Stability of Heterogeneous Ecological Systems

Gang Yan$^{1,2}$, Yang-Yu Liu$^{1,2,3}$

September 23, 2014

$^{1}$Center for Complex Network Research and Department of Physics, Northeastern University, Boston, Massachusetts 02115, USA

$^{2}$Center for Cancer Systems Biology, Dana Farber Cancer Institute, Boston, Massachusetts 02115, USA

$^{3}$Channing Division of Network Medicine, Brigham and Women’s Hospital, Harvard Medical School, Boston, Massachusetts 02115, USA

Stability of ecological system measures the tendency of a community to return to equilibrium after small perturbation\cite{1,2}, which is severely constrained by the underlying network structure\cite{3,4}. Despite significant advances in uncovering the relationship between stability and network structure\cite{12,13,14,15,16}, little attention has been paid to the impact of the degree heterogeneity that exists in real ecological networks\cite{17,18}. Here we show that for networks with mixed interactions of competition and mutualism the degree heterogeneity always destabilizes ecological system. For ecological networks with predator-prey interactions (e.g., food webs) constructed from either simple network models or a realistic food web model (cascade model) high heterogeneity is always destabilizing, yet moderate heterogeneity is stabilizing.
Surprisingly, for ecological networks generated from the niche model, degree heterogeneity is always destabilizing. These findings deepen our understanding of the stability of real ecological systems and may also have implications in studying the stability of more general complex dynamical systems.

Understanding the intricate relationship between the structure and dynamics of complex ecological systems has been one of the key issues in ecology. Equilibrium stability of ecological systems, a measure that considers an ecological system stable if it returns to its equilibrium after a small perturbation, has been studied for more than four decades. Empirical observations suggest that communities with more species are more stable, i.e., a positive diversity-stability relationship. Yet, these intuitive ideas were challenged by the pioneer work of May, who rigorously proved a negative diversity-stability relationship using linear stability analysis on randomly constructed ecological communities. This launched the “diversity-stability debate.”

In his pioneer work, May considered community matrices $M$ of size $S \times S$, where $S$ is the number of species, the off-diagonal elements $M_{ij} \equiv \frac{\partial f_i(x)}{\partial x_j}|_{x^*}$ captures the impact that species $j$ has on species $i$ around a feasible equilibrium point $x^*$ of an unspecified dynamical system $\dot{x}(t) = f(x(t))$ describing the time-dependent abundance $x(t)$ of the $S$ species. Since empirical parameterization of the exact functional form of $f(x(t))$ is extremely difficult for complex ecological system, May considered $M_{ij}$’s are randomly drawn from a distribution with mean 0 and variance $\sigma^2$ with probability $C$ and are 0 otherwise. Hence $\sigma$ represents the characteristic interaction strength and $C$ is the ratio between actual and potential interactions in the ecological system. For simplicity, the diago-
nal elements are chosen to be the same, $-1$, representing the intrinsic damping time scale of each species so that if disturbed from equilibrium it would return with such a damping time by itself. May found that for random interactions drawn from a Gaussian distribution $\mathcal{N}(0, \sigma^2)$, a randomly assembled system is stable (i.e., all the eigenvalues of the community matrix $M$ have negative real parts) if the so-called ‘complexity’ measure $\sigma\sqrt{CS} < 1$. This implies that more complexity (i.e., larger $CS$) tend to destabilize community dynamics.$^{12}$

May’s result continues to be influential almost four decades later is not because that complex ecological systems have to be unstable, but because real ecological system must have some specific structures that allow them to be stable despite their complexity.$^{4}$ In other words, nature must adopt some devious and delicate strategies to cope with this diversity-stability paradox. One of such specificity is the existence of well-defined interspecific relationships observed in nature, e.g., predator-prey, competition, and mutualism. Recently Allesina and Tang refined May’s result and provided analytic stability criteria for all these interspecific interaction types.$^{15}$ They found remarkable differences between predator-prey interactions, which are stabilizing, and mutualistic and competitive interactions, which are destabilizing. Many of the “devious strategies” adopted by nature can now be tested with the revised stability criteria as a reference point.

Yet, the above results rely on a key assumption that the underlying network structure is completely random. Indeed, the construction of the community matrix $M$ follows almost exactly the same procedure as the classical Erdős-Rényi random graph.$^{28,29}$ However, just like many other real-world complex systems, the underlying networks of ecological systems are far from random.
Instead, they often display non-trivial topological features, e.g., degree heterogeneity (representing the spread between the less and the more connected nodes)\textsuperscript{17-22}, nestedness (the level of sharing of interaction partners among species)\textsuperscript{30}, and modularity (the degree of compartmentalization of the networks)\textsuperscript{31,32}. It has been recently shown that the network architecture favoring stability fundamentally differs between trophic and mutualistic networks\textsuperscript{13}. For example, a highly connected and nested architecture promotes community stability in mutualistic networks, whereas the stability of trophic networks is enhanced in modular and weakly connected architectures.

Despite of these remarkable results, we still lack a comprehensive understanding of the relationship between network structure and stability of complex ecological systems. One fundamental issue is the impact of degree heterogeneity on the stability of ecological systems. Typically the degree heterogeneity can be described by $\xi \equiv \langle k^2 \rangle / \langle k \rangle^2$, where $\langle k \rangle = 1/S \sum_{i=1}^{S} k_i$ is the mean degree of the network, $k_i$ is the degree of species $i$ (i.e., the total number of incoming and outgoing connections species $i$ has), and $\langle k^2 \rangle = 1/S \sum_{i=1}^{S} k_i^2$ is the second moment of the node degree distribution. Note that $\xi \geq 1$ and the higher the degree heterogeneity the larger the value of $\xi$. From the advances towards understanding complex networks accumulated in the last decade, we know that degree heterogeneity fundamentally affects many network properties and dynamical processes, from error and attack tolerance\textsuperscript{33,34}, spectra\textsuperscript{35,36}, epidemic spreading\textsuperscript{37}, interdependent fragility\textsuperscript{38}, to structural controllability\textsuperscript{39}. It is fair to expect that degree heterogeneity would affect stability of complex ecological systems as well.

To approach this issue in a systematic fashion, we follow May’s model-independent framework
helping us avoid parameterizing the exact dynamics of complex ecological systems which is extremely difficult. For an ecological system with random interactions, we generate its underlying directed ecological network first, using three different network models (see SI Sec. 1): multi-modal, Erdős-Rényi, and scale-free, at given mean degree $\langle k \rangle$. (The effective connection probability $C = \langle k \rangle / (2(S − 1))$.) Then we construct the community matrix $M$ as follows: (1) We set all the diagonal elements $M_{ii} = −d$; (2) Whenever there is a link from species $j$ to species $i$ the off-diagonal element $M_{ij}$ is drawn from a normal distribution $N(0, \sigma^2)$. We show that the real part of the most positive eigenvalue of the community matrix $M$ is given by $\text{Re}(\lambda_m) = \sigma \sqrt{\xi \langle k \rangle / 2} − d = \sigma \sqrt{\xi (S − 1)C} − d$ (see SI Sec. 3 for details), where $\xi$ is the degree heterogeneity as defined above. $\text{Re}(\lambda_m)$ has to be negative to ensure the equilibrium stability, yielding the stability criterion $\sigma \sqrt{\xi (S − 1)C} < d$. Apparently, any factor that increases (or decreases) $\text{Re}(\lambda_m)$ will destabilize (or stabilizes) the ecological system, respectively. Increasing $\xi$ will certainly destabilize the ecological system. Note that for random $k$-regular networks, where the degrees of all nodes are $k$, $\xi = 1$, recovering May’s classical result.

Fig. 1a shows the impact of degree heterogeneity on the stability of ecological systems with random interactions. The underlying ecological networks are constructed from different network models at given mean degree $\langle k \rangle$. We find that when the complexity $(S − 1)C$ is fixed, $\text{Re}(\lambda_m)$ increases monotonically as the degree heterogeneity $\xi$ increases, implying that larger $\xi$ is always destabilizing an ecological system with random interactions, consistent with our analytical prediction $\text{Re}(\lambda_m) + d \sim \xi^{1/2}$ (see SI Sec. 3). This result can be further illustrated by the distribution of eigenvalues. We find that with increasing $\xi$, the radius of the cycle encompassing the eigenvalues
becomes larger, hence $\text{Re}(\lambda_m)$ increases, destabilizing the ecological system. Interestingly, we also find that as $\xi$ increases the distribution of the eigenvalues becomes more non-uniform with very high density of eigenvalues around the center of the circle (see Figs. 1b-d).

For ecological systems with predator-prey interactions, i.e., whenever $M_{i,j} > 0$ then $M_{j,i} < 0$, we generate the underlying directed network using five different models (see SI Sec. 1): multi-modal, Erdős-Rényi, scale-free, cascade \textsuperscript{43,44}, and niche model \textsuperscript{23}, at given mean degree $\langle k \rangle$. When there is a directed edge from species $i$ to $j$ we draw the off-diagonal element $M_{ij}$ from an half-normal distribution $|N(0, \sigma^2)|$ and $M_{ji}$ from a negative half-normal distribution $-|N(0, \sigma^2)|$. We still set all the diagonal elements $M_{ii} = -d$. We find that large degree heterogeneity hampers the stability of predator-prey ecological systems constructed from all the network models. Surprisingly, for predator-prey ecological systems constructed from the multi-modal (Fig. 2a), Erdős-Rényi and scale-free (Fig. 2b), and cascade (Fig. 2c) model networks, moderate heterogeneity is stabilizing. This non-monotonic behavior can be further illustrated by the distribution of eigenvalues of the community matrix $M$. We find that as the degree heterogeneity $\xi$ increases, not only the eigenvalue distribution becomes non-uniform but also the shape of the boundary that containing all eigenvalues changes from ellipse to bow-tie (Fig. 2e). This change of the boundary shape induces the non-monotonic behavior of $\text{Re}(\lambda_m)$ as we vary $\xi$. The niche model is the only exception for which the degree heterogeneity is always destabilizing (Fig. 2d). The eigenvalue distributions of niche model networks are shown in Fig. 2f. We do not see drastic shape change of the boundary encompassing all eigenvalues.
For ecological systems with a mixture of competitive and mutualistic interactions, we can construct the community matrix $M$ following very similar approach as the case of predator-prey interactions but constraining $M_{ij}$ and $M_{ji}$ to have the same sign. We find that for both multi-modal (Fig. 3a), Erdős-Rényi and scale-free (Fig. 3b) model networks the $\text{Re}(\lambda_{\text{max}})$ increases monotonically as we increase $\xi$, implying that the degree heterogeneity is always destabilizing the ecological system. This is further demonstrated by the distribution of eigenvalues of the community matrix $M$ (Fig. 3c). Similar as in the predator-prey ecological systems, we find that as the degree heterogeneity $\xi$ increases, not only the eigenvalue distribution becomes non-uniform but also the shape of the boundary that containing all eigenvalues changes from ellipse to bow-tie (Fig. 3c). Despite the change of the eigenvalue distribution, the real parts of the eigenvalues always expand as we increase $\xi$. This explains the monotonic impact of degree heterogeneity on the stability of ecological systems with a mixture of competitive and mutualistic interactions. Note that for symmetric networks with only mutualistic interactions the degree heterogeneity is also destabilizing.

In summary, with extensive numerical and analytical calculations, we find that for ecological networks with random interspecific interactions or a mixture of competitive and mutualistic interactions, the degree heterogeneity always destabilizes the ecological system. For ecological networks with predator-prey interactions (e.g., food webs) constructed from simple network models and a realistic food web model (cascade model), we find that high enough degree heterogeneity is destabilizing, yet moderate heterogeneity is stabilizing. In other words, there is an optimal degree heterogeneity for predator-prey networks generated from those models, where the ecological system is most stable. Interestingly, ecological networks generated from niche model do not have
such beneficial effect of degree heterogeneity at all.

The structure of ecological networks has been recognized as one key ingredient contributing to the coexistence between high complexity and stability in real ecological systems. Our results demonstrate that, depending on the type of interactions, degree heterogeneity of ecological networks has drastically different impact on the community stability. This implies that strong variations in the stability of architectural patterns constrain ecological networks toward different architectures, consistent with previous results. Though the presented results do not solve the notorious diversity-stability paradox, they do offer new opportunities to explore how nature subverts these theoretical predictions and produces diverse, stable ecological systems. Moreover, since we use the model independent framework and linear stability analysis, the findings are not limited to ecological networks, but instead hold for any system of differential equations resting at an equilibrium point. For example, the existence of optimal degree heterogeneity for prey-predator networks could have implications beyond ecological systems. The ubiquity of consumer-resource relationships in nature could be due to their intrinsic dynamical properties.

1. May, R. M. Will a large complex system be stable? *Nature* **238**, 413–414 (1972).

2. May, R. M. *Stability and Complexity in Model Ecosystems* (Princeton University Press, 1974).

3. Pascual, M. & Dunne, J. *Ecological Networks: Linking Structure to Dynamics in Food Webs* (Oxford University Press, 2006).

4. Bascompte, J. Structure and dynamics of ecological networks. *Science* **329**, 765–766 (2010).
5. McNaughton, S. J. Stability and diversity of ecological communities. *Nature* **274**, 251–252 (1978).

6. Pimm, S. L. The complexity and stability of ecosystems. *Nature* **307**, 321 (1984).

7. McCann, K. The diversity-stability debate. *Nature* **405**, 228–233 (2000).

8. Ives, A. R. & Carpenter, S. R. Stability and diversity of ecosystems. *Science* **317**, 58–62 (2007).

9. Gross, T., Ebenhöh, W. & Feudel, U. Enrichment and foodchain stability: the impact of different forms of predator-prey interaction. *J. Theor. Biol.* **227**, 349–358 (2004).

10. Okuyama, T. & Holland, J. N. Network structural properties mediate the stability of mutualistic communities. *Ecol. Lett.* **11**, 208–216 (2008).

11. Gross, T., Rudolf, L., Levin, S. A. & Dieckmann, U. Generalized models reveal stabilizing factors in food webs. *Science* **325**, 747–750 (2009).

12. Bastolla, U. *et al.* The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* **458**, 1018–1020 (2009).

13. Thébault, E. & Fontaine, C. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* **329**, 853–856 (2010).

14. Mougi, A. & Kondoh, M. Diversity of interaction types and ecological community stability. *Science* **337**, 349–351 (2012).
15. Allesina, S. & Tang, S. Stability criteria for complex ecosystems. *Nature* **483**, 205–208 (2012).

16. Suweis, S., Simini, F., Banavar, J. R. & Maritan, A. Emergence of structural and dynamical properties of ecological mutualistic networks. *Nature* **500**, 449–452 (2013).

17. Montoya, J. M. & Solé, R. V. Small world patterns in food webs. *J. Theor. Biol.* **214**, 405 – 412 (2002).

18. Dunne, J. A., Williams, R. J. & Martinez, N. D. Food-web structure and network theory: The role of connectance and size. *Proc. Natl. Acad. Sci. USA* **99**, 12917 (2002).

19. Jordano, P., Bascompte, J. & Olesen, J. M. Invariant properties in coevolutionary networks of plant-animal interactions. *Ecol. Lett.* **6**, 69–81 (2003).

20. Vázquez, D. P. Degree distribution in plant-animal mutualistic networks: forbidden links or random interactions? *Oikos* **108**, 421–426 (2005).

21. Montoya, J. M., Pimm, S. L. & Solé, R. V. Ecological networks and their fragility. *Nature* **442**, 259–264 (2006).

22. Stouffer, D. B. Scaling from individuals to networks in food webs. *Funct. Ecol.* **24**(1), 44–51 (2010).

23. Williams, R. J. & Martinez, N. D. Simple rules yield complex food webs. *Nature* **404**, 180–183 (2000).

24. Luenberger, D. G. *Introduction to Dynamic Systems: Theory, Models, & Applications* (John Wiley & Sons, New York, 1979).
25. Odum, E. P. *Fundamentals of Ecology* (Saunders, Philadelphia, 1953).

26. MacArthur, R. Fluctuations of animal populations and a measure of community stability. *Ecology* **36**, 533–536 (1955).

27. Elton, C. S. *Ecology of Invasions by Animals and Plants* (Chapman and Hall, London, 1958).

28. Erdös, P. & Rényi, A. On the evolution of random graphs. *Publ. Math. Inst. Hung. Acad. Sci.* **5**, 17–60 (1960).

29. Bollobás, B. *Random Graphs* (Cambridge University Press, Cambridge, 2001).

30. Bascompte, J., Jordano, P., Melian, C. J. & Olesen, J. M. The nested assembly of plant-animal mutualistic networks. *Proc. Natl. Acad. Sci. USA* **100**, 9383–9387 (2003).

31. Girvan, M. & Newman, M. E. J. Community structure in social and biological networks. *Proc. Natl. Acad. Sci. USA* **99**, 7821–7826 (2002).

32. Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E. & Taylor, W. W. Compartments revealed in food-web structure. *Nature* **426**, 282–285 (2003).

33. Albert, R., Jeong, H. & Barabási, A.-L. Error and attack tolerance of complex networks. *Nature* **406**, 378–382 (2000).

34. Cohen, R., Erez, K., ben Avraham, D. & Havlin, S. Resilience of the internet to random breakdowns. *Phys. Rev. Lett.* **85**, 4626–4628 (2000).
35. Samukhin, A. N., Dorogovtsev, S. N. & Mendes, J. F. F. Laplacian spectra of, and random walks on, complex networks: Are scale-free architectures really important? *Phys. Rev. E* **77**, 036115 (2008).

36. Dorogovtsev, S. N., Goltsev, A. V., Mendes, J. F. F. & Samukhin, A. N. Spectra of complex networks. *Phys. Rev. E* **68**, 046109 (2003).

37. Pastor-Satorras, R. & Vespignani, A. Epidemic spreading in scale-free networks. *Phys. Rev. Lett.* **86**, 3200–3203 (2001).

38. Buldyrev, S. V., Parshani, R., Paul, G., Stanley, H. E. & Havlin, S. Catastrophic cascade of failures in interdependent networks. *Nature* **464**, 1025–1028 (2010).

39. Liu, Y.-Y., Slotine, J.-J. & Barabási, A.-L. Controllability of complex networks. *Nature* **473**, 167–173 (2011).

40. Valente, A. X. C. N., Sarkar, A. & Stone, H. A. Two-peak and three-peak optimal complex networks. *Phys. Rev. Lett.* **92**, 118702 (2004).

41. Barabási, A.-L. & Albert, R. Emergence of scaling in random networks. *Science* **286**, 509–512 (1999).

42. Goh, K.-I., Kahng, B. & Kim, D. Universal behavior of load distribution in scale-free networks. *Phys. Rev. Lett.* **87**, 278701 (2001).

43. Cohen, J. E. & Newman, C. M. A stochastic theory of community food webs: I. models and aggregated data. *Proc. R. Soc. B* **224**, 421–448 (1985).
44. Karrer, B. & Newman, M. E. J. Random acyclic networks. *Phys. Rev. Lett.* 102, 128701 (2009).

45. Feng, W. & Takemoto, K. Heterogeneity in ecological mutualistic networks dominantly determines community stability. *Sci. Rep.* 4, 5912 (2014).

46. Rohr, R. P., Saavedra, S. & Bascompte, J. On the structural stability of mutualistic systems. *Science* 345 (2014).

47. Sommers, H. J., Crisanti, A., Sompolinsky, H. & Stein, Y. Spectrum of large random asymmetric matrices. *Phys. Rev. Lett.* 60, 1895–1898 (1988).

**Author Contributions** Y.-Y.L and G.Y. conceived and executed the research, wrote the manuscript, and contributed equally to this project.

**Acknowledgments** We thank Hai-jun Zhou for comments and discussions on the manuscript.

**Competing Interests** The authors declare that they have no competing financial interests.

**Correspondence** Correspondence and requests for materials should be addressed to Yang-Yu Liu (email: yyl@channing.harvard.edu).
Figure 1

(a) $\text{Re}(\lambda_m) + d$

C = 0.167: 3-modal SF ER
C = 0.083: 3-modal SF ER
C = 0.016: 3-modal SF ER

(b) $\xi = 1.05$ (ER)

(c) $\xi = 1.35$ (SF)

(d) $\xi = 1.91$ (SF)
Figure 2
Figure 3
Figure 1  The impact of degree heterogeneity on the stability of ecological networks with random interactions. (a) $\text{Re}(\lambda_m) + d$ as a function of the degree heterogeneity, $\xi = \langle k^2 \rangle / \langle k \rangle^2$, in log-log plot. The dots are from numerical simulations on 3-modal, Erdős-Rényi (ER), and scale-free (SF) networks. The network size $S = 1200$, the connection probability $C = 0.167, 0.083, 0.016$ (i.e., the mean degree $\langle k \rangle = 100, 50, 10$), and the strength of edges are drawn from the normal distributions $\mathcal{N}(0, \sigma^2)$ with $\sigma = 1.0$. Each error bar represents the standard deviation of 100 independent runs. The solid lines (all with the slope $1/2$) are derived from our analytical results. (b) The typical distributions of the eigenvalues for Erdős-Rényi ($\xi = 1.05$) and scale-free ($\xi = 1.35, 1.91$) networks. The radius of the boundary circles are $\sigma \sqrt{\xi \langle k \rangle / 2}$.

Figure 2  The impact of degree heterogeneity on the stability of ecological networks with predator-prey interactions. (a-d) $\text{Re}(\lambda_m) + d$ as a function of the degree heterogeneity $\xi$ for 3-modal, Erdős-Rényi (ER), scale-free (SF), cascade, and niche model networks. $S = 1200$, and $\sigma = 1.0$. (e) The eigenvalues distributions of Erdős-Rényi ($\xi = 1.05$) and 3-modal ($\xi = 1.35, 1.91$) networks. The ellipse is the classical result for homogeneous networks, which is drawn for reference. Because of the bow-tie shape of the distribution, when $\xi = 1.35$ the real part of the most positive eigenvalue (solid line) is smaller than that of the ellipse (dashed line); the opposite is true when $\xi = 1.91$. (f) The eigenvalue distributions of niche model networks with different values of $\xi$. As $\xi$ increases the real part of the most positive eigenvalue increases monotonically.
Figure 3  The impact of degree heterogeneity on the stability of ecological networks with mixed interactions of competition and mutualism. (a,b) \( \text{Re}(\lambda_m) + d \) as a function of \( \xi \) for 3-modal, Erdős-Rényi (ER) and scale-free (SF) networks. \( S = 1200 \), and \( \sigma = 1.0 \). The dots are numerical simulations averaging over 100 independent runs. (c) The typical eigenvalue distribution of Erdős-Rényi (\( \xi = 1.05 \)) and 3-modal (\( \xi = 1.35, 1.91 \)) networks. The ellipse (drawn for reference) is the classical result \([15,47]\) for homogeneous networks. Despite the bow-tie shape of the eigenvalue distribution as \( \xi \) increases, the real part of the most positive eigenvalue keeps increasing.