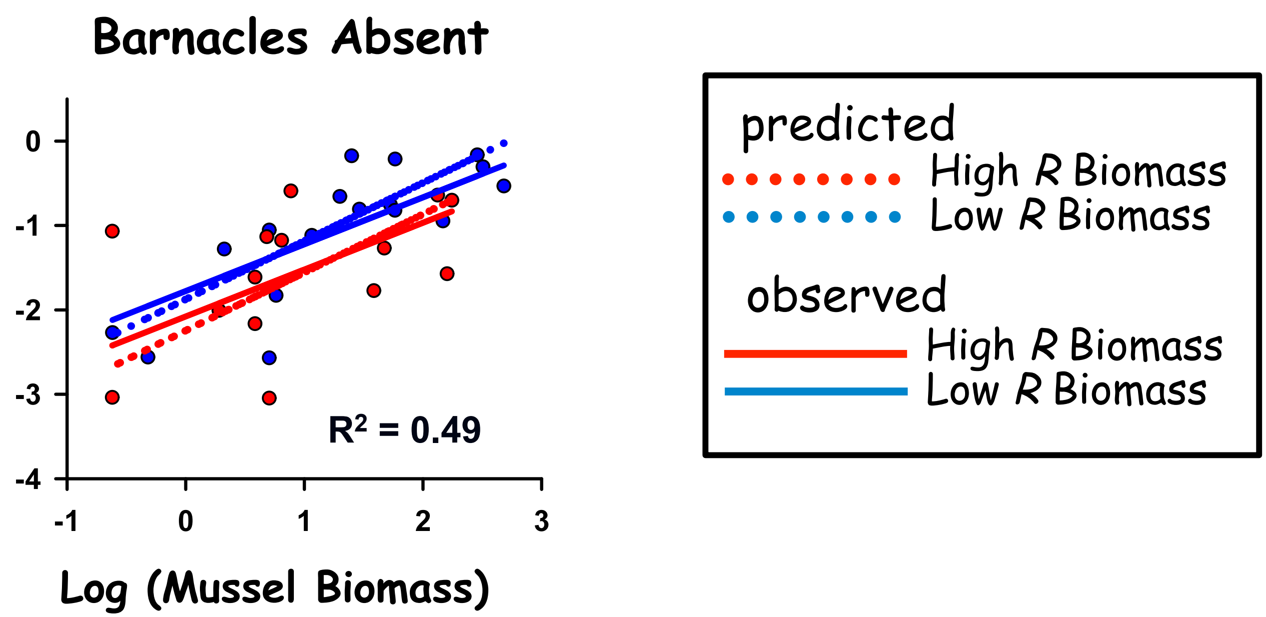
2) 3 species manipulated: R = **predatory whelk**; T = **mussels**

3) Barnacles mediate non-trophic effects of whelks on mussels, since barnacles facilitate mussel recruitment. Whelks eat barnacles:
   → Fewer barnacles means less substrate (negative mussel impact)
   → Thinning helps barnacles survive physical disturbances (positive mussel impact)

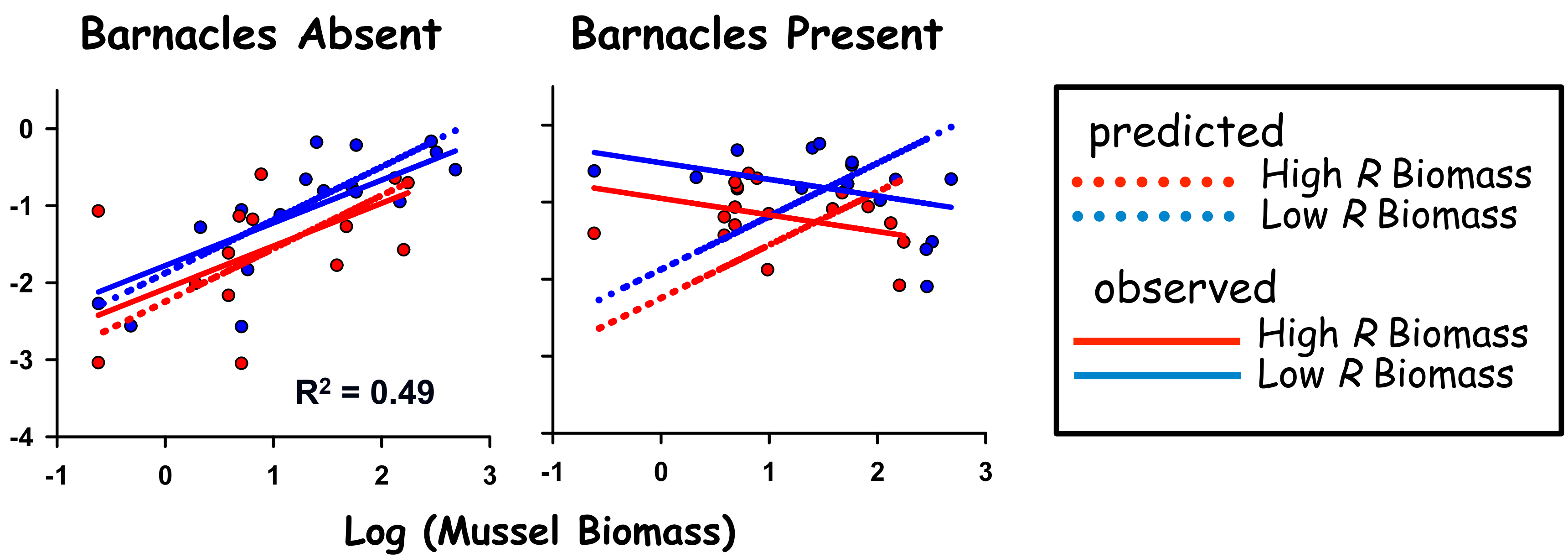
4) Measurements: I and pcI of whelks on mussels; B^{+}_{T} (biomass of mussels with whelk present), B_r (biomass of whelk), M_R (body mass of mussels)

Berlow (1999) Strong effects of weak interactions in ecological communities. *Nature* 398:330–334.

Results



1) <u>Barnacles Absent</u>: ATN model prediction of $\log_{10}|pcI|$ similar to observed at high & low mussel biomass and high & low whelk biomass



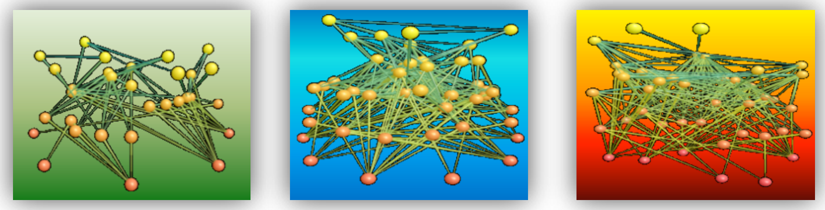
1) <u>Barnacles Absent</u>: ATN model prediction of $\log_{10}|pcI|$ similar to observed at high & low mussel biomass and high & low whelk biomass

2) <u>Barnacles Present</u>: underpredicts *pcI* at low mussel B and overpredicts at high B

Simulation Methods

- STEP ONE:

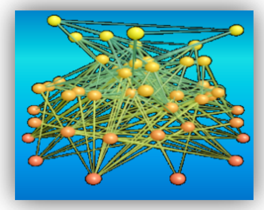
Create 150 Niche model webs (*t*=0)



  - 30 species, initial *C*=0.05, 0.15, 0.30

- STEP TWO:

Create100 niche invaders (*t*=0)



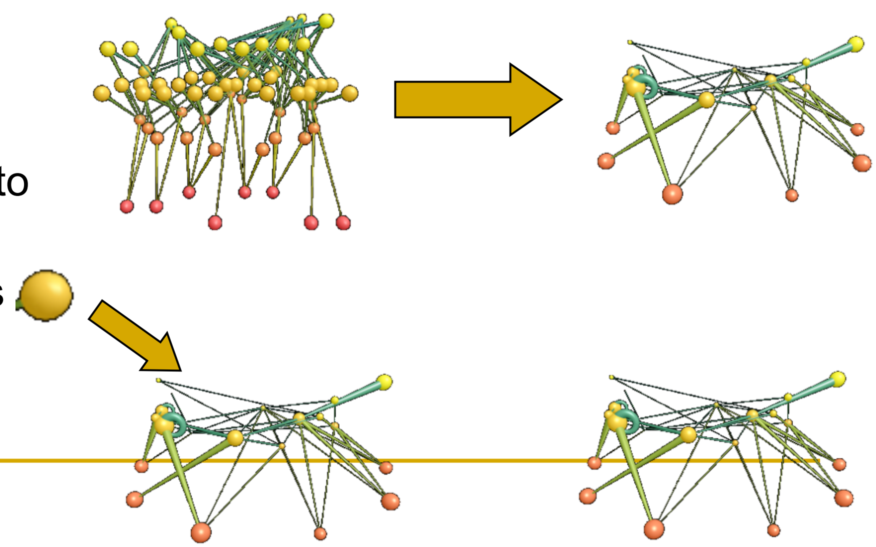
  - 30 species, initial *C*=0.15

- STEP THREE:

Generating persistent webs (*t*=0 to *t*=2000)

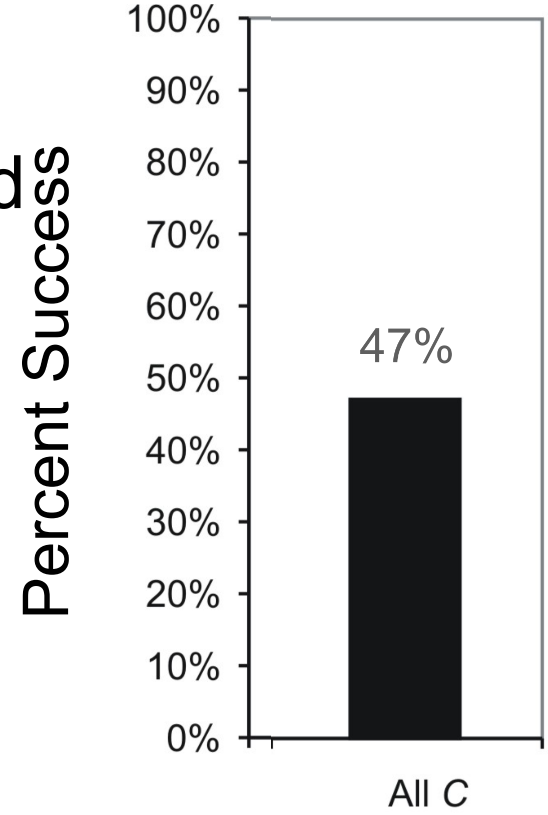
  - S and C range

- STEP FOUR:
  - Introducing invaders in the webs (*t*=2000 to *t*=4000)
  - Running the simulations without invasions (*t*=2000 to *t*=4000)



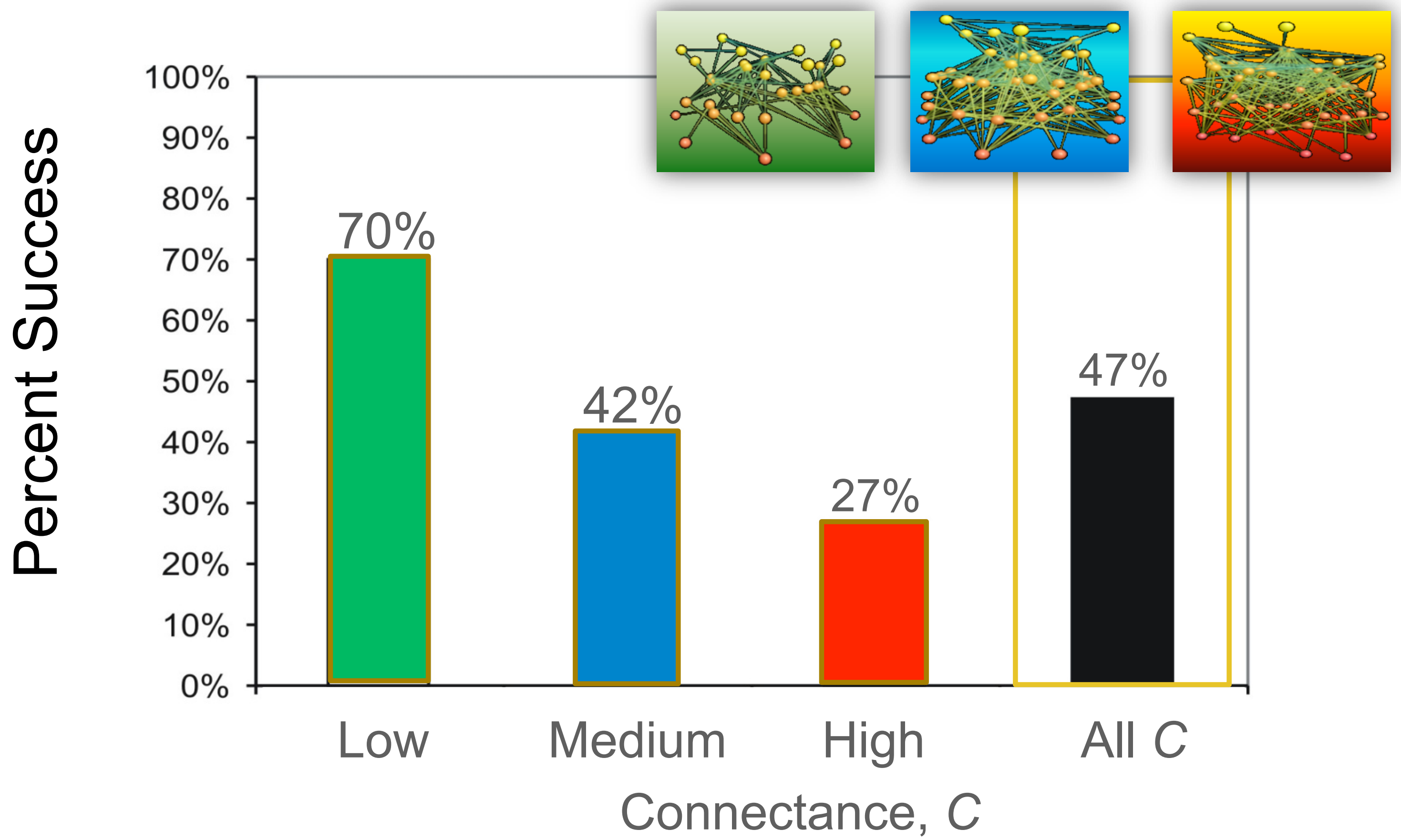
Resistance is not Futile

- 11,438 invasion attempts by non-basal species
- Basal species are eliminated
- 47% of these introductions were successful with the invader persisting till *t*=4000



Theme Issue: '**Food-web assembly and collapse: mathematical models and implications for conservation**', Romanuk *et al*., Phil. Trans. R. Soc. B 2009

Resistance varies with *C*



Romanuk et al., Phil. Trans. Roy. Soc. B 2009

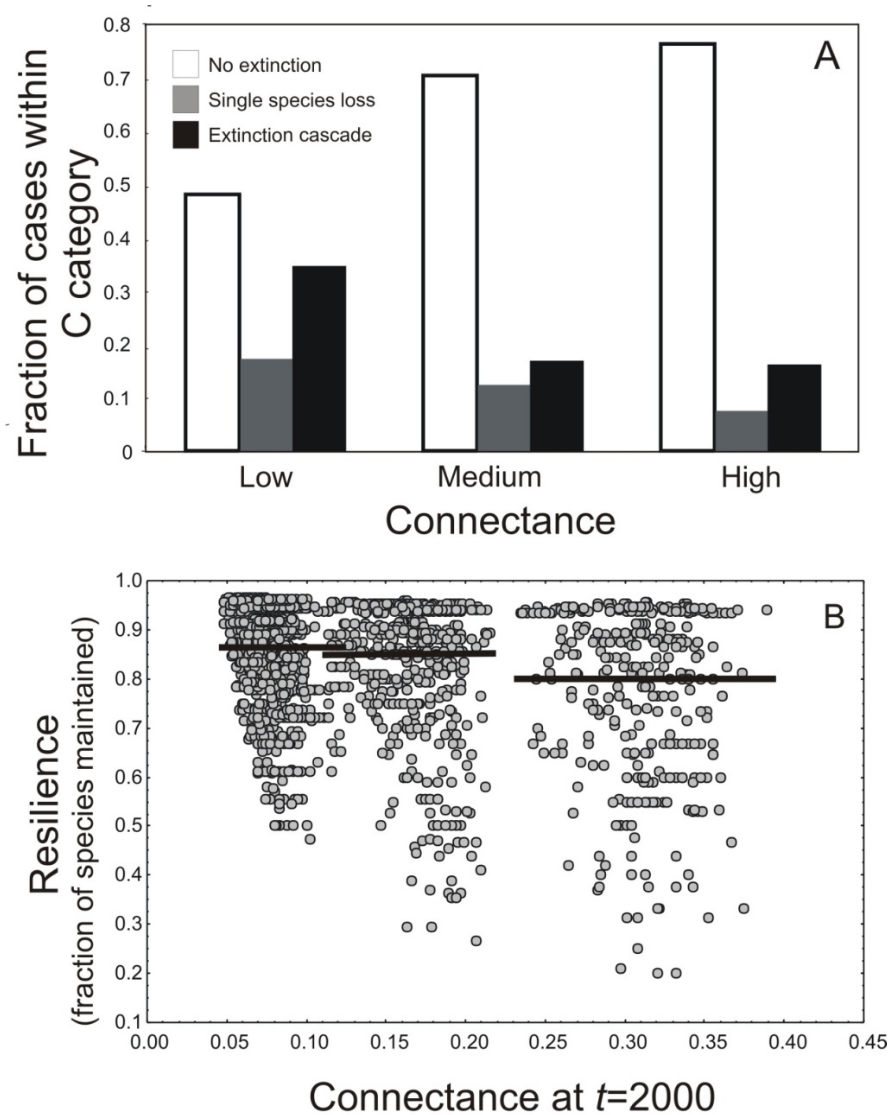


Figure 3a-b

C affects magnitude of secondary extinctions

- The magnitude of the extinctions was much greater in high *C* webs than in the low *C* webs.

Low Connectance Webs most Resilient

Summary

→ A well-developed theory of biodiversity and ecosystem function focuses on the network structure and function of complex food webs

→ This theory has substantial empirical support

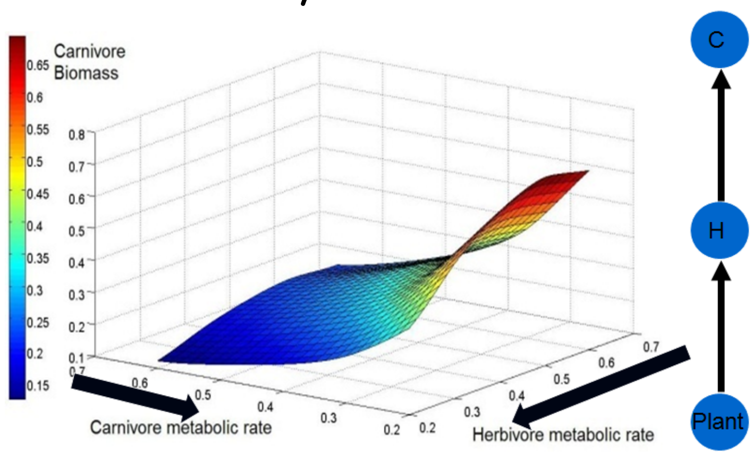
→ The theory is very useful for addressing global change

→ Promising new and synthetic directions need to be pursued.

Economic Effects of Humans on Ecosystems

with Barbara Bauer, Potsdam University

Effects of Body Size on Fish Biomass



Increasing Carnivore Size **Increasing Herbivore Size**

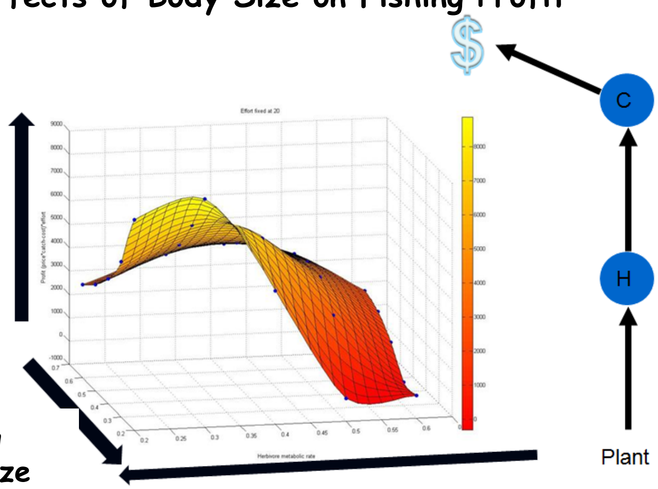
Add economic nodes to ecological networks

$$E_k' = n(pqB_i - c)E_k \quad \text{(Conrad 1999)}$$

- E = exploitation effort
- p = price per unit biomass
- q = catchability
- c = cost per unit effort
- n = economic "openness"

Effects of Body Size on Fishing Profit

Increasing Fishing Profit



Increasing Carnivore Size

Increasing Herbivore Size

→Body size of consumers strongly affect the function of trophic networks

→ Fishing reduces body size which can reduce profits

→ Management can alter body sizes of consumer in exploited ecosystems

ATN Model of a Specific System

Lake Constance

Germany, Austria, Switzerland

w/ Alice Boit & Ursala Gaedke, Potsdam University, Germany

Rich empirical data:

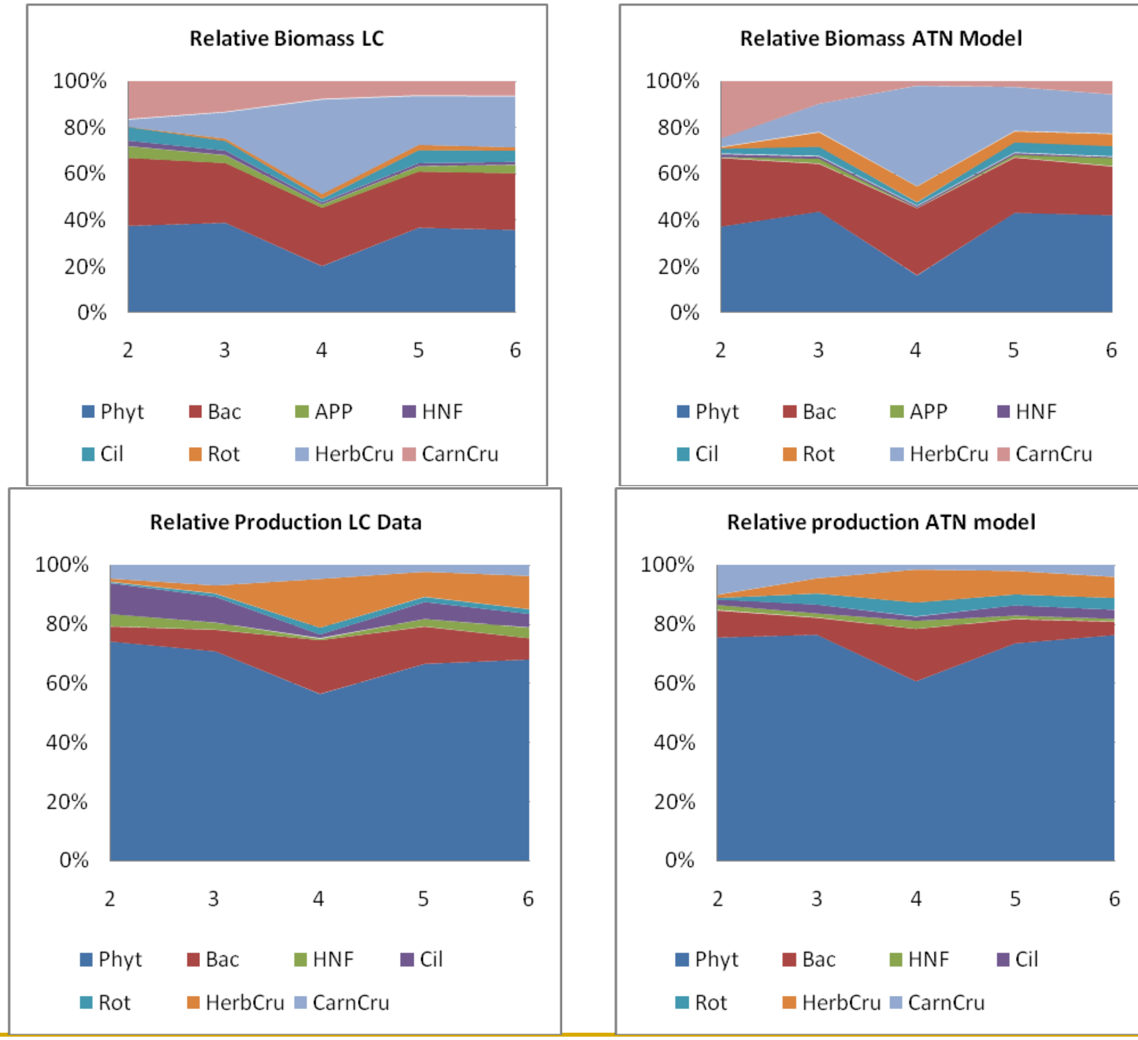
S = 18
Trophic network data
Weekly biomass & productivity data, 10-20 yrs
Metabolic data & body size

Run generic to specific versions of the ATN model and compare output to biomass time series data

(i.e., idealized system, generalized lake pelagic system, highly constrained system)

ATN Model of a Lake Constance

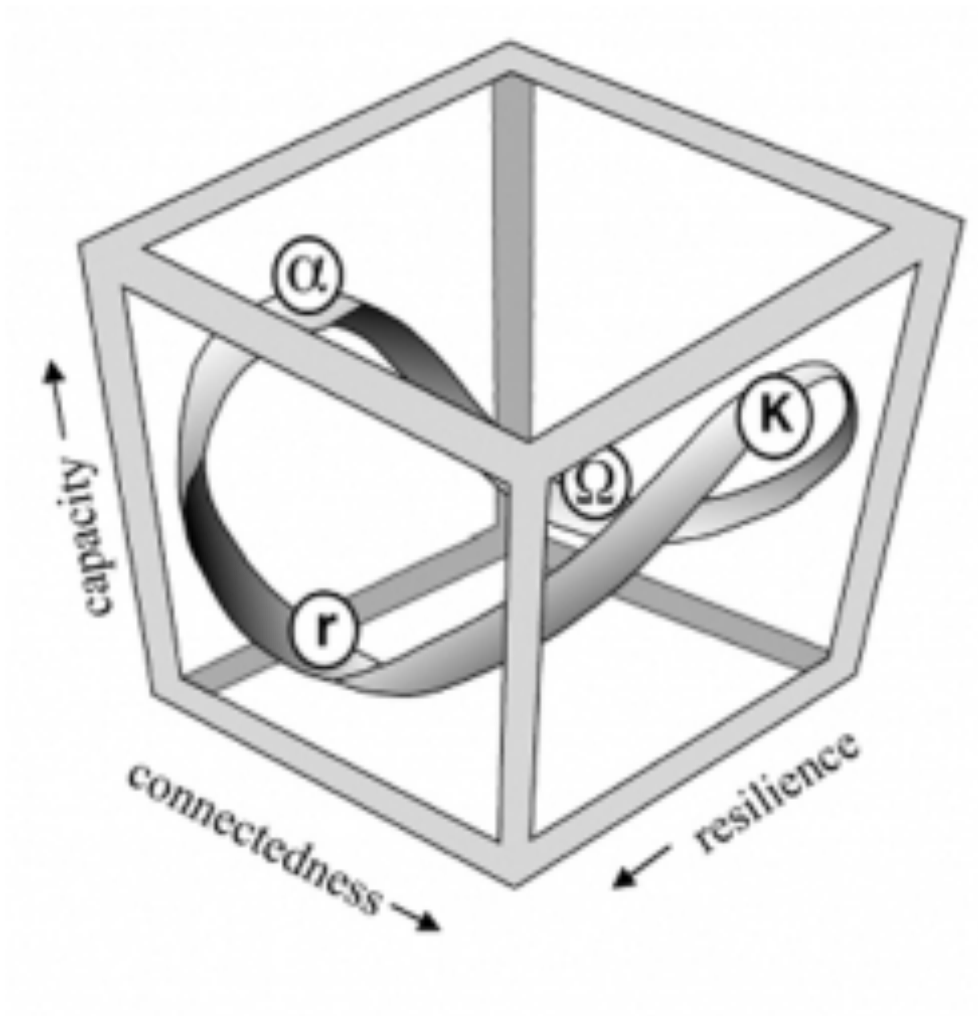
Data



Model

Need to add foraging metabolism to basal metabolism

Resilience Alliance: Panarchy



- A more rigorous framework for exploring fundament al concepts

Future Directions

- Include nontrophic interactions
  - Facilitation, plant-fungal, plant-pollinator
  - Sublethal effects of predators
  - Nutrients, remineralization, decomposition
- Apply computational sciences
  - Constraints, optimization, decision theory
  - Informatics: onologies, semantic web
  - Visualization!