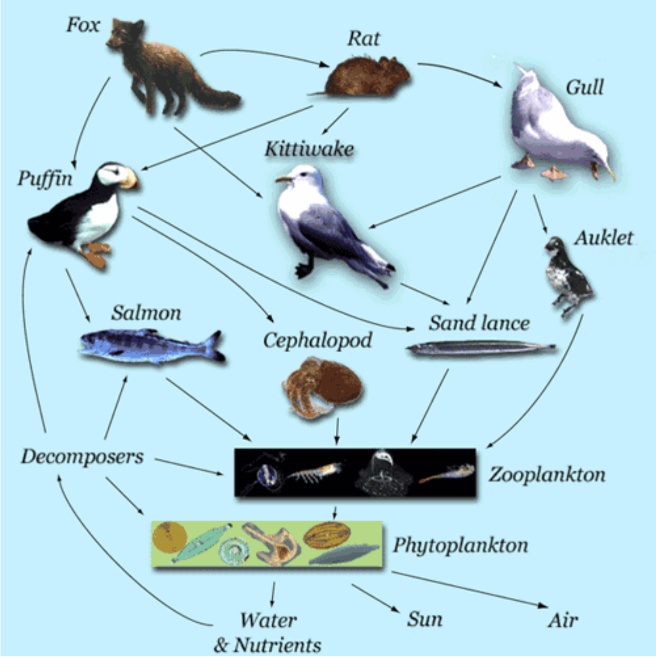
Systems Biology: A Personal View XVII. Food Webs & Stability of Ecological Networks

Sitabhra Sinha

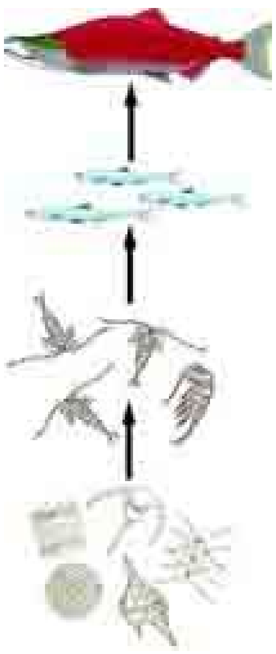
IMSc Chennai

Alaskan food web

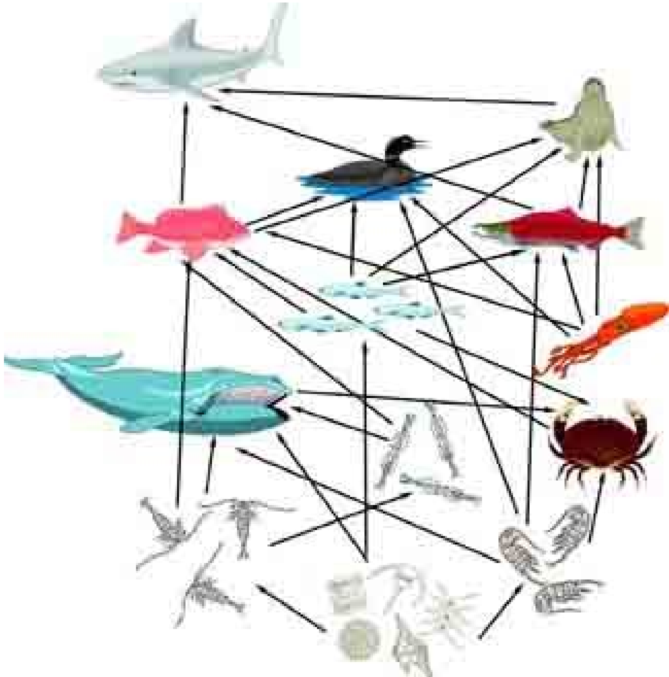


Network of Ecological Interactions

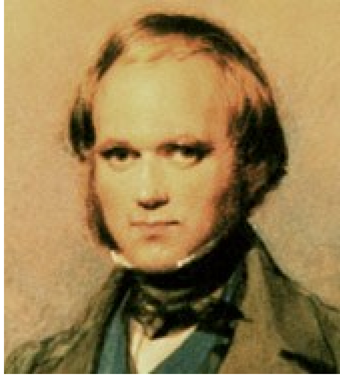
Simple food chains …are embedded in more… Complex food webs



Arrows indicate direction of energy flow



Early understanding of food webs



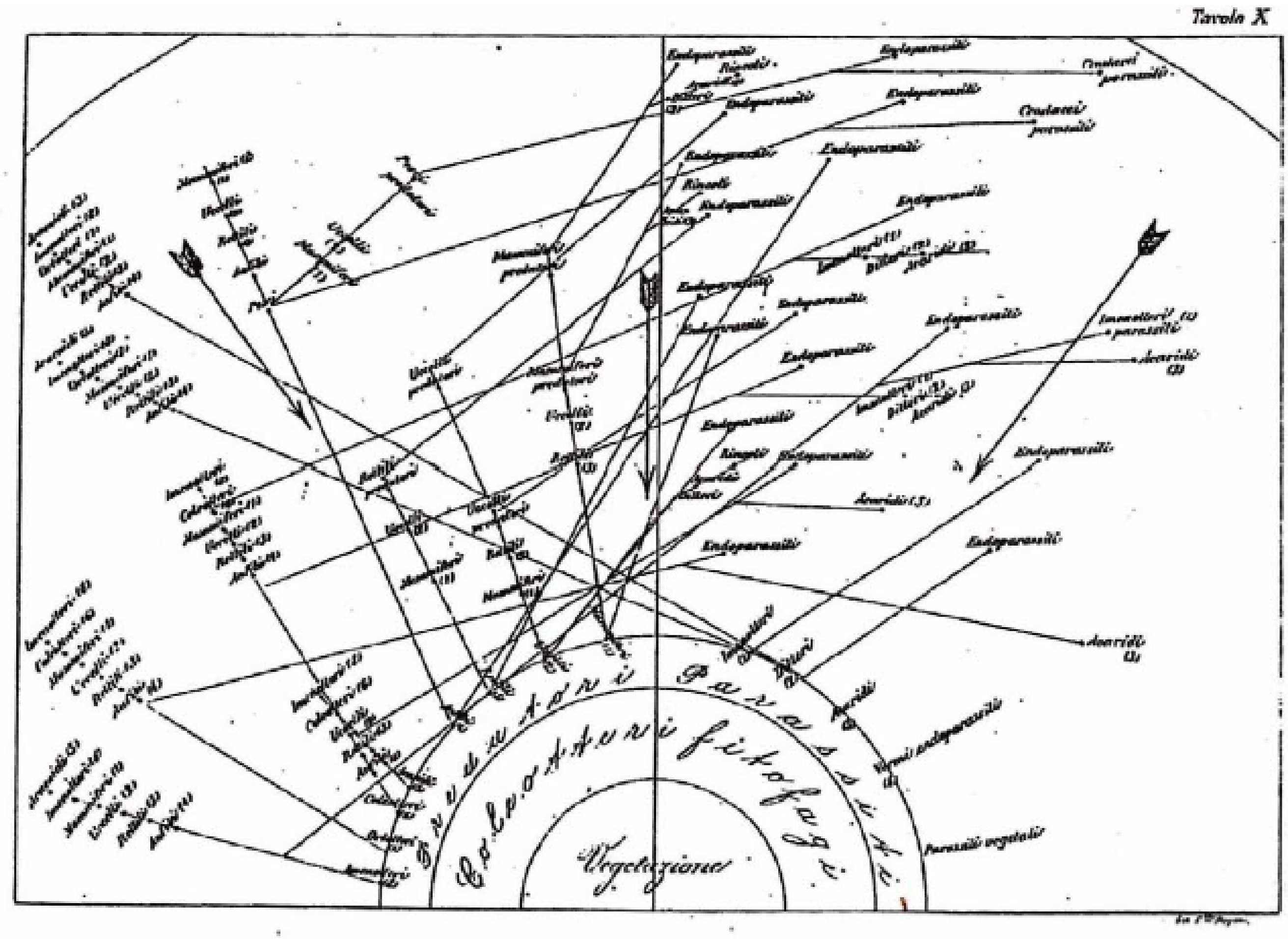
"Not a single plant, not even a lichen, grows on this island; yet it is inhabited by several insects and spiders"
Charles Darwin, 1839

"In February, 1832, Darwin described the food web of St. Paul's Rocks near the equator in the middle of the Atlantic Ocean, and remarked with surprise on the apparent absence of plants."
J E Cohen (1994) in Frontiers of Mathematical Biology (ed S A Levin)

Abundance of each species maintained at a natural equilibrium:
"Moebius in1877... recognized the importance of interspecific nutritive relationships while he was studying the organisms living on the oyster-beds of Schleswig-Holstein. To Moebius is due also the credit for noting that the effect of these interspecific relationships is to establish a state of equilibrium."
U d' Ancona (1954) *The Struggle for Existence*

First known network of trophic relations

Lorenzo Camerano (1880)

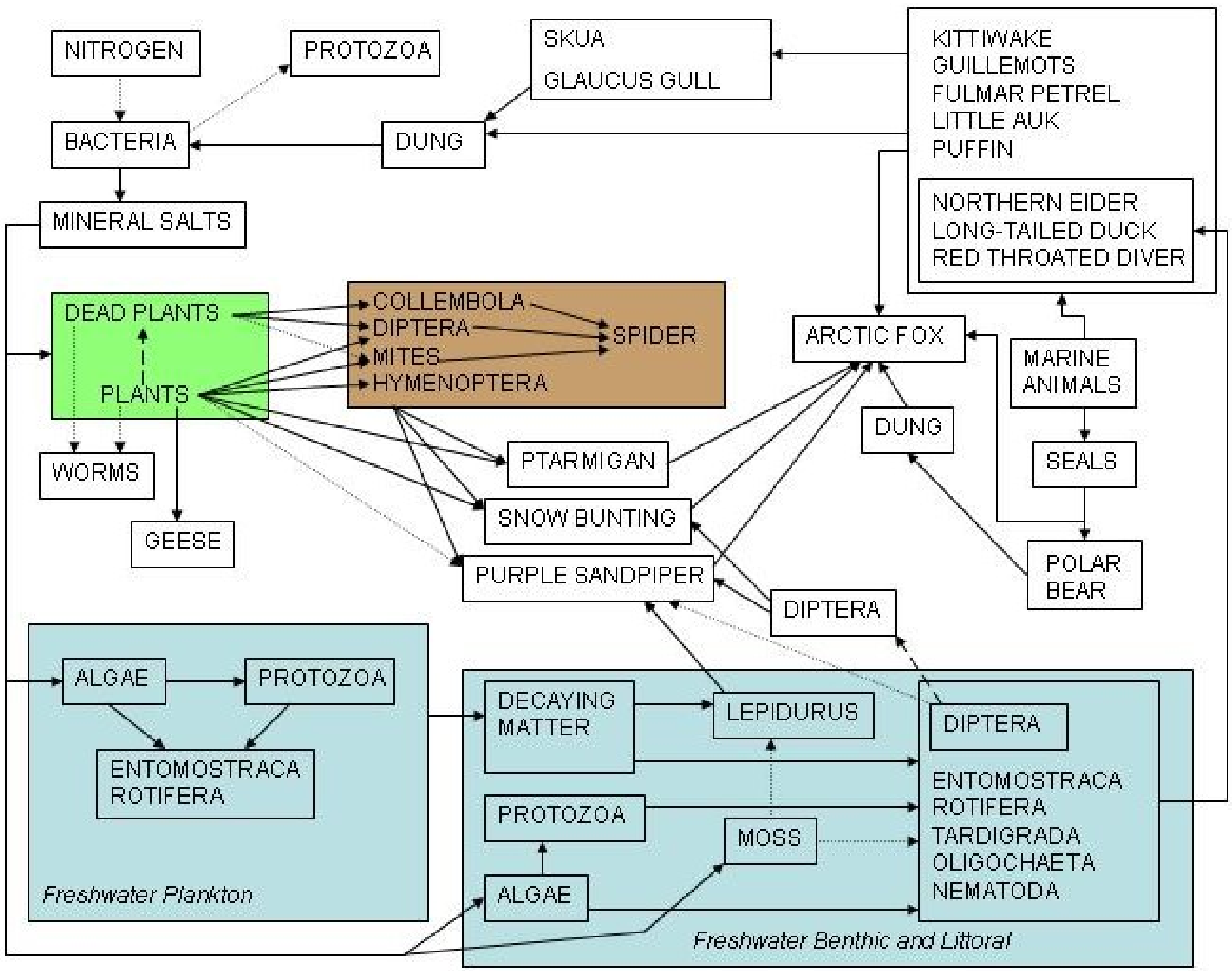


Network nodes classified into several taxa

- Plants
- Parasitic plants
- Insects
- Worms
- Spiders
- Crustaceans
- Fish
- Amphibians
- Reptiles
- Birds
- Mammals

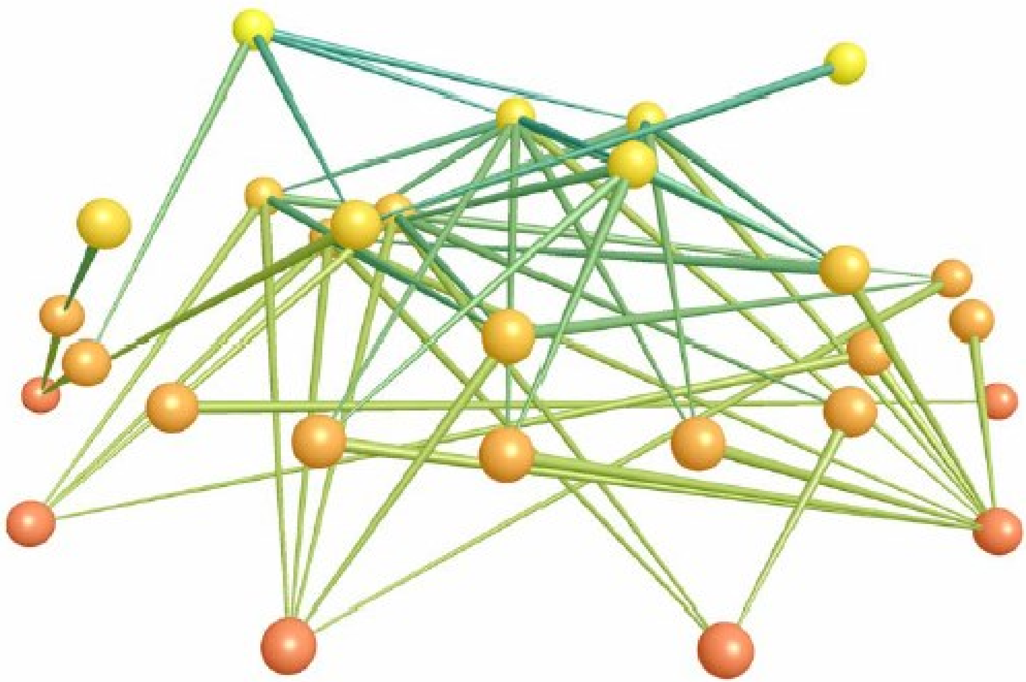
First graphical representation of a food web as a network of groups of species linked by feeding relations

Summerhayes and Elton (1923)
Food web of Bear Island

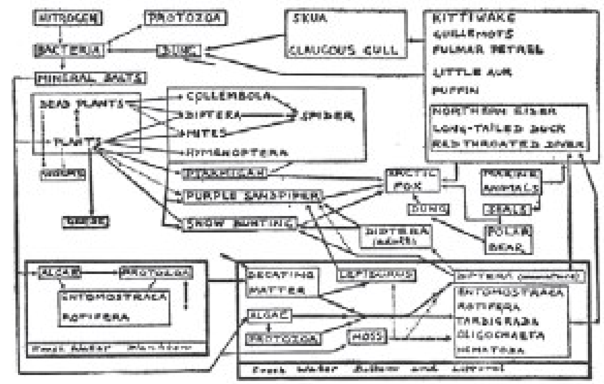


Wikipedia

Bear Island



1 bacteria, 4 autotrophs, 13 invertebrates, 6 birds, 4 mammals

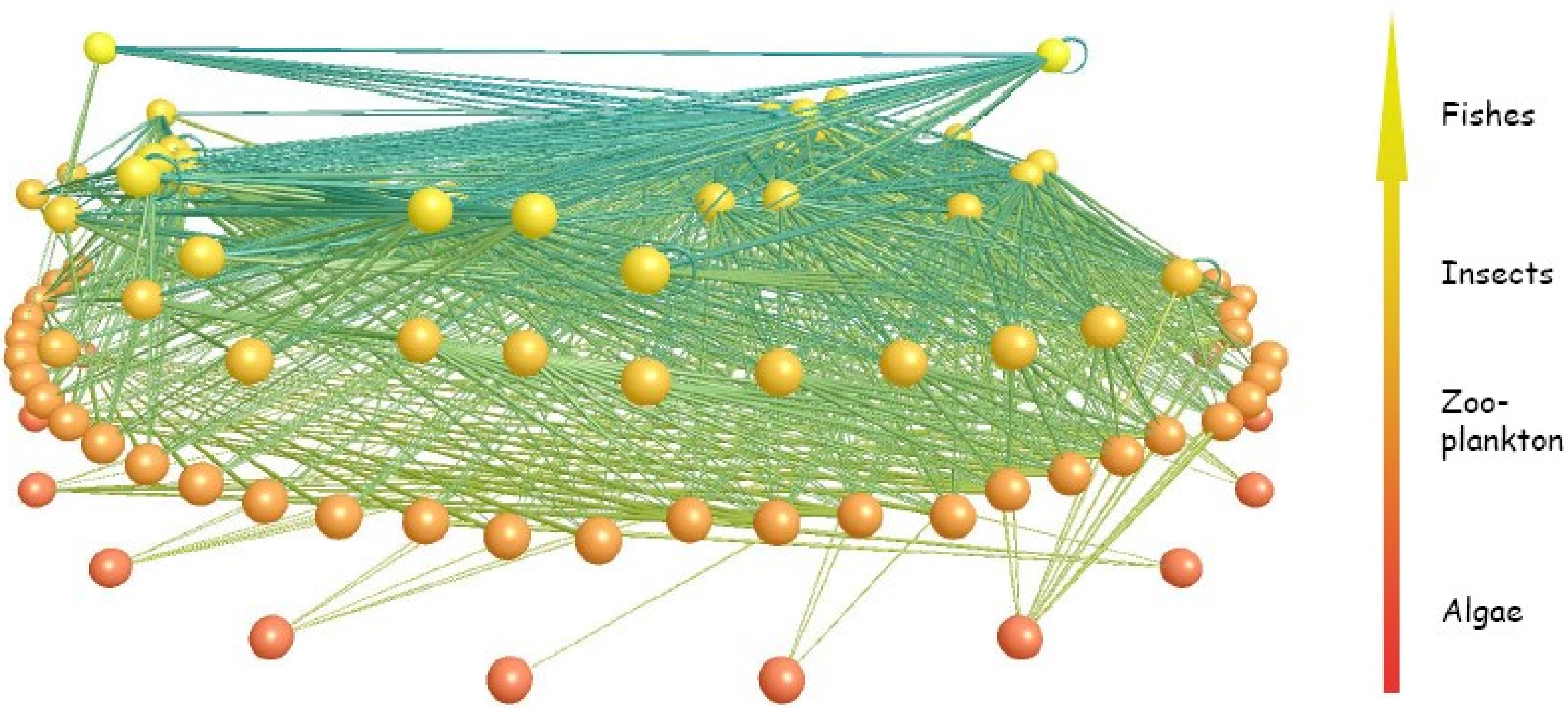


S (# taxa) = 28
L (# links) = 59
L/S (links/species) = 2.1
C (connectance; L/S^2) = 0.075
TL (mean trophic level) = 2.07

Directed Connectance (C): Proportion of possible links (S^2) that are realized (L)

Source: Neo Martinez

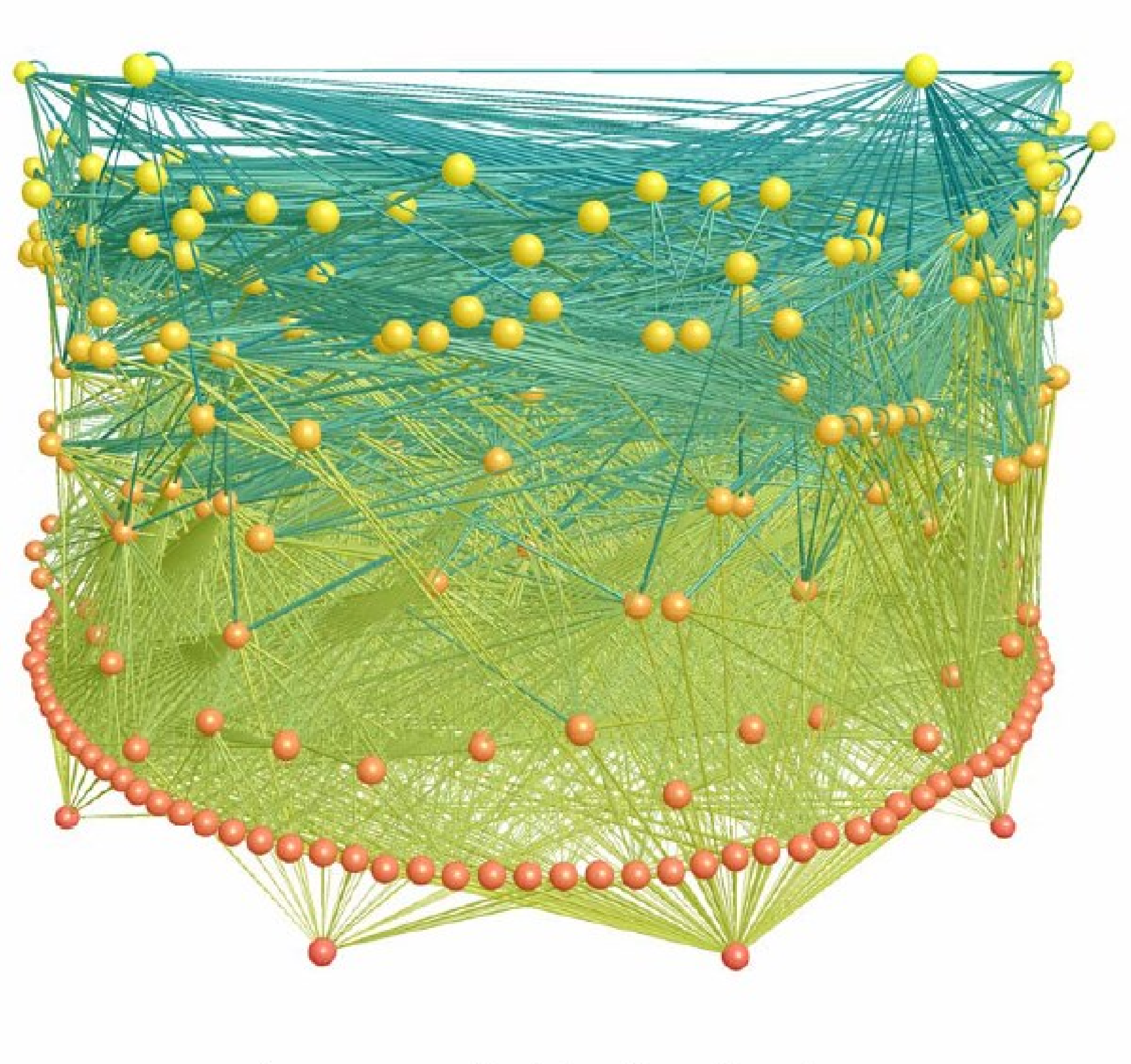
Food web of Little Rock Lake, Wisconsin



S = 92, L = 997, L/S = 11, C = 0.12, TL = 2.40

Martinez 1991

Antarctic Weddell Sea Food Web



Data compiled by Ute Jacob

Highly & Evenly Resolved

Original species = 492

62 autotrophs
4 mixotrophs
345 invertebrates
48 ectotherm vertebrates
29 endotherm vertebrates
3 detritus
1 bacteria

S = 290
L = 7200
L/S = 24.8
C = 0.086
Mean TL = 3.79

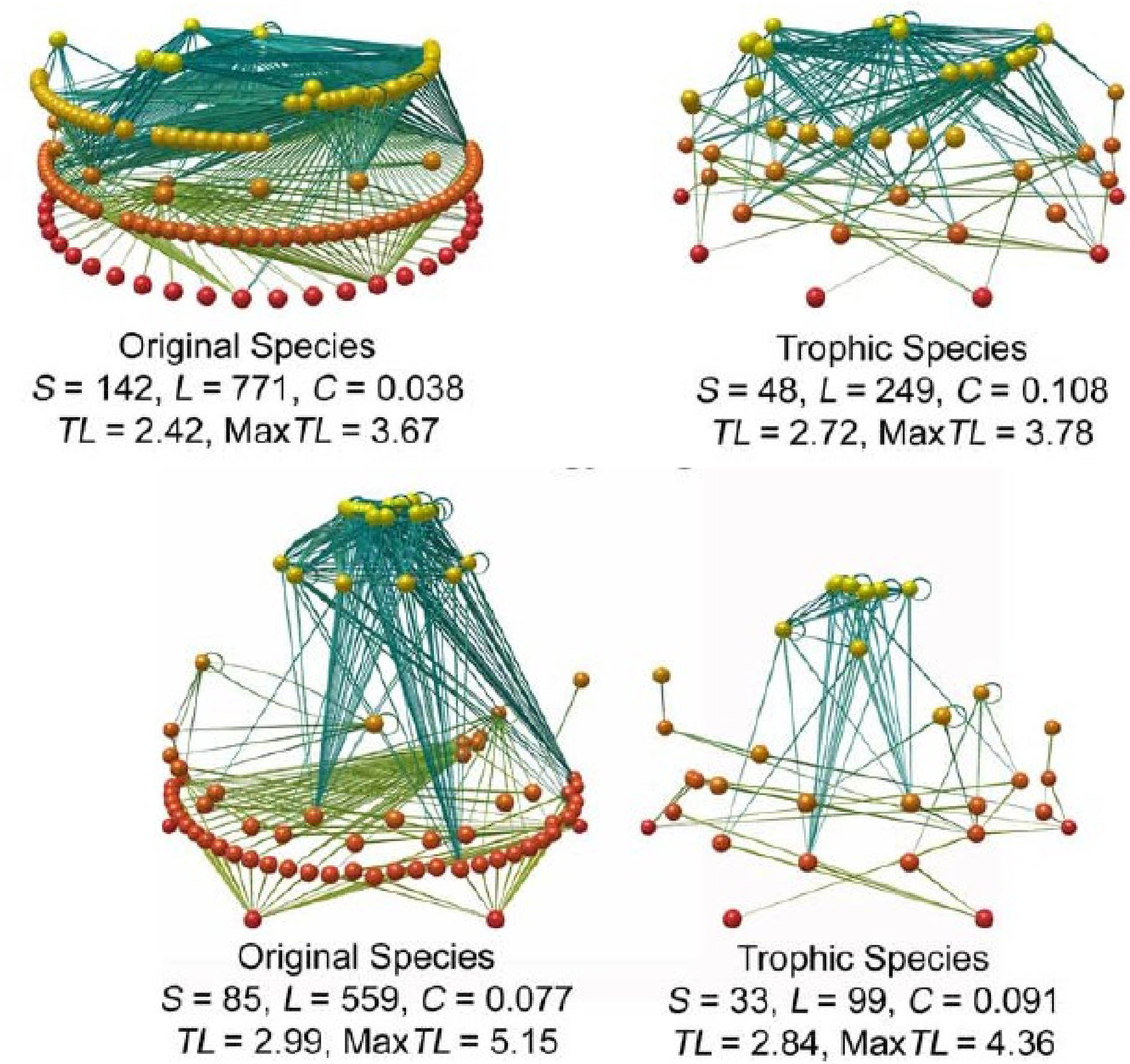
Source: Neo Martinez

Reconstructing Food Webs from the Cambrian Period

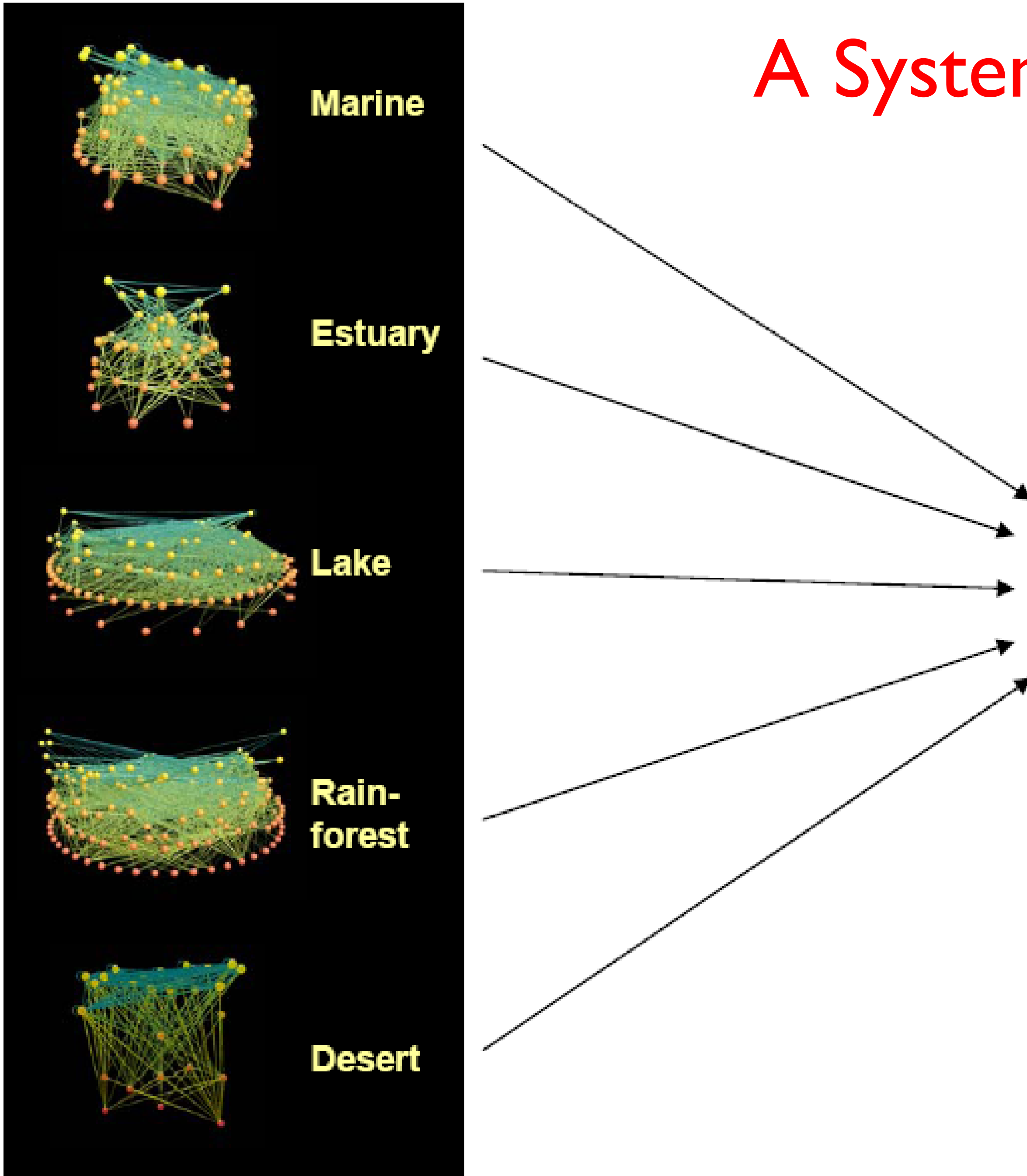
Dunne et al, PLoS Biology (2008)

Burgess Shale

Chengjiang Shale



A Systems-level Question

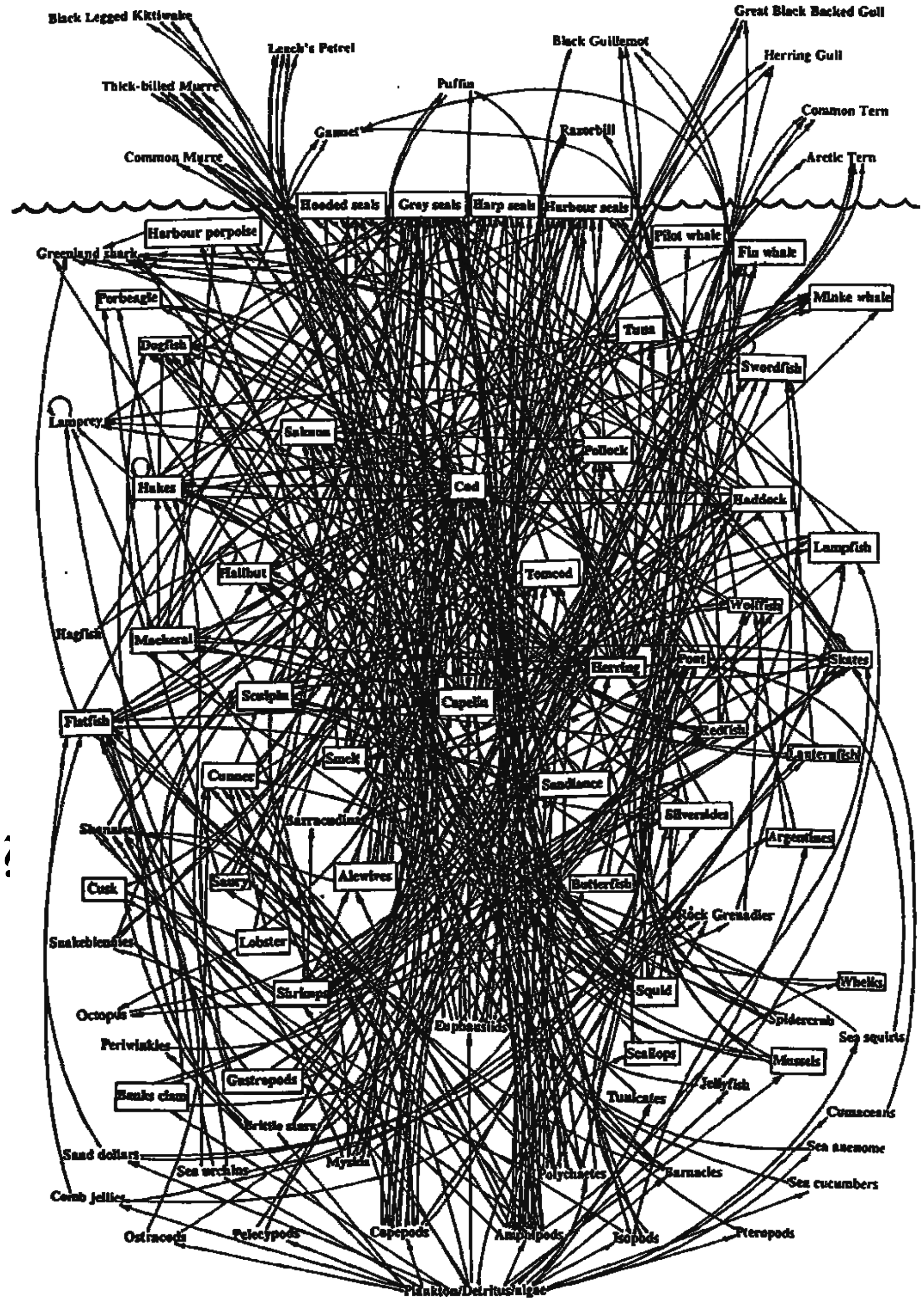


Source: Neo Martinez

Instead of considering each food web in isolation as an unique case, is it possible to understand the general features of such networks ?
To understand why and how such networks occur ?

Robustness of Ecological Networks

- How do ecosystems collapse ?
  Cascades of extinction events triggered by small fluctuations
- Ecosystem management:
  Effect of human intervention ?
- Is higher diversity good or bad for the stability of the network ?
- How do robust networks emerge ?



The Scotian Shelf food web

Are Complex Networks Unstable ?

Do complex networks become more susceptible to perturbations as:

- the number of nodes,
- the density of connections, and,
- the strength of interaction between the nodes,

is increased ?

Puzzle:

Theoretical results imply that complexity <u>decreases</u> stability, while observations (e.g., in ecology) sometimes show the <u>opposite</u>.

But…

Most results were obtained assuming networks are random and at equilibrium (both at level of nodes as well as the network) !


Charles Elton (1900-1991)

The Empiricists' View

Diversity is essential for maintaining network stability

Charles Elton (1958)

Simple ecosystems less stable than complex ones

Field observations:

- ❑ Violent fluctuations in population density more common in simpler communities.
- ❑ Simple communities more likely to experience species extinctions.
- ❑ Invasions more frequent in cultivated land.
- ❑ Insect outbreaks rare in diverse tropical forests – common in less diverse sub-tropical forests.

Robert MacArthur: theoretical attempt at justification

Multiple links ≡ Insurance !

But …

This view was challenged by:

• Numerical experiments on the stability of random networks by Gardner & Ashby (1970).
• Theoretical analysis of randomly constructed ecological networks by May (1972).

Observation: Stability decreases as network size, connectivity and interaction strength increases.

The Theorist's View

Increasing diversity leads to network instability

www.topbritishinnovations.org

Robert M May (1936-)

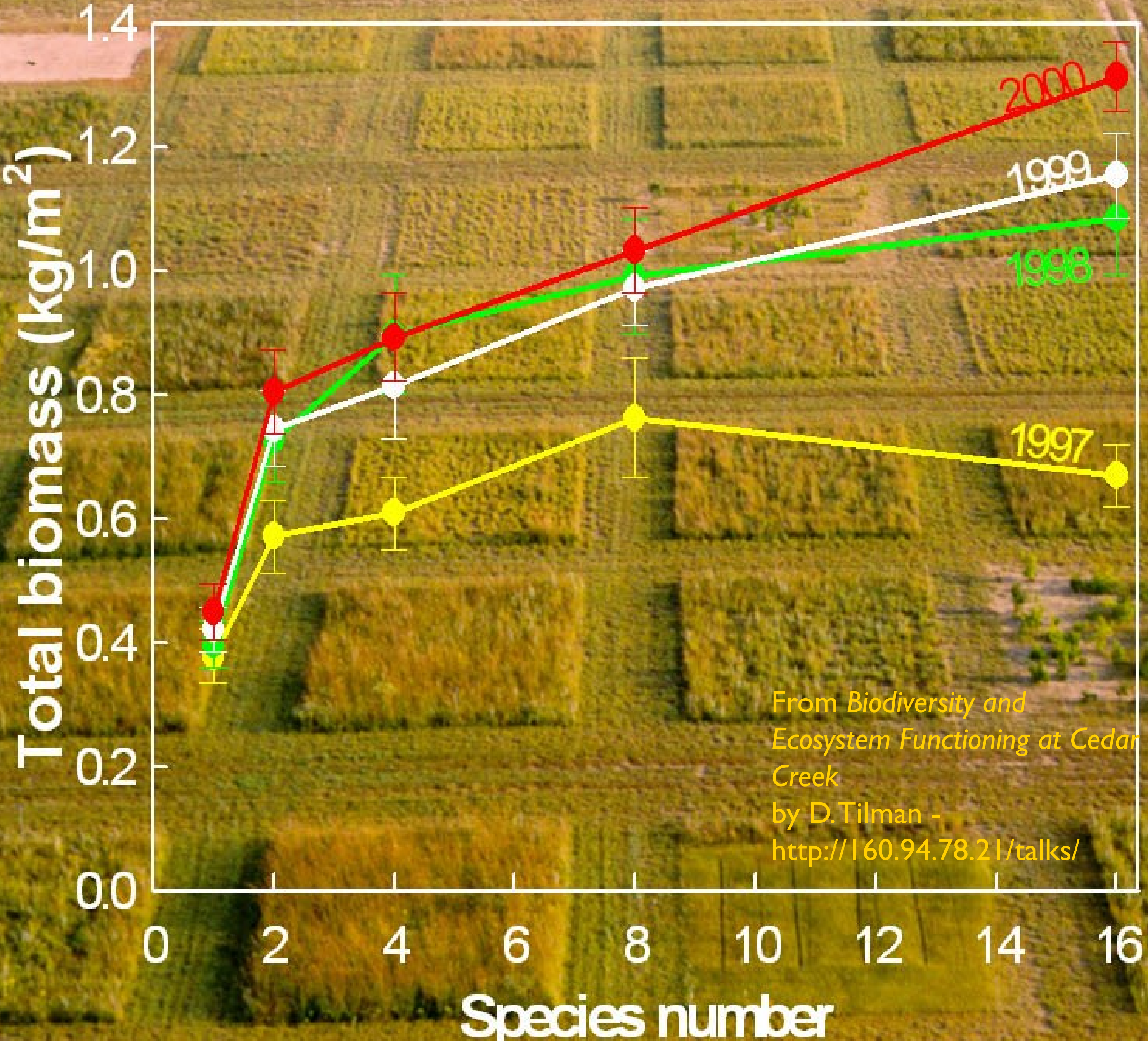
Basis for the Stability vs. Diversity debate in ecology.

Experimental evidence:
Common garden experiments (e.g. Cedar Creek)

- diversity treatments divided over hundreds of experimental plots.
- examine response of population and community level biomass to environmental perturbation.

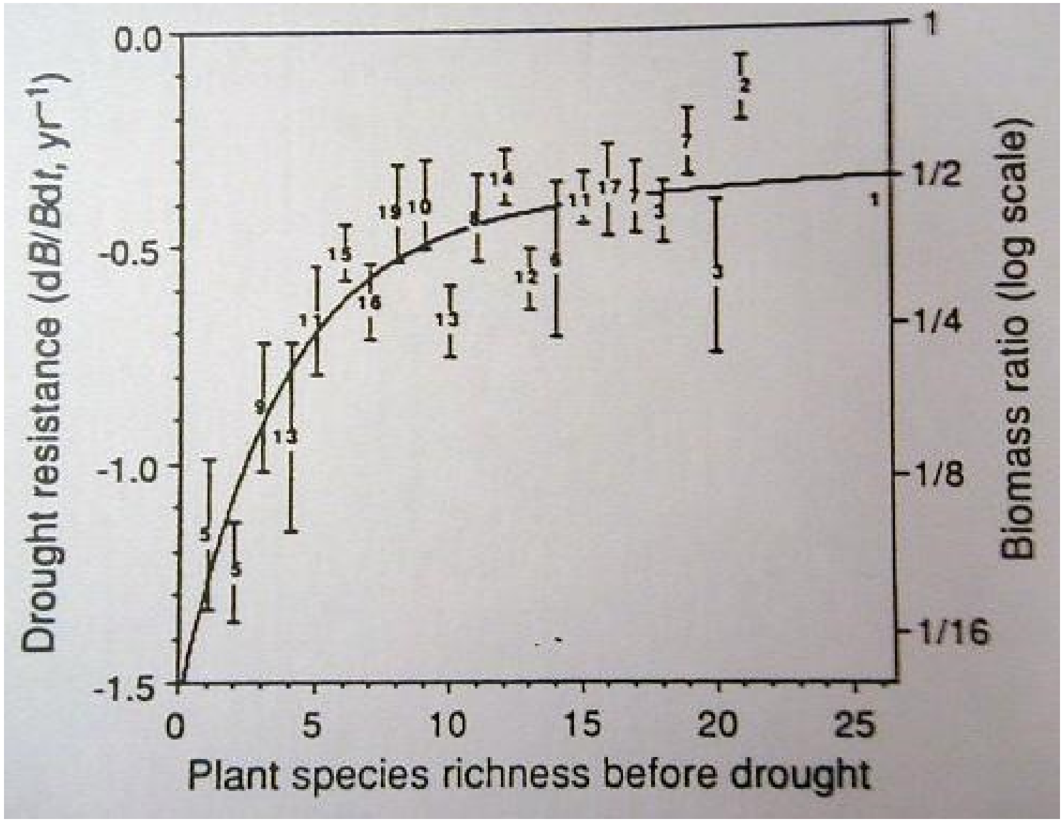
D.

Diverse Systems Are More Productive



D.Tilman

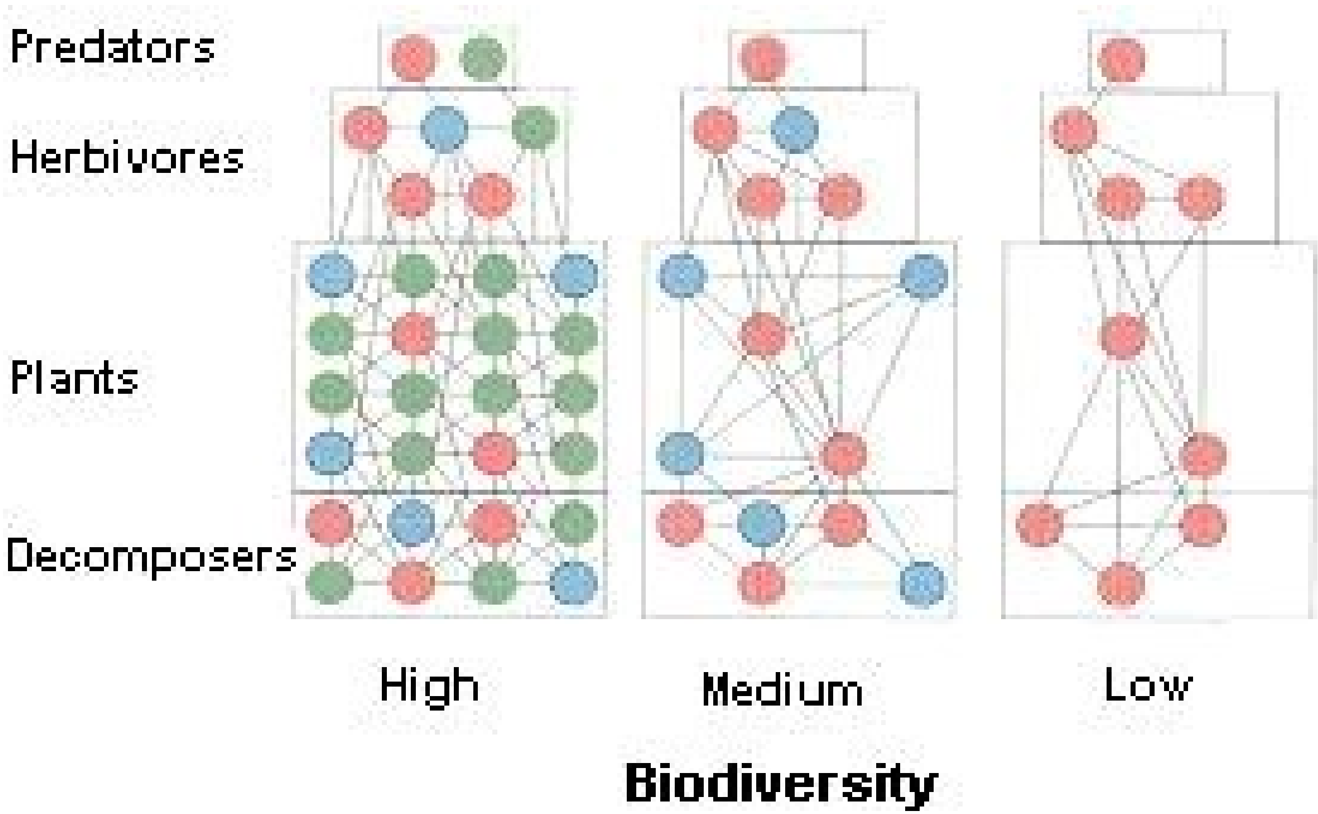
…and more resistant



Tilman et al. (1996)

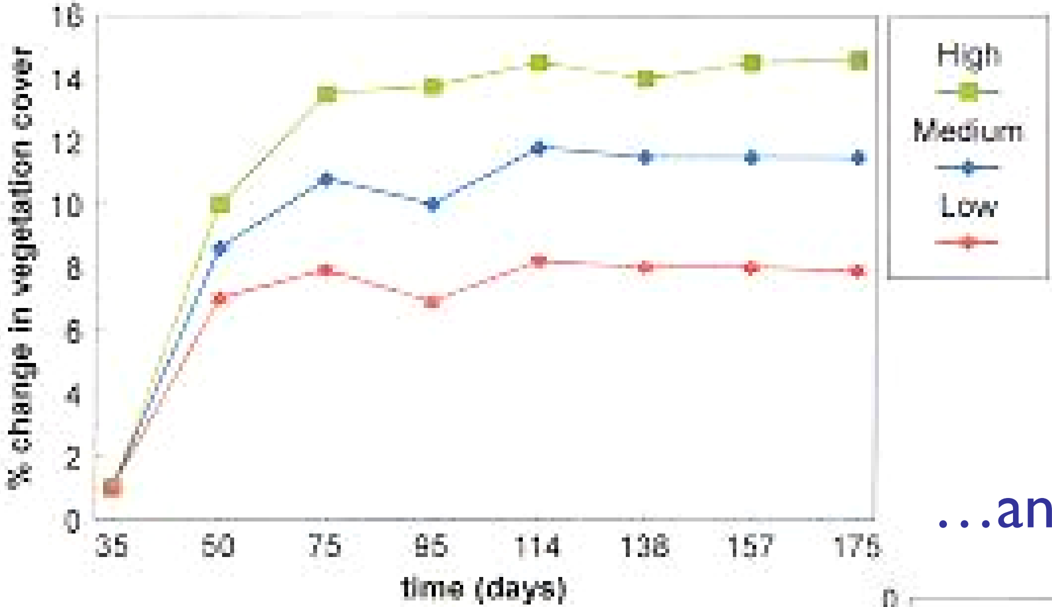
- ❑but no effect on population variability.
- ❑indicates averaging effect.

Experimental evidence:
Bottle Experiments (e.g. Ecotron)

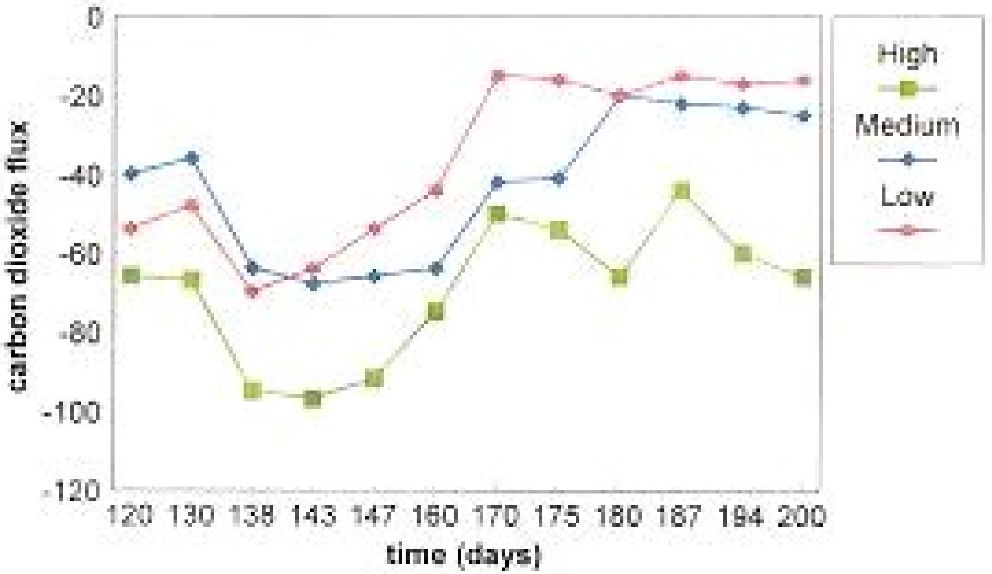


Setup allows manipulating diversity while maintaining food web structure.

High diversity communities are more productive than low diversity ones.



…and consume more CO_2…



…but its unclear how these results scale to real communities.

The Theorist's View

Increasing diversity leads to network instability

Consider a simple community of one predator and one prey

$$f_1 = \frac{dX}{dt} = X(a - bY)$$

$$f_2 = \frac{dY}{dt} = Y(-d + cX)$$

Taylor expansion around the equilibrium yields the Jacobian or "community matrix"

$$J = \begin{pmatrix} a & -bd/c \\ ac/b & -d \end{pmatrix}$$

The system is stable if the largest real component of the eigenvalues $Re(\lambda_{max}) < 0$.

The Theorist's View

Increasing diversity leads to network instability

NATURE VOL. 238 AUGUST 18 1972

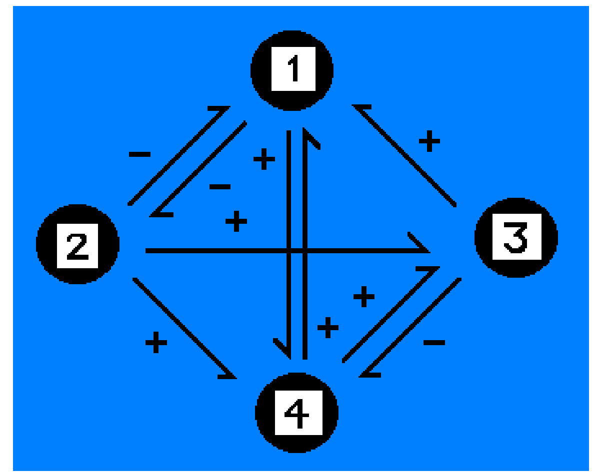
Will a Large Complex System be Stable?

ROBERT M. MAY

Robert May (1972) constructed *randomly* generated matrices representing interaction strengths in a network of N nodes whose isolated nodes are stable (J_{ii} = -1)

J =

	-1.15	0	0.33
-1.66		0.17	2.18
0.12	0		-0.14
0.29	0	0.73	



obtained its eigenvalues λ…

…used the criterion that if $\lambda_{max} > 0$, the system is unstable.

Observation: Stability decreases as network size, connectivity and interaction strength increases.

Stability of large networks:

State of the network of N nodes: N-d vector $x = (x_1, x_2, \ldots, x_N)$, x_i : state of the i^{th} node.

Time evolution of x is given by a set of equations (e.g., Volterra-Lotka)

$d x_i / d t = f_i(x)$ (i = 1, 2, …, N)

Fixed point equilibrium of the dynamics : $x^0 = (x^0_1, x^0_2, \ldots, x^0_N)$ such that $f(x^0) = 0$

Local stability of x^0 : Linearizing about the eqlbm: $\delta x = x - x^0$

$d\, \delta x / d t = A\, \delta x$ where Jacobian A: $A_{ij} = \partial f_i / \partial x_j |_{x = x0}$

Long time behavior of δx dominated by λ_{max} (the largest real part of the eigenvalues of A)
$| \delta x | \sim \exp(\lambda_{max} t)$

The equilibrium $x = x^0$ is stable if $\lambda_{max} < 0$.

What is the probability that for a network, $\lambda_{max} < 0$?

Each node is independently stable $\Rightarrow$ diagonal elements of A < 0 (choose $A_{ii} = -1$).

Let A = B - I where B is a matrix with diagonal elements 0 and I is $N \times N$ identity matrix.

For matrix B, the question: What is the probability that $\lambda'_{max} < 1$?

Applying Random Matrix Theory:

Simplest approximation: no particular structure in the matrix B, i.e., B is a random matrix.

B has connectance C, i.e., $B_{ij} = 0$ with probability 1 - C .

The non-zero elements are independent random variables from $(0, \sigma^2)$ Normal distribution.

For large N, Wigner's theorem for random matrices apply.

Largest real part of the eigenvalues of B is $\lambda'_{max} = \sqrt{(N C \sigma^2)}$.

For eigenvalues of A: $\lambda_{max} = \lambda'_{max} - 1$

For large N, probability of stability $\rightarrow 0$ if $\sqrt{(N C \sigma^2)} > 1$,
while, the system is almost surely stable if $\sqrt{(N C \sigma^2)} < 1$.

Large systems exhibit sharp transition from stable to unstable behavior when N or C or σ^2 exceeds a critical value.

Numerical computations in good agreement with theory (Gardner & Ashby, 1970; May, 1973).

Early empirical data supporting May (McNaughton, 1978)

Gardner and Ashby

NATURE VOL. 228 NOVEMBER 21 1970

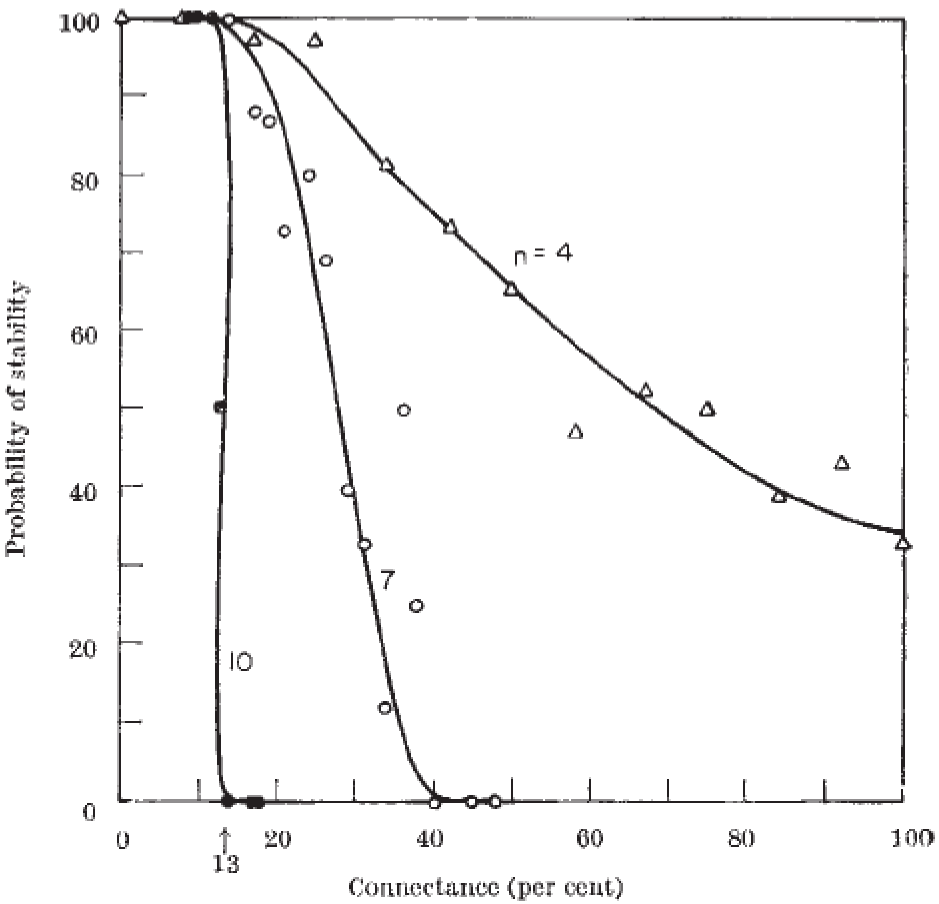
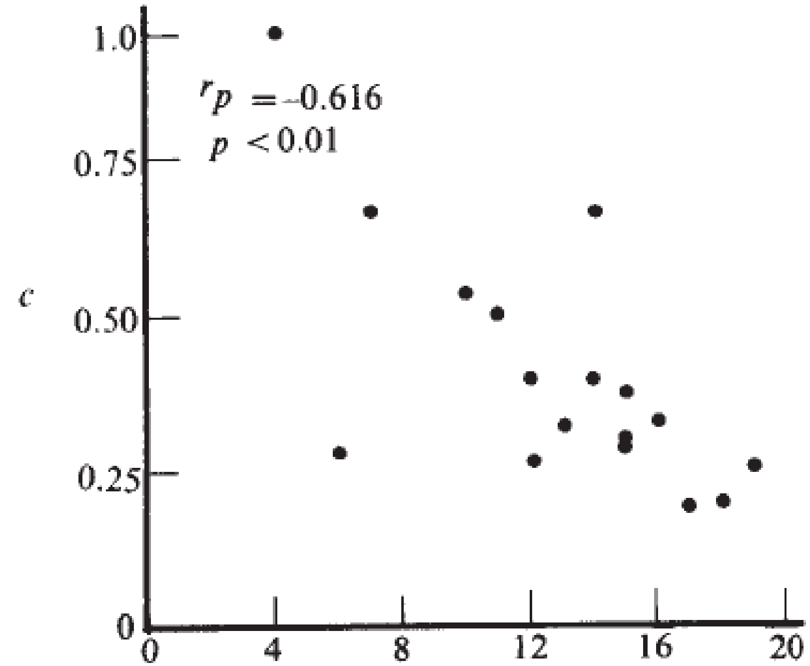


Fig. 1. Variation of stability with connectance.



Inverse relation between connectance and number of species in grassland samples from Serengeti (Tanzania) May-June 1977

NATURE VOL. 307 26 JANUARY 1984 REVIEW ARTICLE 321

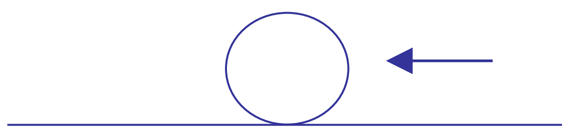
Other "stabilities"

The complexity and stability of ecosystems

Stuart L. Pimm

Global stability : system is stable if it returns to equilibrium after any perturbation (large or small) – size of basin of attraction

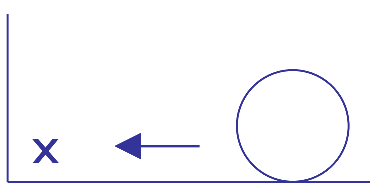
Resistance : the ability of a community to resist change in the face of a potentially perturbing force.



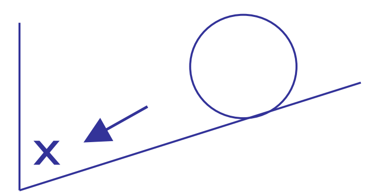
low resistance

high resistance

Resilience : the ability of a community to recover to normal levels of function after disturbance.



low resilience



high resilience

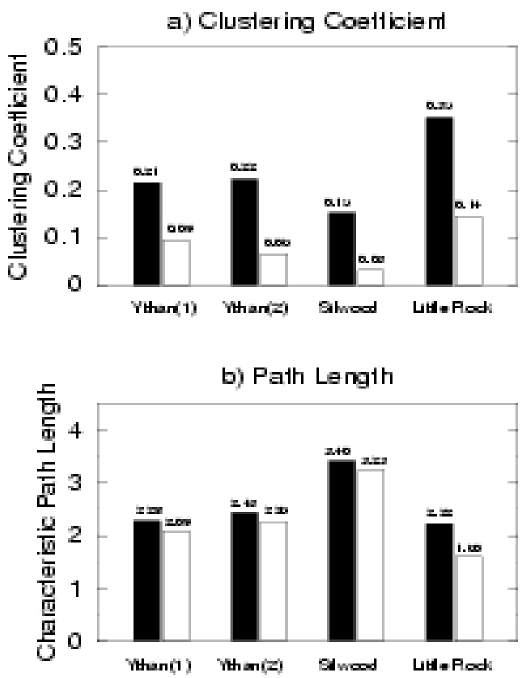
Variability : the variation in population or community densities over time. Usually measured as the coefficient of variation (CV = mean / variance)

In nature, networks are not random – many have certain structural patterns

So…
How does network topological structure affect dynamical stability ?

Small World Structure in Ecological Networks ?

Montoya and Sole (2001)



Network analysis of some food webs:

- Ythan estuary : freshwater-marine interface
- Silwood Park: field site
- Little Rock Lake: freshwater habitat

High clustering → small-world !

Challenged by Dunne et al (2002): Analysis of 16 food webs

"Most food webs do not display typical small-world topology"

Does small-world topology affect the stability of a network ?

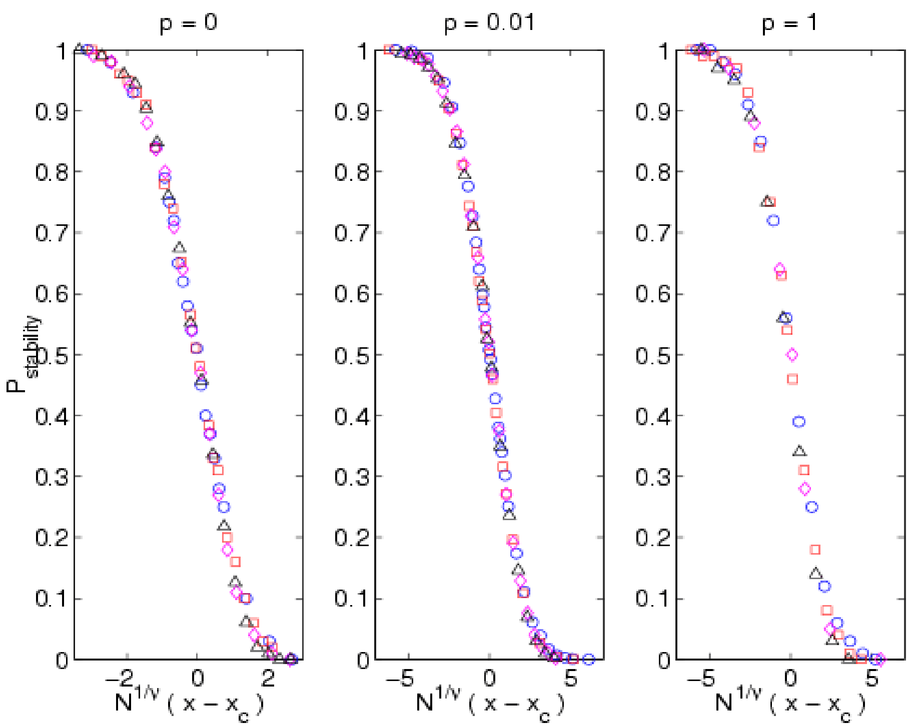
Question:

Does small-world topology affect the stability of a network ?

Answer: NO! (Sinha, 2005)

Probability of stability in a network
Finite size scaling: N = 200, 400, 800 and 1000.

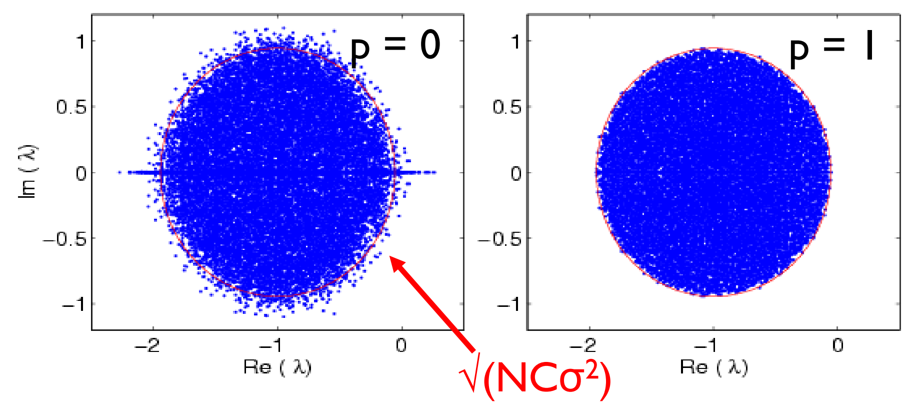
$\nu \approx 2.0$ $\nu \approx 1.72$ $\nu \approx 1.5$



Regular vs Random Networks

The stability-instability transition occurs at the <u>same</u> critical value as random network ….
but transition gets sharper with randomness

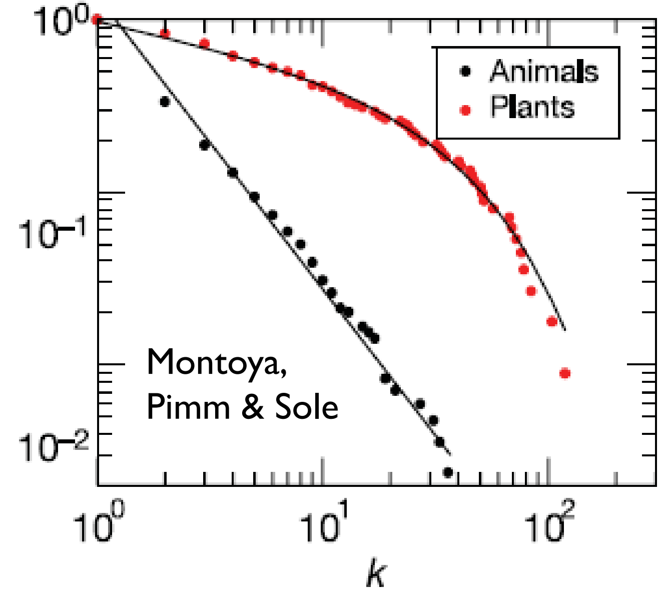
The eigenvalue plain

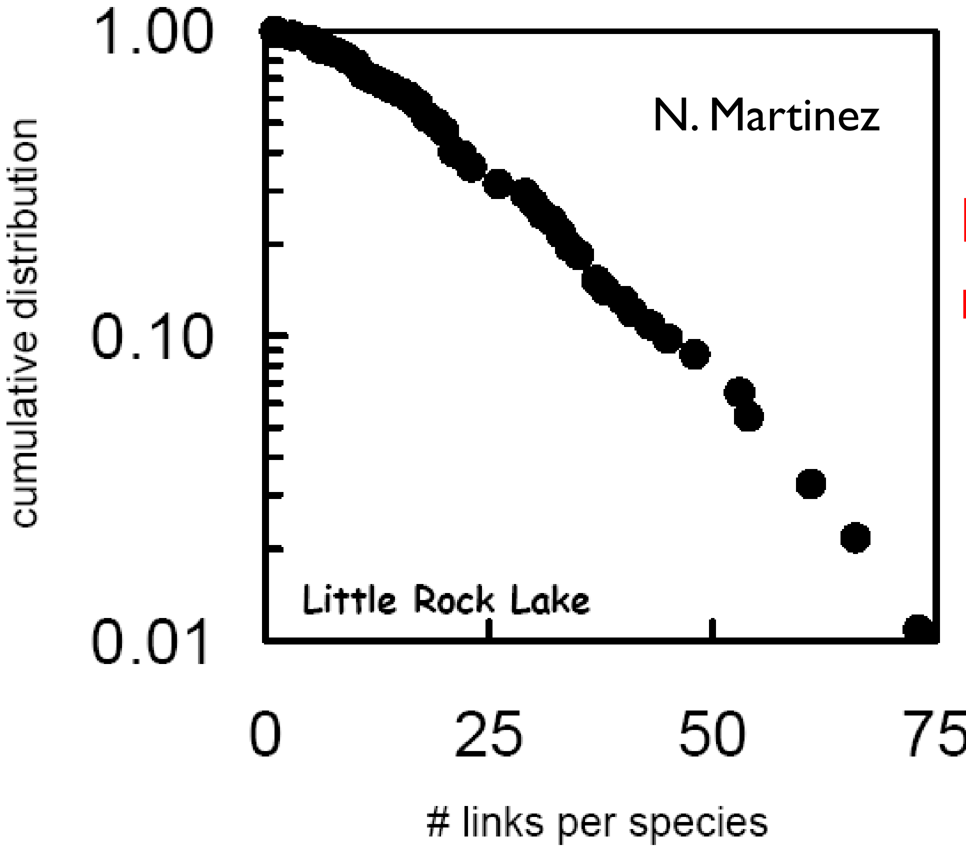


N = 1000, C = 0.021, σ = 0.206

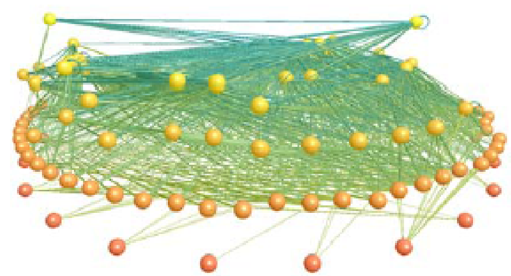
Scale-Free Degree Distribution in Ecological Networks ?

Montoya and Sole (2006): power-law distribution ! [Kyoto plant-pollinator web]
Challenged by Martinez et al





Exponential distribution, not power law



N Martinez

So how can complex networks be robust at all ?

We have not yet considered the dynamics *of* networks!

Possible solution: Network Evolution

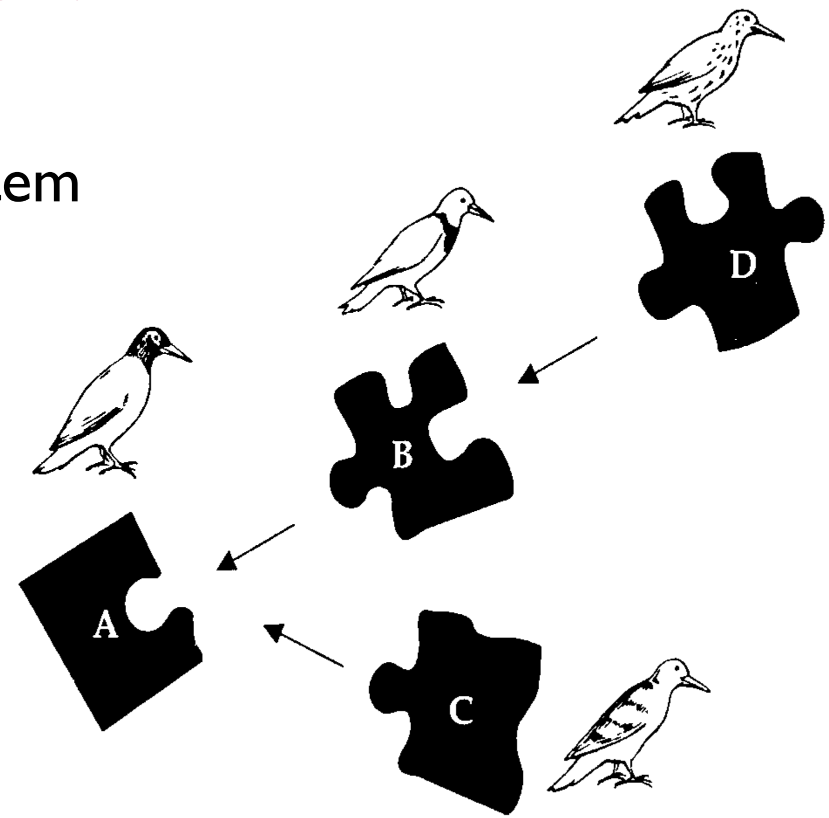
Predator Adaptation or Prey Switching at short time scales
The trophic links between species may change depending on their relative densities

Community Assembly at long time scales
Networks do not occur fully formed but gradually evolve over time

Example:
Assembling ecological communities

How are ecological networks gradually organized over time by species introduction and/or extinction ?

Community Assembly Rules decide
- ❑ which species can coexist in a system
- ❑ the sequence in which species are able to colonize a habitat



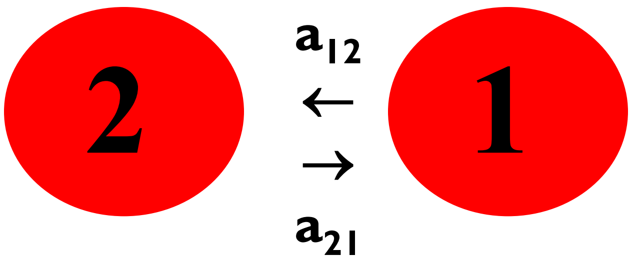
E. O. Wilson

Network Evolution

WSB Network Assembly Model

(Wilmers, Sinha & Brede, 2002)

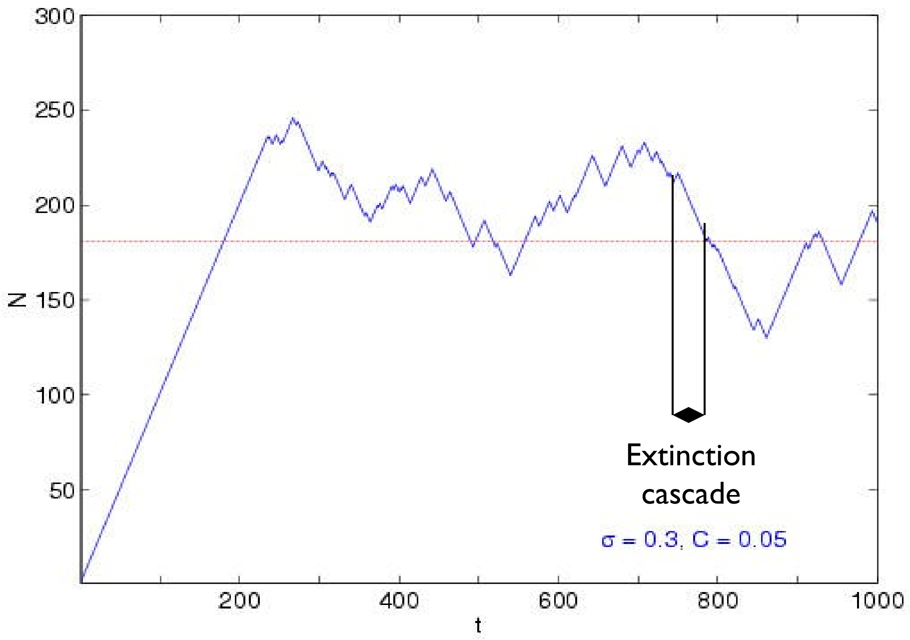
- Start with one node.

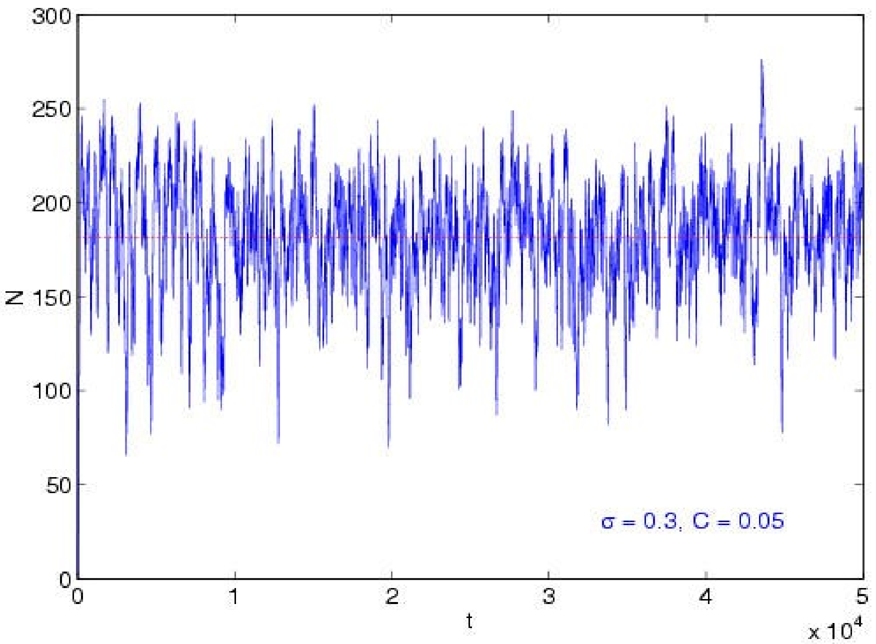


- Add another node with random number of links, and randomly chosen interaction strengths a_{ij} .

- Check stability of the resultant network :
  - If unstable, remove a node at random and analyze the stability again.
  - If stable, add another node.

Network initially grows in size monotonically …

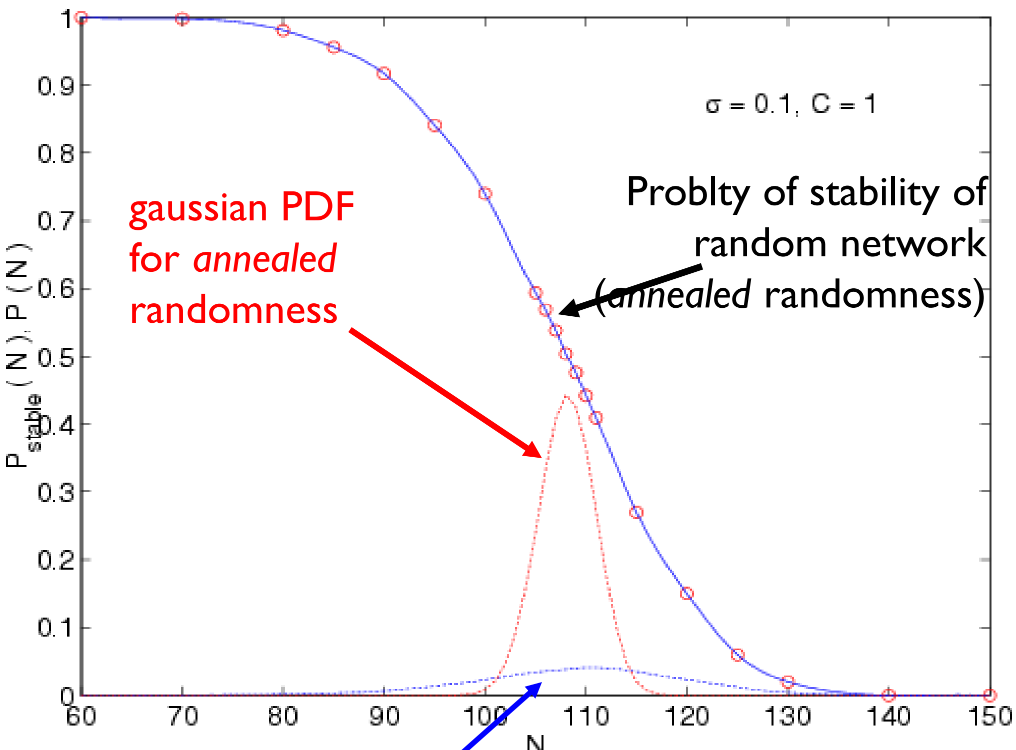




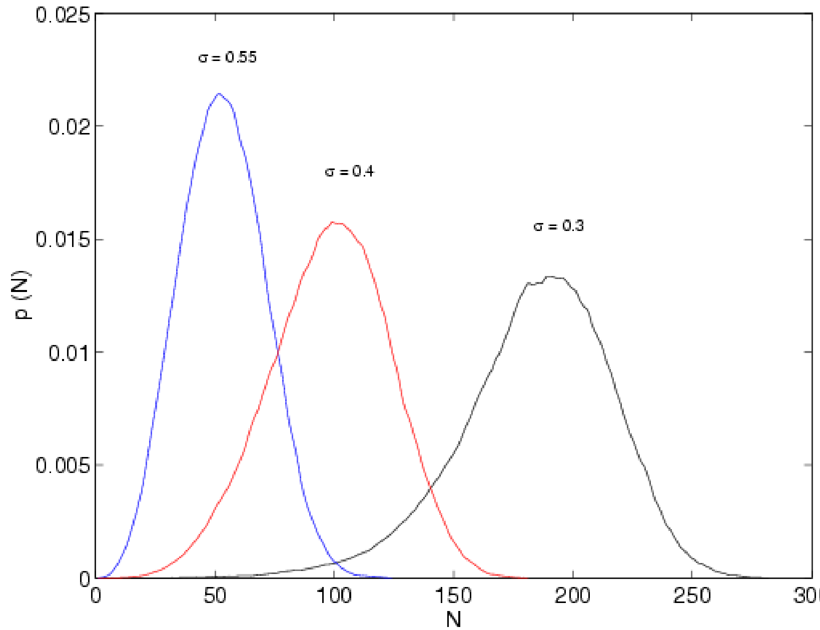
…and then settles down to a pattern of growth spurts & collapses

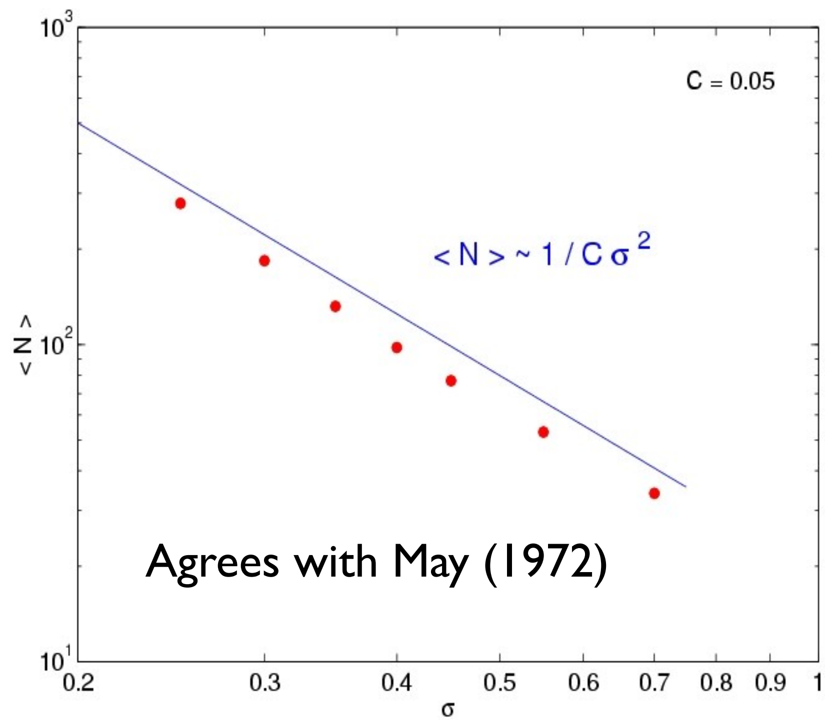
Communities with overall weaker interactions support a larger mean number of species
→ weak links are stabilizing (R. May).

The randomness in network connectivity is *quenched* → long-range memory!



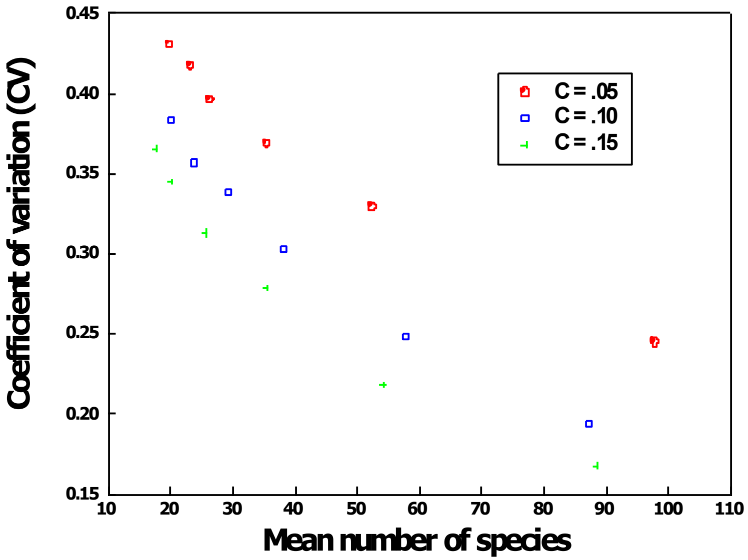
observed PDF for *quenched* randomness

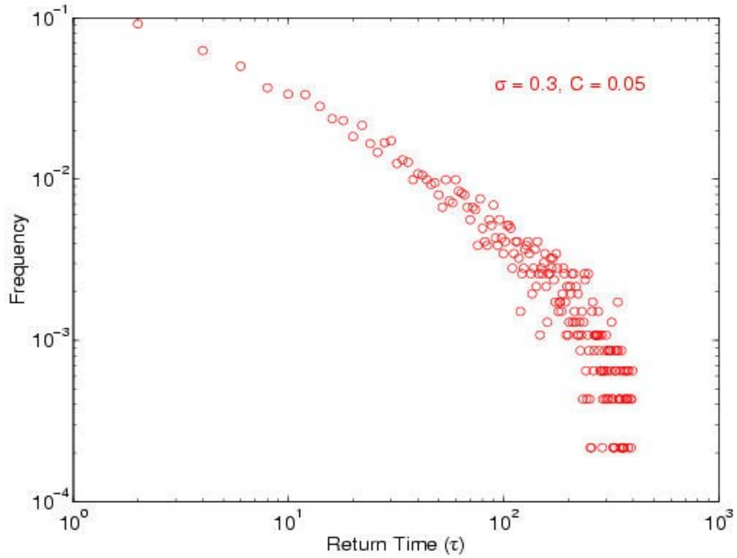




Surprise!

For the evolved networks : complexity → robustness

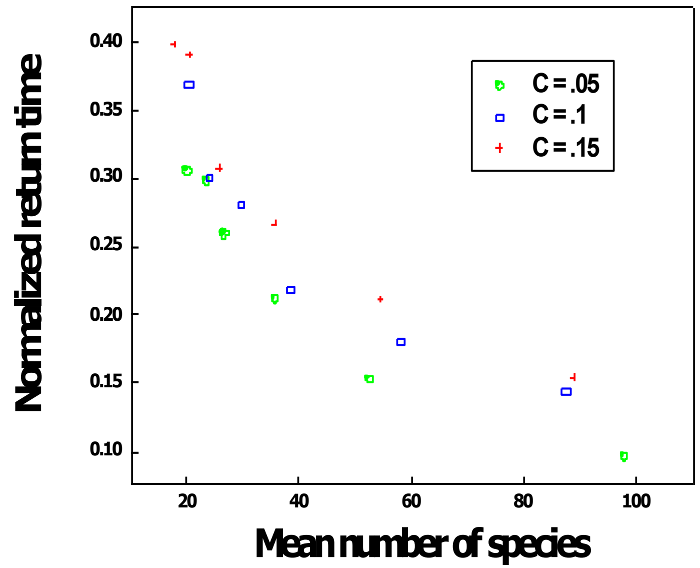




Larger networks are

• less variable (i.e., more robust)

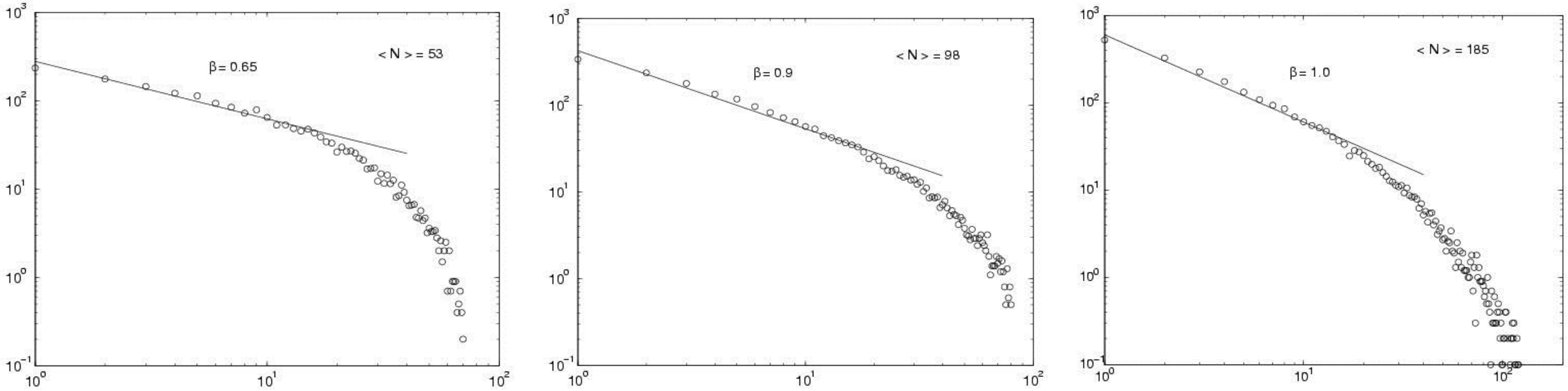
• more resilient
(resilience = normalized mean return time to average network size)



Surprise!

For the evolved networks : complexity → robustness

Frequency Distribution of Extinction Cascades:



Larger networks have smaller chance of a large magnitude collapse → increased resistance

Implications

- ❑ Introducing explicit dynamics and/or complex structure into networks: does <u>not</u> change the likelihood of a network to become unstable at increased complexity

- ❑ Introducing network evolution → Complex yet stable networks can evolve !

- ❑ The results imply that the traditional approach of taking snapshot views of networks may be inadequate to build an understanding of their stability.