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Dynamical Modeling of Complex Food Webs

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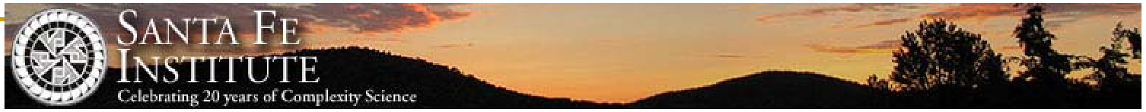

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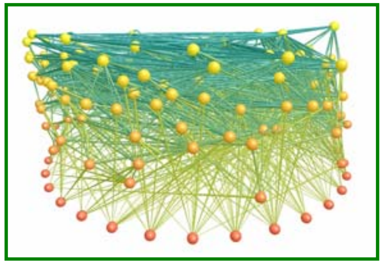
PEaCE Lab: www.foodwebs.org

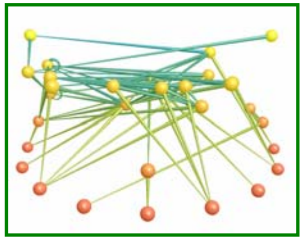
1950's Paradigm:

Complex communities MORE
stable than simple communities



1970's Challenge:

Complex communities LESS
stable than simple communities



Current & Future Research:

"Devious strategies" that promote
stability and species coexistence

1880s: Early thoughts on feeding & community stability

Stephen A. Forbes:

It is a general truth, that those animals and plants are least likely to oscillate widely which are preyed upon by the greatest number of species, of the most varied habitat. Then the occasional diminution of a single enemy will not greatly affect them, as any consequent excess of their own numbers will be largely cut down by their other enemies, and especially as, in most cases, the backward oscillations of one set of enemies will be neutralized by the forward oscillations of another set. But by the operations of natural selection, most animals are compelled to maintain a varied food habit, --so that if one element fails, others may be available.

Forbes, S.A. (1880) On some interactions of organisms. *Illinois Laboratory of Natural History Bulletin* 1(3):3-17.

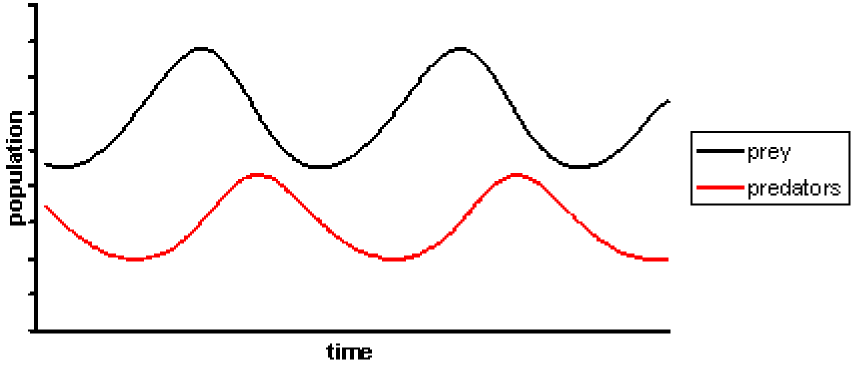
Early 20th Century: Lotka & Volterra predator-prey dynamics

Alfred J. Lotka (1925) & Vito Volterra (1926)

A pair of first order, non-linear differential equations, representing the change in numbers of a predator y and prey x over time t due to their interaction.

$$\frac{dx}{dt} = \alpha x - \beta xy \qquad \frac{dy}{dt} = \delta xy - \gamma y$$

αx is the intrinsic exponential growth of prey
βxy is the rate of predation of y on x, which is proportional to rate at which y and x meet
δxy is the growth rate of the predator
γy is the natural death rate of the predator (exponential decay)



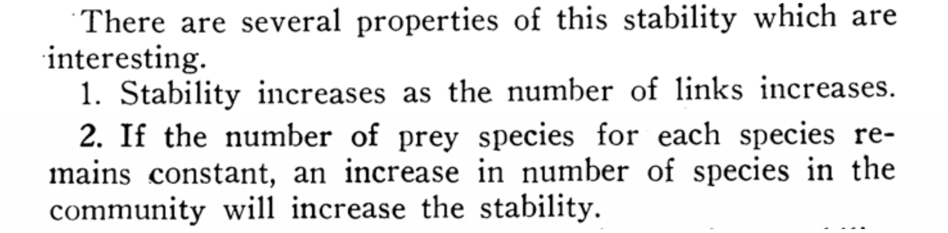
Lotka (1925) Elements of physical biology. Williams and Wilkins, Baltimore
Volterra (1925) Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Mem R Accad Naz dei Lincei* 2:31-113

1920s to 50s: Complexity begets stability

Odum (1953) Fundamentals of Ecology. Saunders.

MacArthur (1955) Fluctuation of animal populations and a measure of community stability. *Ecology* 36: 533-536.

> ***"…a large number of paths through each species is necessary to reduce the effects of overpopulation of one species…"***



There are several properties of this stability which are interesting.

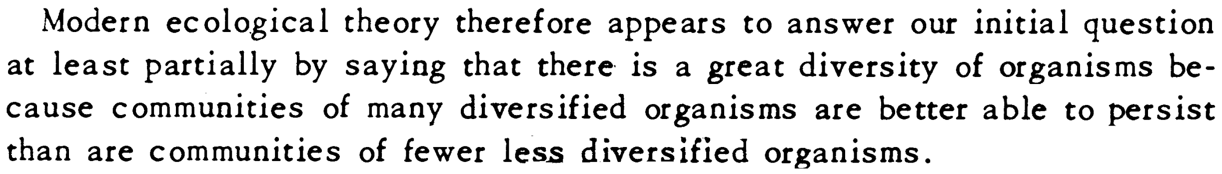
1. Stability increases as the number of links increases.
2. If the number of prey species for each species remains constant, an increase in number of species in the community will increase the stability.

Information Theory/Entropy

Stability: how many different paths energy can take from top to bottom of a food web.

Elton (1958) Ecology of Invasions by Animal and Plants. Chapman and Hall.

Hutchinson (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *The American Naturalist* 93: 145-159.



Modern ecological theory therefore appears to answer our initial question at least partially by saying that there is a great diversity of organisms because communities of many diversified organisms are better able to persist than are communities of fewer less diversified organisms.

Early 1970s: Complexity inhibits stability

May's Stability Criterion: $i\,(SC)^{1/2} < 1$

Local stability analyses of randomly structured, competitive community matrices of species with random interaction strengths indicate that they will be stable if:

i (interaction strength), *or*
S (diversity- number of species), *or*
C (connectance- probability that two species interact)

do not exceed critical values (following Ashby & Gardner 1970 *Nature*).

Implications:

→ Increased links or species tend to increase destabilizing positive feedback loops

→ If we assume i is constant, for communities with increasing S to be stable, C must decrease accordingly (or vice-versa)

→ Mathematically speaking, increasing diversity (S) and complexity (C) destabilizes idealized communities, contrary to earlier ecological intuition

May RM (1972) Will a large complex system be stable? *Nature* 238:413-414.
May RM (1973) Stability and Complexity in Model Ecosystems. Princeton University Press

Post 1970s: “Devious strategies”

In short, there is no comfortable theorem assuring that increasing diversity and complexity beget enhanced community stability; rather, as a mathematical generality the opposite is true. The task, therefore, is to elucidate the devious strategies which make for stability in enduring natural systems.

-May (1973) Stability and Complexity in Model Ecosystems

Modeling species interactions, S>2

1) **Community Matrices**: Species interaction coefficients describe the impact of species *i* on growth of species *j* at equilibrium population densities.
LOCAL STABILITY (May, De Angelis, Pimm, Lawton, Levins, de Ruiter…)

2) **Food-Web Modules**: Population dynamics of S = 3-9 trophically interacting species via numerical integration of linked ordinary differential equations.
POPULATION STABILITY (Hastings, Yodzis, McCann…)

3) **Complex Food Webs**: Population dynamics of $S \geq 10$ trophically interacting species.
POPULATION STABILITY, SPECIES PERSISTENCE, etc.

→ **Population Dynamics + Structure**: run trophic dynamics on *a priori* complex network structures (Chen/Cohen, Kondoh, **Williams/Martinez/Brose/Berlow/Dunne**)

→ Population + Evolutionary Dynamics: evolve complex webs from a few species (McKane/Caldarelli/Drossel, Yoshida, Rossberg)

→ EcoPath with EcoSim: a black-box software package based on static, linear, steady-state, mass-balance snapshots of specific systems (fisheries) + dynamic projections (Christensen/Walters/Pauly)

→ Genetic algorithms: explore structure related to specific dynamical properties in linear and nonlinear systems (Tononi, Ruiz-Moreno/Pascual/Riolo)

→ Individual-based models/digital organisms (Bell, Melian, Ofria/Wilke/Chow)

Bioenergetic dynamics/structure model for complex food webs

The basic framework:

- Generate a set of model network structures, S ~ 10 to 50, C ~ 0.1 to 0.2
- Run allometrically scaled, non-linear trophic dynamics on the networks
- Explore conditions for population stability, species persistence, etc.

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

- Basal species exhibit exponential growth bounded by carrying capacity, or grow according to resource competition or other models
- Other species grow according to feeding rates and assimilation efficiencies
- All species lose energy due to metabolism and consumption
- Non-linear functional responses determine how feeding rates vary with abundances of consumer and/or resource species
- Biological rates of production, metabolism, and maximum consumption are scaled with the species' body masses (Brown/West/Enquist)

Yodzis & Innes (1992) Body size and consumer-resource dynamics. *Am Nat* 139: 1151- 1175.

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

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

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.)

Initial Conditions

B_i (biomass of each species)

Parameters

$G_i(B)$: Gross primary production (of basal species)
Depends on r_i (intrinsic growth rate) and K_i (carrying capacity)

x_i : metabolic rate

y_{ij} : rate of maximum biomass gain

a_{ij} : resource preference

e_{ji} : assimilation efficiency

F_{ij} : Functional response: consumption rate of resource species j by consumer species i

Exploring the basic model:

1) Functional responses
2) Generalist behavior
3) Overall network structure
4) Primary productivity

1) Functional responses (Holling 1959)

F: Predator's relative consumption rate as fraction of maximum ingestion rate

Type I

- linear (used in Lotka-Volterra models)
- ecologically unrealistic

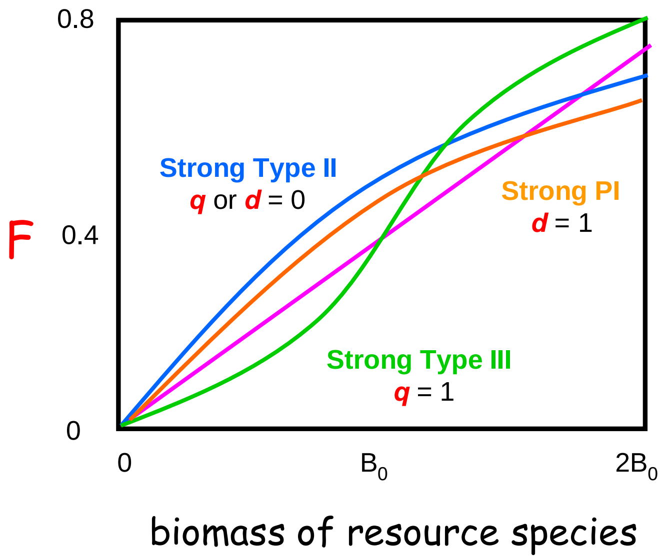
Type II (Murdoch 1973)

- saturating curve (dominates non-linear modeling)
- *ƒ* (resource density)
- function of consumer search and resource handling times
- lab studies

Type III (Real 1977, 1978) (parameter ***q***)

- S curve
- *ƒ* (prey density)
- consumption of low-density resources relaxed
- successful food searches increases consumer's search effort
- field studies

Functional Response Forms



Predator Interference (Beddington 1975, DeAngelis *et al.* 1975) (parameter ***d***)

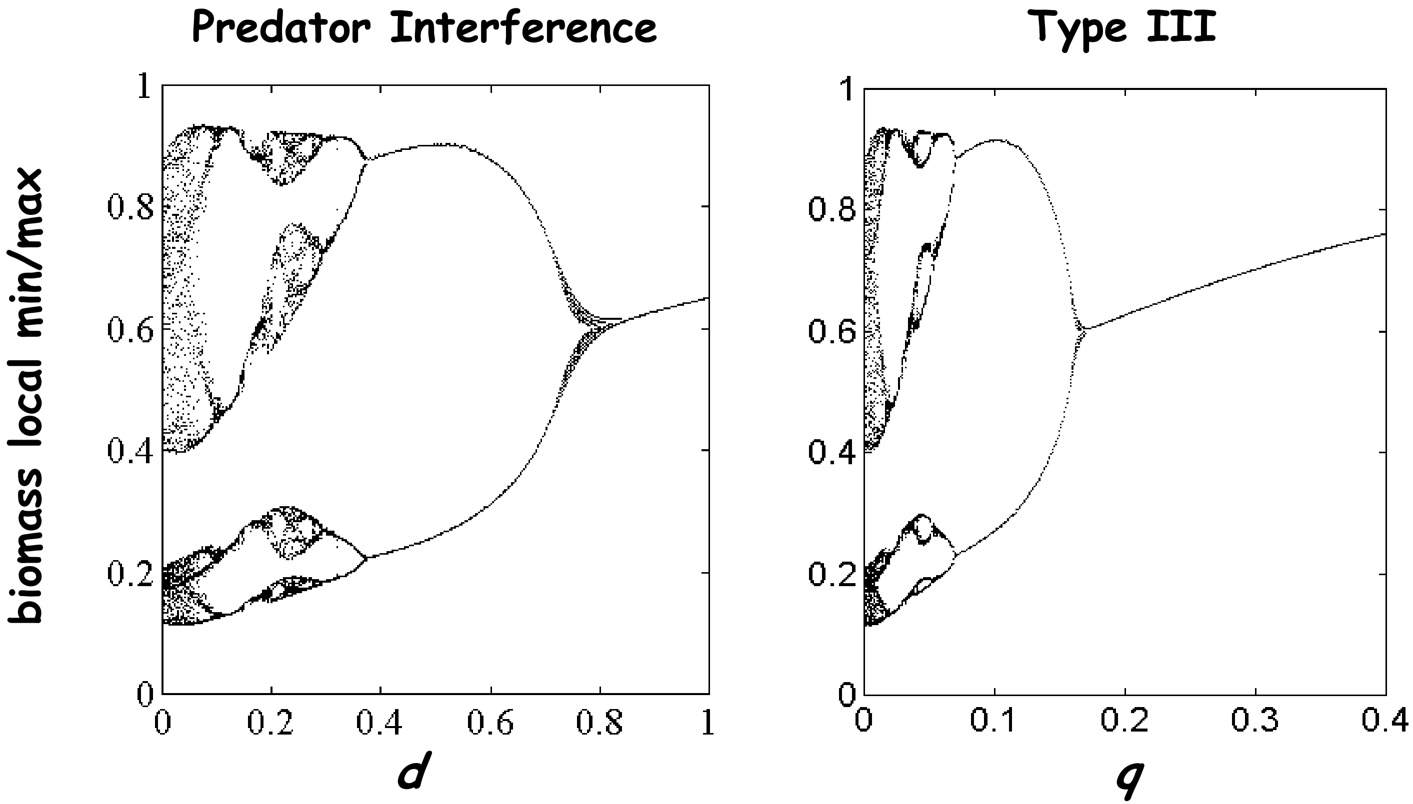
- pushes Type II curve down
- *ƒ* (resource & consumer densities)
- increase in consumer biomass decreases consumption due to interference among consumers
- field studies (best empirical support- Skalski & Gilliam 2001)

Multispecies functional response (Williams & Martinez 2004)

$$F_{ij}\left(\vec{B}\right) = \frac{\left(B_j/B_{0ij}\right)^{1+q}}{1 + d_i B_i + \sum\limits_{k-\mathrm{prey}} \left(B_k/B_{0ik}\right)^{1+q}}.$$

B_i : biomass of species i
B_{0ij} : half-saturation biomass of predator i consuming prey j
q : positive constant that controls the strength of Type III
d_i: positive constant that controls the strength of Pred. Int.

2-species dynamics & functional response



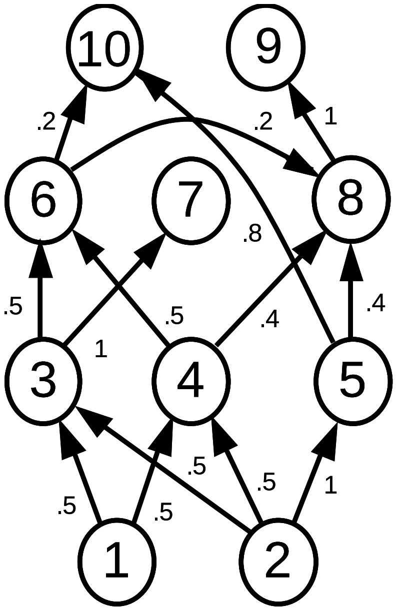
functional response parameters

(when *d* or *q* = 0, the functional response is Type II)

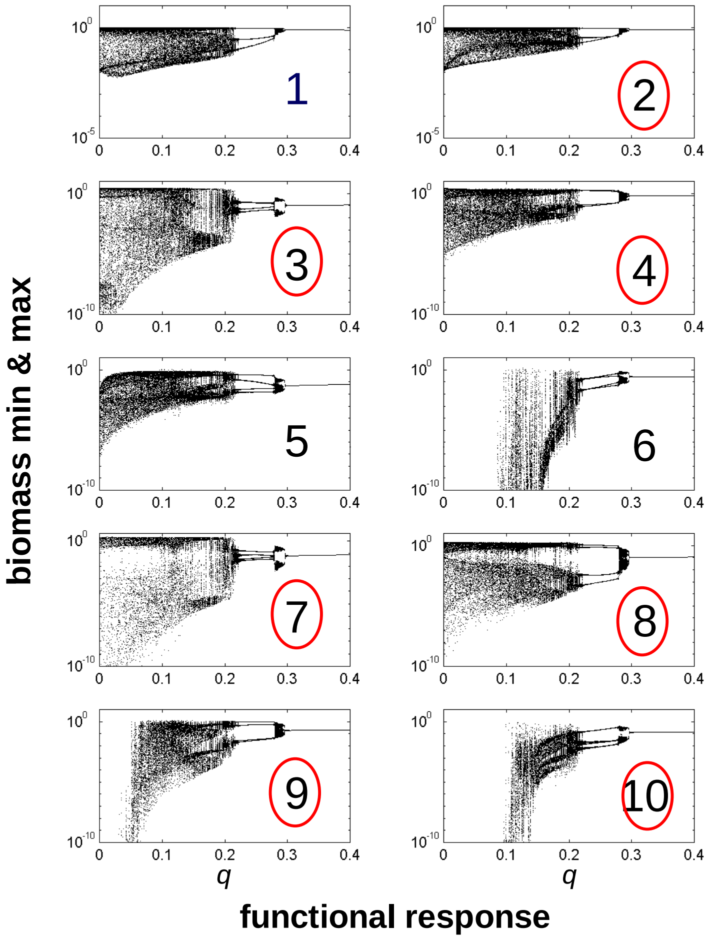
chaotic dynamics → period doubling reversals → stabilization of limit cycles → stable stationary solution

Increases in PI or Type III stabilize dynamics

10-species dynamics & functional response



Weak Type III FR (e.g., q = 0.1) stabilize dynamics by decreasing feeding on rarer spp., increasing it on more abundant spp.



Red circles show species that go extinct with Strong Type 2 (q = 0) functional responses.

Williams & Martinez 2004

2) Generalist behavior

$$F_{ij}\left(\vec{B}\right) = \frac{\left(B_j/B_{0ij}\right)^{1+q}}{1 + d_i B_i + \sum\limits_{k-\text{prey}} \left(B_k/B_{0ik}\right)^{1+q}}. \quad \longrightarrow \quad F_{ij}\left(\vec{B}\right) = \frac{\omega_{ij} B_j^{1+q}}{B_0^{1+q} + d_i B_i B_0^{1+q} + \sum\limits_k \omega_{ik} B_k^{1+q}}$$

$w_{ij} = (B_0 / B_{0ij})^{1+q}$: relative half-saturation densities or relative inverse attack rate, interpreted as the relative preference of *i* for *j*. (B_0 is a reference value)

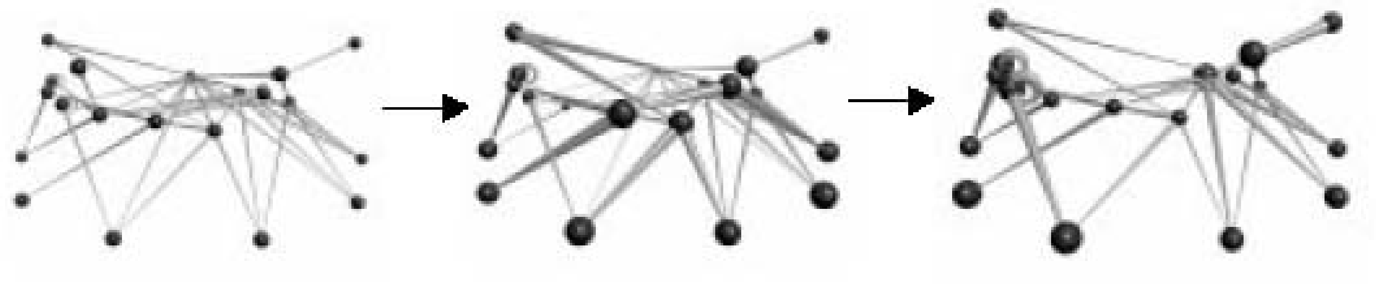
Passive Prey Switching, driven by different relative resource abundances

Depending on how you constrain w_{ij}, it alters the strength of consumption by consumers with more than one resource:

1) "***Weak generalist model***" : total rate of consumption of a generalist is lower than that of a specialist given same total density of resource species.

2) "***Strong generalist model***" : generalists and specialists consume at the same rates when they encounter the same total density of resource species.

3) Overall network structure



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	$n_j \geq n_i$*

4) Primary producer growth rate G_i (B)

1) **Logistic Model**: assumes each basal species i has an independent growth rate constrained by its carrying capacity K_i.
(Limitation: K of system, and thus system-wide maximum possible rate of primary production, are dependent on the number of primary producers)

2) **System-Wide K Model**: defines a system-wide carrying capacity K ($K_i = K/n_{producers}$).

3) **Lotka-Volterra Competition Model**: has primary producers compete for a system-wide carrying capacity K.

Effect of different factors on species persistence?

1) 3 functional response models
2) 2 generalist behavior models
3) 4 network structure models
4) 3 primary production models

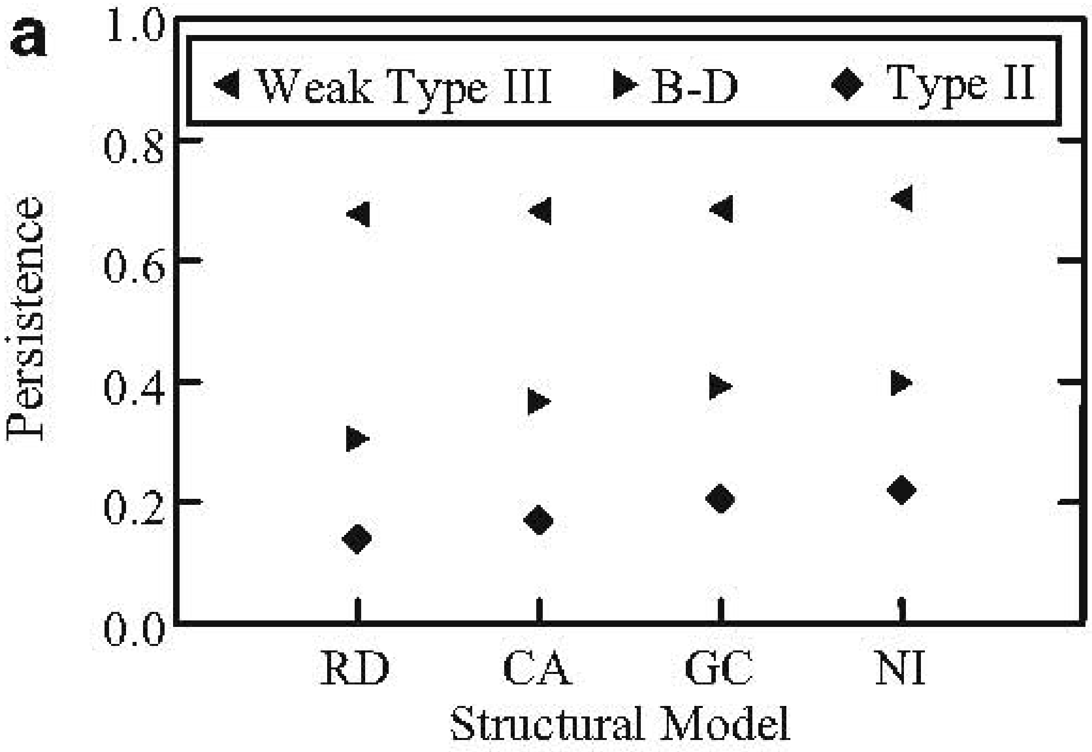
→ Fully factorial design, 200 replicates of 72 factor combinations

→ Initial S = 30 and C = 0.15

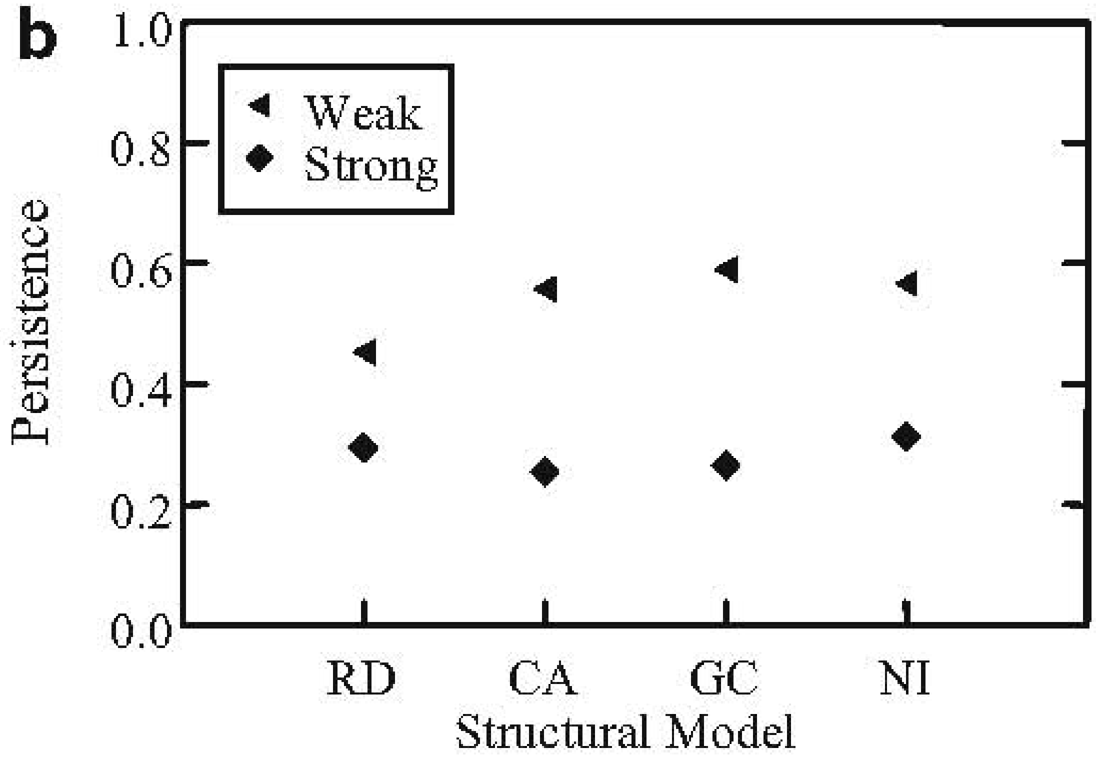
→ Persistence: Fraction S with $B_i > 10^{-15}$ at $t = 4{,}000$

(Williams 2008)

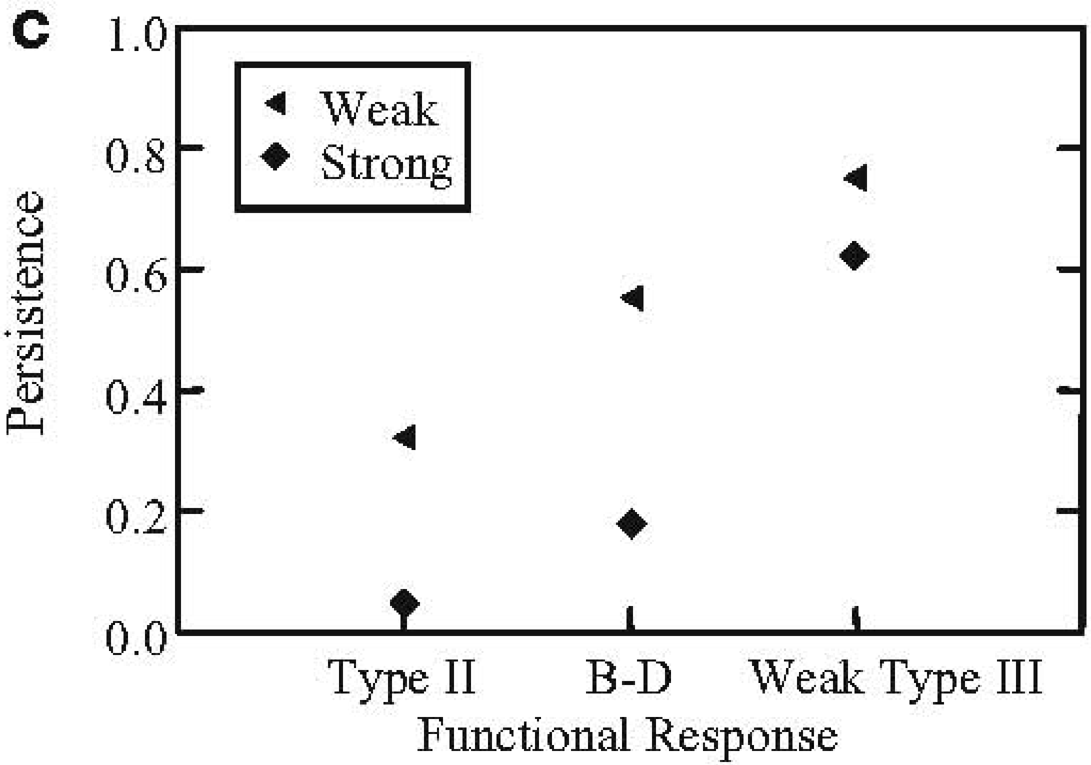
Functional Response & Structural Model



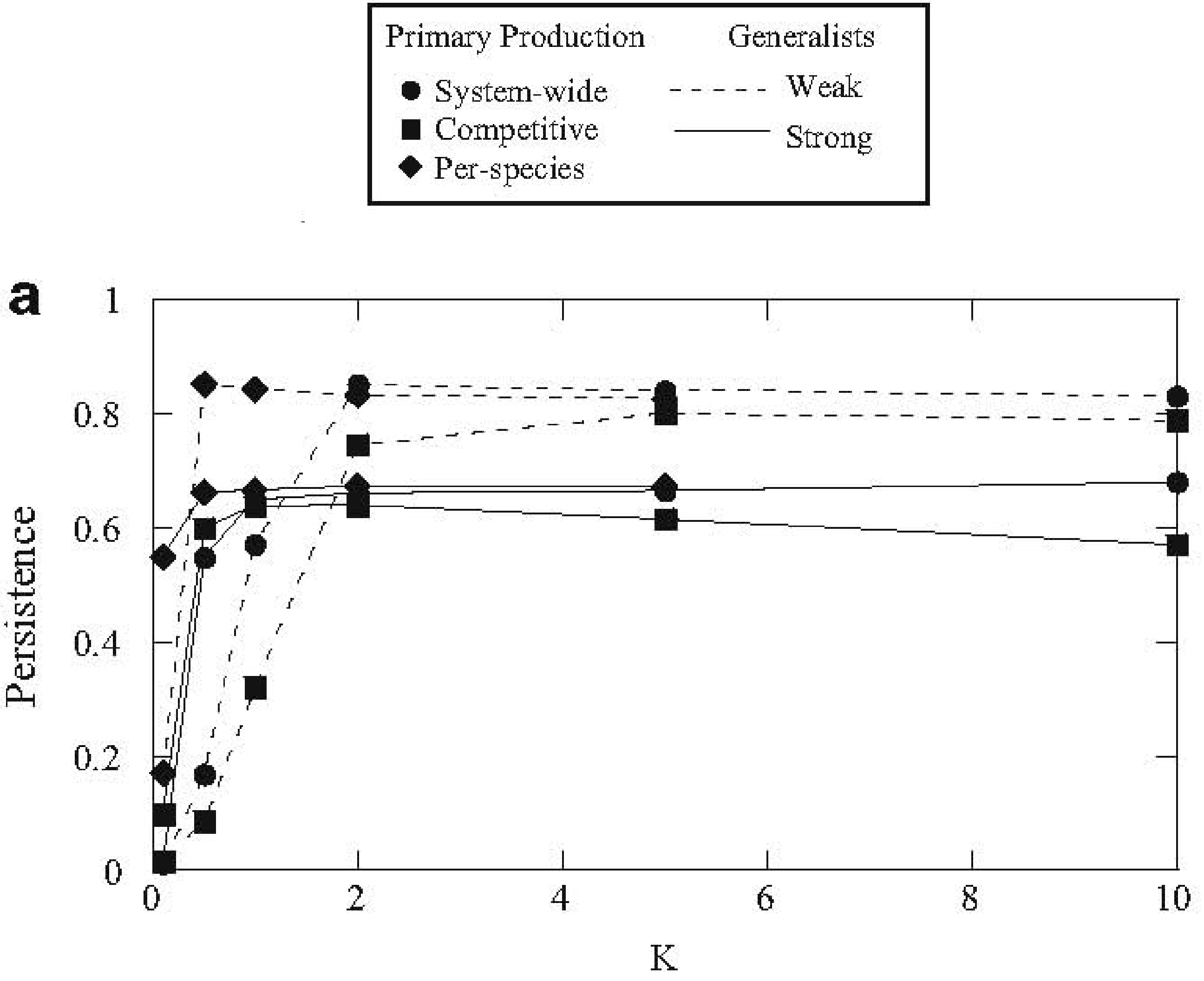
Generalist Behavior & Structural Model



Generalist Behavior & Functional Response



Primary Production & Generalist Behavior



Relative impact of factors on persistence

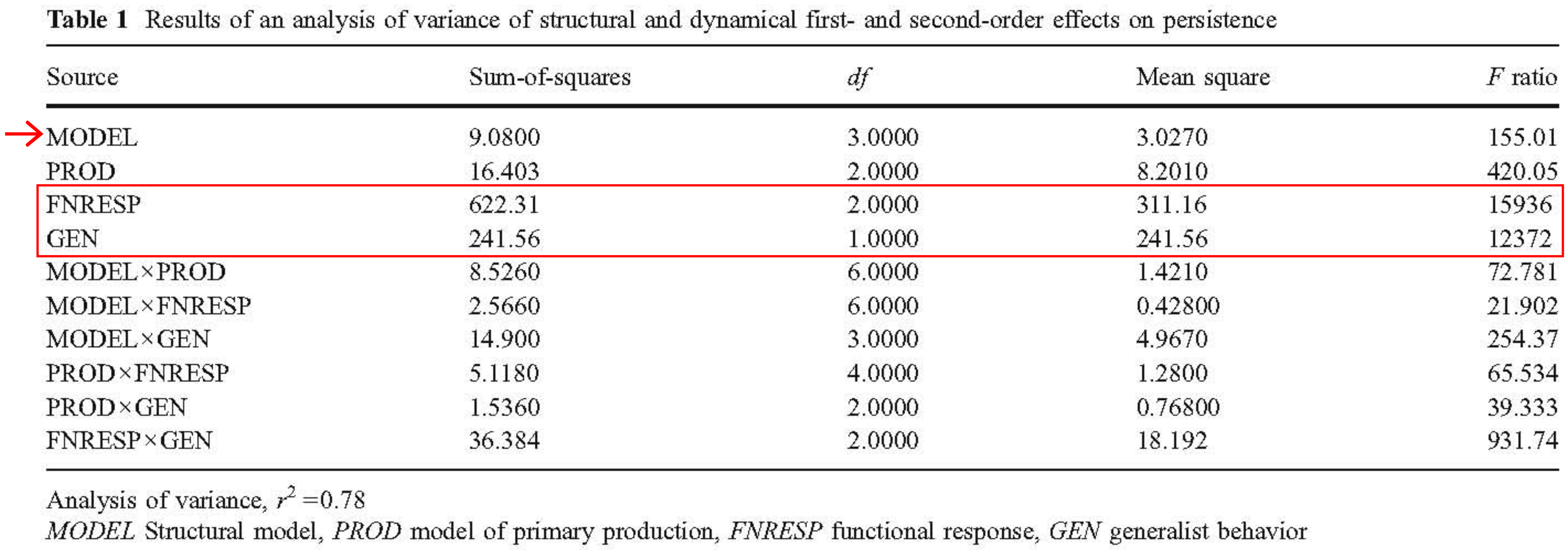


Table 1 Results of an analysis of variance of structural and dynamical first- and second-order effects on persistence

Source	Sum-of-squares	*df*	Mean square	*F* ratio
MODEL	9.0800	3.0000	3.0270	155.01
PROD	16.403	2.0000	8.2010	420.05
FNRESP	622.31	2.0000	311.16	15936
GEN	241.56	1.0000	241.56	12372
MODEL × PROD	8.5260	6.0000	1.4210	72.781
MODEL × FNRESP	2.5660	6.0000	0.42800	21.902
MODEL × GEN	14.900	3.0000	4.9670	254.37
PROD × FNRESP	5.1180	4.0000	1.2800	65.534
PROD × GEN	1.5360	2.0000	0.76800	39.333
FNRESP × GEN	36.384	2.0000	18.192	931.74

Analysis of variance, $r^2 = 0.78$

MODEL Structural model, *PROD* model of primary production, *FNRESP* functional response, *GEN* generalist behavior

→ In model systems where species have identical body sizes, the structural model used has a large effect on persistence (Niche>>Cascade>>Random).

Case studies:

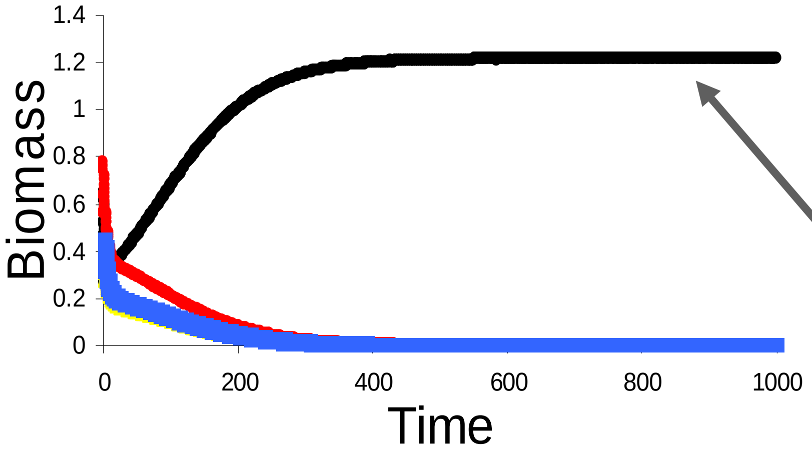
- Keystone species
- Consumer-resource body-size ratios
- Interaction strength
- Human impacts

1) Keystone species

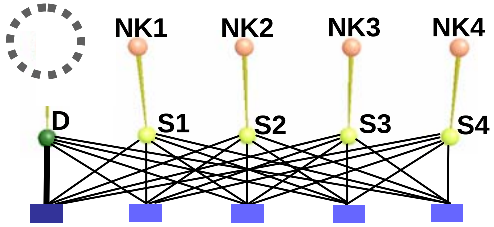
Keystone predation: strong predation on a competitively dominant prey species promotes system diversity

Pisaster* & *Mytilus (R.T. Paine)

Dynamical model, S=9, no keystone



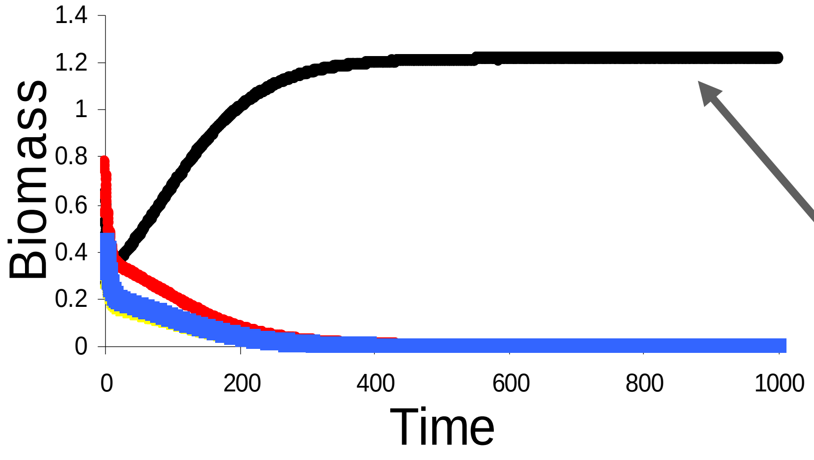
No keystone: diversity lost



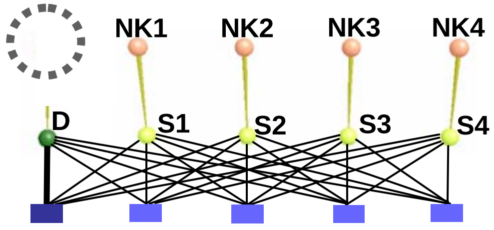
competitive dominant

D = Competitive dominant, K = Keystone consumer, NK = Non-keystone consumer
S = Producer, Blue boxes = Nutrients

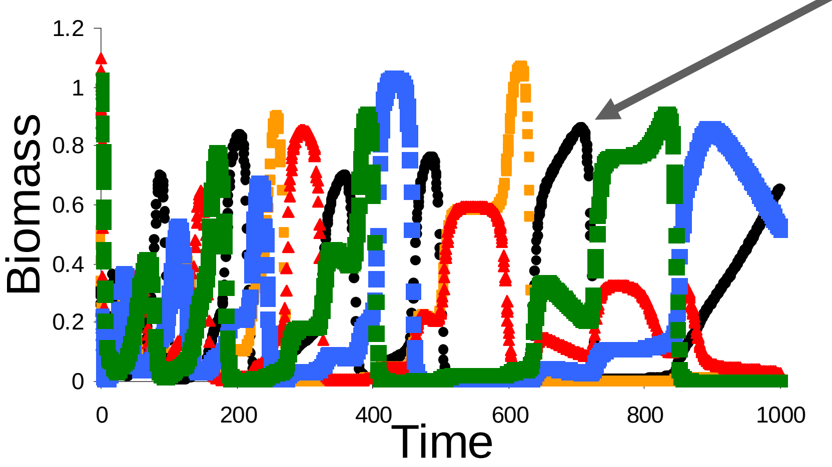
Dynamical model, S=10, no keystone



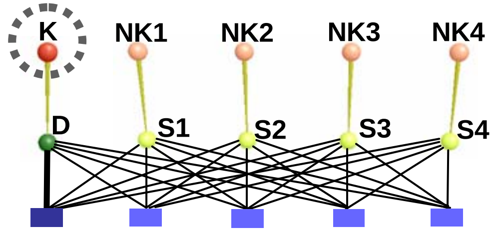
No keystone: diversity lost



competitive dominant

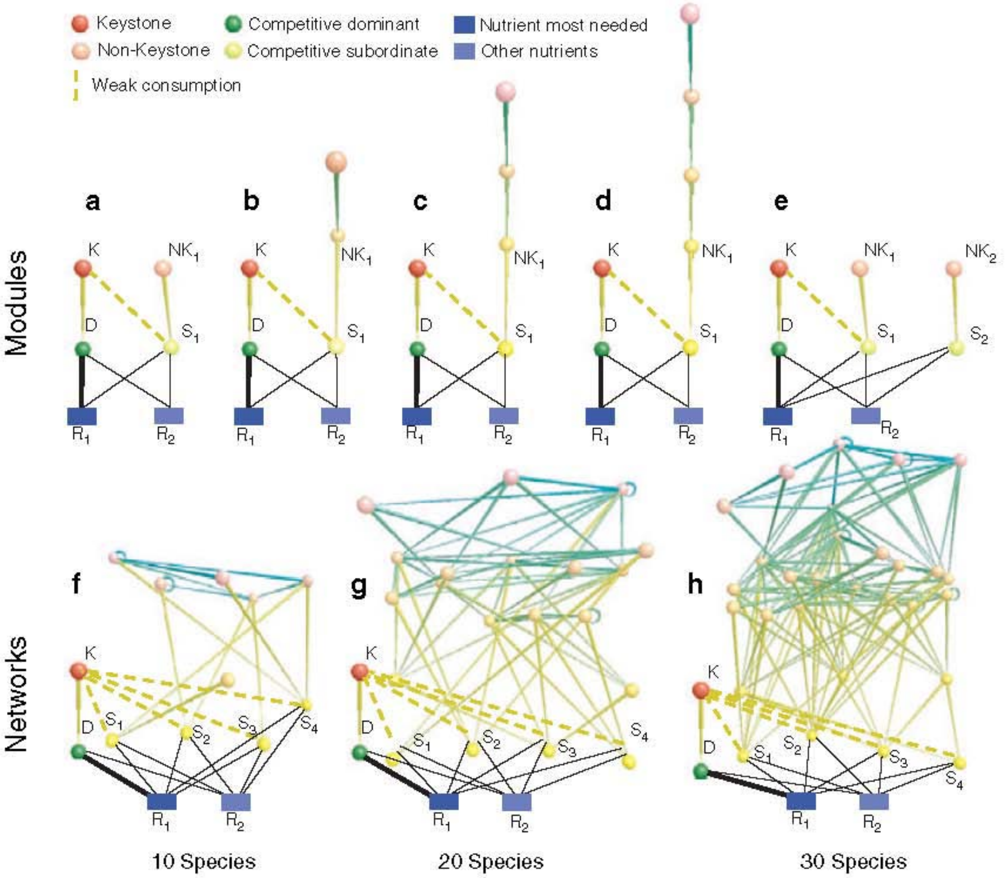


Keystone: diversity maintained



D = Competitive dominant, K = Keystone consumer, NK = Non-keystone consumer
S = Producer, Blue boxes = Nutrients

Brose *et al.* 2005

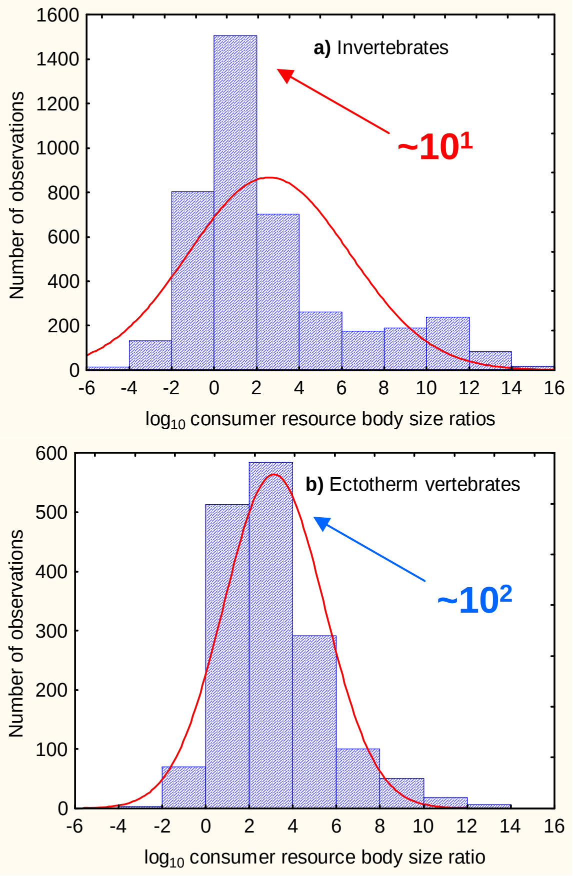


In both small modules (***S*** = 4-7) and larger webs (***S*** = 10-30):

→ ***K*** promotes coexistence of species
→ In absence of ***K***, ***D*** excludes other ***S*** and their consumers
→ Predictability of ***K*** effects on ***S*** similarly high
→ Predation, competition, resource supply & interactions explain ***K*** → ***S***

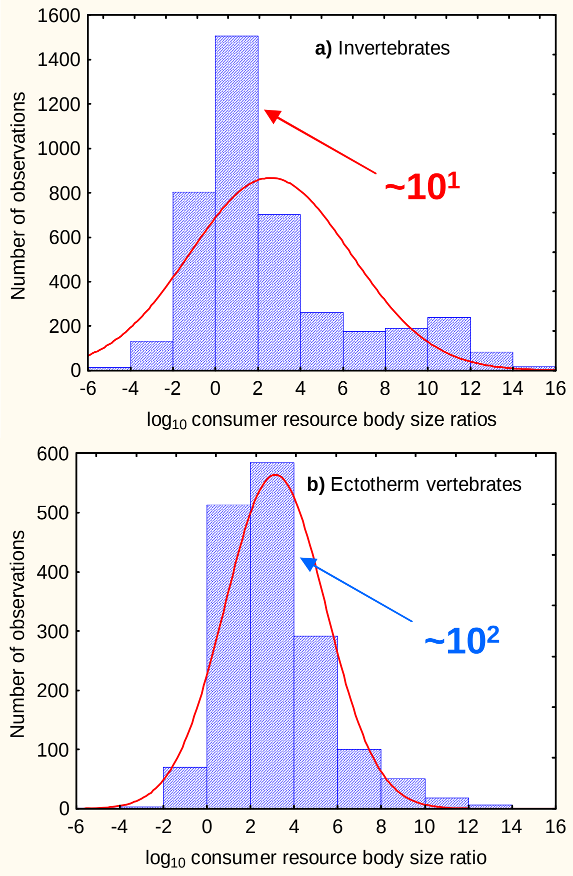
2) Consumer-resource body-size ratios

Empirical Body-Size Ratios

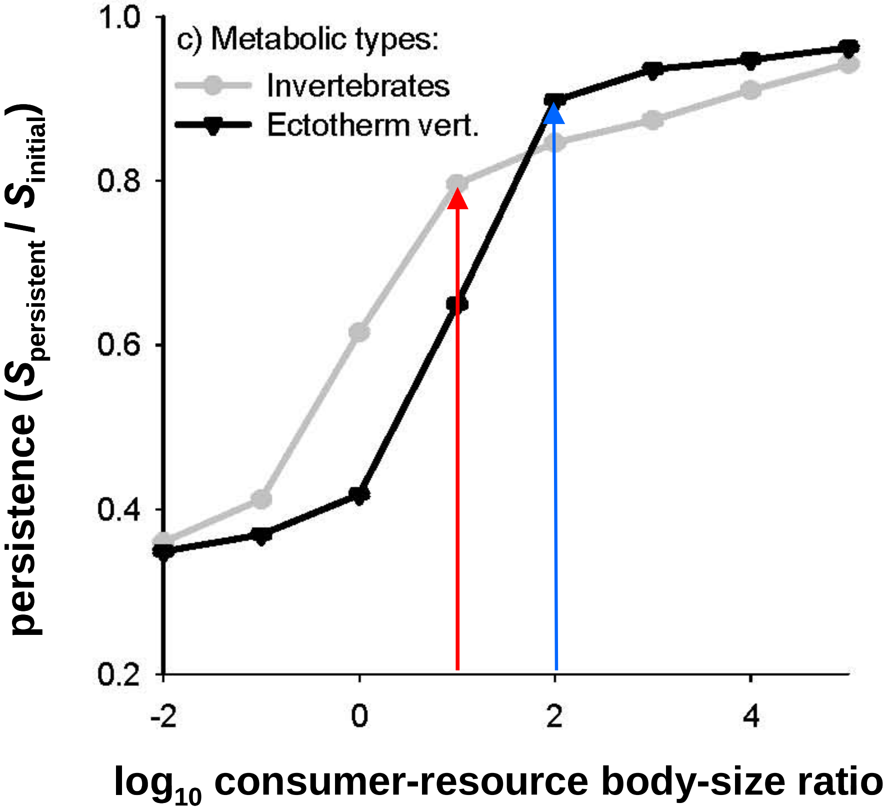


Brose *et al.* 2006a

Empirical Body-Size Ratios



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



Brose *et al.* 2006b

3) Interaction strength

→ Remove individual species from 600 webs, S = 10-30, C = 0.1 to 0.2

→ Measure effect of each "removed species" R on the biomass of every other species in each web (T, "target species").

→ Mean biomass and densities for time steps 50-200 used to calculate **Interaction strengths**:

1) **Population level**: $I = B^{+}_{T} - B^{-}_{T}$
(i.e., biomass of T with R present – biomass of T without R)

2) **Per capita**: $pcI = I/N_r$ (N_r = population density of R)

→ For each of 254,032 possible R & T interactions, record 90 species, link, and network structure attributes

→ Assess which attributes best explains variation in I and pcI using a Classification and Regression Tree (CART) algorithm (a nonlinear modeling algorithm).

Berlow *et al.* 2009

1) Global Structure
-S_i, S_f, C_i, C_f
-# & prop. of T, I, B, Herb, Carn, Omn
-# links TI, TB, II
-# links, L/S
-mean, max, sd of TL (resource average, shortest chain)
-clustering coefficient

2) Local Structure around R & T
-TL, #, total biomass, and mean # of consumer & resource spp. 1, 2, 3 degrees from R & T

3) R & T Attributes
-mean biomass before R removed
-mean body mass
-functional response shape
-consumer interference
-half-sat. conc. of nutrient uptake for producers

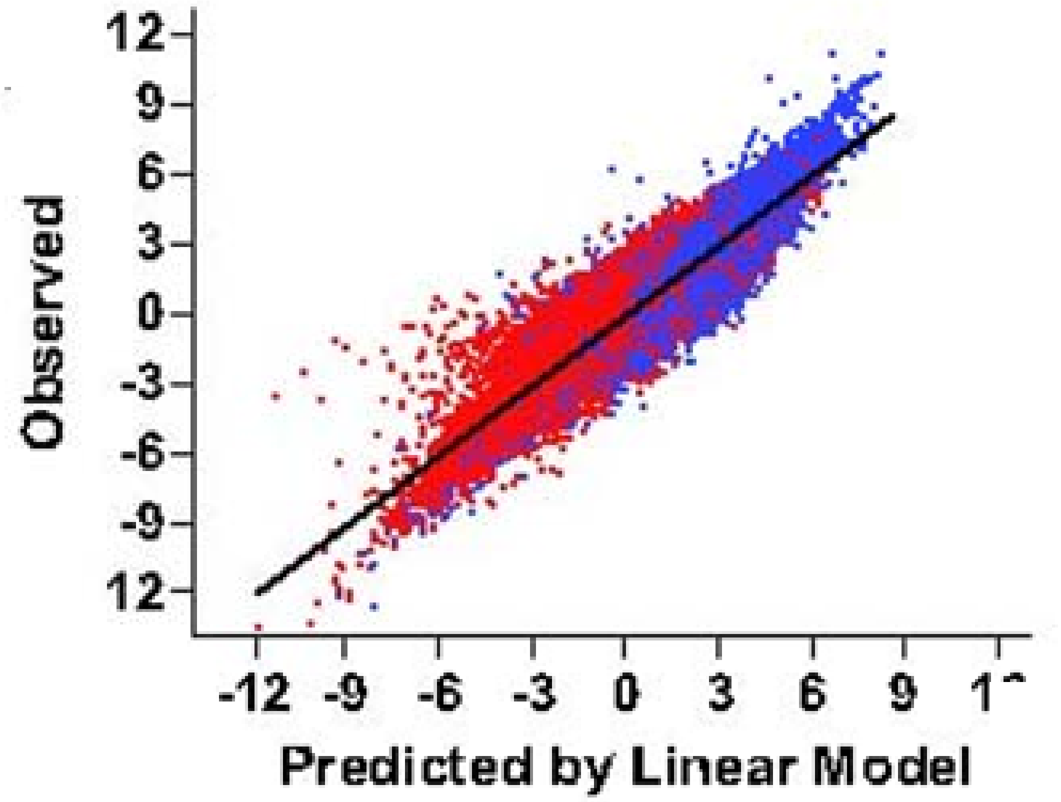
4) Attributes of R-T Pair
-degrees of separation
-single vs. multiple paths from R to T
-net sign of all shortest paths and next-shortest
-sum of those, weighted sum of those

1) 45% positive interactions, 55% negative interactions

2) Modeling $\log_{10}$ of $|I|$ and $|pcI|$ reveals a simpler pattern that describes all of the interactions (not just strong ones) with few variables

3) $\log_{10}|I|$ largely explained by B^{+}_{T} (biomass of T with R present), and B_r (biomass of R)

4) $\log_{10}|pcI|$ largely explained by M_R (body mass of R), B^{+}_{T}, & B_r



$$\log_{10}|pcI| = -1.14 + 0.88\log_{10}(M_R) + 0.71\log_{10}(B^{+}_{T}) - 0.79\log_{10}(B_r)$$

$$R^2 = 0.88$$

red: upper 50% of B_r
blue: lower 50% of B_r

More complex is more simple…

$\log_{10}$ |Interaction Strength| $\log_{10}$ |per capita *I*|

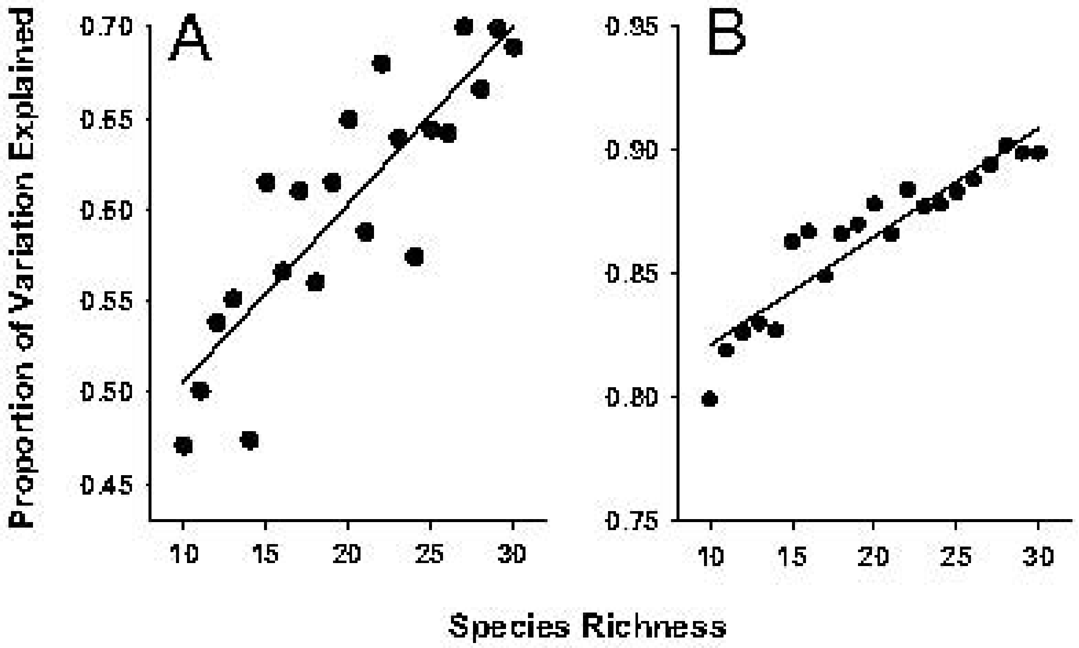


Fig. 4. More complex is more simple. The proportion of variation in (*A*) $\log_{10}|I|$ and (*B*) $\log_{10}$|per capita *I*| explained by the most parsimonious multiple linear regressions described in Figs. 1*D* and 2*C* for different levels of species richness that each included a range of connectance values. The absolute magnitude of both *I* and per capita *I* explained increases with web size (R^2 = 0.74 and 0.88 for *A* and *B*, respectively).

Simple empirical test

Hypotheses

1) Prediction of I or pcI using multiple linear regressions should work well when trophic effects dominate

2) Where non-trophic effects are important, deviation from regressions should indicate sign and magnitude of effect

System

1) Small experimental intertidal systems, $S \sim 30$

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

3) Barnacles mediate non-trophic effects of whelks on mussels: act as mussel substrate

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

Results

1) Barnacles excluded: regression explains 48% of variation in $\log_{10}|pcI|$

2) Barnacles present: under predicts pcI at low mussel biomass and over predicts at high B

3) Barnacle cover low: negative effects of whelks on mussels stronger than predicted

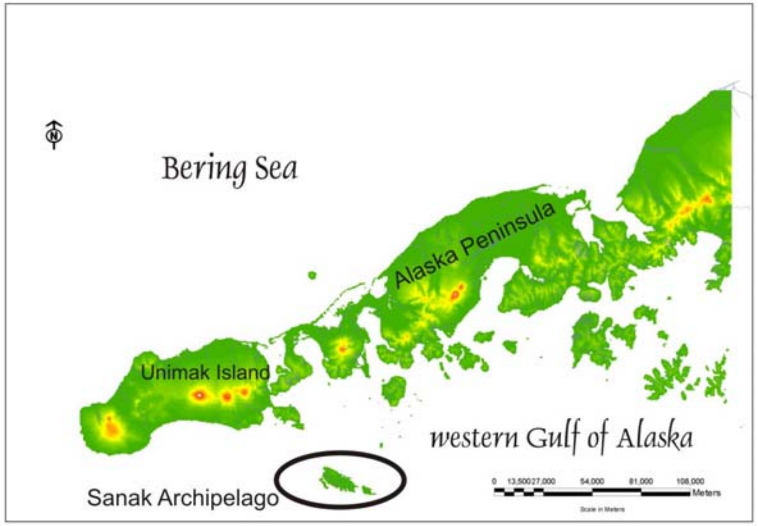
→ whelks reduce barnacle abundance, impeding mussel recruitment

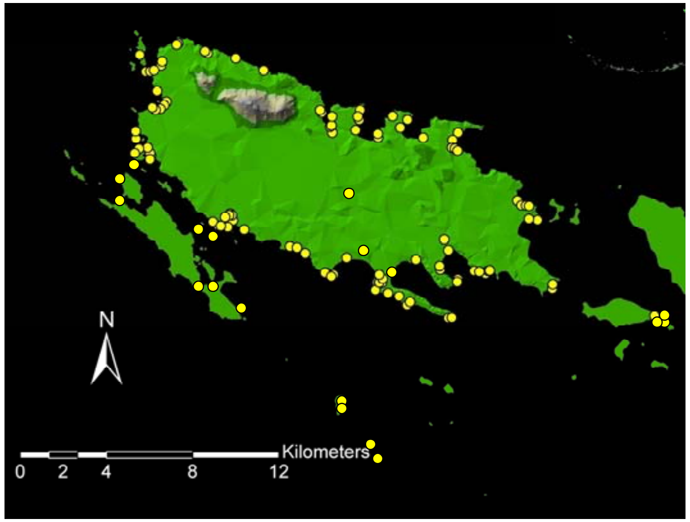
4) Barnacle cover high: negative effects of whelks on mussels weaker than predicted

→ whelks stabilize barnacle abundance, augmenting mussel recruitment

4) Humans as predators in complex food webs

Sanak Archipelago, Western Gulf of Alaska





→ Sanak Aleut: ~6000 years of sustainable culture & habitation

→ A local economy tied directly to ecosystem goods & services

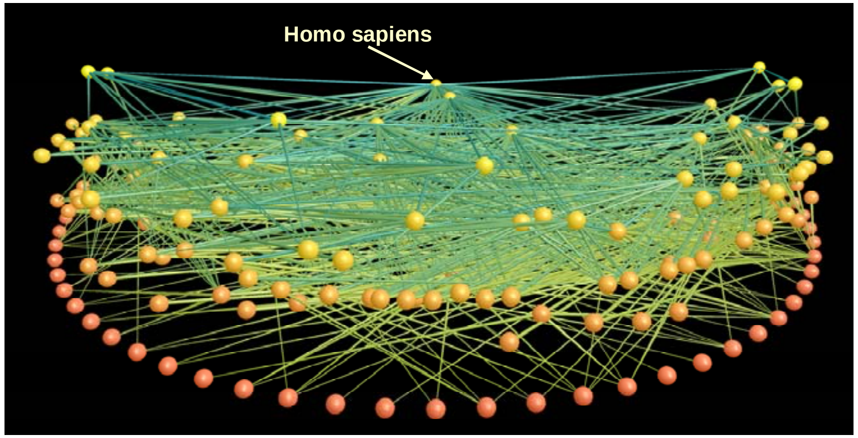
→ How did their roles as hunter-gatherers affect 'sustainability'?

Trophic roles of Aleut in local ecosystems

Data and analyses show:

- Aleut were super-generalists
- Aleut were super-omnivores
- Aleut did temporal, habitat & trophic level prey-switching
- Aleut could increase efficiency of gathering and consumption through technology and planning

Sanak Intertidal Food Web



$S = 164$, $C = 0.03$

Impact on food-web persistence and stability?

Impacts of Aleut on Sanak food webs

$$\underbrace{B_i'(t)}_{\text{Rate of change in biomass}} = \underbrace{G_i(B)}_{\text{Production rate of basal spp.}} - \underbrace{x_i B_i(t)}_{\text{Loss of biomass to metabolism}} + \sum_{j=1}^{n}\Big(\big(\underbrace{x_i\, y_{ij}\, \alpha_{ij}\, F_{ij}(B)\, B_i(t)}_{\text{Gain of biomass from resource spp.}} - \underbrace{x_j\, y_{ji}\, \alpha_{ji}\, F_{ji}(B)\, B_j(t)\big) / e_{ji}}_{\text{Loss of biomass to consumer spp.}}\Big)$$

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.)

Initial exploration of 'Aleut-type' effects:

1) Create "zoo" of model webs: Niche structure, persistent dynamics, *S* ~ 50

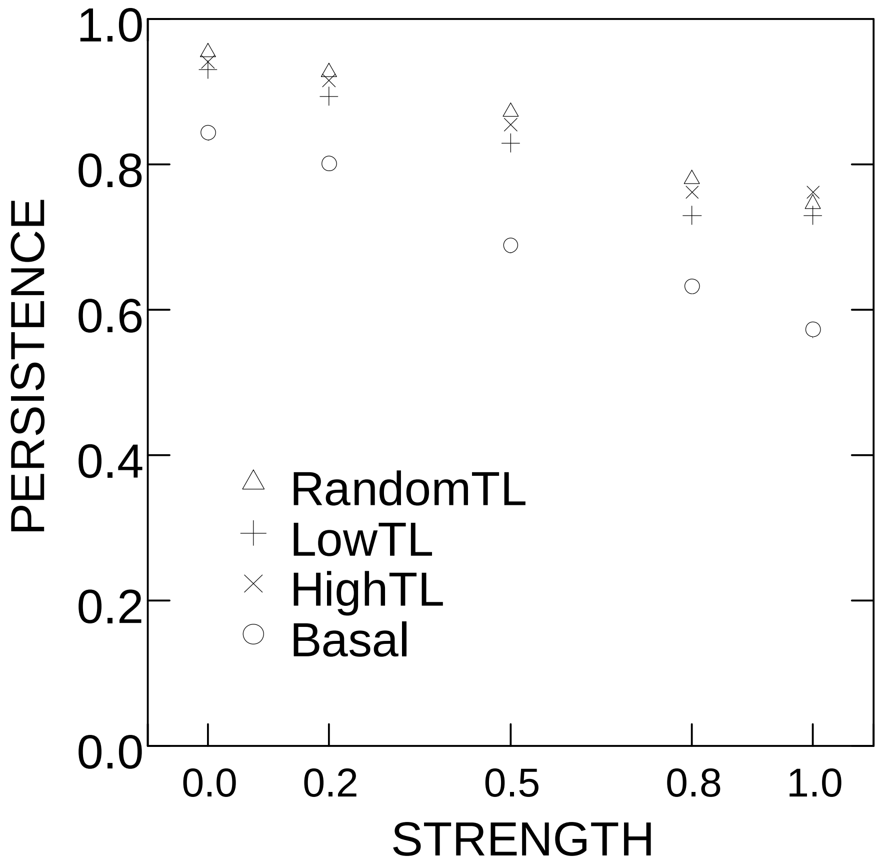
strc 2) Invade webs with a super-generalist (consumes 25-50% of taxa)

strc 3) Generalist consumes on high, low, or random trophic level taxa

dyn 4) Vary fraction of the generalist's links that are strong

5) How many species persist after "invasion" ?

Some initial results: species persistence



- → Lower fraction of strong links results in greater persistence
- → TL of prey has little effect, except…
- → Allowing predation on basal taxa decreases persistence

Dunne & Williams (in prep)

A few last comments

1) Flexible framework for exploring stability/persistence
2) High dimensionality → strategic simplifications
3) Connecting models to data: inputs & outputs
4) Pedagogy versus prediction…

Some Related PEaCE Lab publications:

Berlow, E.L., J.A. Dunne, N.D. Martinez, P.B. Stark, & U. Brose (2009) Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences USA* 106: 187-191.

Brose, U. (2008) Complex food webs prevent competitive exclusion among producer species. *Proceedings of the Royal Society B* 275: 2419-2536.

Brose, U., E.L. Berlow, & N.D. Martinez (2005) Scaling up keystone effects from simple to complex ecological networks. *Ecology Letters* 8: 1317-1325.

Brose et al. (2006a) Consumer-resource body size relationships in natural food webs. *Ecology* 87: 2411-2417.

Brose, U., R.J. Williams, & N.D. Martinez (2006b) Allometric scaling enhances stability in complex food webs. *Ecology Letters* 9: 1228-1236.

Dunne, J.A., U. Brose, R.J. Williams, & N.D. Martinez (2005) Modeling food-web dynamics: complexity-stability implications. pp.117-129 in Aquatic Food Webs: An Ecosystem Approach. A. Belgrano, U. Scharler, J.A. Dunne, and R.E. Ulanowicz, eds. Oxford University Press.

Otto, S.B., B.C. Rall, & U. Brose (2007) Allometric degree distributions facilitate food web stability. *Nature* 450: 1226-1230.

Williams, R.J. (2008) Effects of network and dynamical model structure on species persistence in large model food webs. *Theoretical Ecology* 1: 1874-1746.

Williams, R.J., U. Brose, & N.D. Martinez (2007) Homage to Yodzis and Innes 1991: Scaling up feeding-based population dynamics to complex ecological networks. Pp. 37-52 *in* From Energetics to Ecosystems: The Dynaics and Structure of Ecological Systems. N. Rooney *et al.,* eds. Springer.

Williams, R.J., & N.D. Martinez (2004) Stabilization of chaotic and non-permanent food-web dynamics. *European Physics Journal B* 38: 297-303.

www.FoodWebs.org

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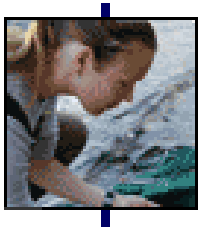

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