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Are Complex Networks Unstable?

Examining the Effects of Species Richness on Community Stability: An Assembly Model Approach

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Are Complex Networks Unstable ?

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Chris Wilmers (Berkeley)
Markus Brede (Leipzig)

- S. Sinha and S. Sinha, *Phys Rev E*, **2005**, *71*, 020902 (R).
- S. Sinha, *Physica A*, **2005**, *346*, 147.
- C. C. Wilmers, S. Sinha and M. Brede, *Oikos*, **2002**, *99*, 3.

Are Complex Systems Unstable ?

ABSTRACT:
Is a large inter-connected network of elements (e.g., power grids, ecologies, computer networks) more stable or less stable to perturbations as more and more elements are added to it ?
Results based on random matrix theory due to Wigner & May, seem to suggest that *complexity implies fragility* in a large network. This runs counter to many empirical studies which claim that *diversity is essential for stability*, and, has led to the famous *complexity vs. stability* debate in ecology.

We have shown that the two main objections against the May-Wigner argument, namely, (i) it is based on *local stability* and (ii) it is only valid for *random networks*, are not tenable and that the original May-Wigner result may be universally applicable to networks.
We also show that, in the specific context of a network assembly model, the apparently contradictory claims of the opposing groups in the *complexity vs. stability* debate can be resolved. In our study of model networks assembled over time subject to stability constraints, we observe that while stronger interactions and increased connectivity do indeed result in smaller networks, yet, given a large, highly connected network generated by the assembly process, it is much more likely to be robust than its smaller, sparsely connected counterpart. The network growth algorithm proposed by us acts as a very efficient search algorithm for stable yet complex network structures which are very rare in the space of all possible networks.

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Instability of complex networks affect our lives at all times

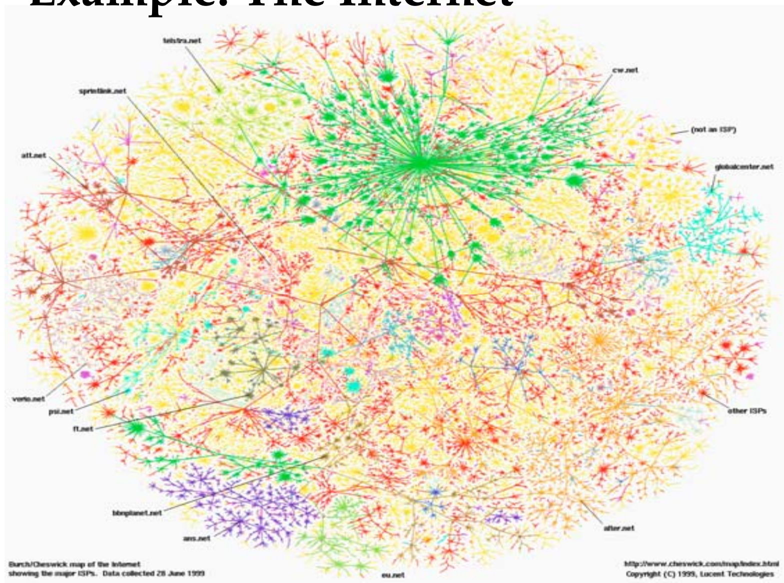
Example: Transportation Network

Non-local effects of delays in air traffic network!

Fog in Delhi delays flights from Chennai to Kolkata !

How do perturbations at one node propagate through the network and affect other distant nodes ?

Example: The Internet



Powerful attack cripples majority of key Internet computers
YAHOO! News Tue Oct 22, 2002 7:30 PM ET

By TED BRIDIS, Associated Press Writer

WASHINGTON - An unusually powerful electronic attack briefly crippled nine of the 13 computer servers that manage global Internet traffic this week, officials disclosed Tuesday. But most Internet users didn't notice because the attack only lasted one hour.

The FBI and White House were investigating. One official described the attack Monday as the most sophisticated and large- scale assault against these crucial computers in the history of the Internet. The origin of the attack was not known.

Seven of the 13 servers failed to respond to legitimate network traffic and two others failed intermittently during the attack, officials confirmed. Service was restored after experts enacted defensive measures and the attack suddenly stopped.

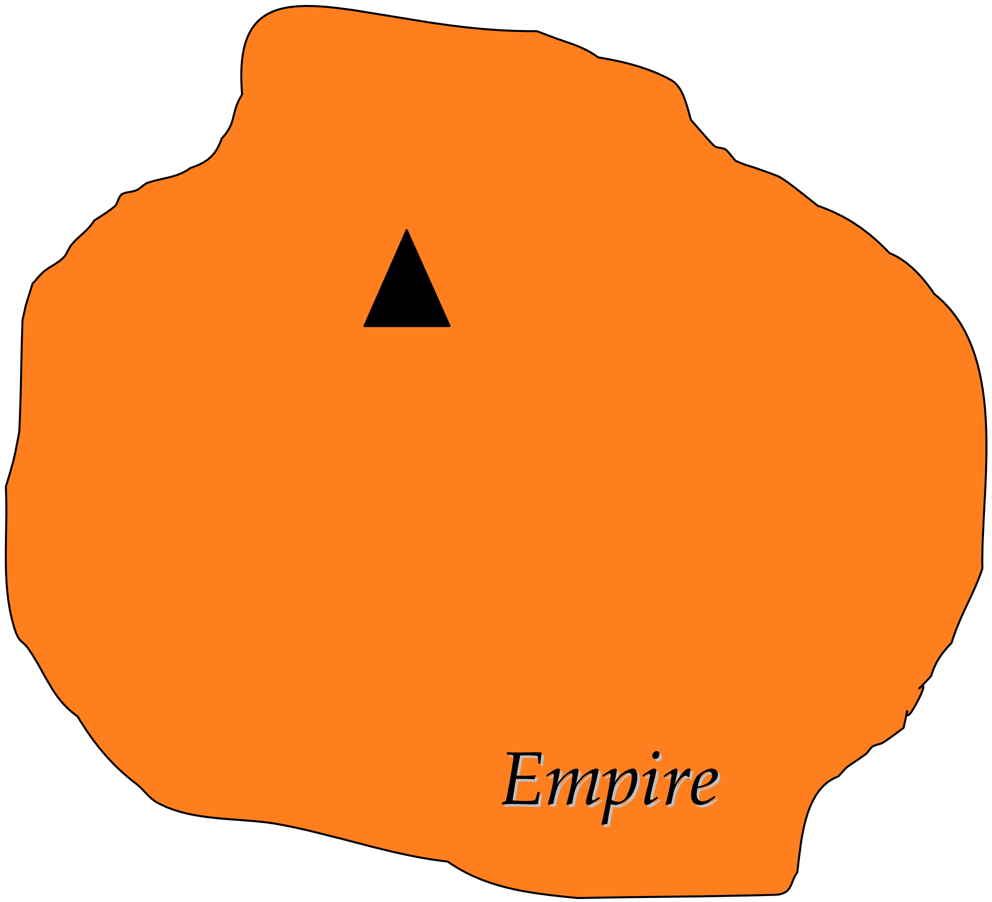
The 13 computers are spread geographically across the globe as precaution against physical disasters and operated by U.S. Government agencies, universities, corporations and private organizations.

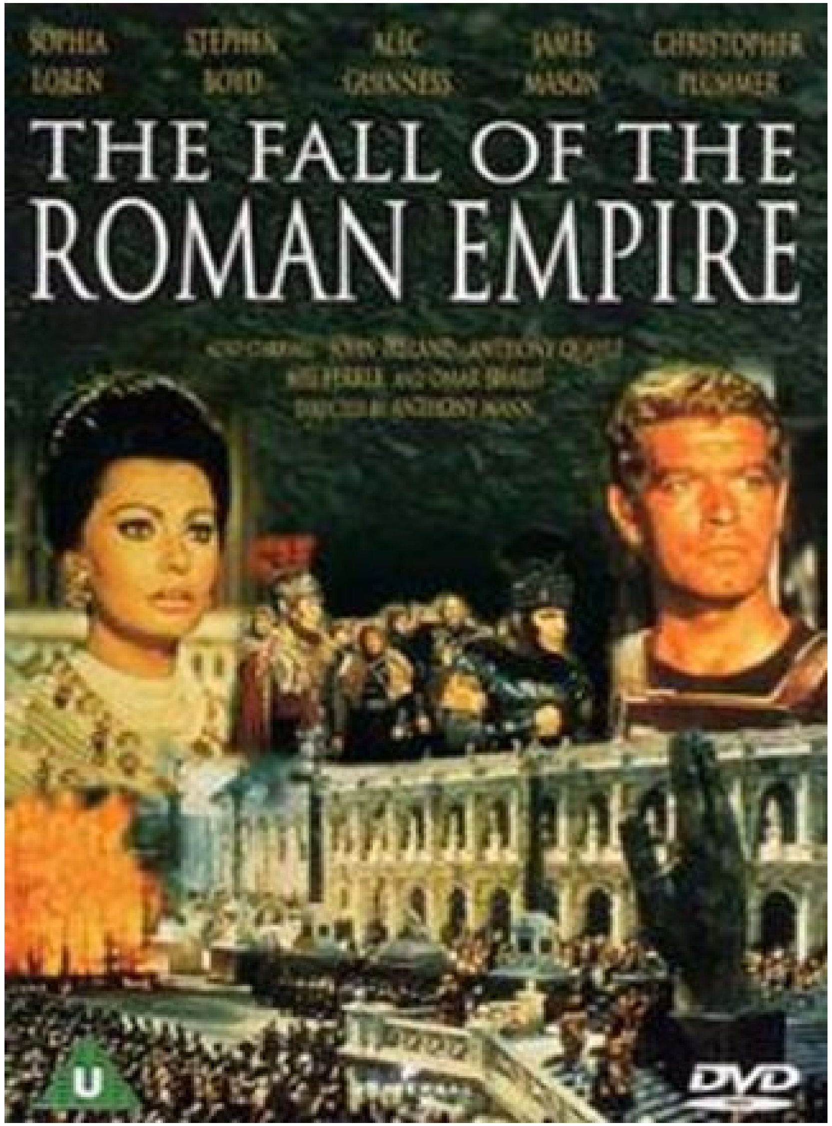
Example: Failures in the power transmission network

New York power outage (Aug 14, 2003)

Example: Instabilities in the global financial network

Collapse of complex societies





…and even longer timescales

- Collapse of ecosystems

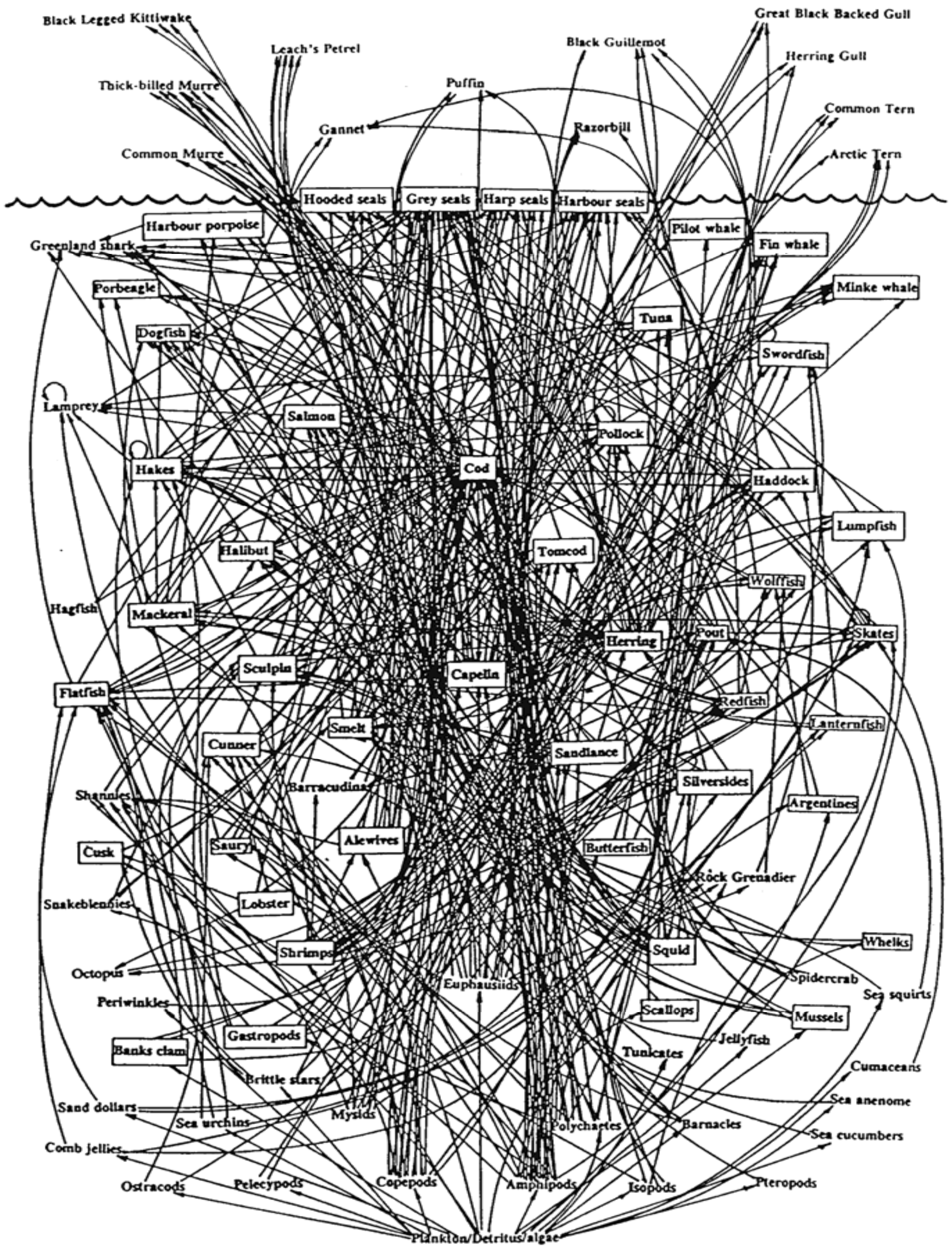
- Cascades of extinction events triggered by small fluctuations

- Ecosystem management:
  Effect of human intervention

- Is higher diversity good or bad for an ecosystem ?

The relation of stability to complexity has been debated for a long time in the context of food webs and ecological interaction networks.

The Scotian Shelf food web



Aim

To understand the stability of network dynamics with many interacting components:

- **Species (Ecology): predator-prey, competitive & cooperative interactions.**
- **Markets/economic agents (Economics): producer-consumer, competitive and cooperative interactions.**
- **Biological distributed information processing (Neural networks): excitatory & inhibitory interactions.**
- **Human groups (Social networks)**

The Question

How does the stability (response to perturbations) of networks change as a function of :

- **network size (number of interacting components in the network)**
- **degree of connectivity between the nodes of the network**
- **the strength of interaction between the nodes of the network**

The Empiricists' View

Complexity is essential for 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

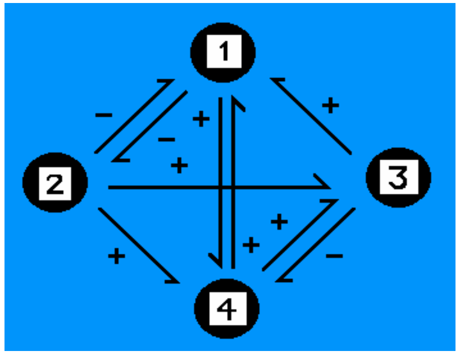
Multiple links ≡ Insurance !

The Physicists' View

Increasing complexity leads to network instability

Robert May (1972)

Randomly constructed networks become less stable with complexity



Construct *randomly* generated matrices representing interaction strengths in a network, whose individual nodes are stable ($J_{ii} = -1$)

J =

-1	-1.15	0	0.33
-1.66	-1	0.17	2.18
0.12	0	-1	-0.14
0.29	0	0.73	-1

Obtain the eigenvalues λ of J and use the criterion that if $\lambda_{max} > 0$, the system is unstable.

May-Wigner Theorem: Stability of a network decreases as its size, connectivity and interaction strength increases

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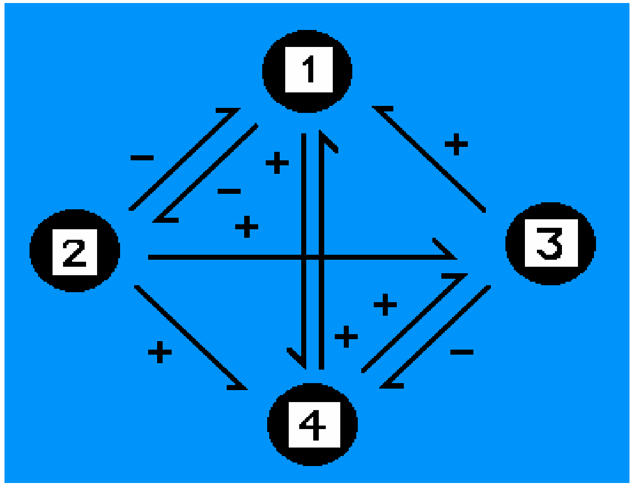

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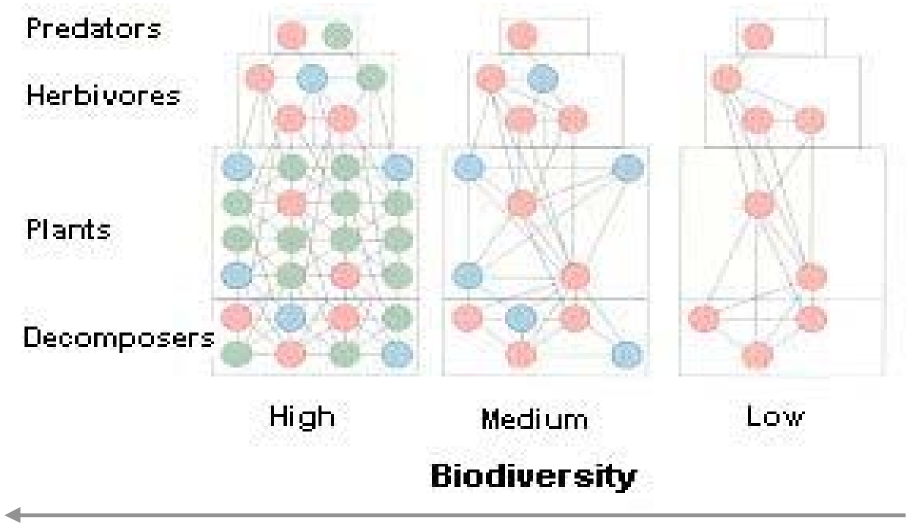
Experimental evidence:

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.

``Bottle'' Experiments: *Ecotron*



Setup allows manipulation of diversity while maintaining food web structure.

Diverse systems are more productive and more resistant, but…
no effect on population variability and may indicate averaging effect.

Also, its unclear how these results scale to real communities.

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 ×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).

Objections to the May-Wigner theorem :
Complexity → Instability

- ❑ Assumes random network of interactions (although the presence of trophic levels clearly imply the existence of structures in the network)

- ❑ Based on linear stability (does not take into account periodic or chaotic dynamics of populations)

- ❑ Does not consider evolution of the network (in terms of network growth by incorporating new nodes and links, or, reduction in size of network through extinction of nodes and/or deletion of links)

A Fresh look at Complexity → Instability

- **Consider networks which have structures in the arrangement of their interactions**

Small-world connectivity: S. Sinha, *Physica A*, **2005**, *346*, 147.
Hierarchical modular connectivity: R. K. Pan and S. Sinha, *forthcoming*

- **Consider networks with full dynamics (fixed point, oscillatory, chaotic) at each node**

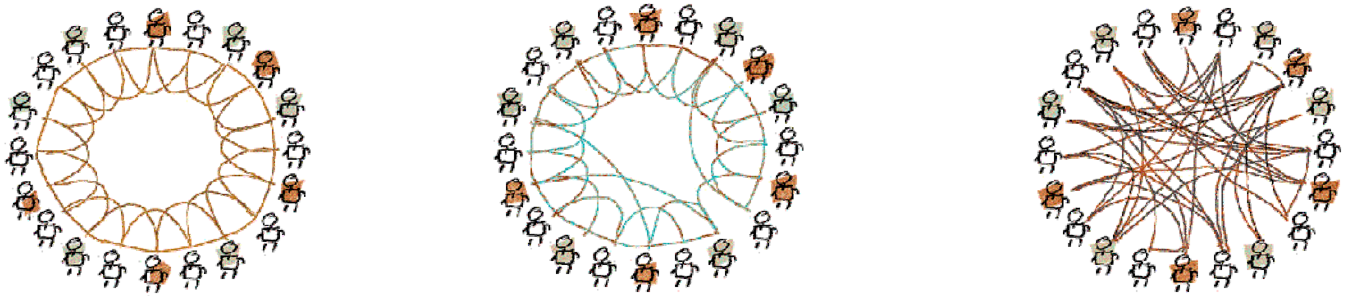
S. Sinha and S. Sinha, *Phys Rev E*, **2005**, *71*, 020902 (R).

- **Consider networks which grow or shrink over time through addition (migration) or deletion (extinction) of nodes**

C. C. Wilmers, S. Sinha and M. Brede, *Oikos*, **2002**, *99*, 3.

In nature, networks are not random – they have structure.

Example: *small-world* networks



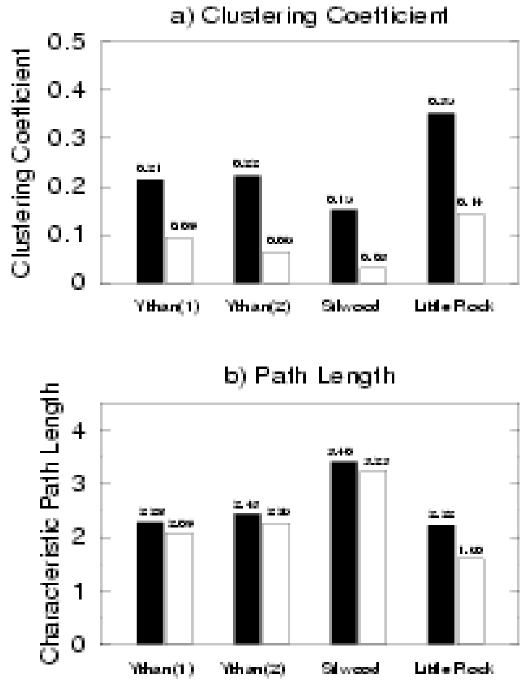
Regular Network
p = 0

"Small-world" Network
0 < p < 1

Random Network
p = 1

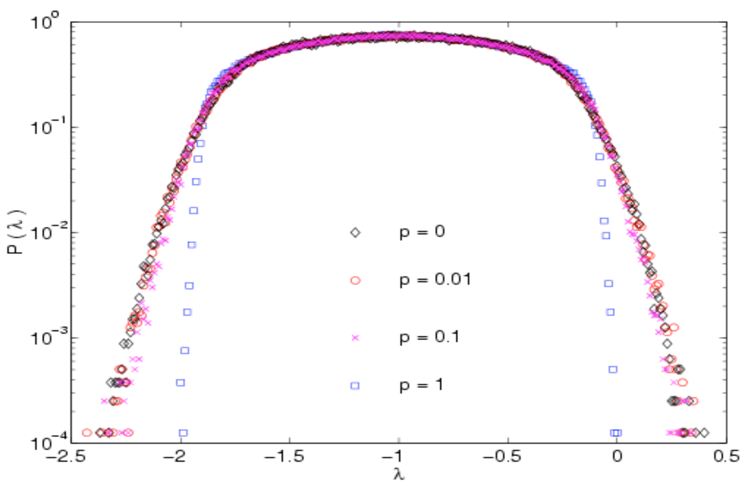
Increasing Randomness

Watts and Strogatz (1998): Many biological, technological and social networks have connection topologies that lie between the two extremes of completely regular and completely random.



Montoya and Sole (2001): Ecological networks are small-world!
Challenged by Dunne et al (2002)

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



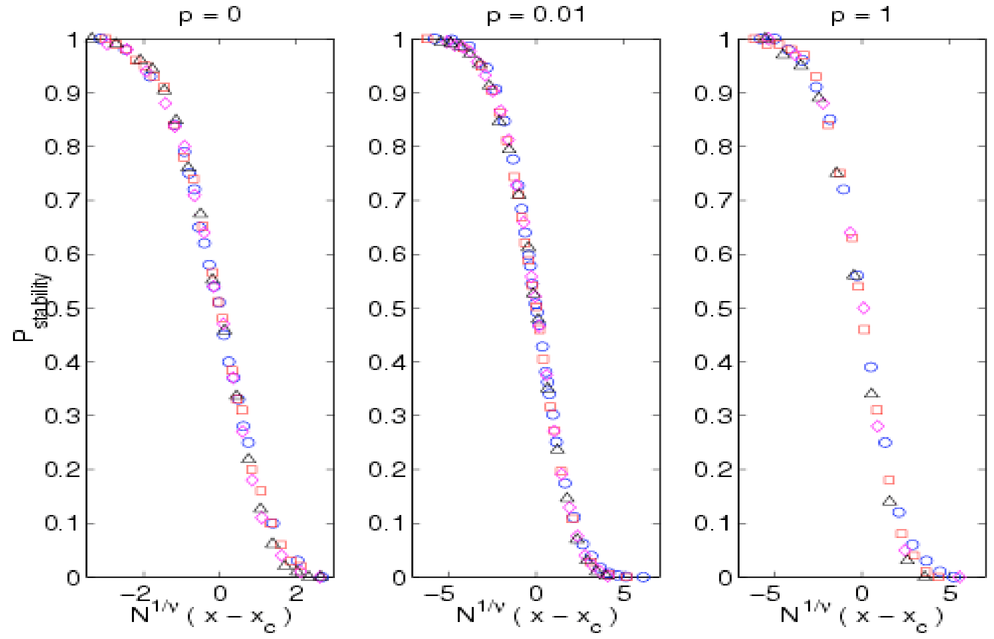
Sinha (2005): Eigenvalue distribution for networks with different topologies.

Extended tail of the eigenvalue distrn for p < 1.

Stability-instability transition in Small-World Networks (Sinha, 2005)

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

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



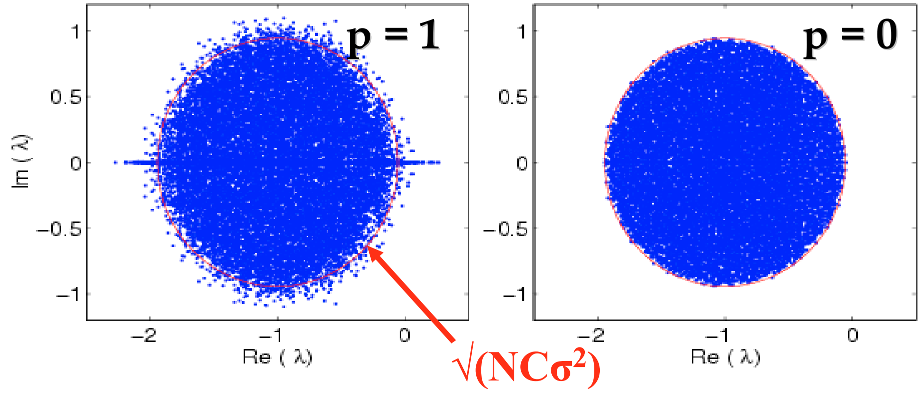
$x = \sqrt{(N\,C\,\sigma^2)} - 1,$

$x_c \rightarrow 0$ as $N \rightarrow \infty$

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

Regular vs Random Networks

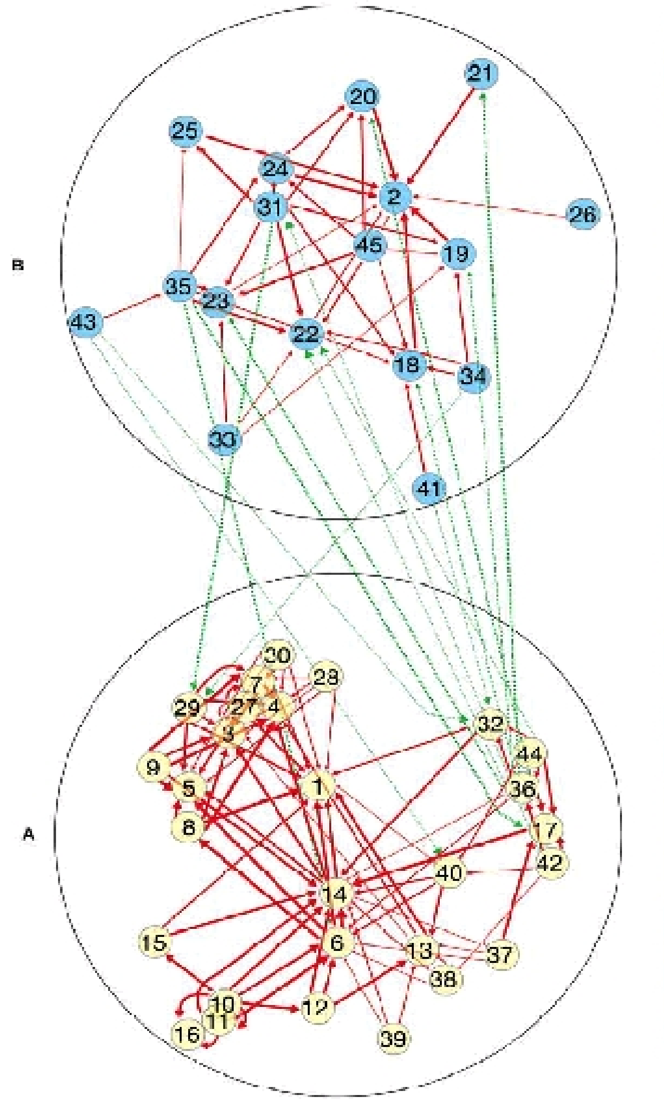
The eigenvalue plain



N = 1000, C = 0.021, σ = 0.206

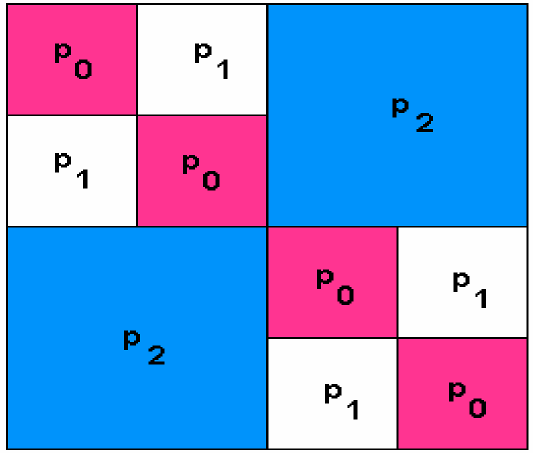
Hierarchical Modular Networks (Pan & Sinha, forthcoming)

Modularity in ecological networks



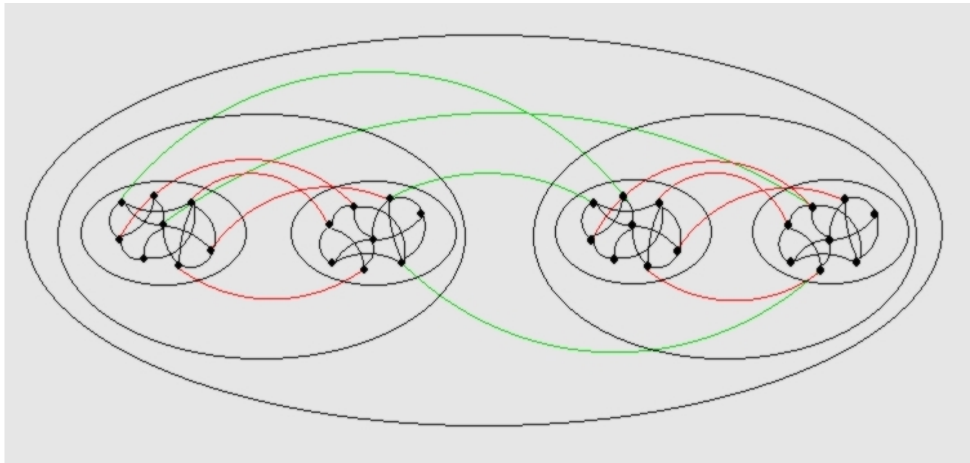
ID	Scientific name or classification
1	Phytoplankton
2	Benthic producers
3	Bacteria <1 µm (small)
4	Bacteria >1 <2 µm (medium)
5	Bacteria >2 µm (large)
6	*Acartia tonsa* (copepod)
7	Micro ciliates
8	Macro ciliates
9	Predaceous ciliates
10	*Chrysaora quinquecirrha* (sea nettle)
11	*Mnemiopsis leidyi* (comb jelly)
12	*Nemopsis bachei* (jellyfish)
13	Cladocera
14	Other zooplankton
15	*Anchoa mitchilli* larvae (anchovy)
16	*Anchoa mitchilli* eggs
17	Fish larvae
18	*Marenzelleria viridis* (polychaete)
19	*Nereis succinea* (polychaete)
20	*Heteromastus filiformis* (oligochaete)
21	Other polychaetes
22	*Corophium lacustre* (amphipod)
23	*Leptocheirus plumulosus* (amphipod)
24	Other meiofauna
25	*Macoma balthica* (Baltic clam)
26	*Macoma mitchelli* (rosy clam)
27	*Rangia cuneata* (wedge clam)
28	*Mulinia lateralis* (coot clam)
29	*Mya arenaria* (soft-shelled clam)
30	*Crassostrea virginica* (oyster)
31	*Callinectes sapidus* (blue crab)
32	*Anchoa mitchilli* (bay anchovy)
33	*Micropogon undulatus* (croaker)
34	*Trinectes maculatus* (hogchoker)
35	*Leiostomus xanthurus* (spot)
36	*Cynoscion regalis* (weakfish)
37	*Alosa sapidissima* (American shad)
38	*Alosa pseudoharengus* (alewife)
39	*Alosa aestivalis* (blue-back herring)
40	*Brevoortia tyrannus* (menhaden)
41	*Morone americana* (white perch)
42	*Morone saxatilis* (striped bass)
43	*Pomatomus saltatrix* (bluefish)
44	*Paralichthys dentatus* (flounder)
45	*Arius felis* (catfish)

Chesapeake Bay foodweb (Ulanowicz et al)

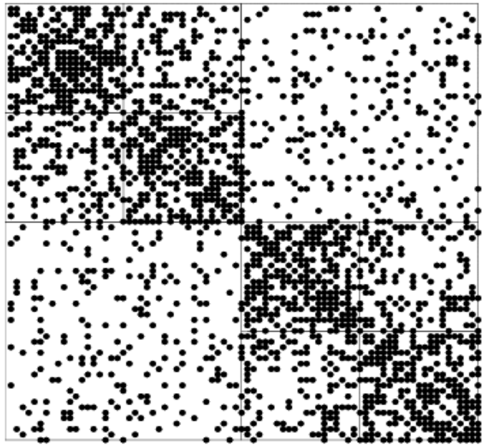


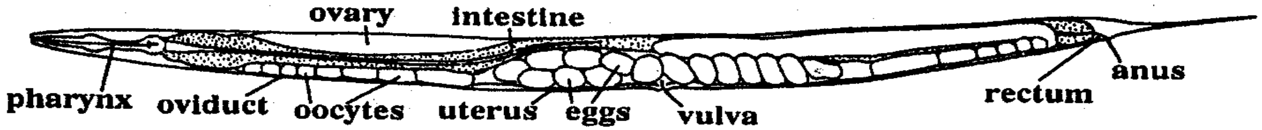
$$\frac{p_1}{p_0} = \frac{p_2}{p_1} = r$$

- $r = 1$: randomly coupled network.
- $r = 0$: isolated sub-networks (modules)
- $0 < r < 1$: hierarchically structured network.

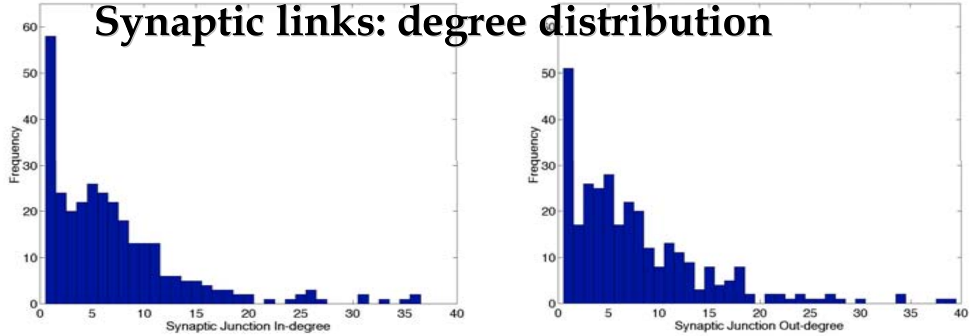


Hierarchical Modular Networks (Pan & Sinha, forthcoming)





C. Elegans neural network: 302 neurons



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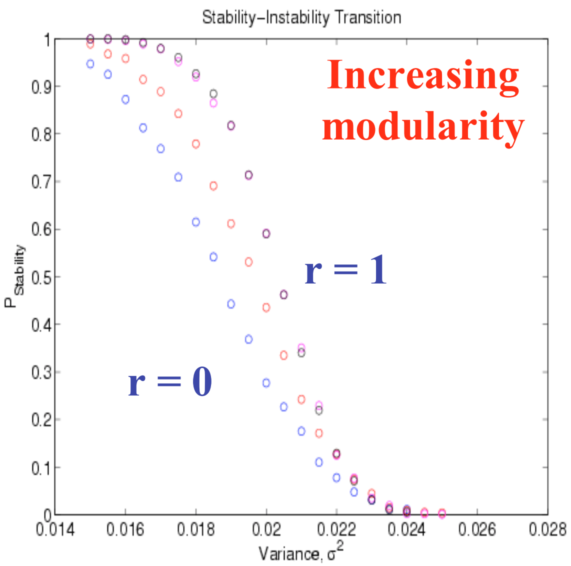
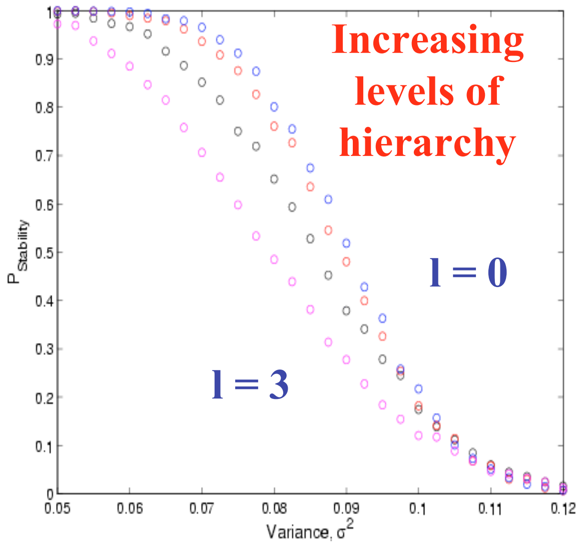
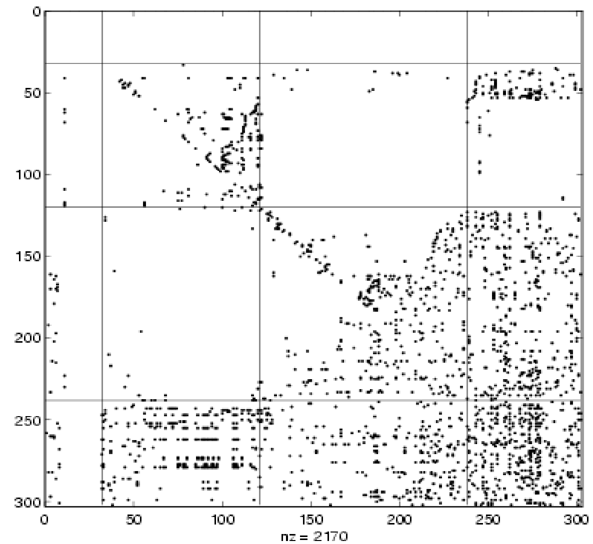




C. Elegans synaptic connectivity matrix



Networks with structure

Introducing certain structures in the network topology does <u>not</u> significantly change the May-Wigner result!

Network dynamics

Is linear stability a proper measure ?

Nodes may have non-trivial dynamics. (Sinha & Sinha, 2005)

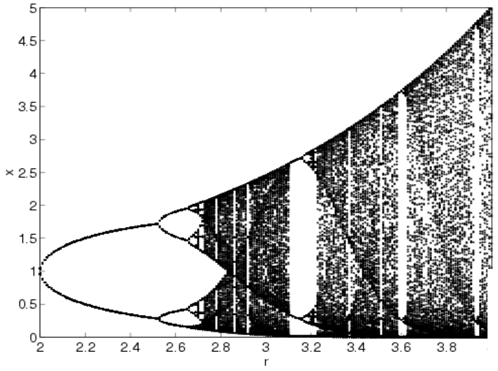
Introduce explicit dynamics at the nodes : X (n+1) = F(X (n))

What happens when such nodes are coupled together via a sparse random network ?

Dynamics of network nodes : X (n+1) = F(X (n)) (Sinha & Sinha, 2005)

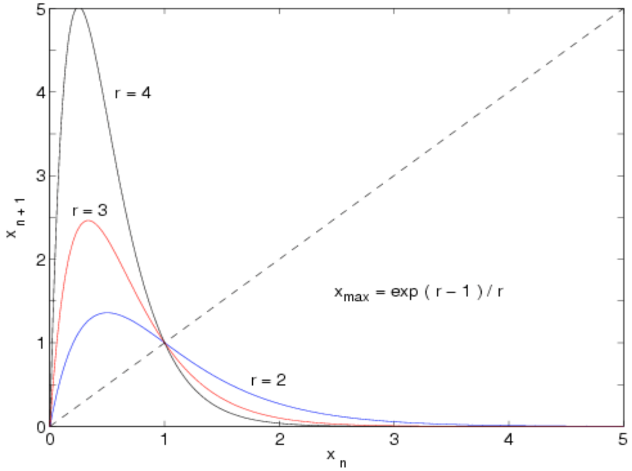
Example: Discrete exponential logistic growth model

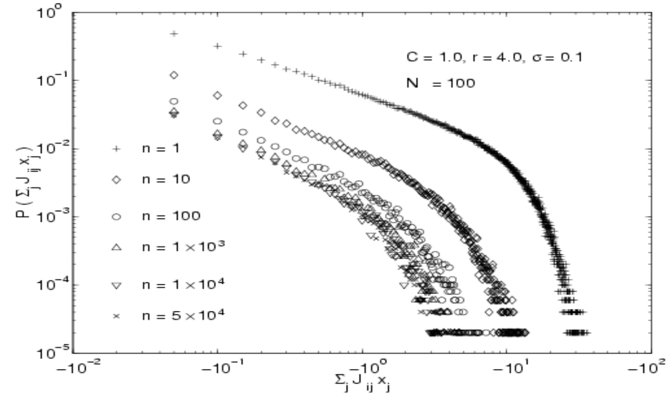
$$X_{n+1} = X_n \exp[r(1 - X_n)]$$



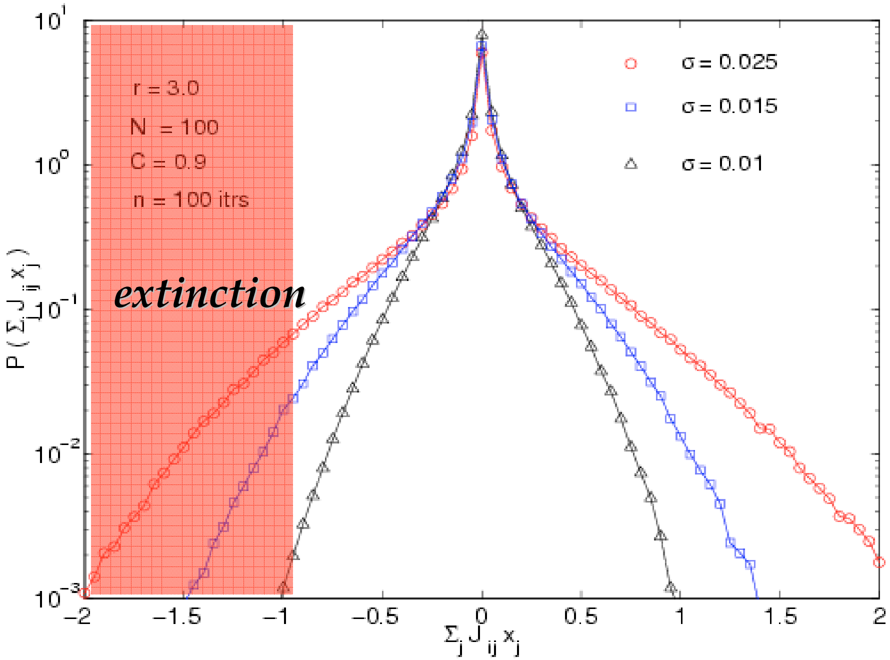
Network dynamics:

Xi (n+1) = F(Xi (n) [1+Σ Jij Xj (n)])





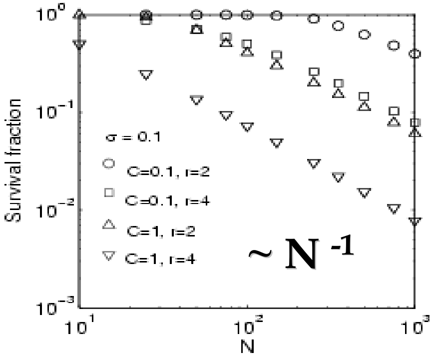
Fixed-point, period and chaotic dynamics

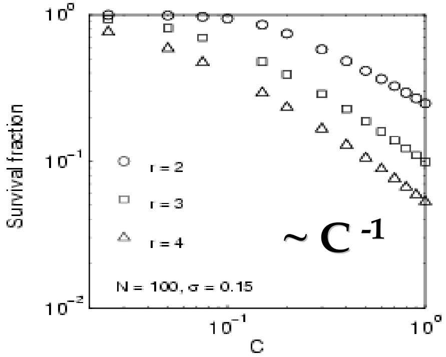


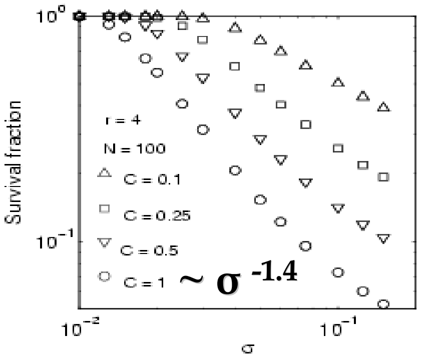
A node is extinct if Σ Jij Xj < -1

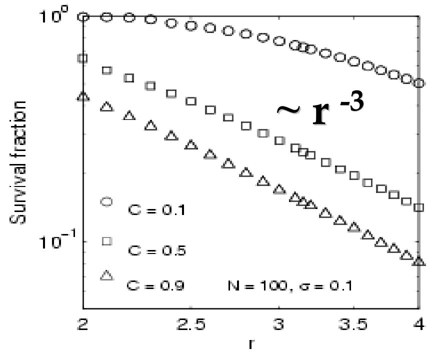
Question: **How many nodes survive asymptotically ?**

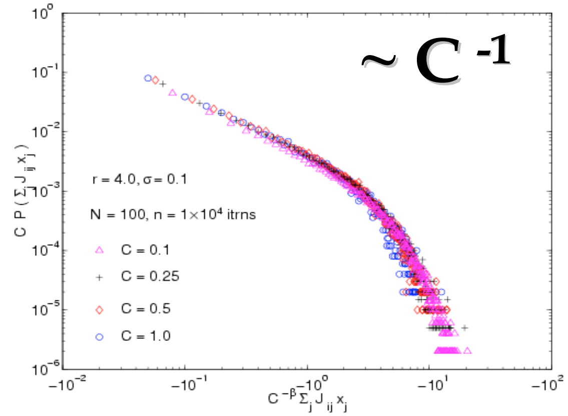
Global stability of network ~ Probability of persistence of active nodes

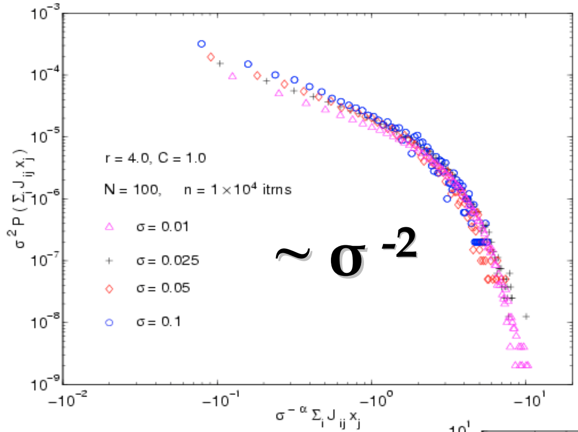


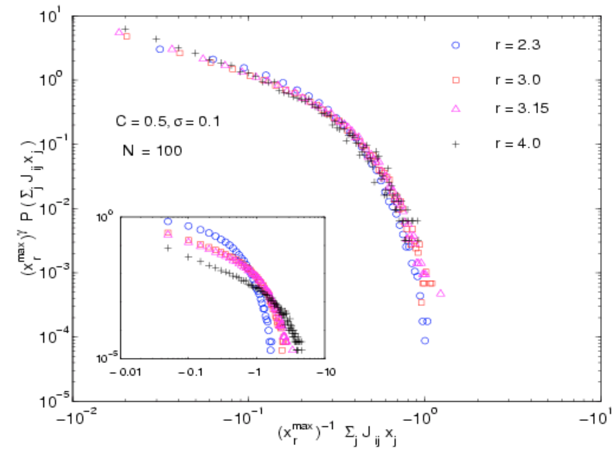












Scaling of Σ J_{ij} X_j distribution confirms the May-Wigner results

Probability of stability depends not on details of map dynamics …but on the extent of the attractor as ~ $[x_r^{max}]^{-3}$

Network dynamics

No change in results for global stability with dynamics at nodes:
Complexity → Instability

Probability of stability $\sim N^{-1}$

$\sim C^{-1}$

$\sim \sigma^{-2}$

Universal feature of network dynamics!

Puzzle !

How can complex networks be robust at all ?

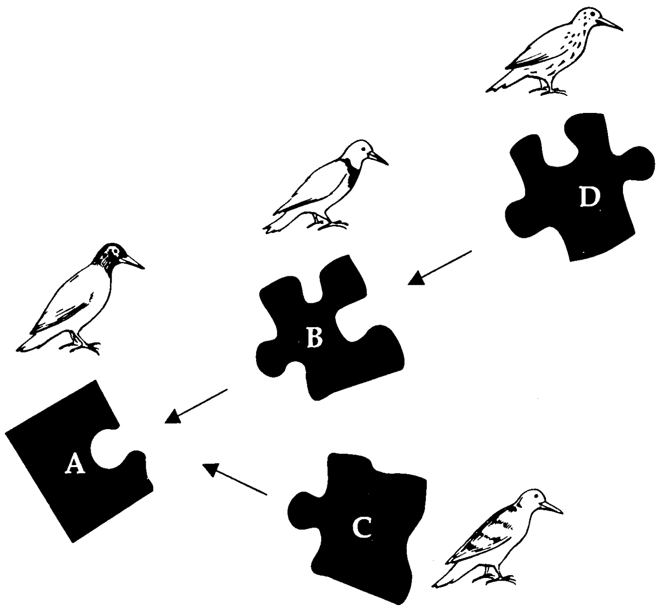
Possible solution: Network Evolution

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 invasion and/or extinction ?

Community Assembly rules decide which species can coexist in an ecosystem, and the sequence in which species are able to colonize a habitat.



Network Evolution

WSB Network Assembly Model : Algorithm

(Wilmers-Sinha-Brede, 2002)

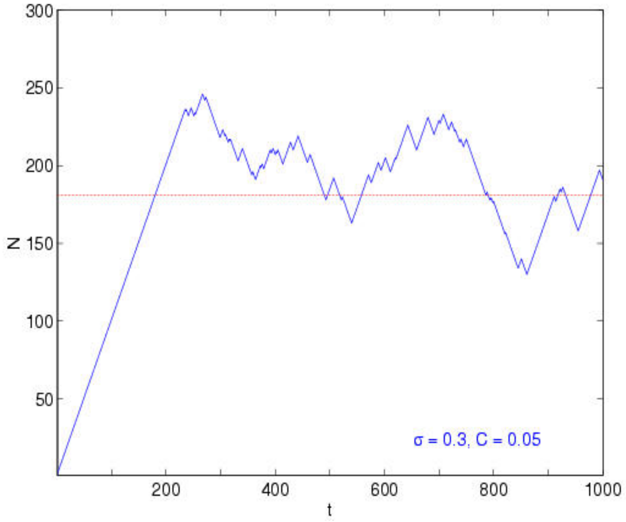
- **Start with one node.**

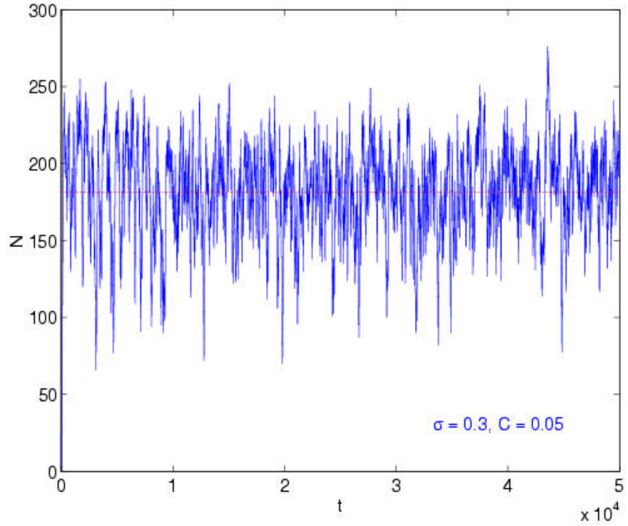
a_{12}
$\leftarrow$
$\rightarrow$
a_{21}

- **Add another node with Poisson distributed number of links, and Normal $(0,\sigma^2)$ distributed interaction strengths a_{ij} .**

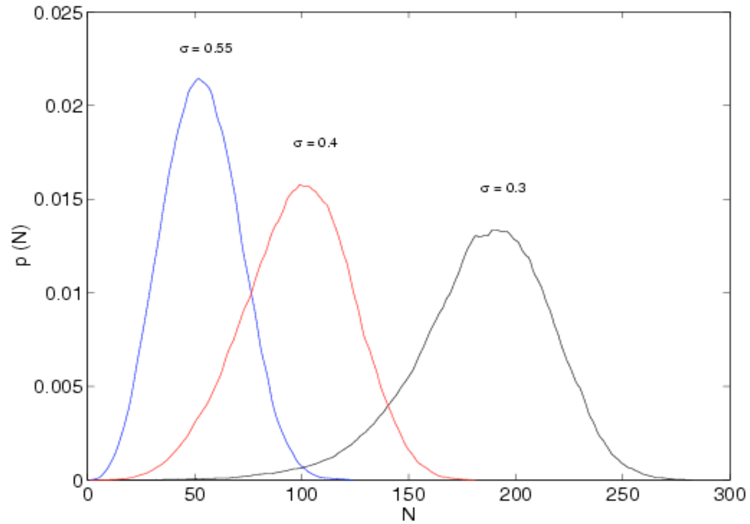
- **Check stability of the resultant network interaction matrix:**
  - **If unstable, remove a node at random and analyze the stability again.**
  - **If stable, add another node.**

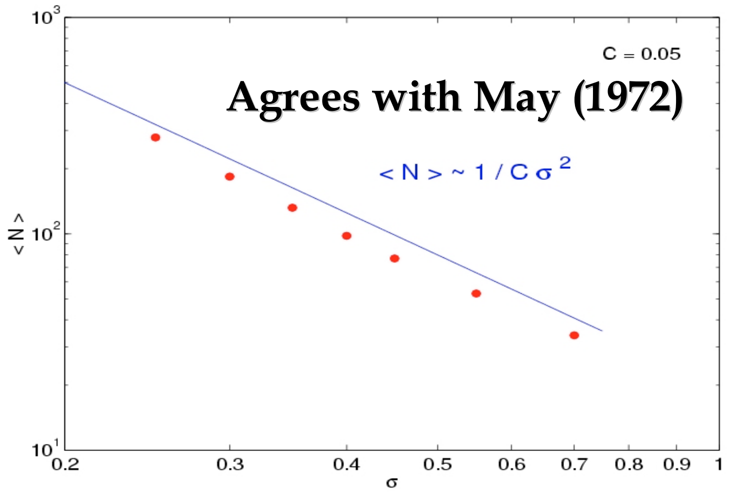
Network initially grow in size monotonically and then settles down to a pattern of growth spurts and collapses.





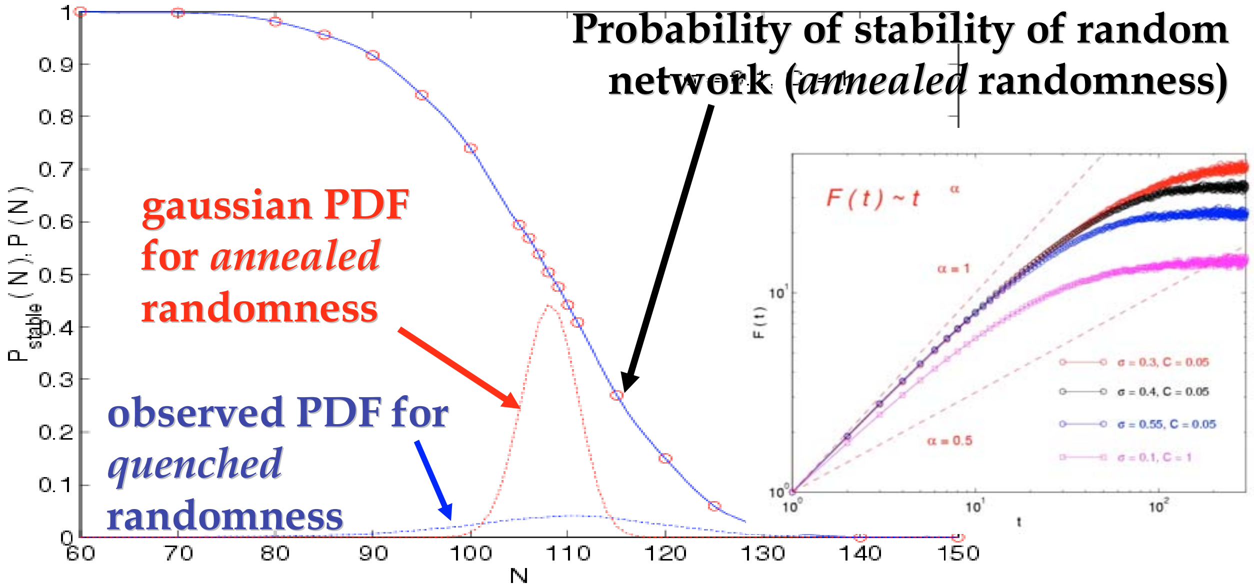
Communities with overall weaker interactions support a larger mean number of species → weak links are stabilizing (R. May).





Agrees with May (1972)

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

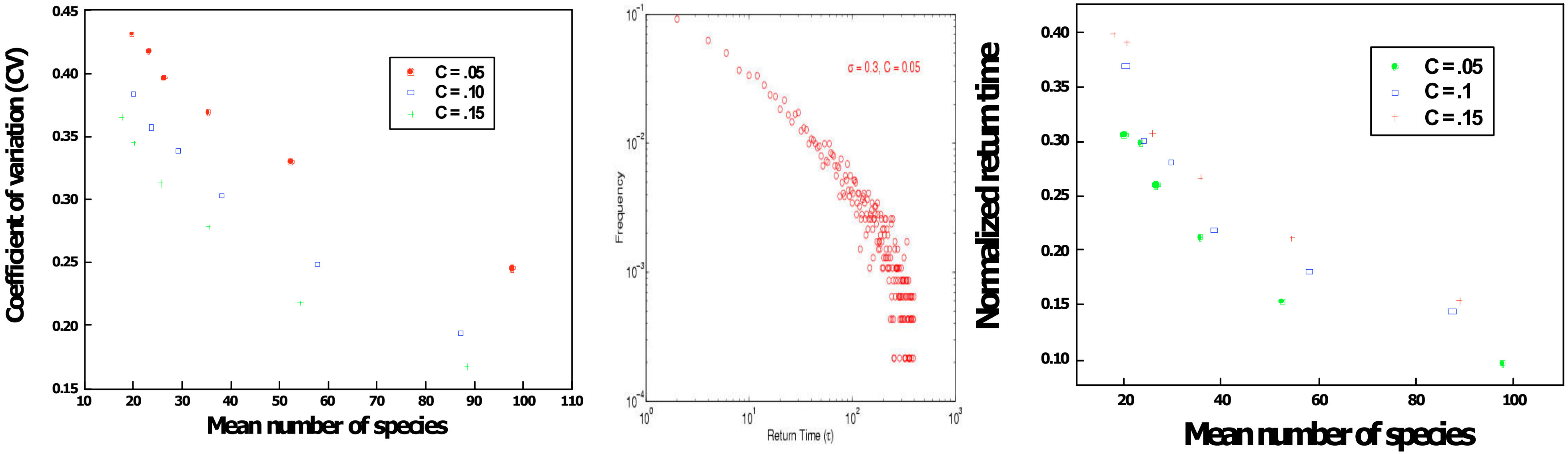


Probability of stability of random network (*annealed* randomness)

gaussian PDF for *annealed* randomness

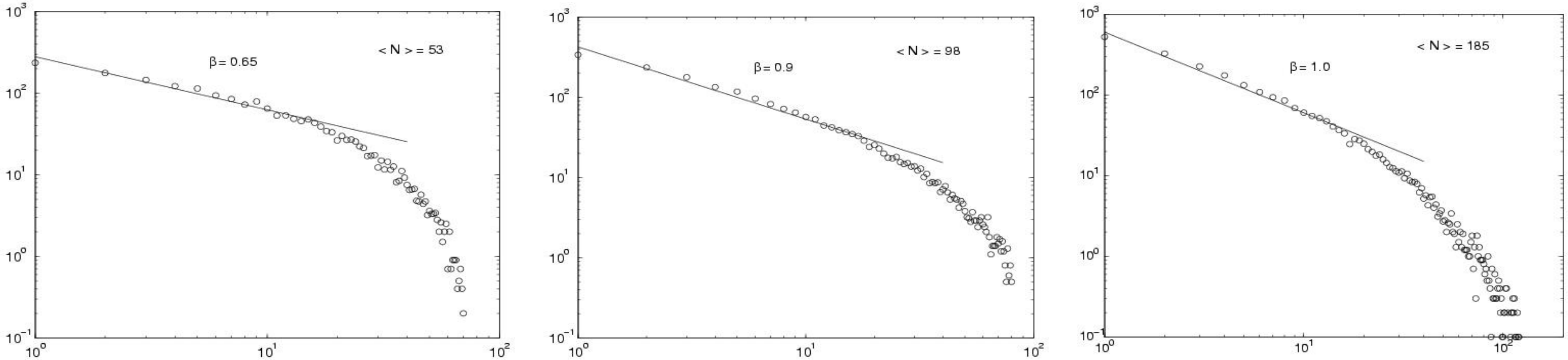
observed PDF for *quenched* randomness

Surprise! For the evolved networks : complexity → robustness



Larger networks are less variable (i.e., more robust) and more resilient
(resilience = normalized mean return time to average network size)

Frequency Distribution of Extinction Cascades:



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

Conclusion

- **Introducing dynamics and/or structure into networks does <u>not</u> change stability-instability transition at increased complexity.**

- **Introducing network evolution →**
  synthesis of opposing views in stability/diversity debate

- **Stronger interactions & increased connectivity lead to smaller networks, yet,**

- **given a large, highly connected network it is more likely to be robust than its smaller, sparsely connected counterpart.**

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

- **Implications not just for ecology, but from cell to society!**

OIKOS 99: 363–367, 2002

Examining the effects of species richness on community stability: an assembly model approach

Christopher C. Wilmers, Sitabhra Sinha and Markus Brede

Wilmers, C. C., Sinha, S. and Brede, M. 2002. Examining the effects of species richness on community stability: an assembly model approach. – Oikos 99: 363–367.

We build dynamic models of community assembly by starting with one species in our model ecosystem and adding colonists. We find that the number of species present first increases, then fluctuates about some level. We ask: how large are these fluctuations and how can we characterize them statistically? As in Robert May's work, communities with weaker interspecific interactions permit a greater number of species to coexist on average. We find that as this average increases, however, the relative variation in the number of species and return times to mean community levels decreases. In addition, the relative frequency of large extinction events to small extinction events decreases as mean community size increases. While the model reproduces several of May's results, it also provides theoretical support for Charles Elton's idea that diverse communities such as those found in the tropics should be less variable than depauperate communities such as those found in arctic or agricultural settings.

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Theoretical studies have generally supported the notion that as community complexity increases, stability decreases (Gardner and Ashby 1970, May 1972, Gilpin 1975, Pimm and Lawton 1978, Hogg et al. 1989). Authors of such work typically analyze the local or species-deletion stability of randomly organized interaction matrices and/or Lotka-Volterra systems. With few exceptions (e.g. in donor-controlled communities) theoretical research has shown a negative relationship between stability and complexity (Pimm 1982). Conversely, empirical work generally shows that as communities increase in species richness they also increase in stability (McNaughton 1978, Tilman and Downing 1994, Tilman et al. 1996, Naeem and Li 1997). Studies conducted in controlled microcosms demonstrate a positive relationship between species richness and aggregate measures of community stability such as total biomass (Tilman et al. 1996, Naeem and Li 1997). Though this disconnect between theory and experiment is partially due to varying definitions of stability, it has nevertheless led to what has become the 'diversity-stability debate' in ecology (McCann 2000).

An alternative approach to modeling communities as randomly constructed entities is to assemble them one species at a time. Models of this kind typically draw species from a limited pool of resources and consumers until a final community state is reached (Post and Pimm 1983, Drake 1990, Law and Morton 1996). A clear advantage to this approach is the realism embodied in the methodology. As such, models of this kind have closely corroborated experimental manipulations in microcosm experiments. While much effort has been focused on analyzing the invasibility of these models, there has been little work analyzing their statistical properties.

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Here we construct dynamic models of community assembly starting with one species and then adding colonists to our hypothetical ecosystem. As with previous studies, we find that the number of species initially increases, then fluctuates about some level. We ask: how large are these fluctuations and how can we characterize them statistically? We present the results through an ecological lens, though much like previous work in this area, the model may have broader application to other networked systems such as those found in economics, sociology and computing.

Methods

We begin with one species in our model ecosystem and add colonists to the network one at a time. New colonists interact with resident species with probability p, where p is chosen such that the resultant connectance C (where $E(C) = p$), of our ecological network approximates the values reported in empirical food web studies. We compare scenarios $p = 0.05$, 0.10 and 0.15. Once a link has been established between two species, interaction strengths are then assigned from a specified distribution. We focus our analysis on normal (0, σ) distributed interactions, where σ is a joint measure of the population of a species and average interaction strength between species. For the remainder of the paper we refer to σ simply as interaction strength, though it can be (as in equations containing nonlinear terms) a weighted measure of interaction strength and populations size depending on the specific form of the underlying equations. We focus on normally distributed interactions because weak interactions are thought to be more common in nature than strong ones but we also test uniform (−a, a) and beta (r, s) distributions where beta parameters r and s are chosen such that the distribution of interaction strengths is basin shaped thus emphasizing strong interactions. Species interactions in our community are represented by a matrix A with elements a_{ij} such that perturbations of species from a community equilibrium satisfy the equation,

$$\frac{dx}{dt} = Ax, \qquad (1)$$

where A is the Jacobian matrix resulting from a Taylor expansion of a set of nonlinear first-order differential equations around one of their equilibrium points, retaining only the linear terms. The variable x indicates deviation from the equilibrium. As in May (1972), we do not specify the form of these equations, so that our model remains simple and general. This also means that we do not need to consider feasibility issues (Roberts 1974) since such considerations are only relevant when explicit dynamics (e.g. Lotka-Volterra) are specified. Diagonal terms a_{ii} are set to -1 so that populations are self regulated and normalized with respect to their intrinsic growth rates. We then analyze the local stability of the system by calculating the eigenvalues of the community matrix A. We use the condition that if the real part of the dominant eigenvalue is greater than zero, then the equilibrium point at which the community exists is unstable (May 1972). If it is unstable, we remove a species at random. Conversely, if it is stable, we add another species with a binomial (n, p) distributed number of links, where n is the number of species, and randomly chosen interaction strengths as described above. We then analyze the local stability of the system and repeat the process. The model is then allowed to run for $5 \times 10^5 – 10^6$ iterations, which is more than sufficient to assess the statistical properties of the system.

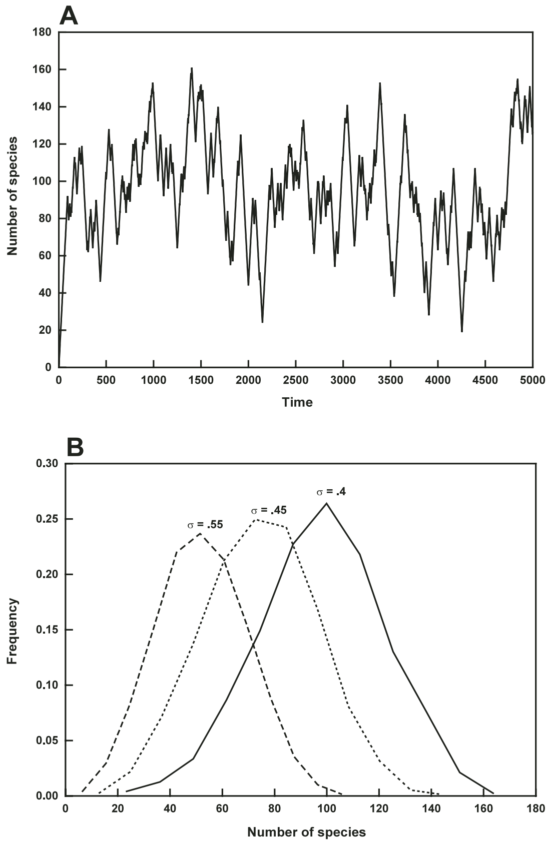

Fig. 1. (A) The number of species in the model ecosystem is plotted over time for a connectance = 0.05 and interaction strength σ = 0.4 from a normal distribution. (B) The corresponding distribution of species diversity of such communities is plotted for three different mean interaction strength levels σ.

Results

Communities in our model initially grow monotonically and then settle into a pattern of growth spurts and collapse (Fig. 1A). This process of community growth and decline ultimately defines a stationary stochastic process in the sense that a limiting distribution of states is approached asymptotically. A Fourier transform of the resulting time series can be modeled by a power law of the form,

$$P = \gamma f^{\alpha}, \qquad (2)$$

where P is the power spectral density of the time series, f is the frequency and γ and α are constants. An exponent of $\alpha \approx -3$ indicates that the process of community growth and collapse is more correlated than a random walk, which has exponent $\alpha \approx -2$ (Feller 1966).

Previous studies, both empirical and theoretical, have shown that as communities grow, they settle into a climax state thus becoming less invasible (Post and Pimm 1983, Dickerson and Robinson 1986, Robinson and Edgemon 1988, Drake 1990, Law and Morton 1996). Studies of this kind focus on a limited set of species interacting over a narrow time horizon. The pattern we observe is similar to other community assembly models in its initial growth, but it differs markedly in that a final climax state is never reached. Our model may be thought of as acting on a longer time scale such that a balance of colonization and extinction is maintained.

In Fig. 1B we illustrate the size distribution of the communities for the values 0.4, 0.45 and 0.55 of average interaction strength σ from a normal distribution. The mean of the distribution shifts to higher values as σ decreases. This indicates that communities with overall weaker interactions can support a larger number of species, which agrees, in principle, with the general theoretical result that weak links are more stabilizing (May 1974, McCann et al. 1998). Communities with strong links in our system cannot sustain as many species as those with weaker links because the probability of becoming unstable, as species are added to communities with strong interactions, increases more rapidly than in communities with weaker interactions.

Due to the stationarity of this stochastic process, it is appropriate to analyze the stability of the system in terms of variation in community size. Communities that vary widely around the mean are less stable than communities that stick more closely to the mean. A cursory glance at the variance of community distribution (Fig. 1B) indicates that it gets larger as community size increases. We do not believe, however, that variance is an accurate descriptor of stability here, so instead we investigate the variability of our communities by calculating the coefficient of variation (CV), which standardizes the measure of fluctuation in community size for different means. Large communities are more likely to lose more species than small communities because they have more to lose. It is how many species these communities lose on a percentage basis that we are concerned with.

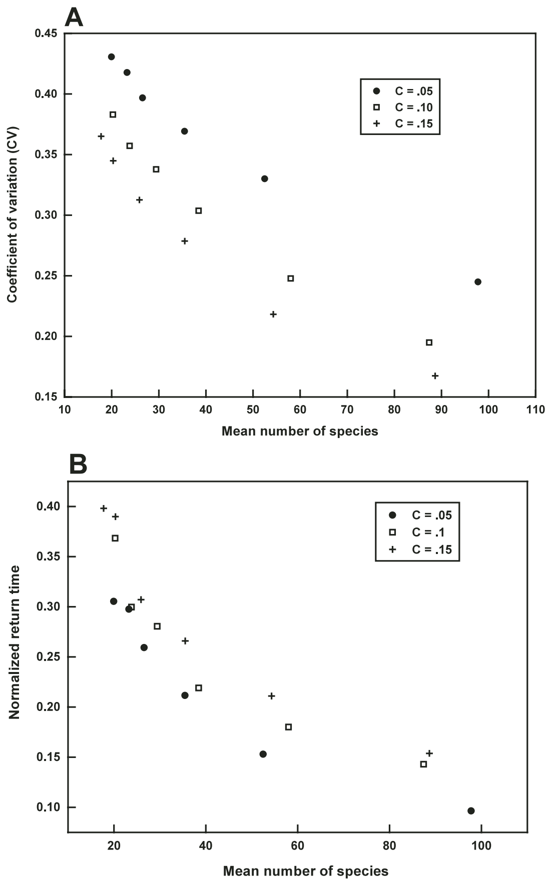

Fig. 2. (A) The coefficients of variation and (B) return times to equilibrium are plotted for communities with different mean number of species for three different connectance levels C.

Our results indicate (Fig. 2A) that increasing mean community size leads to decreasing values of CV indicating that more diverse communities are less variable. To be more specific, diverse communities in absolute terms lose more species than depauperate ones, but as a percentage of their members they lose less.

The distribution from which interaction strengths were drawn did not change our results qualitatively. Communities assembled from uniform and basin shaped beta distributions both showed the same pattern of decreasing CV with increasing diversity. What appears to be driving the reduction in CV is the assembly process itself. Figure 2A also reveals that as connectance C increases for a given community size, CV decreases.

Another way to investigate the variation of our communities is to look at the size distribution of species extinction cascades. Communities with more large cascades relative to small ones may be thought of as more variable than communities with more small cascades relative to large ones. The distribution of these extinction cascades generally showed a power law variation with exponent β (represented as slope on a log-log plot) over one decade followed by an exponential cut-off due to the finite size of our system (Fig. 3). Specifically,

$$N = \alpha S^{-\beta} \tag{3}$$

where S is the cascade size, N is the number of such cascades and α and β are constants. The value of β increases with increasing mean community size where α and β are greater than zero. The larger the value of the exponent, the more negative the slope of the power law and thus the smaller the frequency of large cascades, corroborating our previous result that communities decrease in variation as they get larger.

In addition to analyzing the variation in community size, we investigated return times to mean community size. We did this using two approaches. In the first, we used the mean of our time-series as a threshold, and evaluated the number of time-steps between each departure and subsequent return to this threshold. In the second, we looked at return times to the mean from points a maximum or minimum distance away from the mean. The length of each of these interval periods was stored in a vector. We then take the mean of this vector and divide by the variance of the time series. Normalizing the mean by the variation is analogous to the normalization procedure we previously used for variance. In that case we compared the variance of distributions drawn from different means. Here, we compare means drawn from distributions of different variance. The qualitative results of both measures of return time were the same. Namely, as seen in Fig. 2B, return times decrease with increasing mean community size and decreasing connectance.

Discussion

Robert May's results and subsequent work indicate that large randomly assembled ecosystems tend to be less dynamically stable as they increase in complexity (May 1972, Gilpin 1975, Pimm 1982, Hogg et al. 1989). Specifically, if $\sigma^2 nC > 1$ then the system will almost surely be unstable. Real ecosystems are not randomly constructed, however, but rather gradually assembled through a long series of invasions and extinctions. This is a non-equilibrium situation where – driven by external factors such as weather, species invasion or some other kind of disturbance – the system is constantly changing over time. Our assembly model simulates this process of gradual formation, and thereby builds a more realistic ecosystem.

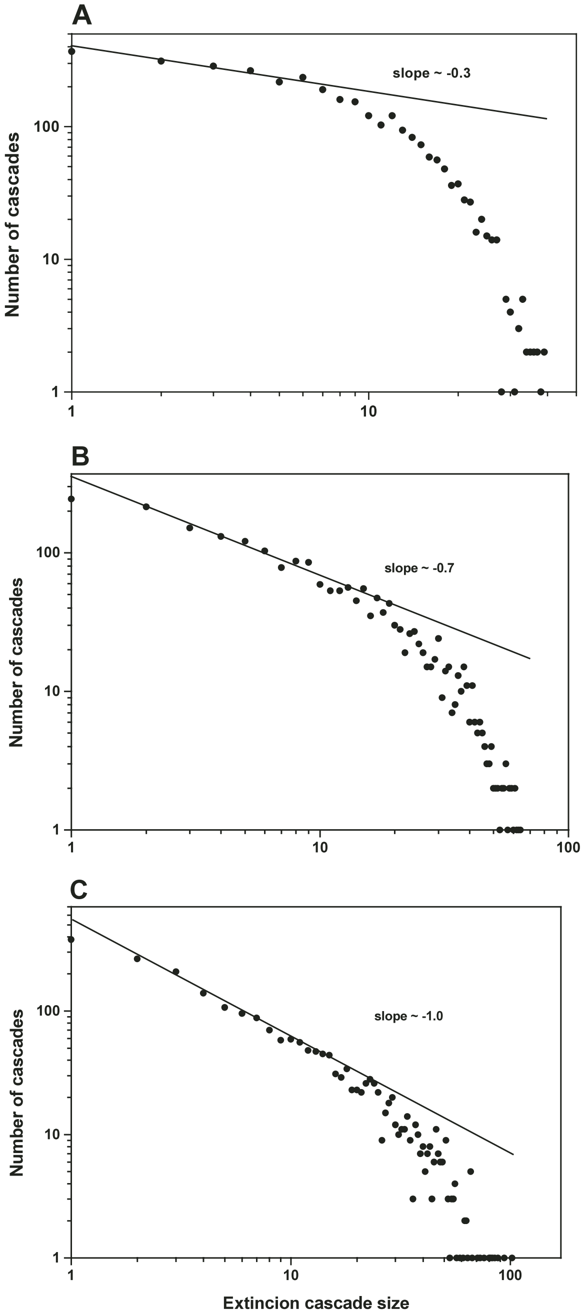

Fig. 3. The distributions of extinction cascades is plotted for communities with a mean of (A) 20 species (B) 52 species and (C) 98 species. Cascade distributions are power law with exponential tails due to the finite size of the system. As community size increases the slope of this power law decreases indicating that the smaller a community gets, the more likely it is to experience large extinctions on a relative basis.

Our model shows the same directional relationship between the variables σ, n and C on community size that May demonstrated on community stability. Because our method of constructing communities progresses according to a specified algorithm that reflects the community assembly process, however, our systems are not subject to the same stability criterion as May. In order to build larger and larger communities, we must decrease mean interaction strength or connectance, but once a community is established, species-rich communities are less variable and return more quickly to mean levels than do less diverse ones.

Our results lend theoretical support to the view, espoused by Charles Elton, that more diverse ecosystems such as those found in the tropics are less prone to large oscillations in species abundance, and hence more stable, than less diverse ecosystems such as those found in the arctic or horticultural fields (Elton 1958). This idea originally received theoretical justification based on the assumption that a multiplicity of predator-prey associations in a community frees it from dramatic changes in abundance when one of the prey or predator species declines in density (MacArthur 1955). May's result, however, ran counter to this argument. Our model corroborates both views. Stronger interactions and increased connectivity lead to smaller communities, yet when the system is diverse and highly connected, it is likely to be less variable than its sparsely connected and less diverse counterpart.

Our focus on CV should give conservation biologists pause. Are we worried about species loss on an absolute basis or on a relative basis? Because large communities have more species, we should expect them to lose more species. The fact that we predict that they will lose less on a percentage basis, however, implies that being large is stabilizing.

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