

Stability of Degree Heterogeneous Ecological Networks

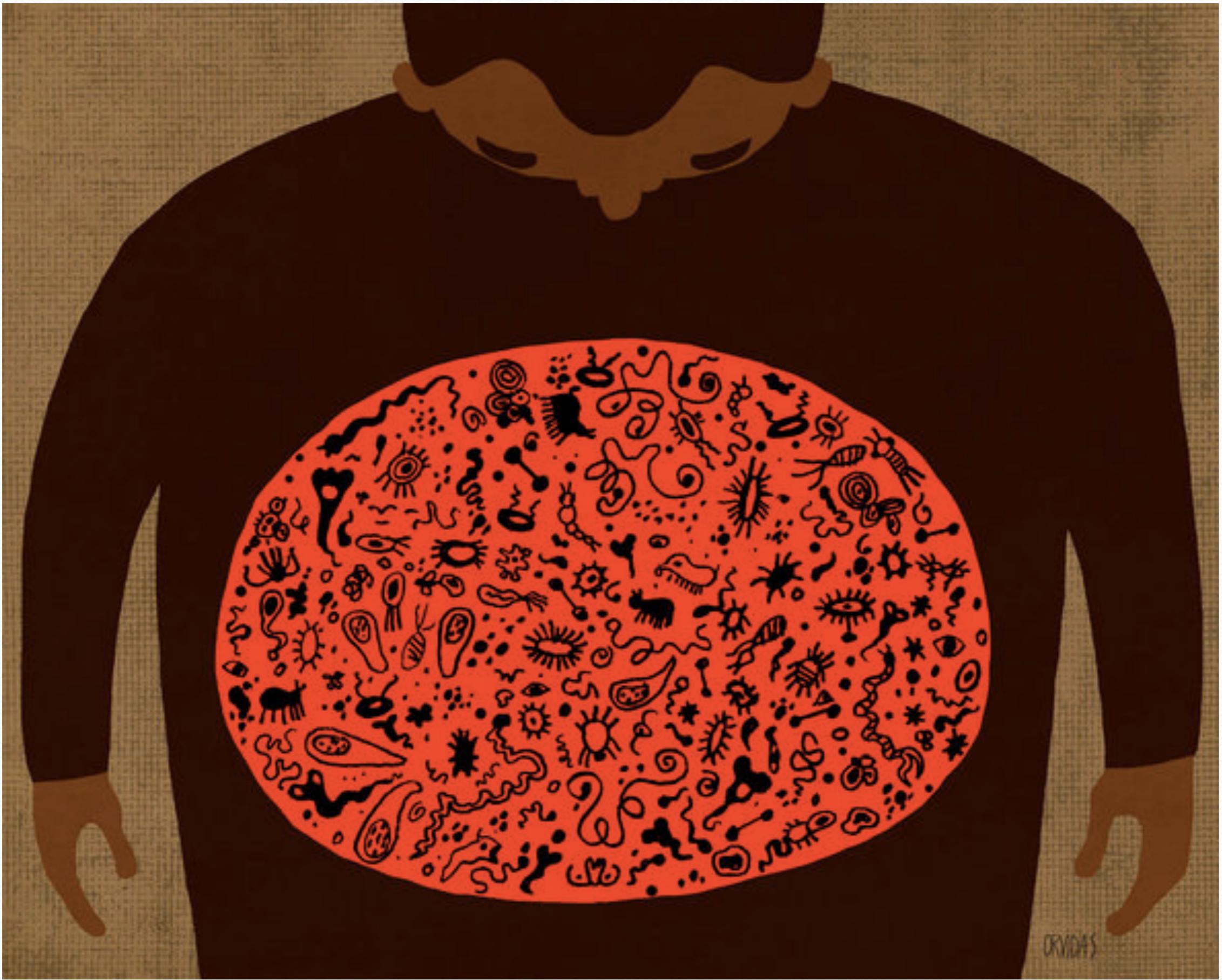
Yang-Yu Liu

*Channing Division of Network Medicine
Brigham and Women's Hospital
Harvard Medical School*



Collaborators: Gang Yan (Northeastern Univ.), Neo Martinez (Univ. of Arizona)
arXiv:1409.4137v3





ORIGAS

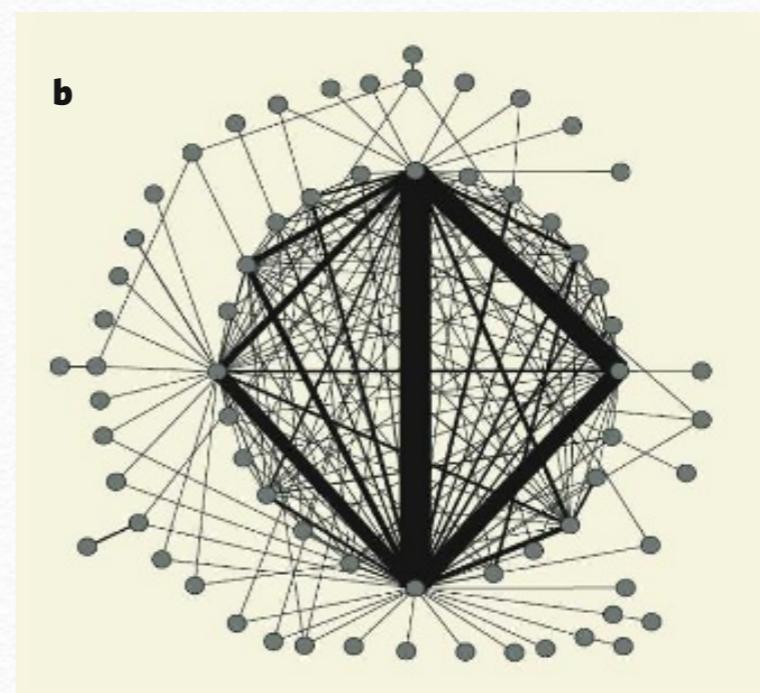
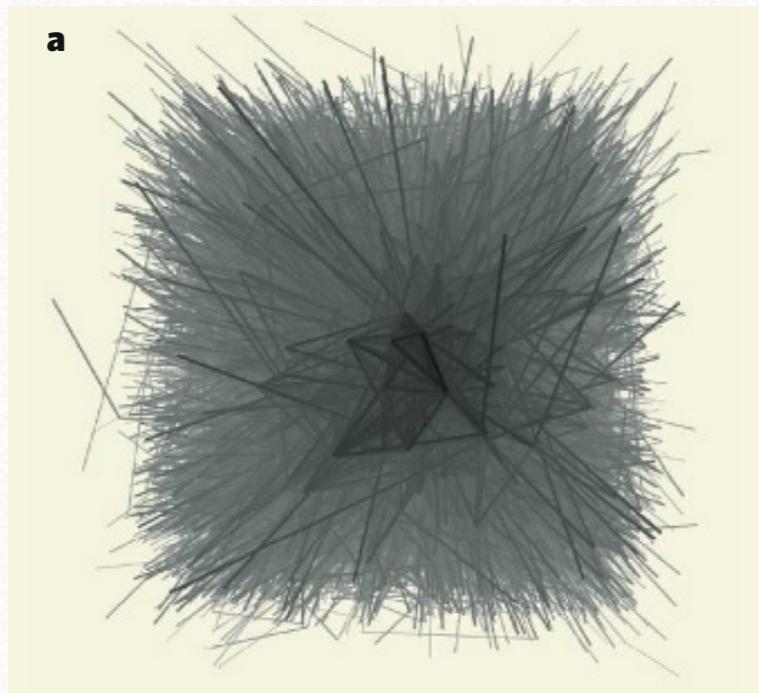
NEWS & VIEWS

COMPLEX SYSTEMS

Ecology for bankers

Robert M. May, Simon A. Levin and George Sugihara

There is common ground in analysing financial systems and ecosystems, especially in the need to identify conditions that dispose a system to be knocked from seeming stability into another, less happy state.



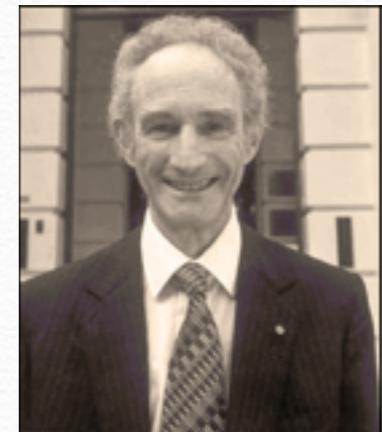
The Fedwire interbank payment network

Diversity–Stability Paradox

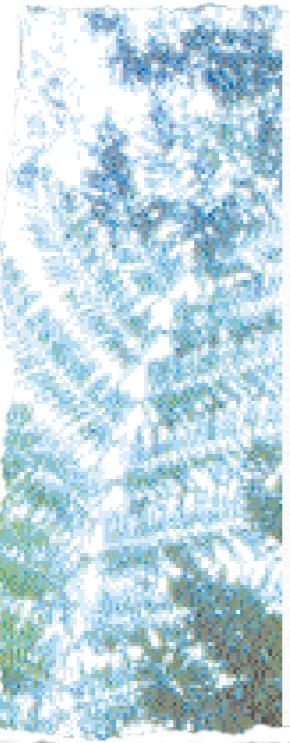
Before the 1970s, ecologists believed that more diverse communities enhanced ecosystem stability.

Simple communities were more easily upset than that of richer ones; that is, more subject to destructive oscillations in populations, and more vulnerable to invasions.

These early intuitive ideas were challenged by the theoretical work of Robert May in 1973, who found that diversity tends to destabilize community dynamics.



Yet, real ecosystems are undoubtedly complex and diverse.



insight review articles

The diversity–stability debate

Kevin Shear McCann

1205 Docteur Penfield Avenue, Department of Biology, McGill University, Montreal, Quebec, Canada H3A 1B1

There exists little doubt that the Earth's biodiversity is declining. The Nature Conservancy, for example, has documented that one-third of the plant and animal species in the United States are now at risk of extinction. The problem is a monumental one, and forces us to consider in depth how we expect ecosystems, which ultimately are our life-support systems, to respond to reductions in diversity. This issue — commonly referred to as the diversity–stability debate — is the subject of this review, which synthesizes historical ideas with recent advances. Both theory and empirical evidence agree that we should expect declines in diversity to accelerate the simplification of ecological communities

McCann, *Nature* (2000)

REVIEW

Stability and Diversity of Ecosystems

Anthony R. Ives¹ and Stephen R. Carpenter²

Understanding the relationship between diversity and stability requires a knowledge of how species interact with each other and how each is affected by the environment. The relationship is also complex, because the concept of stability is multifaceted; different types of stability describing different properties of ecosystems lead to multiple diversity-stability relationships. A growing number of empirical studies demonstrate positive diversity-stability relationships. These studies, however, have emphasized only a few types of stability, and they rarely uncover the mechanisms responsible for stability. Because anthropogenic changes often affect stability and diversity simultaneously, diversity-stability relationships cannot be understood outside the context of the environmental drivers affecting both. This shifts attention away from diversity-stability relationships toward the multiple factors, including diversity, that dictate the stability

perturbations occur rarely, stability can be measured by the rate at which the system returns to equilibrium (15). If shocks occur frequently and stochastically, the impact of these shocks depends on community resistance (5), which can be measured by the variability in the change in combined densities, from one time point to the next, caused by repeated shocks. These two concepts of stability—the rate of return to equilibrium, and the change in combined densities in response to repeated shocks—together determine a third measure of stability: the overall system variability. For example, a more resistant system is knocked less by environmental shocks, and rapid return rates pull the system more quickly toward its equilibrium, both of which lead to lower overall community variability (16).

Ives & Carpenter, *Science* (2007)

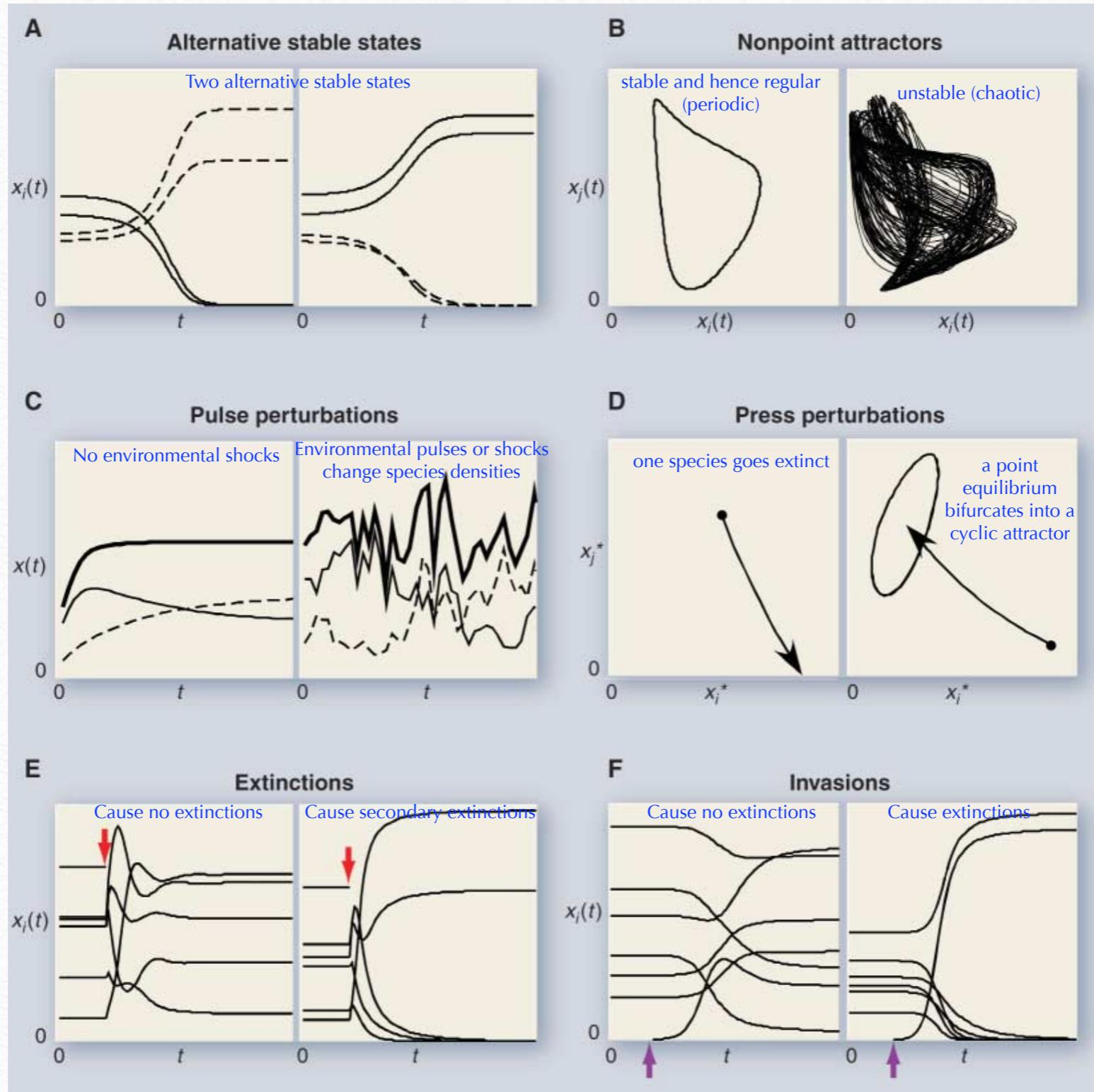
Table S1. Sixty-four diversity-stability relationships as stated by the authors of 52 studies.

First author	Year	Citation	System	Trophic levels	Diversity	Type of stability	Perturbation	Response	Claimed relationship
Directly manipulated diversity									
Allison	2004	(S118)	marine algae	1	spp	resistance	temperature	cover/biomass	0
Arenas	2006	(S119)	marine algae	1	fnct	invasibility	invasion	invader biomass	0
Beisner	2006	(S120)	rock pools	1	spp	invasibility	invasion	success	+
Britton-Simmons	2006	(S121)	seaweed	1	fnct	invasibility	invasion	success	+
Brown	1987	(S122)	forest/crops	1	spp	variability	herbivory	leaf area	+
Caldiera	2005	(S123)	grassland	1	spp	variability	drought	biomass	+
						return time	drought	biomass	0
Craine	2003	(S124)	grassland	1	spp	variability	weather	biomass	+
Crawley	1999	(S125)	grassland	1	spp	invasibility	invasion	success	+
Dimitrakopoulos	2005	(S126)	grassland	1	spp	invasibility	invasion	success	+
Dukes	2001	(S113)	grassland	1	spp/fnct	invasibility	invasion	biomass	+
						impact of invasion	invasion	biomass	+
Fargione	2005	(S127)	grassland	1	spp	invasibility	invasion	biomass/ number	+
France	2006	(S128)	seagrass	2	herbivore spp	variability	weather	biomass	-
Giffiths	2001	(S116)	microbes	?	spp	return time	temperature	CO2 production	0
						press	toxin	CO2 production	0
Gonzalez	2004	(S129)	microbes	2	spp	variability	temperature	biomass	-
Hector	2001	(S130)	grassland	1	spp	invasibility	invasion	success	+
Kennedy	2002	(S131)	grassland	1	spp	invasibility	invasion	success/size	+
Knops	1999	(S132)	grassland	1	spp	invasibility	invasion	success	+
Levine	2000	(S133)	tussock plants	1	spp	invasibility	invasion	success	+
McGrath-Steed	2000	(S115)	microbes	3	spp	variability	none	abundance	+
Morin	2004	(S134)	microbes	4	spp	variability	none	CO2 production	+
Mulder	2001	(S135)	mosses	1	spp	resistance	drought	biomass	+
Petchey	1999	(S117)	microbes	3	spp/fnct	press	temperature	productivity	0
						press	temperature	number of species	0
Petchey	2002	(S136)	microbes	1	spp	variability	temperature	biomass	0
Pfisterer	2002	(S137)	grassland	1	spp	resistance	drought	biomass	-
						return time	drought	biomass	-
Prieur-Richard	2000	(S138)	grassland	1	spp/fnct	invasibility	invasion	biomass/fecundity	+

Romanuk	2006	(S139)	rock pools	1?	spp	variability	none	abundance	0
Stachowitz	1999	(S98)	intertidal	1	spp	invasibility	invasion	success	+
Steiner	2005	(S140)	microbes	4	spp	variability	none	biomass	+
Steiner	2006	(S141)	microbes	4	spp	return time	dilution	biomass	+
Symstad	2000	(S142)	grassland	1	fnct	invasibility	invasion	success	+
Tilman	2006	(S143)	grassland	1	spp	variability	weather	biomass	+
van Ruijven	2003	(S144)	grassland	1	spp	invasibility	invasion	# spp/density	+
von Holle	2005	(S145)	herbs	1	spp	invasibility	invasion	success	0
Wardle	2000	(S146)	plants	2	spp/fnct	resistance	drought	numerous	0
Zalalata	2004	(S147)	grassland	1	spp	invasibility	invasion	biomass/fecundity	+
Zhang	2006	(S148)	algae	1	spp	resistance	temperature	biomass	-
Zhang	2006	(S149)	algae	1	spp	variability	none	biomass	+
Indirectly manipulated diversity									
Bai	2004	(S150)	grassland	1	spp	variability	climate	biomass	+
Dodd	1994	(S151)	grassland	1	spp	variability	weather	biomass	+
Frank	1991	(S152)	grassland	1	index	resistance	drought	biomass	+
Giffiths	2000	(S112)	microbes	?	spp/fnct?	return time	temperature	CO2 production	+
						press	toxin	CO2 production	+
Hurd	1971	(S153)	old field	3	spp	resistance	fertilizer	plant biomass	+
								insect numbers	-
Kahmen	2005	(S154)	grassland	1	spp	resistance	drought	productivity	+
Leps	2004	(S155)	meadow	1	spp/index	variability	extinction	biomass	0
						variability	nutrient	biomass	+
MacDougall	2005	(S156)	grassland	1	spp	invasibility	fire	success	+
						return time	fire	light	+
McNaughton	1977	(S157)	grassland	1	index	return time	drought	biomass	+
						return time	grazing	biomass	+
Mellinger	1975	(S158)	grassland	1	index	resistance	nutrients	biomass	+
Robinson	1995	(S159)	grassland	1	spp	invasibility	invasion	success	-
Rodriquez	1994	(S160)	grassland	1	index	resistance	drought	biomass	-
Tilman	1996	(S55)	grassland	1	spp	variability/resistance	none/drought	biomass	+
						return time	drought	biomass	+
Tilman	1997	(S161)	grassland	1	spp/fnct	invasibility	invasion	success	+
Valone	2003	(S162)	desert plants	1	spp	variability	none	number	+

Concept of Stability is Multifaceted

What's the total number of alternative stable states?
fewer => more stable.



whether its attractor is periodic or chaotic?

What's the overall system variability under environmental shocks?

When an extinction occurs, what's the number of other species that go secondarily extinct?

Whether it can sustain greater press perturbations before its dynamics undergoes a qualitative change?

When invasions occur, what's the number of extinctions it causes if it is successful?

Difficulty: Parameterization

Empirical parameterization of the exact functional form of the dynamics $f(x(t))$ is rather difficult for complex ecosystems.

$$\dot{\mathbf{x}}(t) = \mathbf{f}(\mathbf{x}(t))$$

Generalized Lotka-Volterra model

$$\dot{x}_i = x_i(b_i + \sum_{j=1}^S a_{ij}x_j)$$

b_i is the intrinsic growth rate of the i -th species and a_{ij} is the per capita effect of the j -th species on the i -th species and are the elements of the per capita interaction matrix $\mathbf{A} = [a_{ij}]$.

How did May resolve the parameterization issue in 1973?

- 1. Linear Stability Analysis**
- 2. Random Community Matrix**

May's Approach

1. Linear Stability Analysis

- Consider a **unspecified** dynamical system describing the time-dependent abundance $\mathbf{x}(t)$ of the S species.
- **Linearization:** Linearize $\mathbf{f}(\mathbf{x})$ around a feasible equilibrium point \mathbf{x}^* . The corresponding Jacobian matrix is called the community matrix (\mathbf{M}), with M_{ij} captures the impact that species j has on species i around the equilibrium point .
- **Stability Criterion:** If all the eigenvalues of \mathbf{M} have negative real part (i.e., \mathbf{M} is Hurwitz), then the equilibrium point is stable: the system will return to \mathbf{x}^* after a small perturbation away from \mathbf{x}^* .

$$\dot{\mathbf{x}}(t) = \mathbf{f}(\mathbf{x}(t))$$

$$M_{ij} \equiv \frac{\partial f_i(\mathbf{x})}{\partial x_j} \Big|_{\mathbf{x}^*}$$

$$\text{Re}(\lambda_i^{\mathbf{M}}) < 0, \forall i \in [1, S]$$

May's Approach

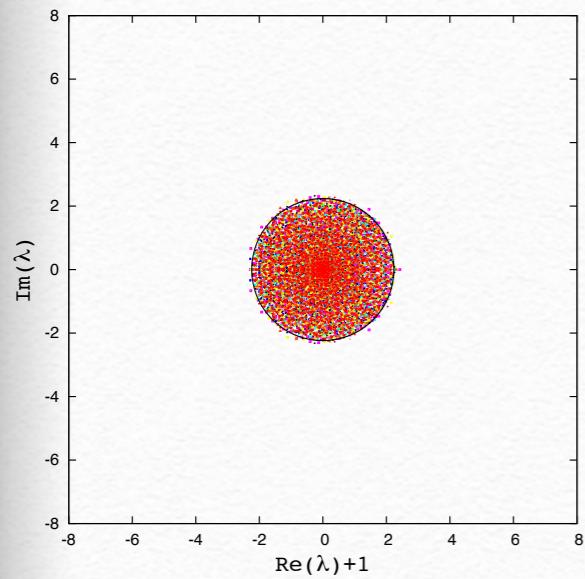
2. Random Community Matrix

-1	0	X	X	0	X	0	X	0	X	X
0	-1	X	0	0	X	0	X	0	0	0
0	X	-1	0	X	X	X	0	X	X	0
X	0	X	-1	0	0	X	0	0	X	X
X	X	0	0	-1	X	0	X	X	0	X
0	0	X	0	X	-1	X	0	X	X	0
X	X	0	0	X	0	-1	X	X	0	X
X	0	X	0	X	X	0	-1	0	X	0
0	X	0	X	0	X	0	X	-1	X	0
0	X	X	0	X	0	X	0	X	-1	X
X	X	0	0	0	X	0	X	X	0	-1

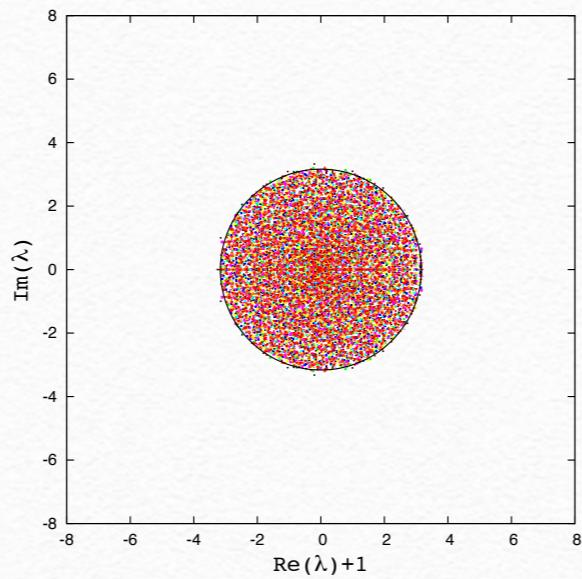
- Diagonal elements M_{ii} are chosen to be $-d=-1$, representing the intrinsic damping time scale of each species.
- Off-diagonal elements M_{ij} are randomly drawn from a distribution with mean 0 and variance σ^2 with probability C and are 0 otherwise.

Eigenvalues of Community Matrix

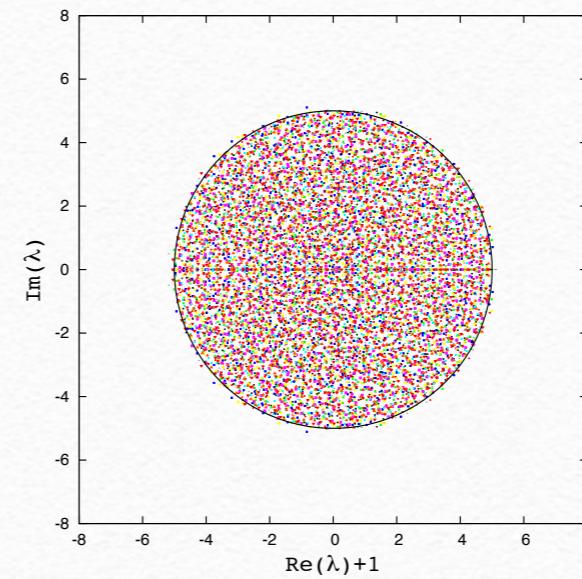
$S=1000$, $X \sim \mathcal{N}(0, \sigma^2)$ with $\sigma=1$



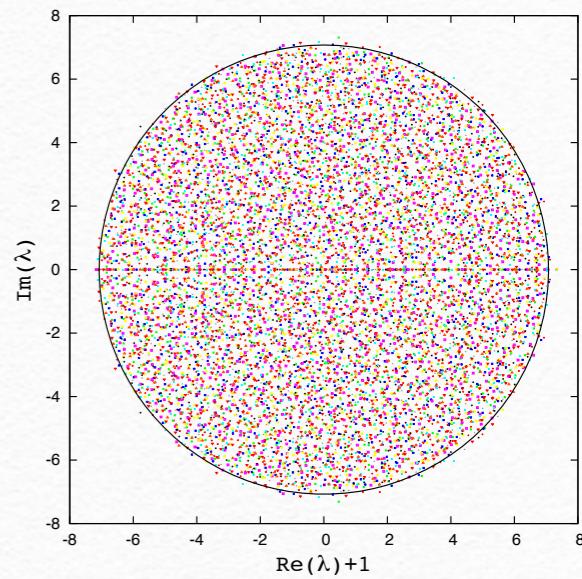
$C=0.005$



$C=0.01$



$C=0.025$



$C=0.05$

$$\text{Re}(\lambda_{\max}) + d = \sqrt{SC}\sigma$$

Stability Criterion: $\text{Re}(\lambda_{\max}) < 0 \Rightarrow \boxed{\sqrt{SC} < \theta = d/\sigma}$

Diversity and connectivity tend to destabilize ecosystem.

Circular Law

(fully connected limit: $C=1$)

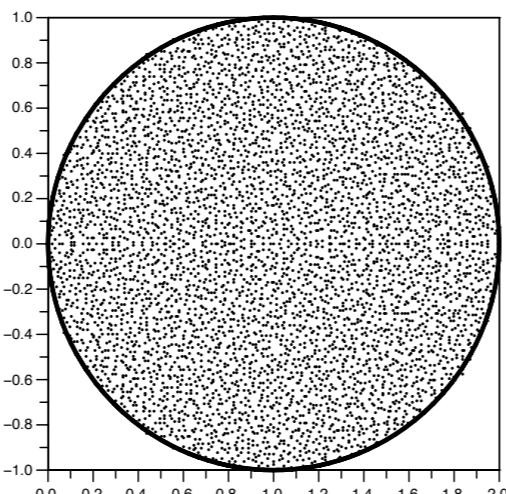
Girko's circular law (1985): Consider a random $S \times S$ real matrix \mathbf{A} with entries independent and taken randomly from normal distribution $\mathcal{N}(0, \sigma^2)$. Then as $S \rightarrow \infty$, the eigenvalues of $\mathbf{A}/\sqrt{S\sigma^2}$ is uniformly distributed on the unit disk centered at $(0,0)$ in the complex plane.

Girko, Theor. Probab. Appl. (1985)

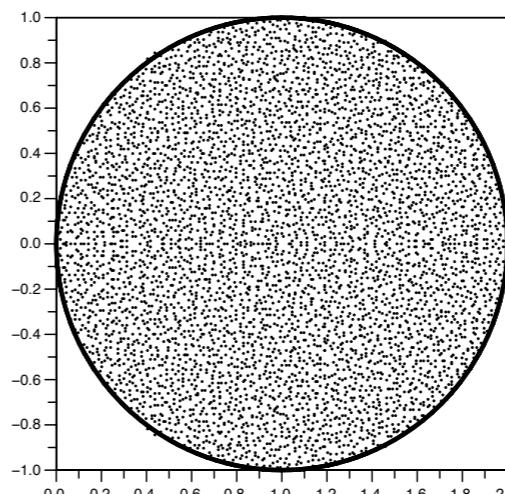
Tao et. al. (2010): Consider a random $S \times S$ real matrix \mathbf{A} with entries independent and taken randomly from a distribution with mean 0 and bounded variance σ^2 . Then as $S \rightarrow \infty$, the eigenvalues of $\mathbf{A}/\sqrt{S\sigma^2}$ is uniformly distributed on the unit disk centered at $(0,0)$ in the complex plane.

Tao, et al., Ann. Prob. (2010)

Bernoulli



Gaussian



Elliptic Law

(fully connected limit: C=1)

Consider a $S \times S$ matrix \mathbf{A} with $A_{ii} = 0$, and off-diagonal elements follow a normal distribution with

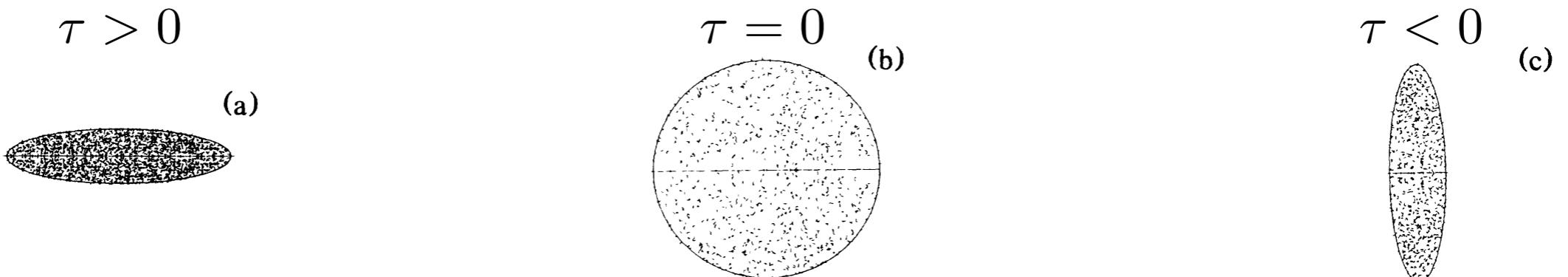
$$\mathbb{E}(A_{ij})_{i \neq j} = 0 \quad (1)$$

$$\text{Var}(A_{ij})_{i \neq j} = 1/S \quad (2)$$

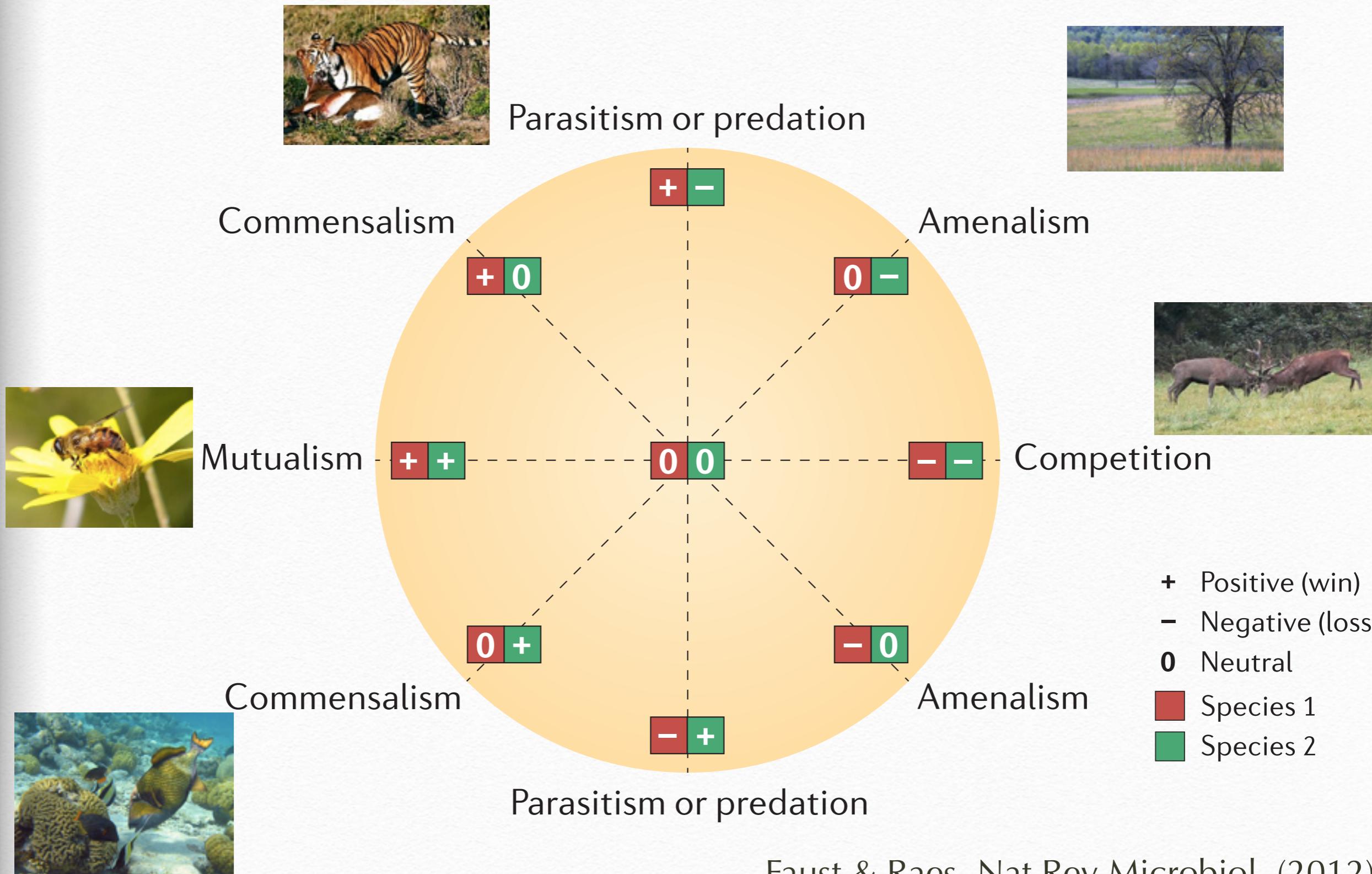
$$\mathbb{E}(A_{ij}A_{ji})_{i \neq j} = \tau/S \quad (3)$$

and $\tau := \mathbb{E}(A_{ij}A_{ji})_{i \neq j}/\text{Var}(A_{ij})_{i \neq j}$. In the limit of $S \rightarrow \infty$, the eigenvalues of \mathbf{A} , $\lambda = x + iy$, are uniformly distributed in an ellipse

$$(x/a)^2 + (y/b)^2 = 1, \quad \text{with } a = 1 + \tau, b = 1 - \tau \quad (4)$$



Ecological Interactions



Stability criteria for complex ecosystems

Stefano Allesina^{1,2} & Si Tang¹

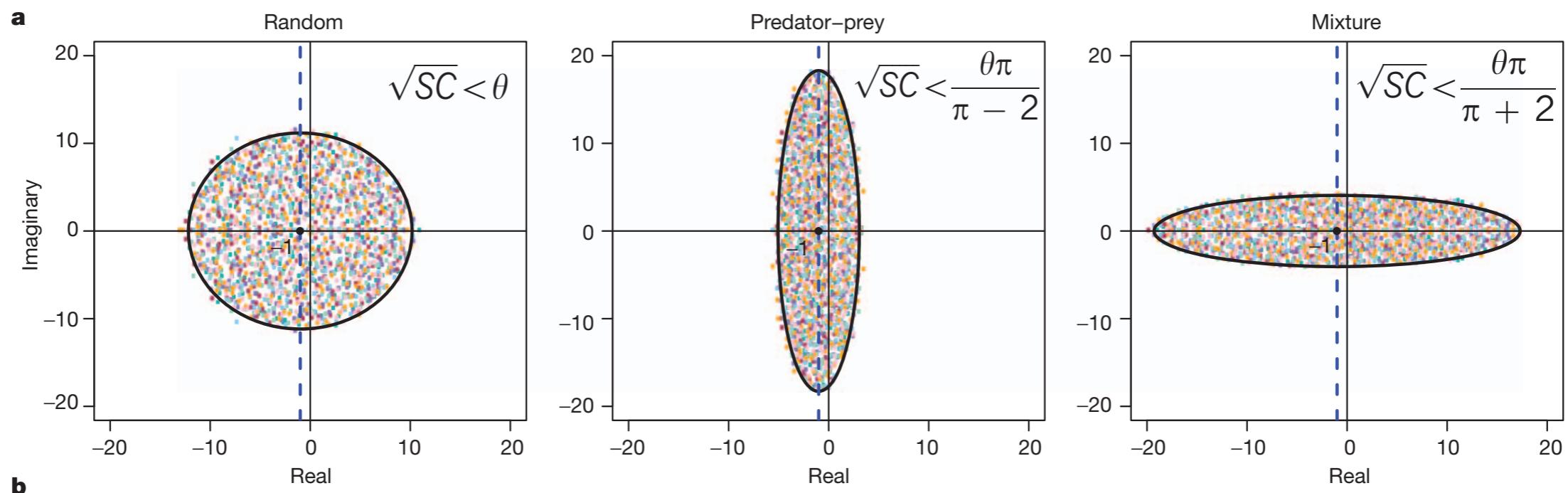
Forty years ago, May proved^{1,2} that sufficiently large or complex ecological networks have a probability of persisting that is close to zero, contrary to previous expectations^{3–5}. May analysed large networks in which species interact at random^{1,2,6}. However, in natural systems pairs of species have well-defined interactions (for example predator-prey, mutualistic or competitive). Here we extend May's results to these relationships and find remarkable differences between predator-prey interactions, which are stabilizing, and mutualistic and competitive interactions, which are destabilizing. We provide analytic stability criteria for all cases. We use the criteria to prove that, counterintuitively, the probability of stability for predator-prey networks decreases when a realistic food web structure is imposed^{7,8} or if there is a large preponderance of weak interactions^{9,10}. Similarly, stability is negatively affected by nestedness^{11–14} in bipartite mutualistic networks. These results are found by separating the contribution of network structure and interaction strengths to stability. Stable predator-prey networks can be arbitrarily large and complex, provided that predator-prey pairs are tightly coupled. The stability criteria are widely applicable, because they hold for any system of differential equations.

$\text{Var}(X) = \sigma^2$. The diagonal elements of the community matrix, representing self-regulation, are set to $-d$. For large systems, the eigenvalues are contained in a circle¹⁸ in the complex plane (Fig. 1 and Supplementary Information). The circle is centred at $(-d, 0)$ and the radius is $\sigma\sqrt{SC}$. In stable systems, the whole circle is contained in the left half-plane (that is, all eigenvalues have negative real parts). Thus, the system is stable when the radius is smaller than d : $\sqrt{SC} < \theta = d/\sigma$.

In predator-prey networks, interactions come in pairs with opposite signs: whenever $M_{ij} > 0$, then $M_{ji} < 0$. With probability C , we sample one interaction strength from the distribution of $|X|$ and the other from $-|X|$, whereas with probability $(1 - C)$ both are zero. The eigenvalues of large predator-prey matrices are contained in a vertically stretched ellipse¹⁹, centred at $(-d, 0)$, with horizontal radius $\sigma\sqrt{SC}(1 - \mathbb{E}^2(|X|)/\sigma^2)$ and thus the stability criterion is $\sqrt{SC} < \theta/(1 - \mathbb{E}^2(|X|)/\sigma^2)$ (Fig. 1 and Supplementary Information).

When we constrain M_{ij} and M_{ji} to have the same sign, and thus impose a mixture of competition and mutualism with equal probability, the eigenvalues are enclosed in a horizontally stretched ellipse¹⁹ and the criterion becomes $\sqrt{SC} < \theta/(1 + \mathbb{E}^2(|X|)/\sigma^2)$ (Fig. 1 and Sup-

Stability criteria for complex ecosystems



- Predator-prey interactions is **stabilizing**.
- Competitive and mutualistic interactions are **destabilizing**.

What else can we do?

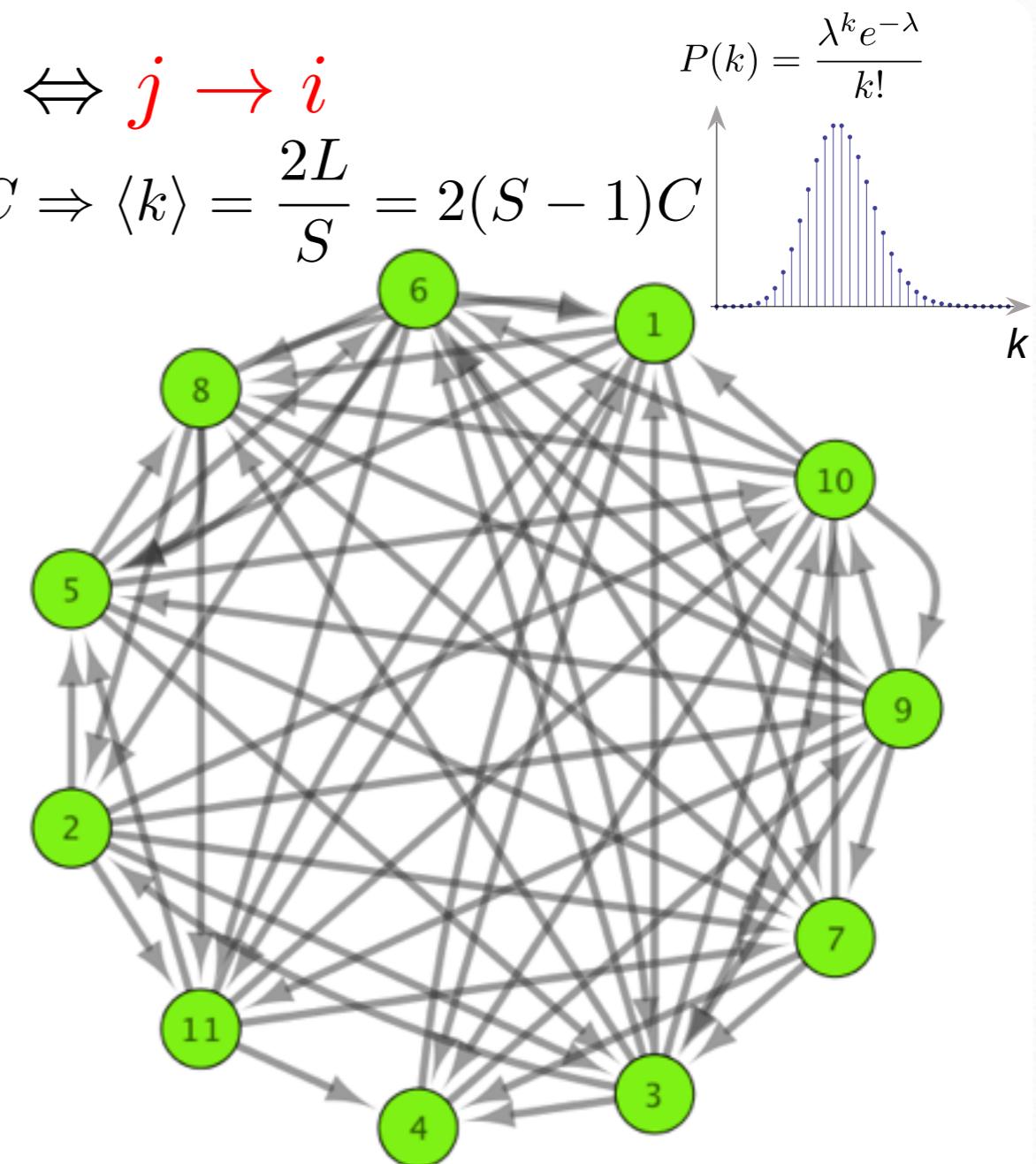
What else can we do?

Off-diagonal elements M_{ij} are randomly drawn from a distribution with mean 0 and variance σ^2 with probability C and are 0 otherwise.

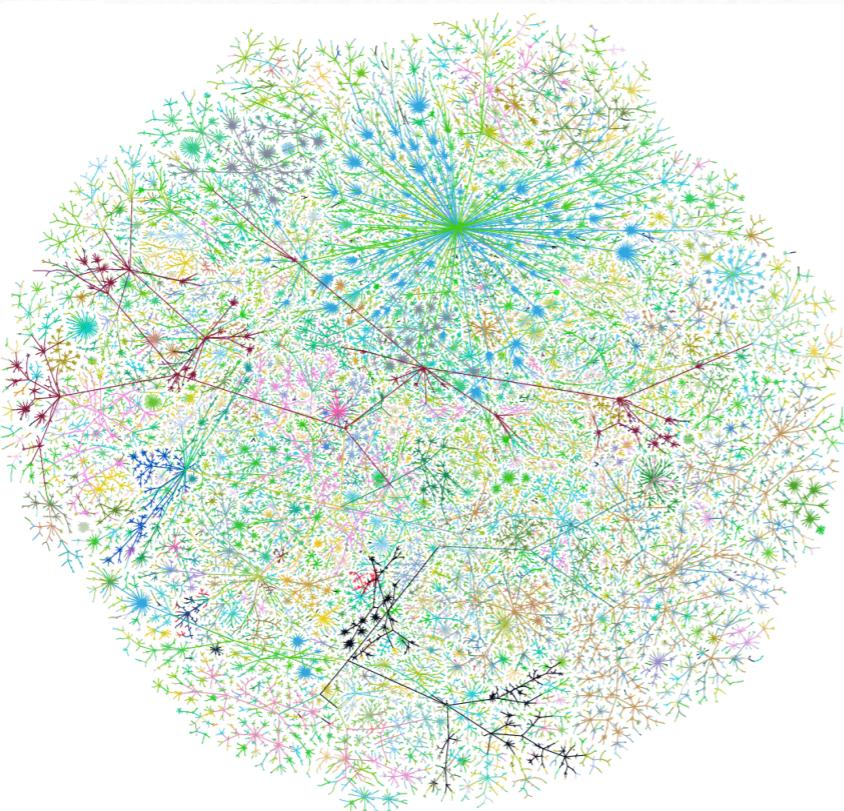
$$M_{ij} \neq 0 \Leftrightarrow j \rightarrow i$$

$$L = S(S - 1) \cdot C \Rightarrow \langle k \rangle = \frac{2L}{S} = 2(S - 1)C$$

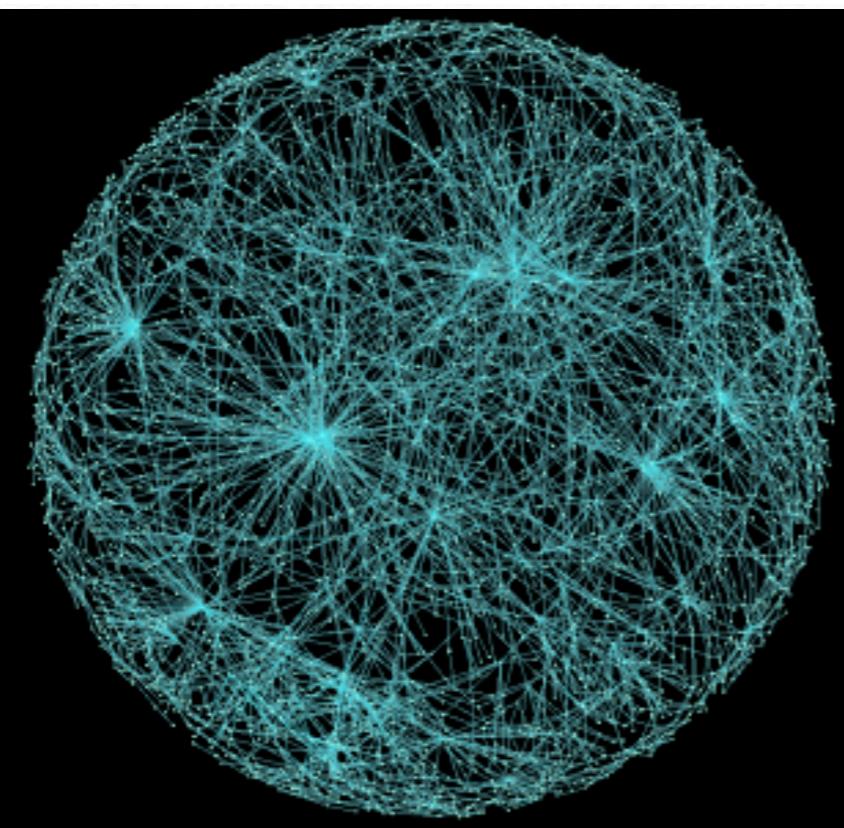
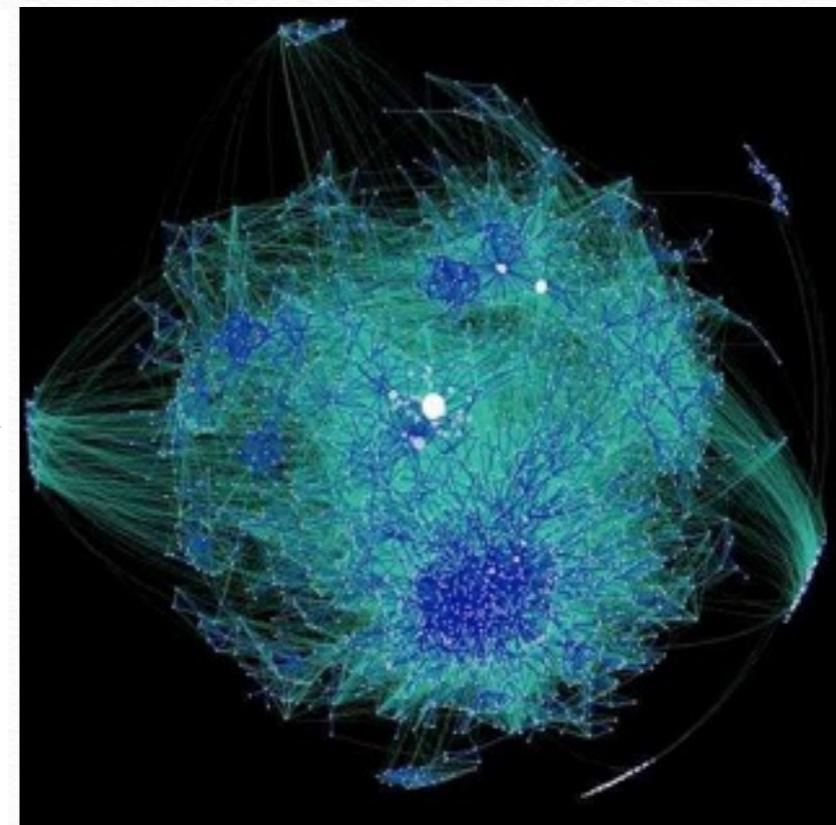
-1	0	X	X	0	X	0	X	0	X	X
0	-1	X	0	0	X	0	X	0	0	0
0	X	-1	0	X	X	X	0	X	X	0
X	0	X	-1	0	0	X	0	0	X	X
X	X	0	0	-1	X	0	X	X	0	X
0	0	X	0	X	-1	X	0	X	X	0
X	X	0	0	X	0	-1	X	X	0	X
X	0	X	0	X	X	0	-1	0	X	0
0	X	0	X	0	X	0	X	-1	X	0
0	X	X	0	X	0	X	0	X	-1	X
X	X	0	0	0	X	0	X	X	0	-1



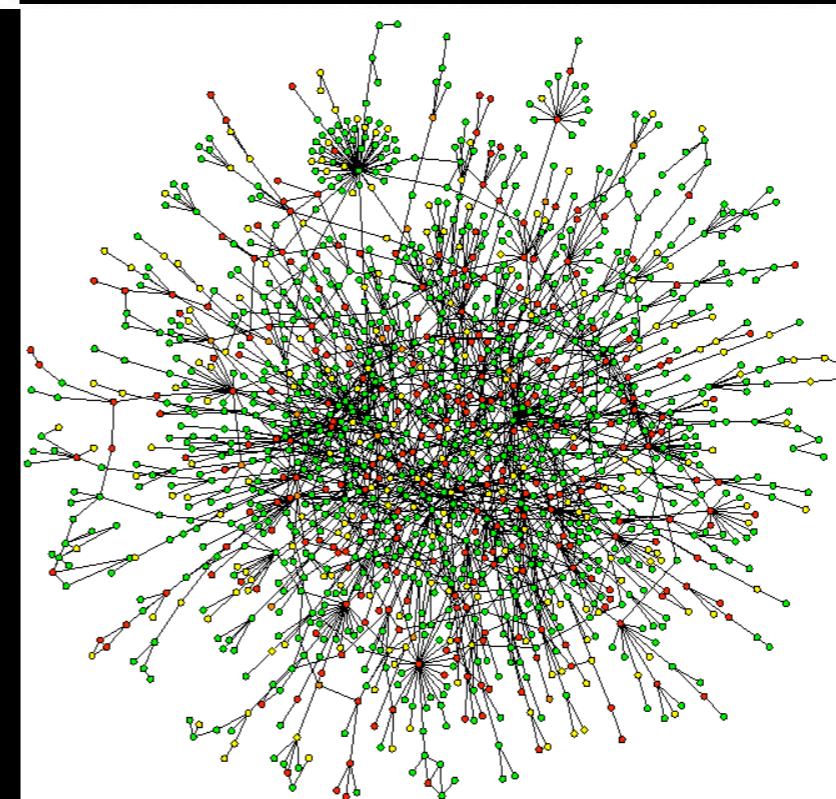
Internet



World wide web



Metabolic Network



Protein Interaction Network

Degree Heterogeneity Matters!

- **Network Robustness**

We remove a fraction f of the nodes. At what threshold f_c will the network fall apart (no giant component)?

Breakdown threshold

$$f_c = 1 - \frac{1}{\frac{\langle k^2 \rangle}{\langle k \rangle} - 1}$$

- **Spreading Phenomenon**

λ : effective spreading rate

$\lambda > \lambda_c$: outbreak; $\lambda < \lambda_c$: die out

Epidemic threshold

$$\lambda_c = \frac{\langle k \rangle}{\langle k^2 \rangle}$$

For scale-free networks ($P(k) \sim k^{-\gamma}$),
in the thermodynamic limit ($N \rightarrow \infty$),

$$\langle k^2 \rangle \rightarrow \infty \text{ for } \gamma < 3 \Rightarrow \lambda_c \rightarrow 0 \text{ and } f_c \rightarrow 1.$$

Albert, Jeong & Barabási, *Nature* (2000)

Cohen et al., *PRL* (2000)

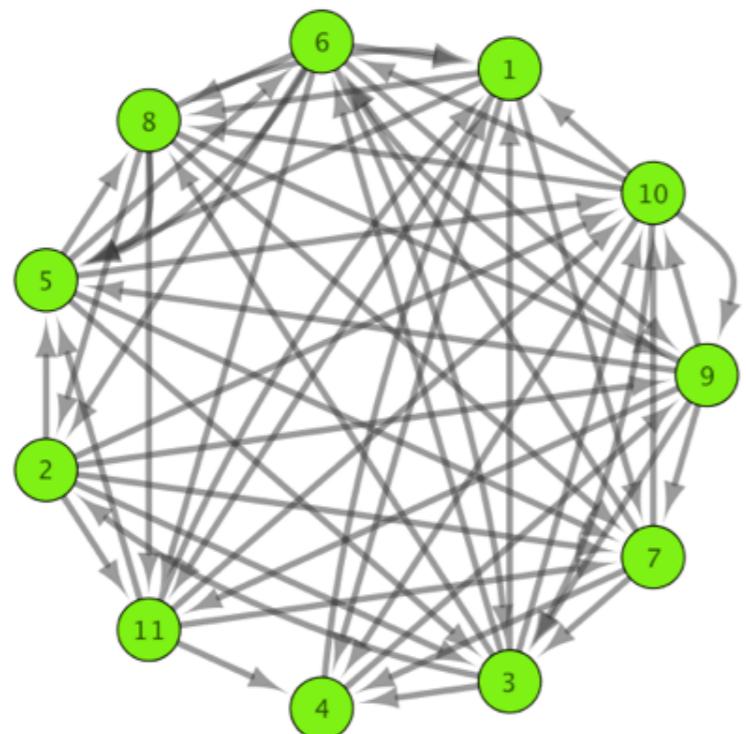
Pastor-Satires et al., *PRL* (2001)

How does degree heterogeneity affect the stability of complex ecosystem?

- 1. Linear Stability Analysis**
- 2. Construct community matrix from network models with prescribed degree distributions and specific interaction types**

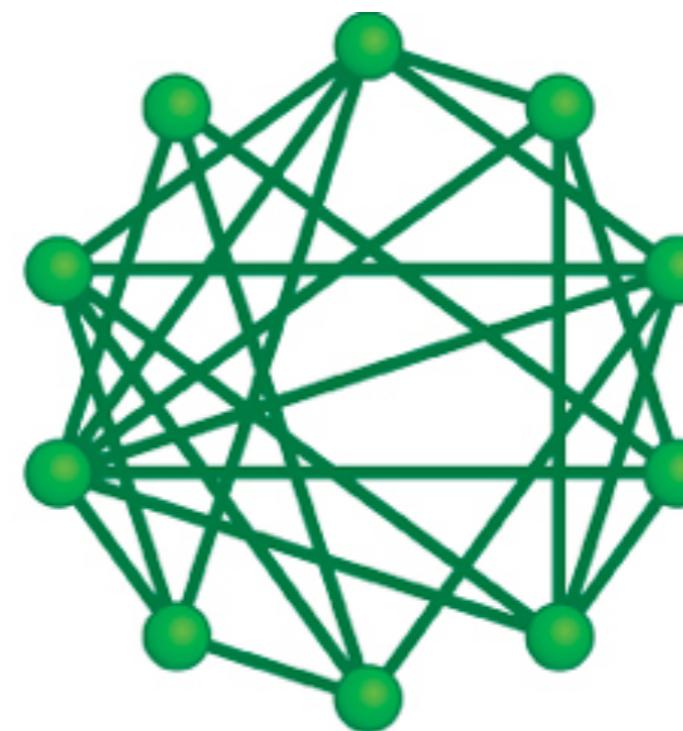
How to construct community matrix from network models with given degree distributions and interaction types?

For ecosystems with **random interactions**, we generated **directed networks first**, and then construct the community matrix accordingly.



$$i \xrightarrow{M_{ji}} j$$

For ecosystems with **predator-prey, competitive, or mutualistic interactions**, we generated **undirected networks first**, and then split each edge into a bidirectional edge, and finally construct the community matrix accordingly.

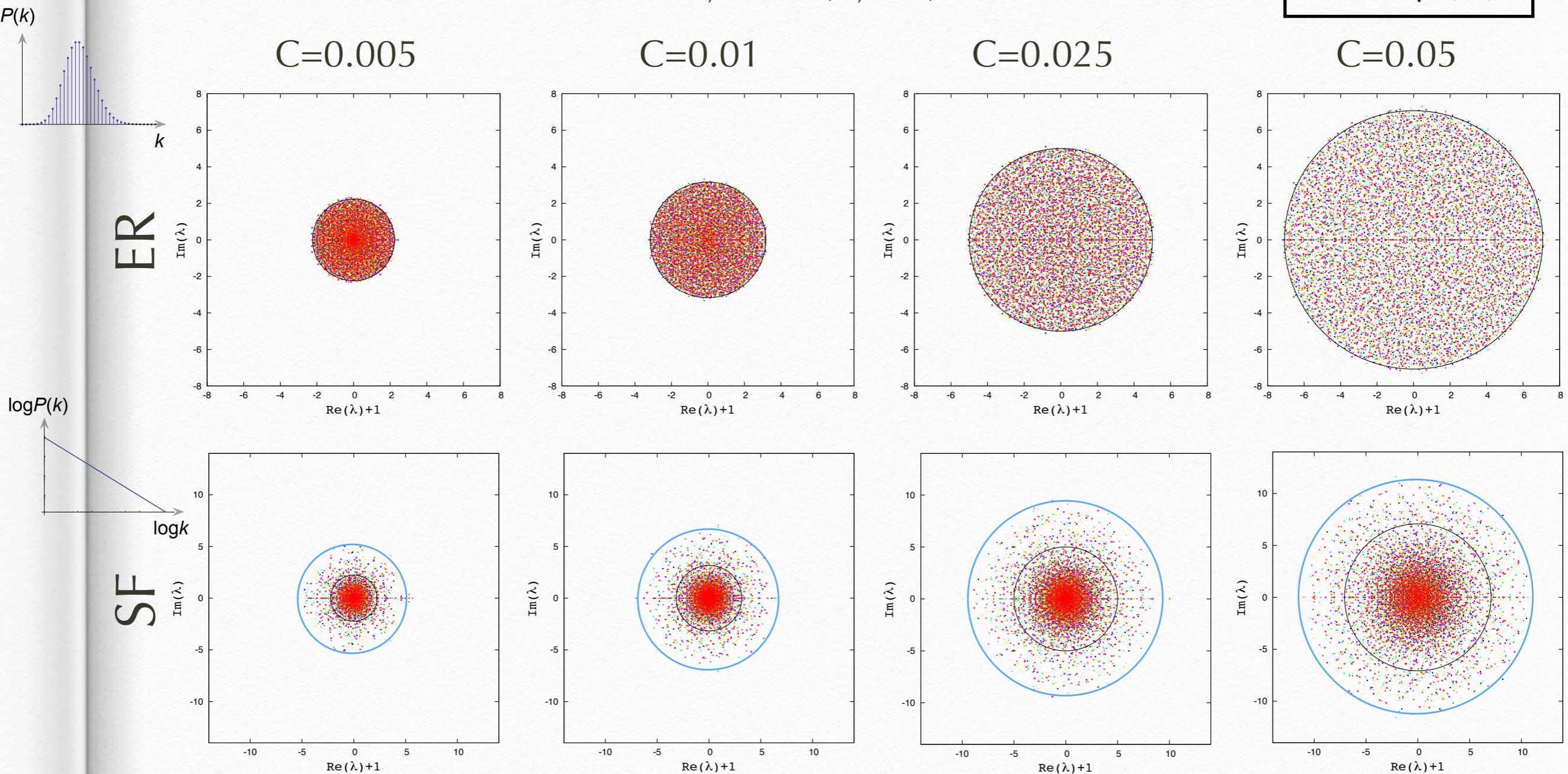


$$i - j \quad \text{means} \quad i \xrightleftharpoons[M_{ij}]{} j$$

Random Interactions

$S=1000$, $X \sim N(0, \sigma^2)$ with $\sigma=1$

$$r \sim \sigma \sqrt{CS}$$

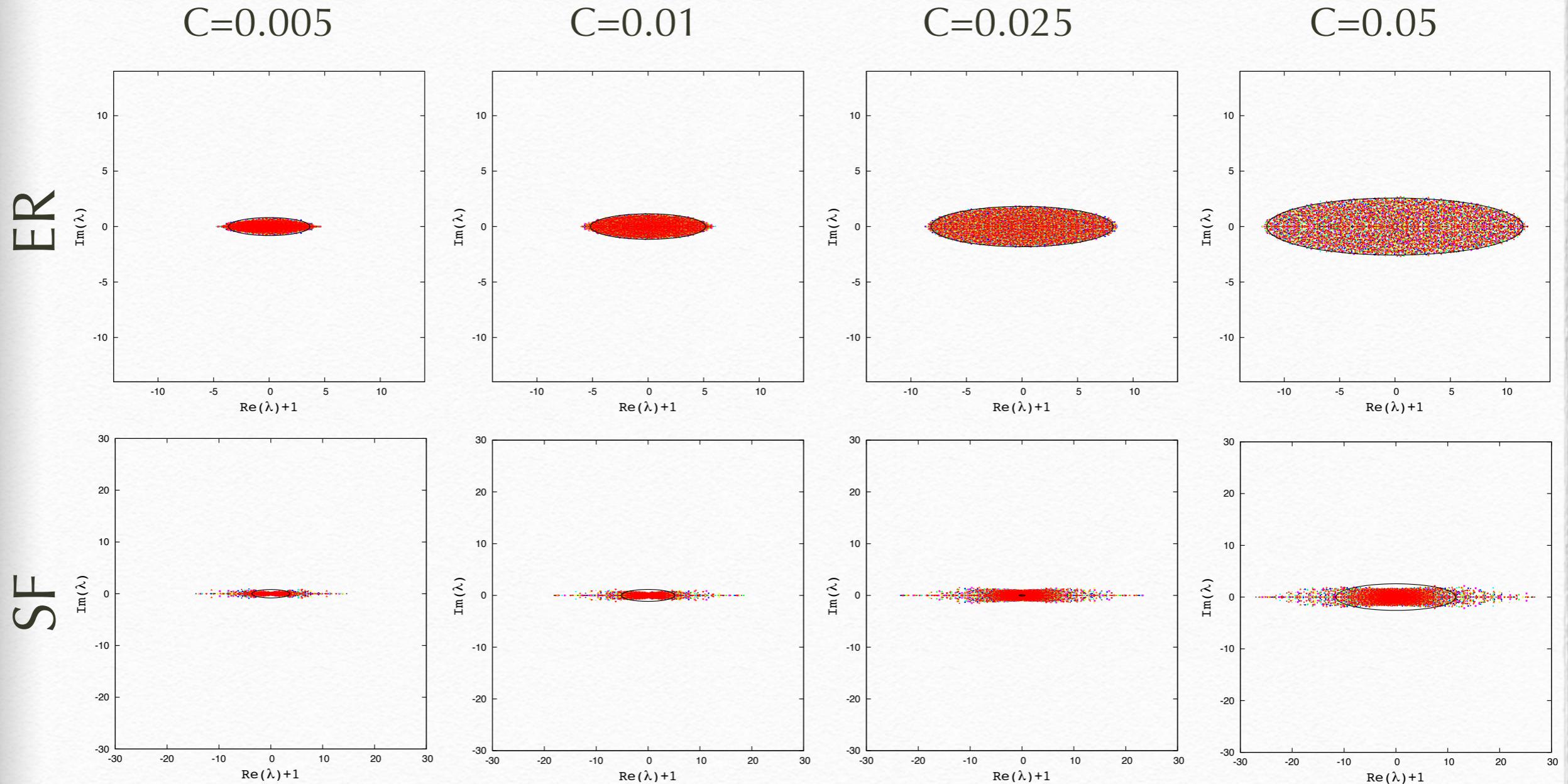


Degree heterogeneity destabilizes
ecosystems with random interactions.

$$r \sim \sigma \sqrt{\xi CS} \quad \xi = \frac{\langle k^2 \rangle}{\langle k \rangle^2}$$

Mixture of Competitive and Mutualistic Interactions

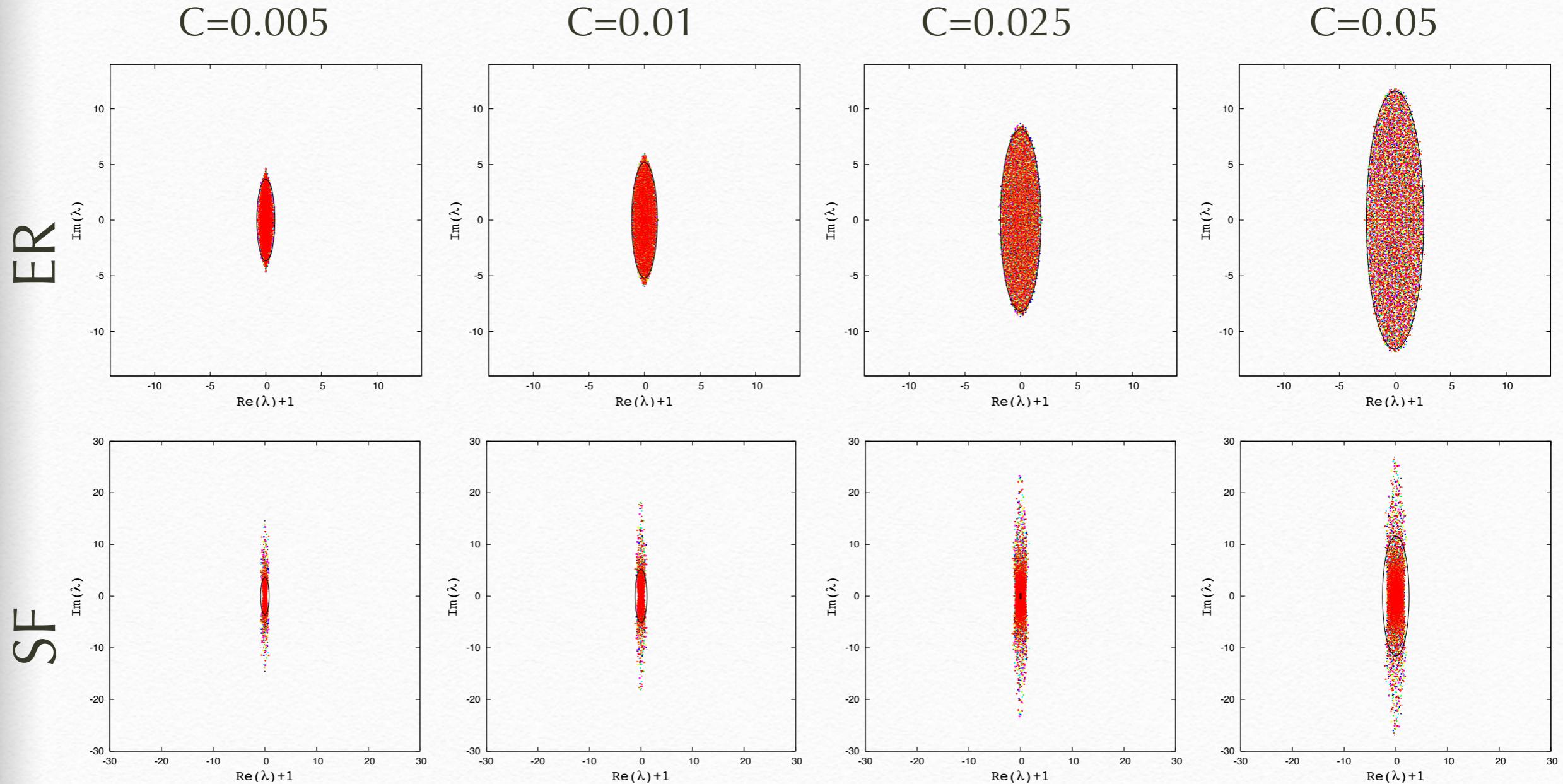
$S=1000$, $X \sim N(0, \sigma^2)$ with $\sigma=1$



Degree heterogeneity destabilizes ecosystems with a mixture of competitive and mutualistic interactions!

Predator-Prey Interactions

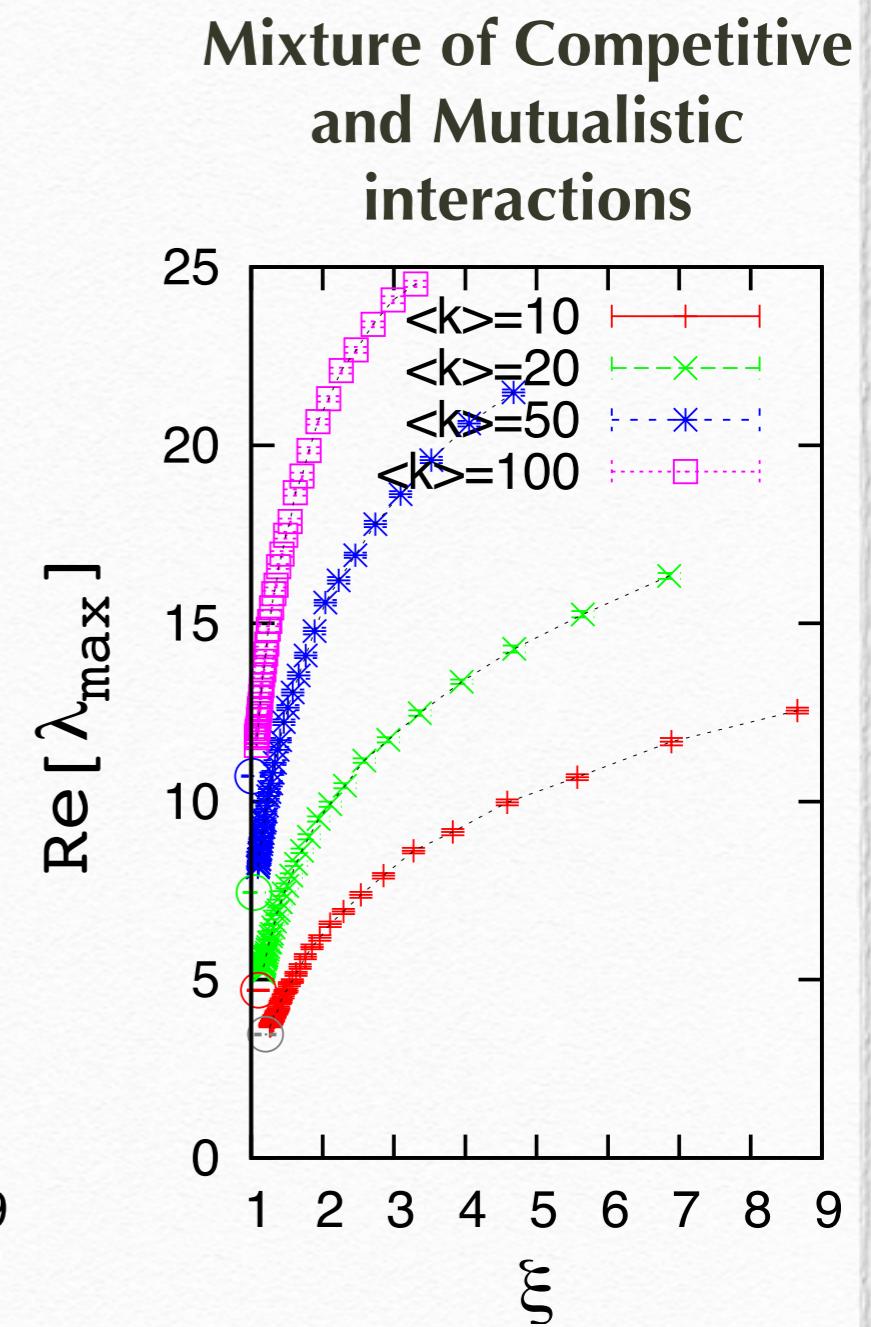
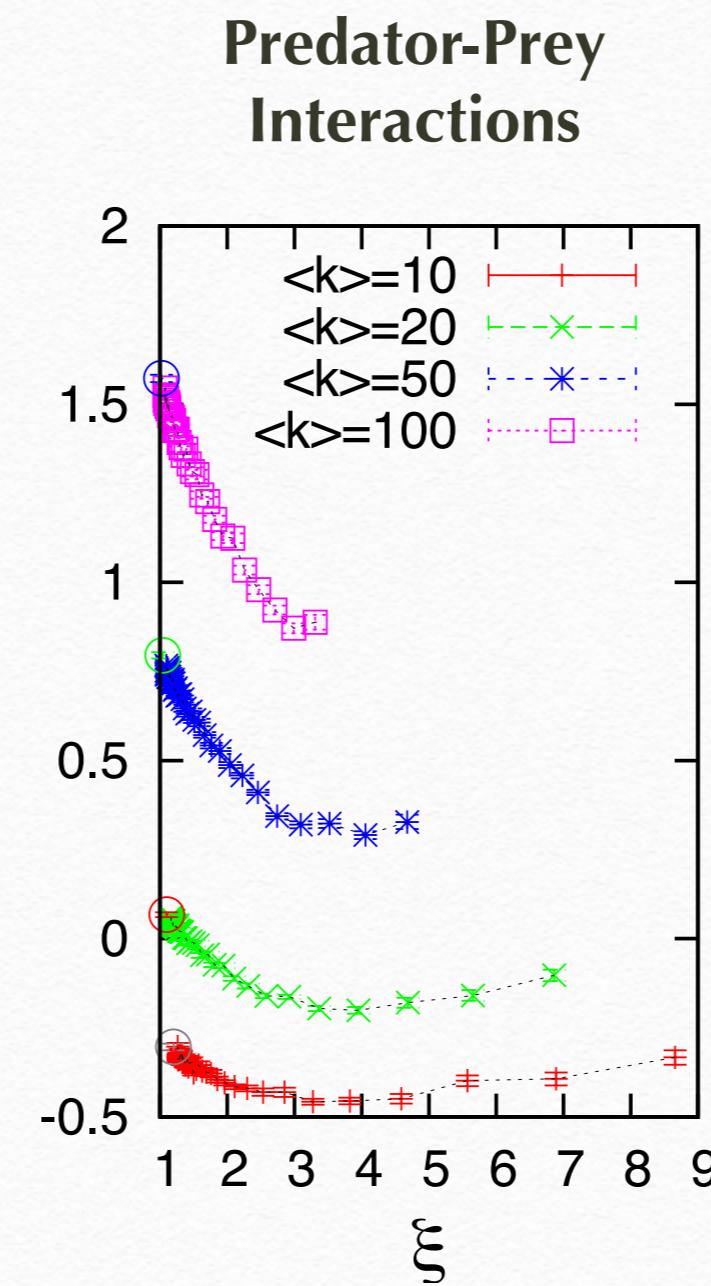
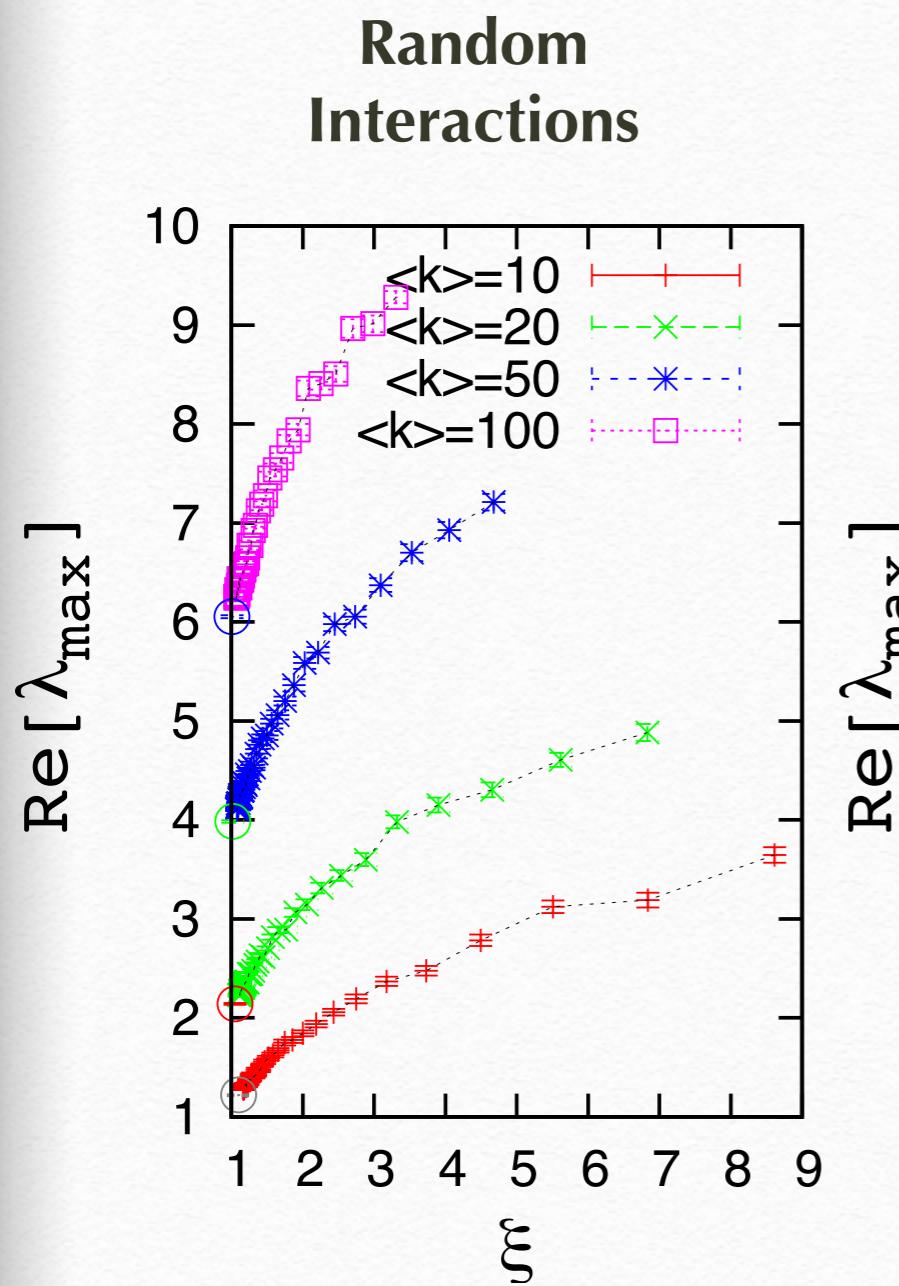
$S=1000$, $X \sim N(0, \sigma^2)$ with $\sigma=1$



Degree heterogeneity stabilizes ecosystems with predator-prey interactions?

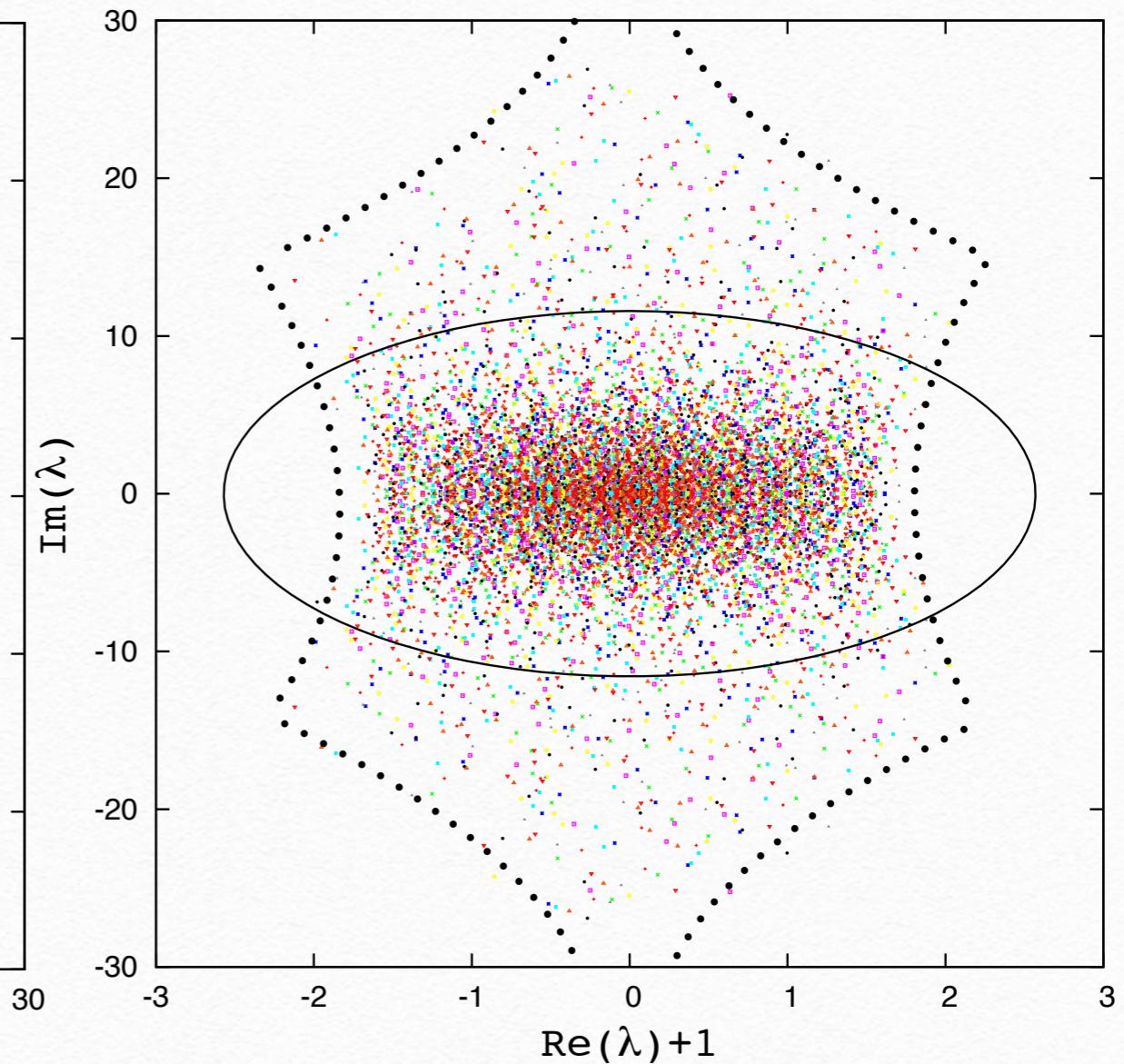
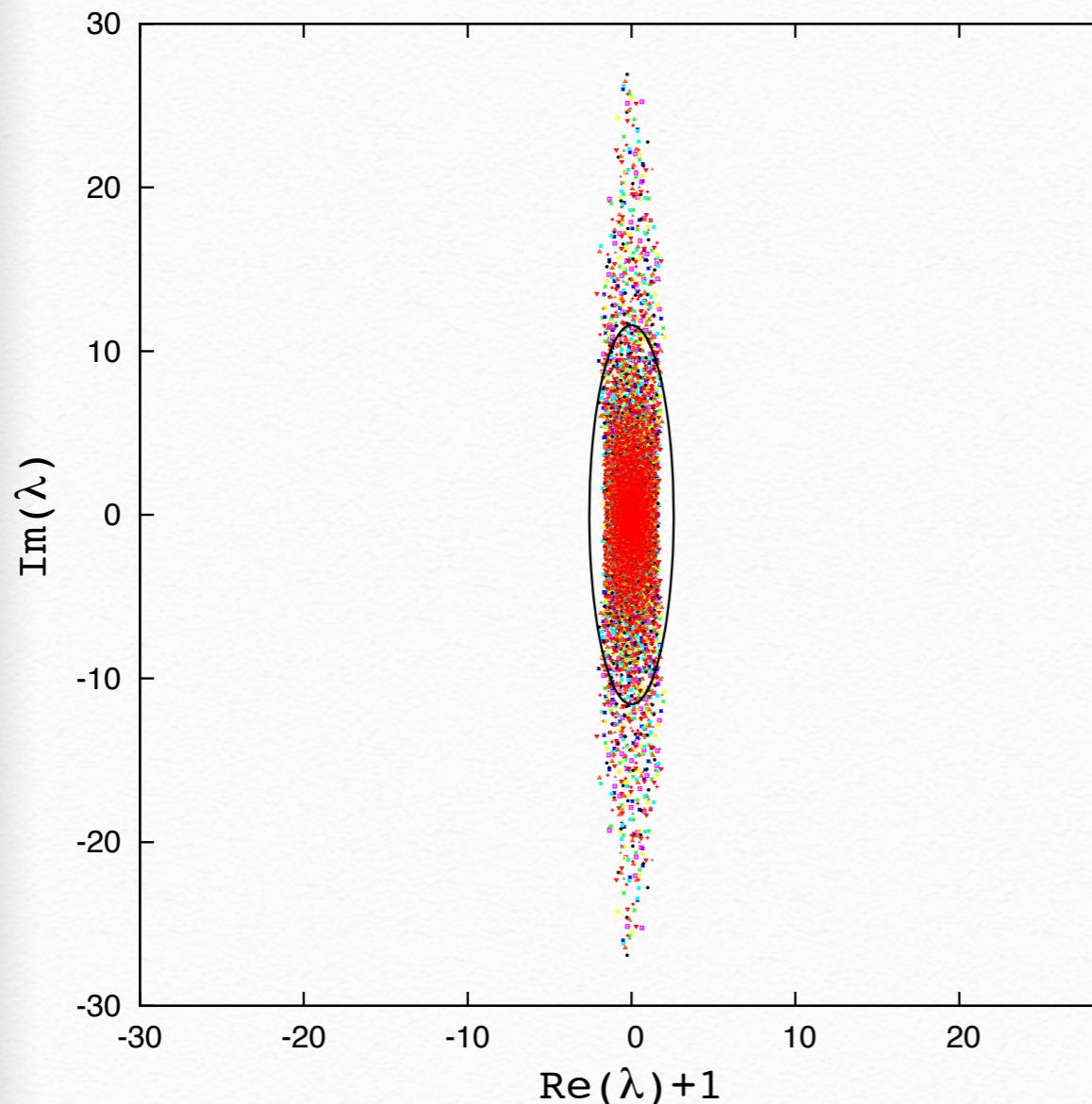
Impact of Degree Heterogeneity on the Stability of Complex Ecosystem

$$\xi = \frac{\langle k^2 \rangle}{\langle k \rangle^2}$$



Predator-Prey Interactions

$S=1000$, $X \sim N(0, \sigma^2)$ with $\sigma=1$, $C=0.05$



Degree heterogeneity stabilizes ecosystems with predator-prey interactions? It depends!

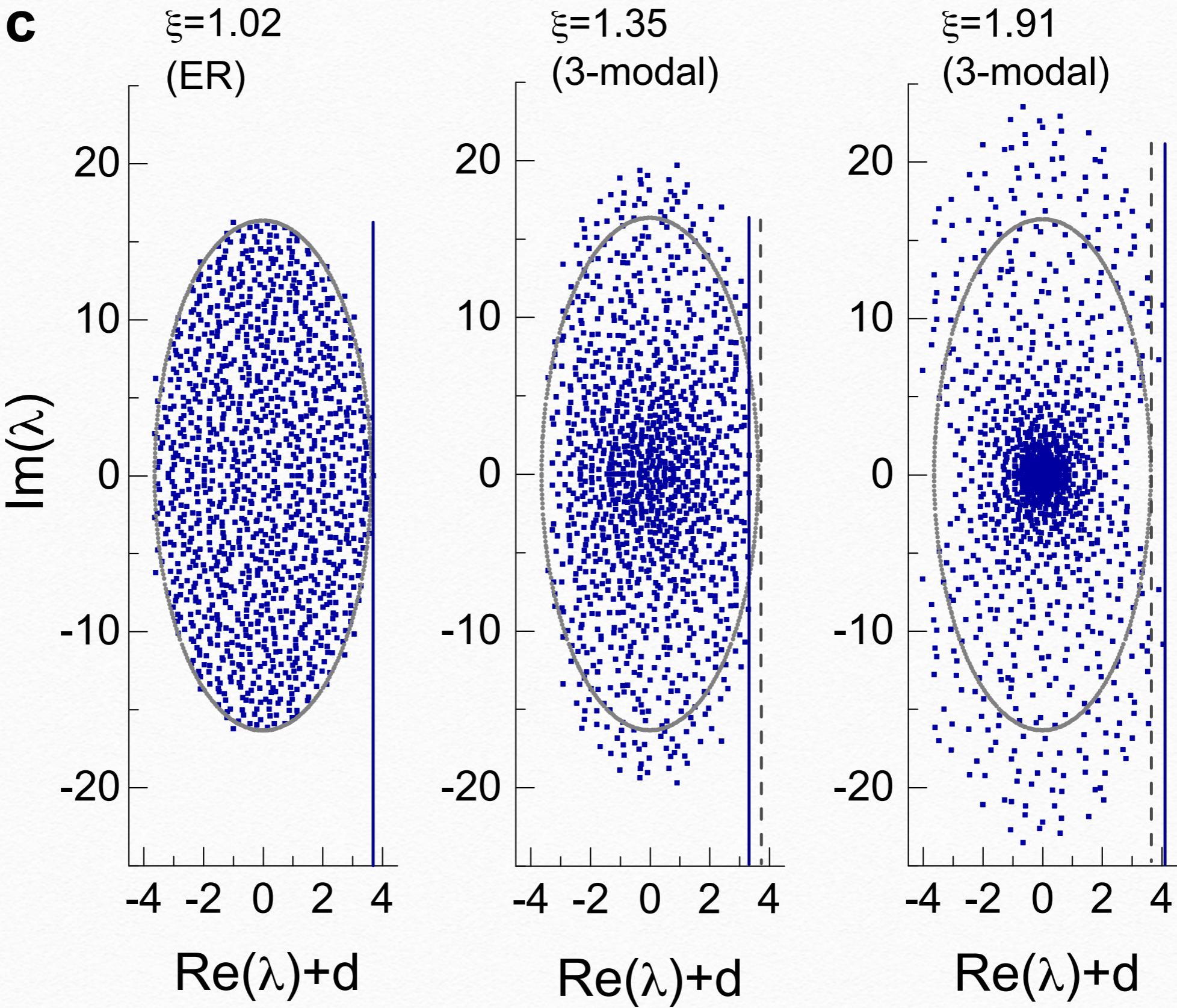
Tune degree heterogeneity in q -modal networks

A q -modal network have q different degrees $\{K_1, K_2, \dots, K_q\}$ for the N nodes. The number of nodes with degree K_a is $N_a = N/q$ for $a = 1, 2, \dots, q$. The mean degree of the network is

$$\langle k \rangle = \frac{1}{N} \sum_{a=1}^q N_a K_a = \frac{1}{q} \sum_{a=1}^q K_a.$$

To tune degree heterogeneity and preserve the average degree $\langle k \rangle$, we can tune the variance of the q types of degrees. For instance, for 3-modal networks with three different degrees $\{K_1, K_2, K_3\}$ in the network. Fix $\langle k \rangle = \frac{K_1 + K_2 + K_3}{3}$ and set $K_1/K_2 = K_2/K_3 = r$, we can change the value of r to explicitly tune the degree heterogeneity of the networks.

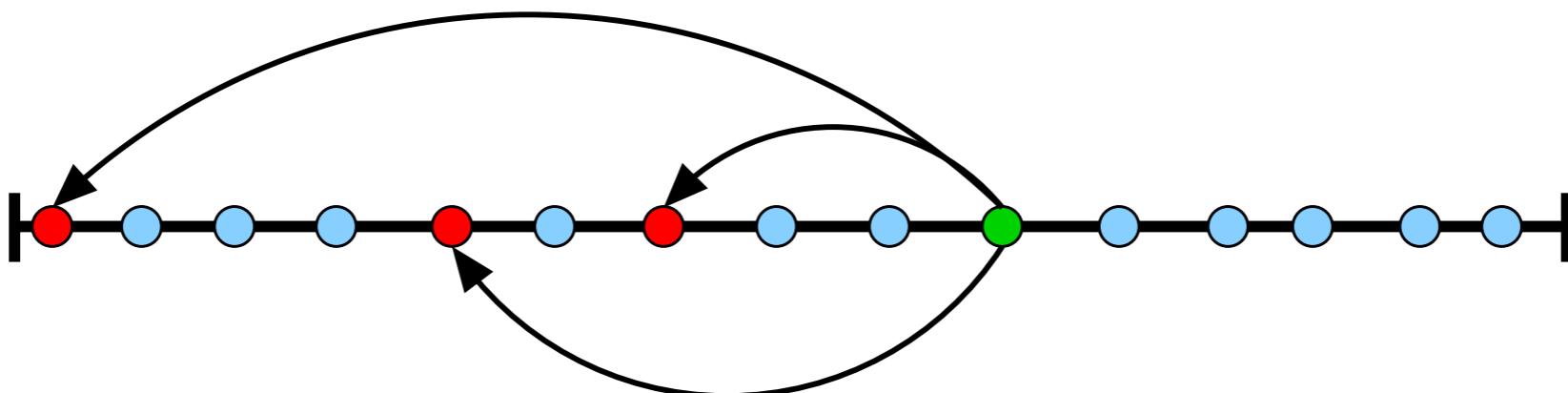
Origin of non-monotonicity



Realistic Model of Food Web: Cascade Model

Species are ordered in a natural cascade or hierarchy such that a given species can prey on only those below it and can be preyed on by those above it in the hierarchy.

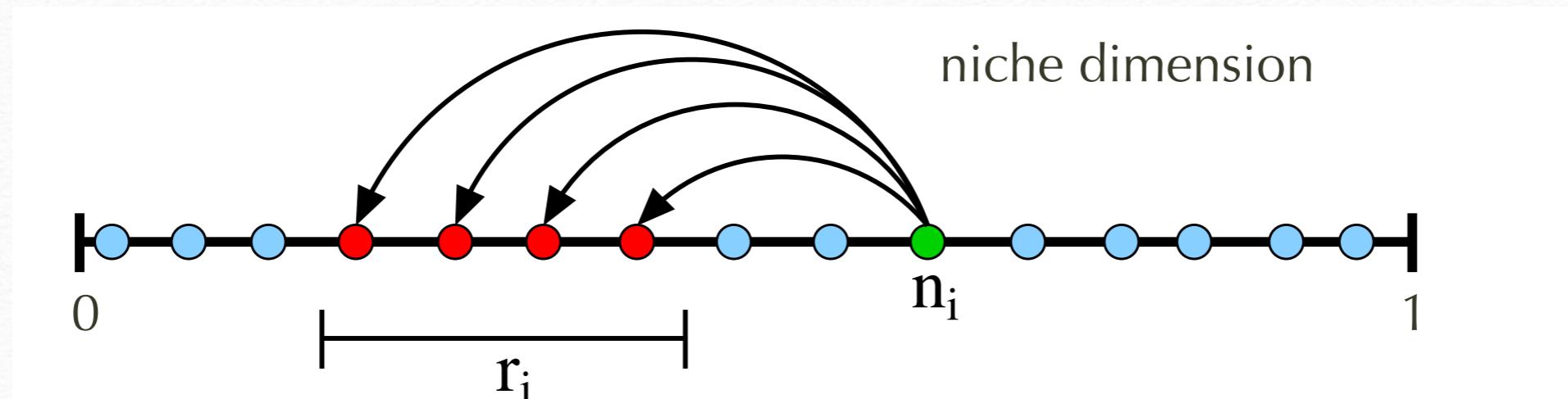
Cohen et al. Proc. R. Soc. B (1985)

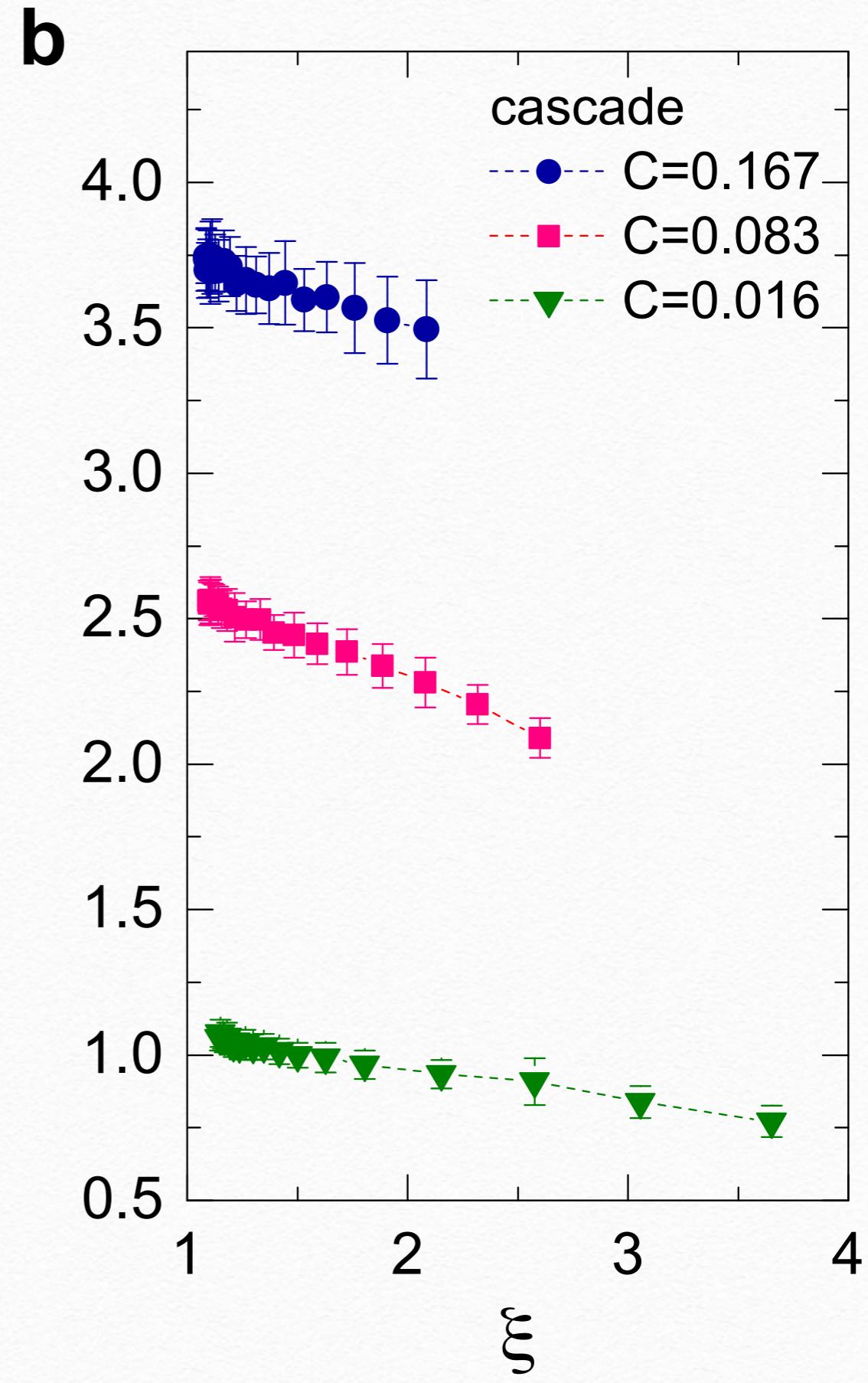
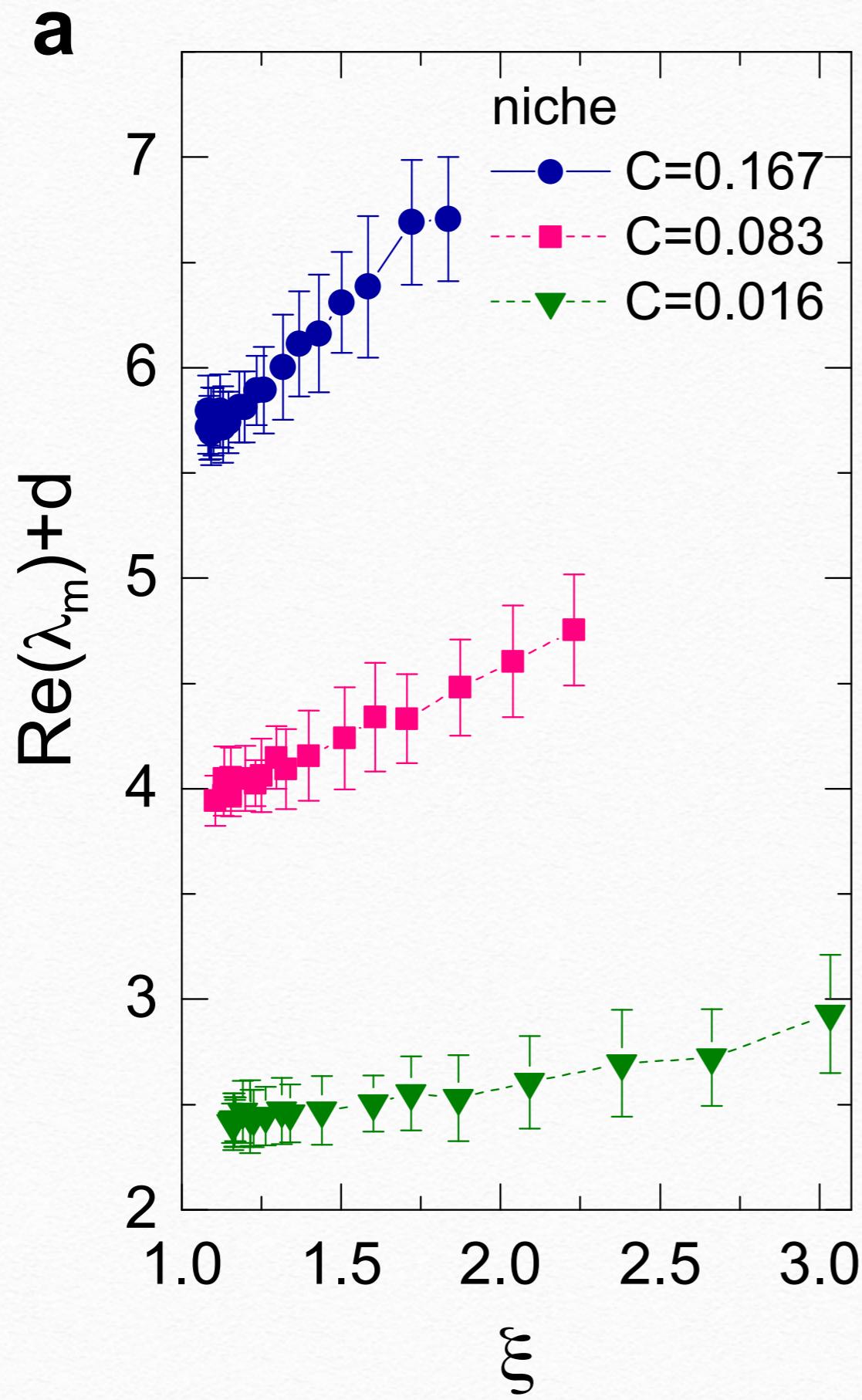


- (1) start from S isolated species with the order $1, 2, \dots, i, \dots, S - 1, S$, and each species i has a weight $\eta_i = i^{-\alpha}$ with $0 < \alpha < 1$.
- (2) select two different species i and j with the probabilities equal to the normalized weights $\eta_i / \sum_{h=1}^S \eta_h$ and $\eta_j / \sum_{h=1}^S \eta_h$ respectively, then add an edge from i to j provided that $i < j$ unless such a directed edge exists already.
- (3) repeat step (2) until $\langle k \rangle S/2$ edges are produced.

Realistic Model of Food Web: Niche Model

1. Order all S species according to a uniformly random ‘niche value’ (n_i) assigned to each species. This value places the species randomly somewhere along a ‘niche dimension’ from 0 to 1 ($0 \leq n_i \leq 1$).
2. A consumer eats all species whose niche values fall within a range (r_i) whose centre (c_i) is a uniformly random number between $r_i/2$ and $\min(n_i, 1-r_i/2)$.
3. The niche range $r_i = xn_i$ where $0 \leq x \leq 1$ is a random variable with beta-distributed probability density function $p(x) = \beta(1 - x)^{(\beta-1)}$ with $\beta = (1/2C)-1$.





Relaxed Niche Model (RNM)

Contiguity (g): varies from 0 to 1 and controls the niche widths relative to their maximum possible widths.

- When $g = 1$, the niche widths are at their narrowest and the model is identical to the original niche model.
- As g is reduced towards zero, feeding ranges are widened while species that fall within the niches have lower probability of being consumed, so that non-interval networks can occur.
- When $g = 0$, niches are as wide as possible and the RNM is equivalent to the generalized cascade model.

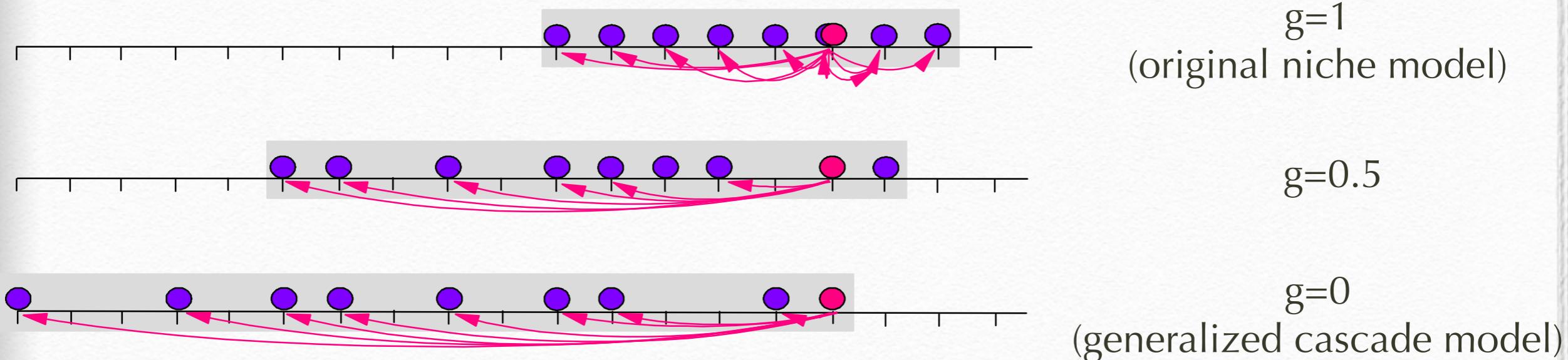
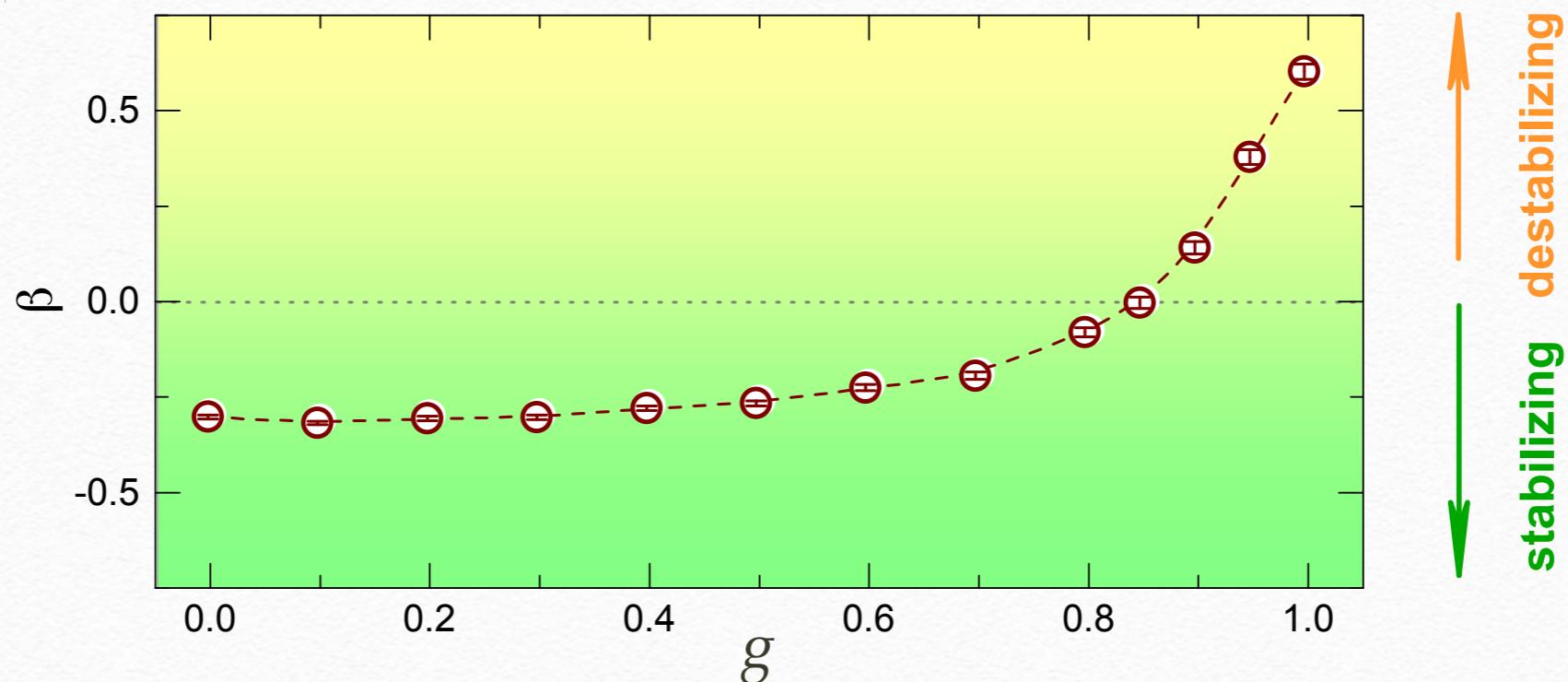
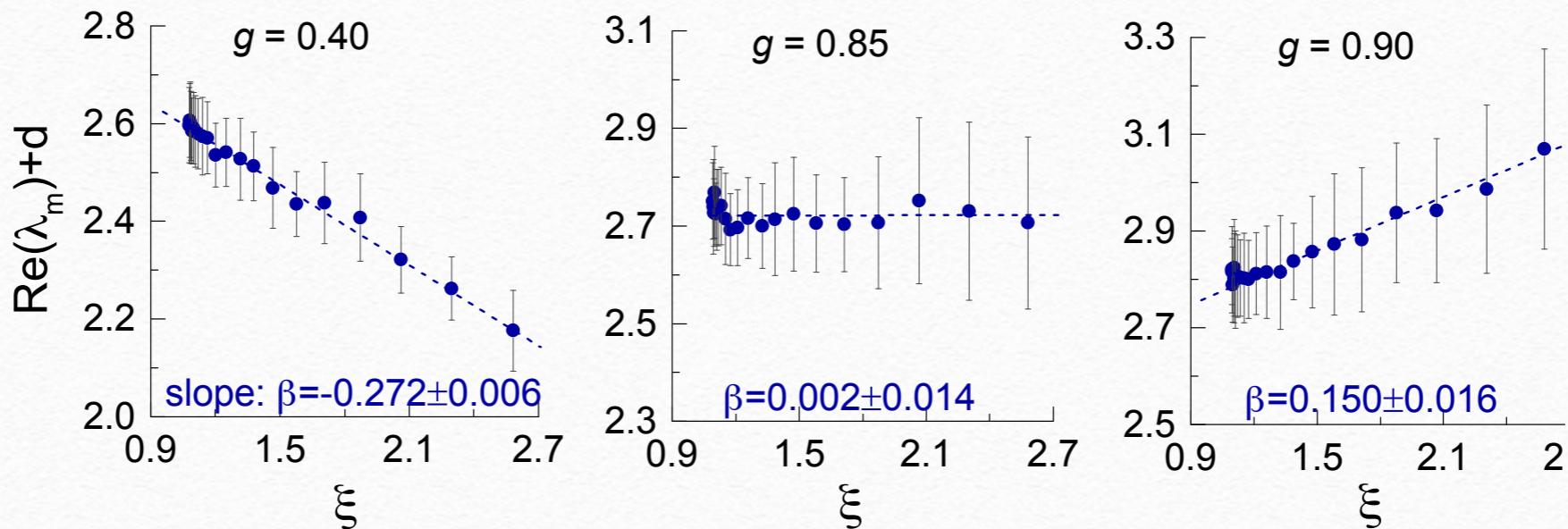


Table 1. Source and basic properties of the empirical food webs analysed here. S is the number of trophic species, C is the connectance, c is the contiguity of the generalized niche model webs and g is the contiguity of relaxed niche model webs that, on average, have the same $dDiet$ as the empirical web. *The generalized niche model could not produce webs with mean $dDiet$ equal to the empirical value for the Skipwith Pond food web

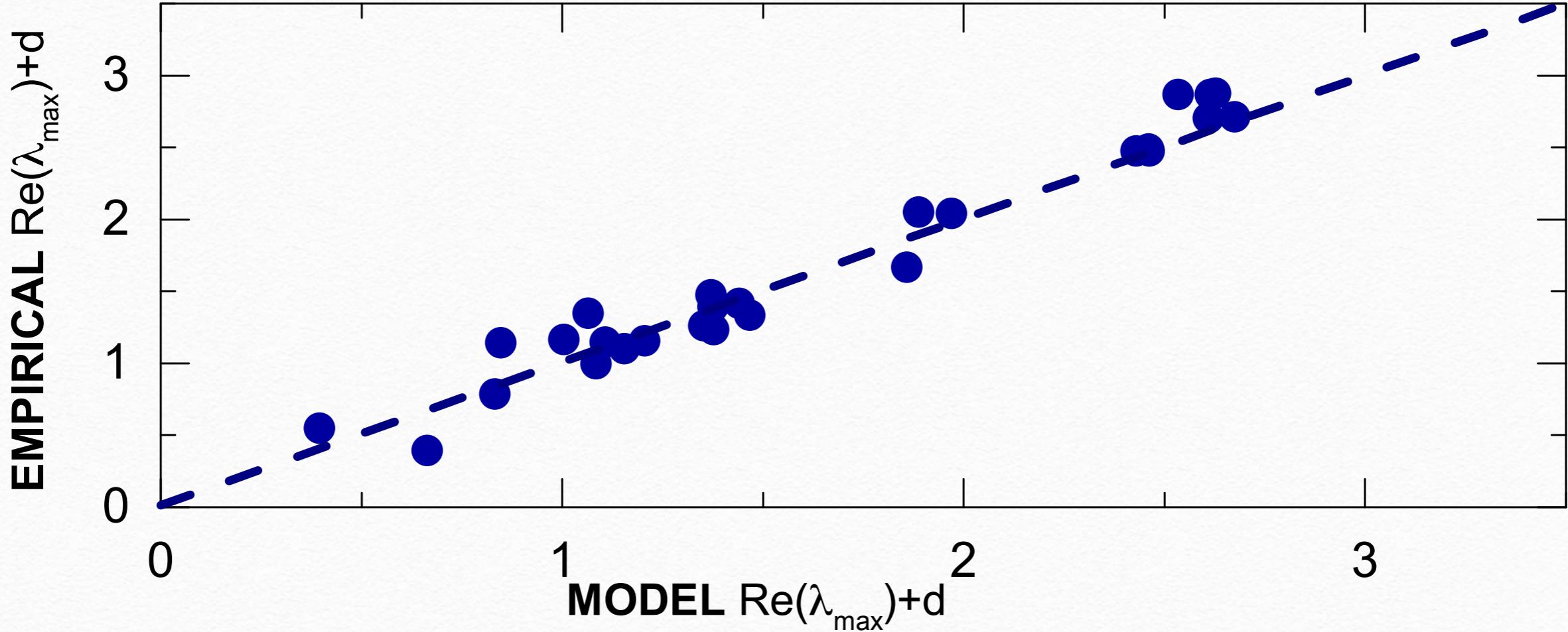
Web	Reference	S	C	c	g
Benguela	(Yodzis 1998)	29	0·241	0·866	0·816
Chesapeake	(Baird & Ulanowicz 1989)	31	0·071	0·784	0·835
Coachella	(Polis 1991)	29	0·312	0·587	0·681
Bridge Brook Lake	(Havens 1992)	25	0·171	0·995	0·994
Little Rock Lake	(Martinez 1991)	92	0·118	0·903	0·890
Reef	(Opitz 1996)	50	0·222	0·686	0·606
Shelf	(Link 2002)	79	0·225	0·836	0·694
Skipwith Pond	(Warren 1989)	25	0·315	*	0·446
St Marks	(Christian & Luczkovich 1999)	48	0·096	0·743	0·722
St Martin	(Goldwasser & Roughgarden 1993)	42	0·116	0·739	0·695

Feeding niches of predators in real food webs are close to contiguous but not completely so (i.e., the prey contiguity g is close to but not exactly 1).

Relaxed Niche Model (RNM)



- Impact of degree heterogeneity on stability depends on the contiguity g .
- The contiguity of most empirical food webs lies in the regime where degree heterogeneity favors community stability.



Degree heterogeneity and prey contiguity together largely determine the stability of food webs.

Summary

The impact of “degree heterogeneity” on linear stability of ecological networks systematically vary with different types of interspecific interactions.

- Degree heterogeneity is always destabilizing in ecological networks with random interactions or mixture of competitive and mutualistic interactions.
- Its effects on networks of predator-prey interactions (e.g. food webs) depend on **prey contiguity**, i.e., the extent to which the species consume an unbroken sequence of prey in community niche space. Increasing degree heterogeneity stabilizes food webs except those with the most contiguity.

These findings help explain previously unexplained observations that food webs are highly but not completely contiguous.

More broadly, the results deepen our understanding of the stability of complex ecological networks with important implications for other types of dynamical systems.

Acknowledgement

**Gang Yan (Northeastern Univ.)
Neo Martinez (Univ. of Arizona)**



John
Templeton
Foundation

Thank you!