

Component response rate variation underlies the stability of complex systems

A. Bradley Duthie

Biological and Environmental Sciences, University of Stirling, Stirling, UK, FK9 4LA
alexander.duthie@stir.ac.uk

The stability of a complex system generally decreases with increasing system size and interconnectivity, a counterintuitive result of widespread importance across the physical, life, and social sciences. Despite recent interest in the relationship between system properties and stability, the effect of variation in the response rate of individual system components remains unconsidered. Here I vary the component response rates (γ) of randomly generated complex systems. I show that when component response rates vary, the potential for system stability is markedly increased. Variation in γ is especially important for stability in highly complex systems, in which the probability of stability would otherwise be negligible. At such extremes of simulated system complexity, the largest stable complex systems would be unstable if not for $\text{Var}(\gamma)$. My results therefore reveal a previously unconsidered aspect of system stability that is likely to be pervasive across all realistic complex systems.

In 1972, May¹ first demonstrated that randomly assembled systems of sufficient complexity are almost inevitably unstable given infinitesimally small perturbations. Complexity in this case is defined by the size of the system (i.e., the number of potentially interacting components; S), its connectance (i.e., the probability that one component will interact with another; C), and the variance of interaction strengths (σ^2)². May's finding that the probability of local stability falls to near zero given a sufficiently high threshold of $\sigma\sqrt{SC}$ is broadly relevant for understanding the dynamics and persistence of systems such as ecological^{1–5}, neurological^{6,7}, biochemical^{8,9}, and socio-economic^{10–13} networks. As such, identifying general principles that affect stability in complex systems is of wide-ranging importance.

Randomly assembled complex systems can be represented as large square matrices (\mathbf{M}) with S components (e.g., networks of species² or banks¹¹). One element of such a matrix, M_{ij} , defines how component j affects component i in the system at a point of equilibrium². Off-diagonal elements ($i \neq j$) therefore define interactions between components, while diagonal elements ($i = j$) define component self-regulation (e.g., carrying capacity in ecological communities). Traditionally, off-diagonal elements are assigned non-zero values with a probability C , which are sampled from a distribution with variance σ^2 ; diagonal elements are set to -1 ^{1,2,4}. Local system stability is assessed using eigenanalysis, with the system being stable if the real parts of all eigenvalues (λ) of \mathbf{M} are negative ($\max(\Re(\lambda)) < 0$)^{1,2}. In a large system (high S), eigenvalues are distributed uniformly¹⁴ within a circle centred at $\Re = -1$ (the mean value of diagonal elements) and $\Im = 0$, with a radius of $\sigma\sqrt{SC}$ ^{1,2,4} (Figs 1a and 2a). Local stability of randomly assembled systems therefore becomes increasingly unlikely as S , C , and σ^2 increase.

May's^{1,2} stability criterion $\sigma\sqrt{SC} < 1$ assumes that the expected response rates (γ) of individual components to perturbations of the system are identical, but this is highly unlikely in any complex system. In ecological communities, for example, the rate at which population density changes following perturbation will depend on the generation time of organisms, which might vary by orders of magnitude among species. Species with short generation times will respond quickly (high γ) to perturbations relative to species with long generation times (low γ). Similarly, the speed at which individual banks respond to perturbations in financial networks, or individuals or institutions respond to perturbations in complex social networks, is likely to vary. The effect of such variance on stability has not been investigated in complex systems theory. Intuitively, variation in γ might be expected to decrease system stability by introducing a new source of variation into the system and thereby increasing σ . Here I show why, despite higher σ , realistic complex systems (such that S is high but finite) are actually more likely to be stable if their individual component response rates vary.

Results

Component response rates of random complex systems. Rows in \mathbf{M} define how a given component i is affected by other components of the system, meaning that the rate of component response time can be modelled by multiplying all row elements by a real scalar value γ_i ¹⁵. The distribution of γ over S components thereby models the distribution of component response rates. An instructive example compares one \mathbf{M} where $\gamma_i = 1$ for all i in S to the same \mathbf{M} when half of $\gamma_i = 1.95$ and half of $\gamma_i = 0.05$. This models one system in which γ is invariant and one in which γ varies, but systems are otherwise identical (note that mean $\gamma_i = 1$ in both cases). I assume $S = 200$, $C = 0.05$, and $\sigma = 0.4$; diagonal elements are set to -1 and non-zero off-diagonal elements are drawn randomly from $\mathcal{N}(0, \sigma^2)$. Rows are then multiplied by γ_i to generate \mathbf{M} . When $\gamma_i = 1$, eigenvalues of \mathbf{M} are distributed uniformly within a circle centred at $(-1, 0)$ with a radius of 1.265 (Fig. 1a). Hence, the real components of eigenvalues are highly unlikely to all be negative when all $\gamma_i = 1$. But when γ_i values are separated into two groups, eigenvalues are no longer uniformly distributed (Fig. 1b). Instead, two distinct clusters of eigenvalues appear (red circles in Fig. 1b), one centred at $(-1.95, 0)$ and the other centred at $(-0.05, 0)$. The former has a large radius, but the real components have shifted to the left (in comparison to when $\gamma = 1$), while the latter cluster has a smaller radius, but real components have shifted to the right; all $\Re(\lambda) < 0$. Overall, for 1 million randomly assembled \mathbf{M} , this division between slow and fast component response rates results in more stable systems: 1 stable given $\gamma = 1$ versus 32 stable given $\gamma = \{1.95, 0.5\}$.

Higher stability in systems with variation in γ can be observed by sampling γ_i values from various distributions. I focus on a uniform distribution where $\gamma \sim \mathcal{U}(0, 2)$ (see Supplementary Information for other distributions, which give similar results). As with the case of $\gamma = \{1.95, 0.5\}$ (Fig. 1b), mean $\gamma = 1$ when $\gamma \sim \mathcal{U}(0, 2)$, allowing comparison of \mathbf{M} before and after the addition of variation in component response rate. Figure 2 shows a comparison of eigenvalue distributions given $S = 1000$, $C = 0.05$, and $\sigma = 0.4$. As expected¹⁴, when $\gamma = 1$, eigenvalues are distributed uniformly in a circle centred at $(-1, 0)$ with a radius of $\sigma\sqrt{SC} = 2.828$. Uniform variation in γ leads to a non-uniform distribution of eigenvalues^{16–18}, some of which are clustered locally near the centre of the distribution, but others of which are spread outside the former radius of 2.828 (Fig 2b). The clustering and spreading of eigenvalues introduced by $Var(\gamma)$ can destabilise previously stable systems or stabilise systems that are otherwise unstable. But where systems are otherwise too complex to be stable given $\gamma = 1$, the effect of $Var(\gamma)$ can often lead to stability above May’s^{1,2} threshold $\sigma\sqrt{SC} < 1$.

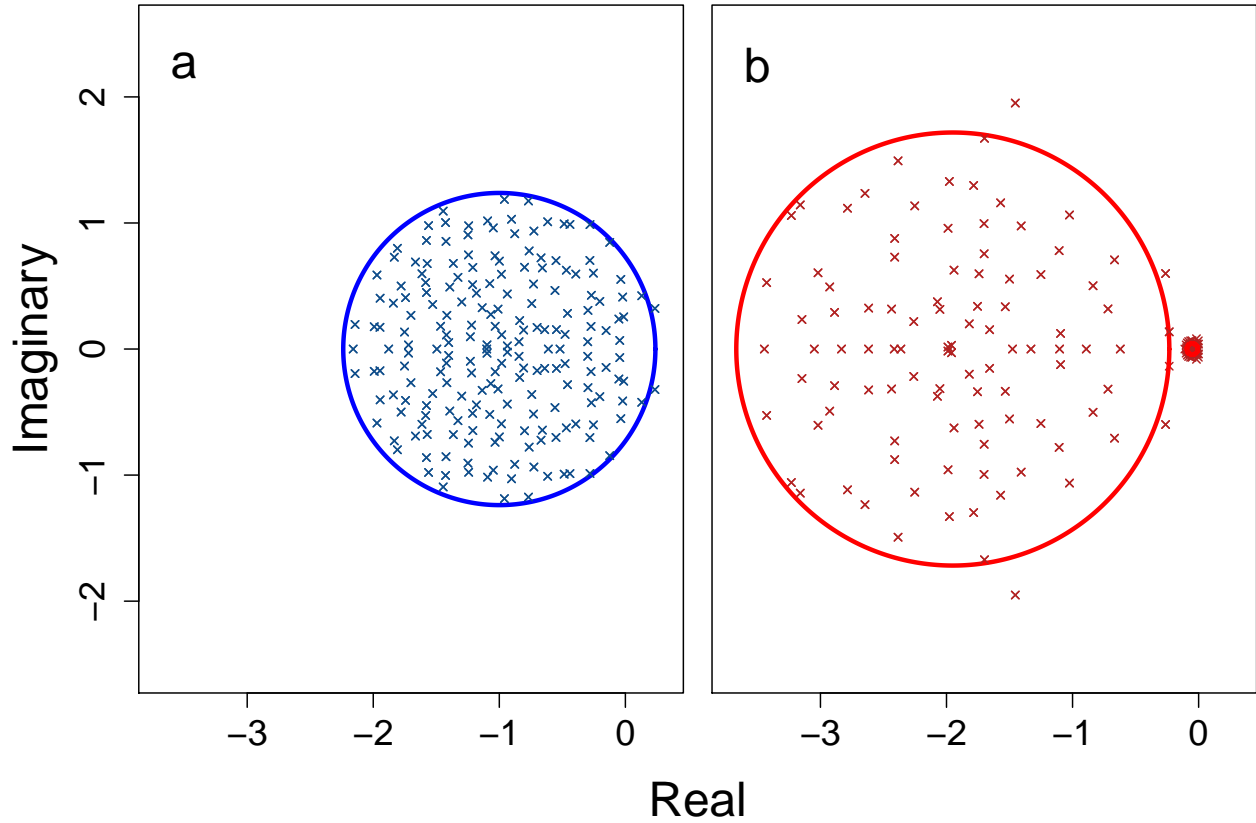
Simulation of random \mathbf{M} across S . To investigate the effect of $Var(\gamma)$ on stability across systems of varying complexity, I simulated random \mathbf{M} matrices at $\sigma = 0.4$ and $C = 1$ across $S = \{2, 3, \dots, 49, 50\}$. One million \mathbf{M} were simulated for each S , and the stability of \mathbf{M} was assessed given $\gamma = 1$ versus $\gamma \sim \mathcal{U}(0, 2)$. For all $S > 10$, I found that the number of stable random systems was higher given $Var(\gamma)$ than when $\gamma = 1$ (Fig. 3; see Supplementary Information for full table of results), and that the difference between the probabilities of observing a stable system increased with an increase in S . In other words, the potential for $Var(\gamma)$ to affect stability increased with system complexity and was most relevant for systems on the cusp of being too complex to be realistically stable. For the highest values of S , nearly all systems that were stable given $Var(\gamma)$ would not have been stable given $\gamma = 1$.

Targeted manipulation of γ . To further investigate the potential of $Var(\gamma)$ to be stabilising, I used a genetic algorithm. Genetic algorithms are heuristic tools that mimic evolution by natural selection, and are useful when the space of potential solutions (in this case, possible combinations of γ values leading to stability in a complex system) is too large to search exhaustively¹⁹. Generations of selection on γ value combinations to minimise $\max(\Re(\lambda))$ demonstrated the potential for $Var(\gamma)$ to increase system stability. Across $S = \{2, 3, \dots, 39, 40\}$, sets of γ values were found that resulted in stable systems with probabilities that were up to four orders of magnitude higher than when $\gamma = 1$ (Fig. 4), meaning that stability could often be achieved by manipulating S γ values rather than $S \times S$ \mathbf{M} elements (i.e., by manipulating component response rates rather than interactions between components).

System feasibility given $Var(\gamma)$ For complex systems in which individual system components represent the density of some tangible quantity, it is relevant to consider the feasibility of the system. Feasibility assumes that values of all components are positive at equilibrium^{5,20,21}. This is of particular interest for ecological communities because population density (N) cannot take negative values, meaning that ecological

systems need to be feasible for stability to be biologically realistic²⁰. While my results are intended to be general to all complex systems, and not restricted to species networks, I have also performed a feasibility analysis on all matrices \mathbf{M} tested for stability, and additionally for specific types of ecological communities² (e.g., competitive, mutualist, predator-prey; see Supplementary Information). I emphasise that γ is not interpreted as population density in this analysis, but instead as a fundamental property of species life history such as expected generation time. Feasibility was unaffected by $Var(\gamma)$ and instead occurred with a fixed probability of $1/2^S$, consistent with a recent proof by Serván et al.²² (see Supplementary Information). Hence, for pure interacting species networks, variation in component response rate (i.e., species generation time) does not affect stability at biologically realistic species densities.

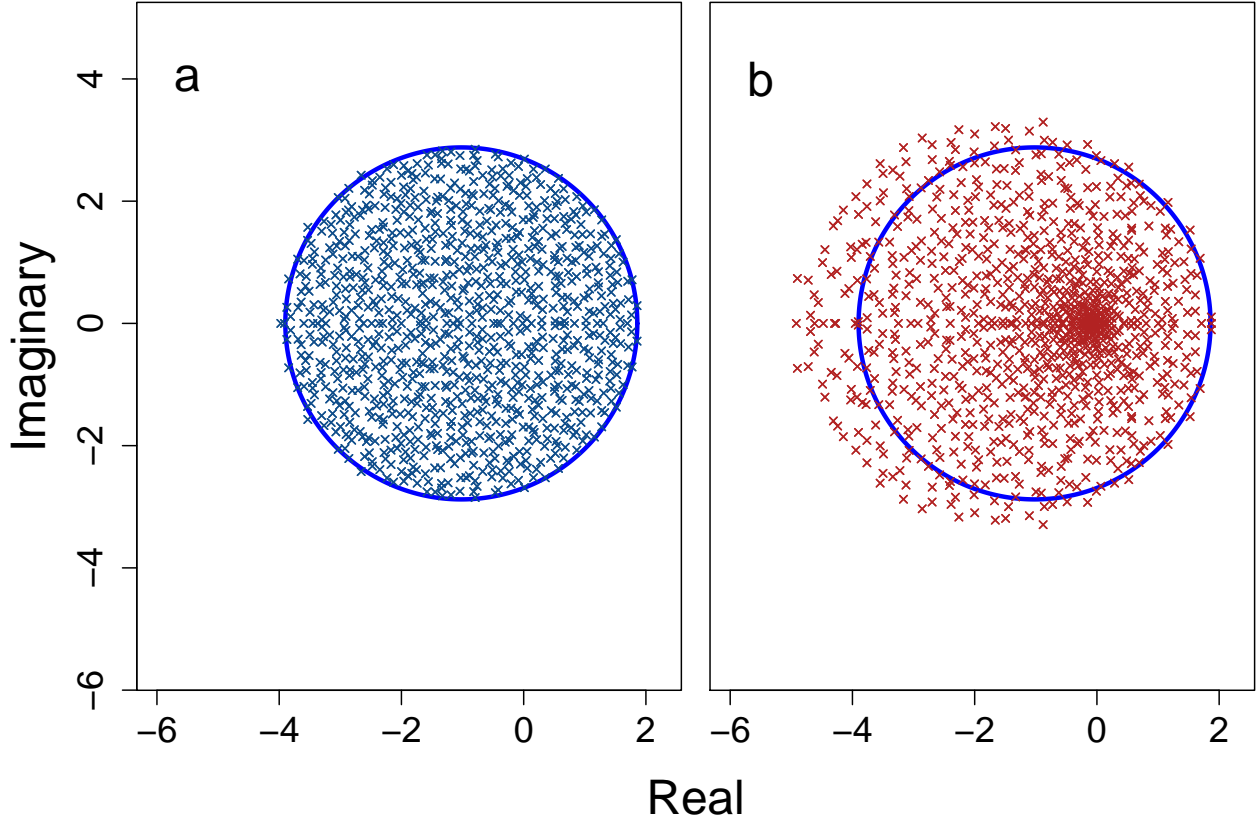
Figure 1: Example distribution of eigenvalues before (a) and after (b) separating a randomly generated complex system into fast ($\gamma = 1.95$) and slow ($\gamma = 0.05$) component response rates. Each panel shows the same system where $S = 200$, $C = 0.05$, and $\sigma = 0.4$, and in each case $E[\gamma] = 1$ (i.e., only the distribution of γ differs between panels). **a.** Eigenvalues plotted when all $\gamma = 1$; distributions of points are uniformly distributed within the blue circle with a radius of $\sigma\sqrt{SC} = 1.238$ centred at -1 on the real axis. **b.** Eigenvalues plotted when half $\gamma = 1.95$ and half $\gamma = 0.05$; distributions of points can be partitioned into one large circle centred at $\gamma = -1.95$ and one small circle centred at $\gamma = -0.05$. In a, the maximum real eigenvalue $\max(\Re(\lambda)) = 0.2344871$, while in b $\max(\Re(\lambda)) = -0.0002273135$, meaning that the complex system in b but not a is stable because in b $\max(\Re(\lambda)) < 0$. In 1 million randomly generated complex systems under the same parameter values, 1 was stable when $\gamma = 1$ while 32 were stable when $\gamma = \{1.95, 0.05\}$. Overall, complex systems that are separated into fast versus slow components tend to be more stable than otherwise identical systems with identical component response rates.



Discussion

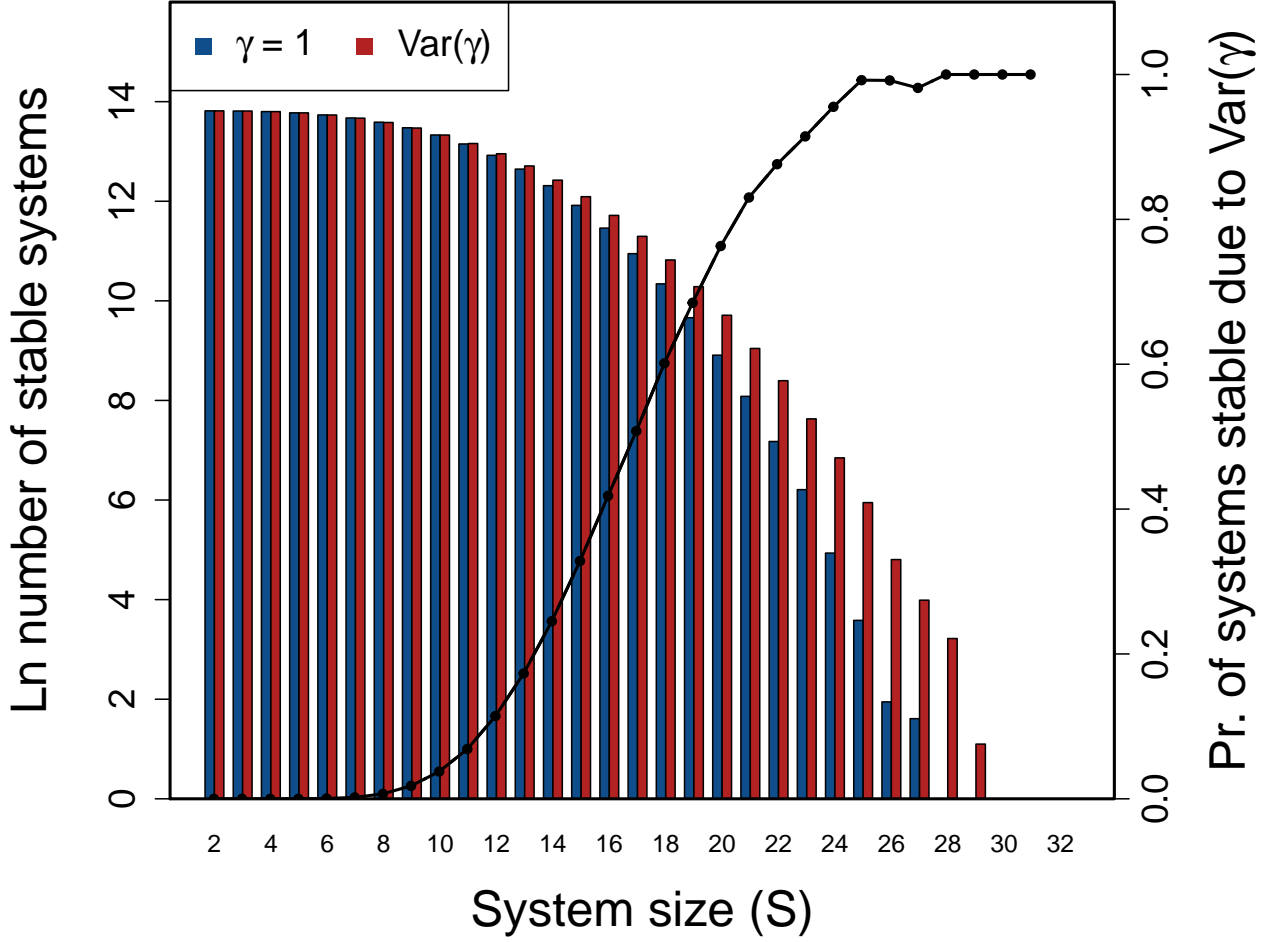
I have shown that the stability of complex systems might often be contingent upon variation in the response rates of their individual components, meaning that factors such as rate of trait evolution (in biological networks), transaction speed (in economic networks), or communication speed (in social networks) need to be considered when investigating the stability of complex systems. Variation in component response rate is more likely to be critical for stability in systems that are especially complex, and it can ultimately increase the probability that system stability is observed above that predicted by May's¹ classically derived $\sigma\sqrt{SC}$ criterion. The logic outlined here is general, and potentially applies to any complex system in which individual system components can vary in their reaction rates to system perturbation.

Figure 2: Distributions of eigenvalues before (a) and after (b) introducing variation in component response rate (γ) in complex systems. Each panel show the same system where $S = 1000$, $C = 0.05$, and $\sigma = 0.4$. **a.** Eigenvalues plotted in the absence of $Var(\gamma)$ where $E[\gamma] = 1$, versus **b.** eigenvalues plotted given $\gamma \sim \mathcal{U}(0, 2)$, which increases the variance of interaction strengths (σ^2) but also creates a cluster of eigenvalues toward the distribution's centre $(-1, 0)$. Blue ellipses in both panels show the circle centred on the distribution in panel a. Proportions of $\Re(\lambda) < 0$ are 0.724 and 0.742 for a and b, respectively.



It is important to recognise that variation in component response rate is not stabilising per se; that is, adding variation in component response rates to a particular system does not increase the probability that the system will be stable. Rather, highly complex systems that are observed to be stable are more likely to have varying component response rates, and for this variation to be critical to their stability (Fig. 3). This is caused by the shift to a non-uniform distribution of eigenvalues that occurs by introducing $Var(\gamma)$ (Fig. 1b, 2b), which can sometimes cause all of the real components of the eigenvalues of the system matrix to become negative, but might also increase the real components of eigenvalues.

Figure 3: Stability of large complex systems with and without variation in component response rate (γ). The ln number of systems that are stable across different system sizes (S , max $S = 50$) given $C = 1$, and the proportion of systems in which variation in γ is critical for system stability. For each S , 1 million complex systems are randomly generated. Stability of each complex system is tested given variation in γ by randomly sampling $\gamma \sim \mathcal{U}(0, 2)$. Stability given $\text{Var}(\gamma)$ is then compared to stability in an otherwise identical system in which $\gamma = E[\mathcal{U}(0, 2)]$ for all components. Blue and red bars show the number of stable systems in the absence and presence of $\text{Var}(\gamma)$, respectively. The black line shows the proportion of systems that are stable when $\text{Var}(\gamma) > 0$, but would be unstable if $\text{Var}(\gamma) = 0$.

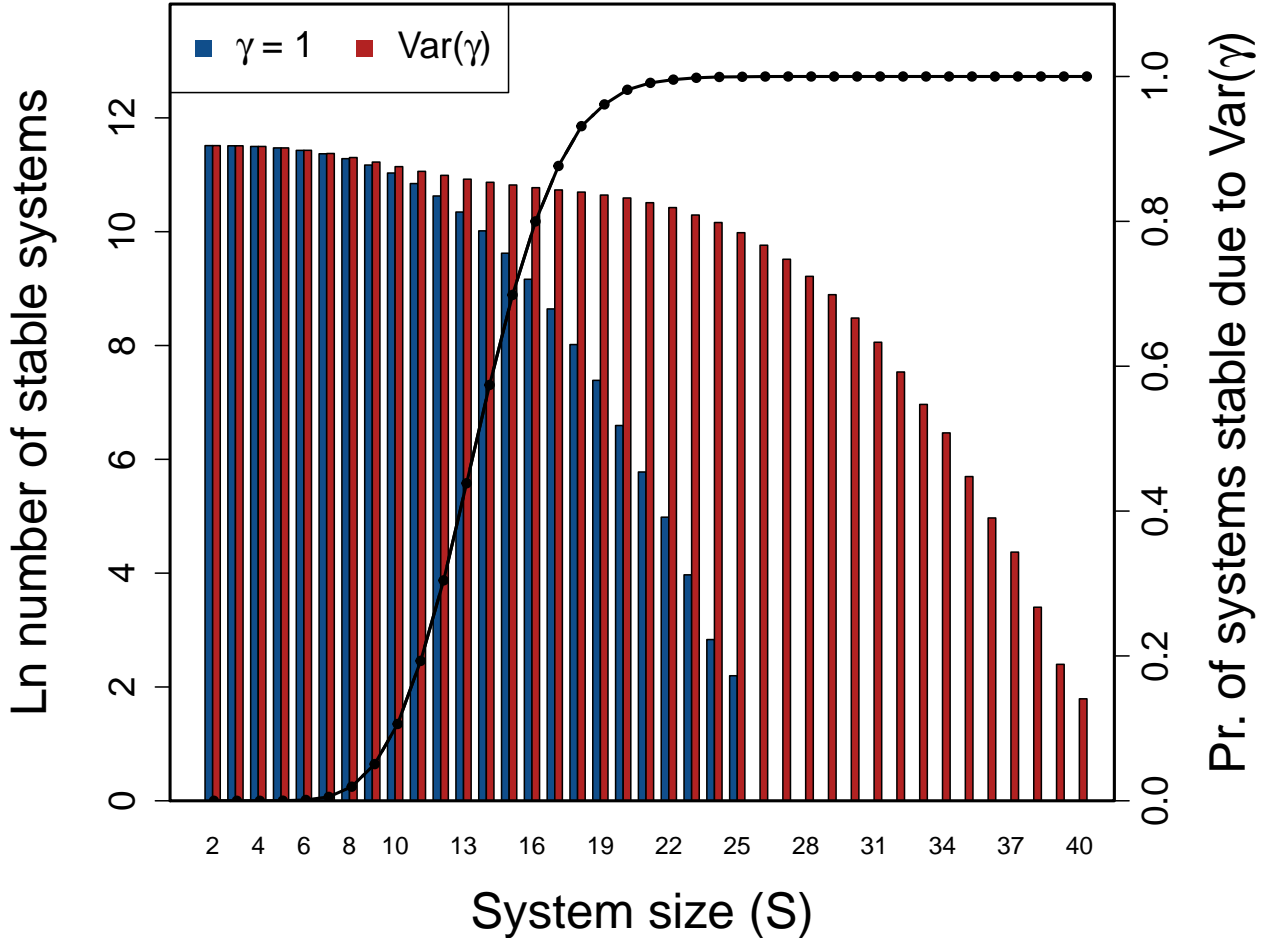


My focus is distinct from Gibbs et al.¹⁷, who applied the same mathematical framework to investigate how a diagonal matrix \mathbf{X} (equivalent to γ in my model) affects the stability of a community matrix \mathbf{M} given an interaction matrix \mathbf{A} within a generalised Lotka-Volterra model, where $\mathbf{M} = \mathbf{XA}$. Gibbs et al.¹⁷ analytically demonstrated that the effect of \mathbf{X} on system stability decreases exponentially as system size becomes arbitrarily large ($S \rightarrow \infty$) for a given magnitude of complexity $\sigma\sqrt{SC}$. My numerical results do not contradict this prediction because I did not scale $\sigma = 1/\sqrt{S}$, but instead fixed σ and increased S to thereby increase total system complexity (see Supplementary Information for results simulated across σ and C). Overall, I show that component response rate variation increases the upper bound of complexity at which stability can be realistically observed, meaning that highly complex systems are more likely than not to vary in their component response rates, and for this variation to be critical for system stability.

The potential importance of component response rate variation was most evident from the results of simulations in which the genetic algorithm was used in attempt to maximise the probability of system stability. The

probability that some combination of component response rates could be found to stabilise the system was shown to be up to four orders of magnitude higher than the background probabilities of stability in the absence of any component response rate variation. Instead of manipulating the $S \times S$ interactions between system components, it might therefore be possible to manipulate only the S response rates of individual system components to achieve stability. Hence, managing the response rates of system components in a targeted way could potentially facilitate the stabilisation of complex systems through a reduction in dimensionality.

Figure 4: Stability of large complex systems given $\gamma = 1$ versus targeted $Var(\gamma)$. The \ln number of systems that are stable across different system sizes (S , max $S = 40$) for $C = 1$, and the proportion of systems wherein a targeted search of γ values successfully resulted in system stability. For each S , 100000 complex systems are randomly generated. Stability of each complex system is tested given variation in γ using a genetic algorithm to maximise the effect of γ values on increasing stability, as compared to stability in an otherwise identical system in which γ is the same for all components. Blue bars show the number of stable systems in the absence of component response rate variation, while red bars show the number of stable systems that can be generated if component response rate is varied to maximise system stability. The black line shows the proportion of systems that are stable when component response rate is targeted to increase stability, but would not be stable if $Var(\gamma) = 0$.



Interestingly, while complex systems were more likely to be stable given variation in component response rate, they were not more likely to be feasible, meaning that stability was not increased when component values were also restricted to being positive at equilibrium. Feasibility is important to consider, particularly for the study of ecological networks of species^{5,18,20,22} because population densities cannot realistically be negative.

My results therefore suggest that variation in the rate of population responses to perturbation (e.g., due to differences in generation time among species) is unlikely to be critical to the stability of purely multi-species interaction networks (see also Supplementary Information). Nevertheless, ecological interactions do not exist in isolation in empirical systems¹⁵, but instead interact with evolutionary, abiotic, or social-economic systems. The relevance of component response rate for complex system stability should therefore not be ignored in the broader context of ecological communities.

A general mathematical framework encompassing shifts in eigenvalue distributions caused by a vector γ has been investigated¹⁶ and recently applied to questions concerning species density and feasibility^{17,18}, but γ has not been interpreted as rates of response of individual system components to perturbation. My model focuses on component response rates for systems of a finite size, in which complexity is high but not yet high enough to make the probability of stability unrealistically low for actual empirical systems. For this upper range of system size, randomly assembled complex systems are more likely to be stable if their component response rates vary (e.g., $10 < S < 30$ for parameter values in Fig. 3). Overall, I suggest that variation in component response rate might therefore be critical for maintaining stability in many highly complex empirical systems. These results are broadly applicable for understanding the stability of complex networks across the physical, life, and social sciences.

Methods

Component response rate variation (γ). In a synthesis of eco-evolutionary feedbacks on community stability, Patel et al. model a system that includes a vector of potentially changing species densities (\mathbf{N}) and a vector of potentially evolving traits (\mathbf{x})¹⁵. For any species i or trait j , change in species density (N_i) or trait value (x_j) with time (t) is a function of the vectors \mathbf{N} and \mathbf{x} ,

$$\frac{dN_i}{dt} = N_i f_i(\mathbf{N}, \mathbf{x}),$$

$$\frac{dx_j}{dt} = \epsilon g_j(\mathbf{N}, \mathbf{x}).$$

In the above, f_i and g_j are functions that define the effects of all species densities and trait values on the density of a species i and the value of trait j , respectively. Patel et al. were interested in stability when the evolution of traits was relatively slow or fast in comparison with the change in species densities¹⁵, and this is modulated in the above by the scalar ϵ . The value of ϵ thereby determines the timescale separation between ecology and evolution, with high ϵ modelling relatively fast evolution and low ϵ modelling relative slow evolution¹⁵.

I use the same principle that Patel et al. use to modulate the relative rate of evolution to modulate rates of component responses for S components. Following May^{1,23}, the value of a component i at time t ($v_i(t)$) is affected by the value of j ($v_j(t)$) and j 's marginal effect on i (a_{ij}), and by i 's response rate (γ_i),

$$\frac{dv_i(t)}{dt} = \gamma_i \sum_{j=1}^S a_{ij} v_j(t).$$

In matrix notation²³,

$$\frac{d\mathbf{v}(t)}{dt} = \gamma \mathbf{A} \mathbf{v}(t).$$

In the above, γ is a diagonal matrix in which elements correspond to individual component response rates. Therefore, $\mathbf{M} = \gamma \mathbf{A}$ defines the values of system components and can be analysed using the techniques of May^{1,16,23}. In these analyses, row means of \mathbf{A} are expected to be identical, but variation around this

expectation will naturally arise due to random sampling of \mathbf{A} off-diagonal elements and finite S . In simulations, the total variation in \mathbf{M} row means that is attributable to \mathbf{A} is small relative to that attributable to γ , especially at high S . Variation in γ specifically isolates the effects of differing component response rates, hence causing differences in expected \mathbf{M} row means.

Genetic algorithm. Ideally, to investigate the potential of $Var(\gamma)$ for increasing the proportion of stable complex systems, the search space of all possible γ vectors would be evaluated for each unique $\mathbf{M} = \gamma\mathbf{A}$. This is technically impossible because γ_i can take any real value between 0-2, but even rounding γ_i to reasonable values would result in a search space too large to practically explore. Under these conditions, genetic algorithms are highly useful tools for finding practical solutions by mimicking the process of biological evolution¹⁹. In this case, the practical solution is finding vectors of γ that decrease the most positive real eigenvalue of \mathbf{M} . The genetic algorithm used achieves this by initialising a large population of 1000 different potential γ vectors and allowing this population to evolve through a process of mutation, crossover (swapping γ_i values between vectors), selection, and reproduction until either a γ vector is found where all $\Re(\lambda) < 0$ or some “giving up” criteria is met.

For each $S = \{2, 3, \dots, 39, 40\}$, the genetic algorithm was run for 100000 random \mathbf{M} ($\sigma = 0.4$, $C = 1$). The genetic algorithm was initialised with a population of 1000 different γ vectors with elements sampled i.i.d from $\gamma_i \sim \mathcal{U}(0, 2)$. Eigenanalysis was performed on the \mathbf{M} resulting from each γ vector, and the 20 γ vectors resulting in \mathbf{M} with the lowest $\max(\Re(\lambda))$ each produced 50 clonal offspring with subsequent random mutation and crossover between the resulting new generation of 1000 γ vectors. Mutation of each γ_i in a γ vector occurred with a probability of 0.2, resulting in a mutation effect of size $\mathcal{N}(0, 0.02)$ being added to generate the newly mutated γ_i (any γ_i values that mutated below zero were multiplied by -1 , and any values that mutated above 2 were set to 2). Crossover occurred between two sets of 100 γ vectors paired in each generation; vectors were randomly sampled with replacement among but not within sets. Vector pairs selected for crossover swapped all elements between and including two γ_i randomly selected with replacement (this allowed for reversal of vector element positions during crossover; e.g., $\{\gamma_4, \gamma_5, \gamma_6, \gamma_7\} \rightarrow \{\gamma_7, \gamma_6, \gamma_5, \gamma_4\}$). The genetic algorithm terminated if a stable \mathbf{M} was found, 20 generations occurred, or if the mean γ fitness increase between generations was less than 0.01 (where fitness was defined as $W_\gamma = -\max(\Re(\lambda))$ for \mathbf{M}).

System feasibility. Dougoud et al.²⁰ identify the following feasibility criteria for ecological systems characterised by S interacting species with varying densities in a generalised Lotka-Volterra model,

$$\mathbf{n}^* = -(\theta\mathbf{I} + (CS)^{-\delta}\mathbf{J})^{-1}\mathbf{r}.$$

In the above, \mathbf{n}^* is the vector of species densities at equilibrium. Feasibility is satisfied if all elements in \mathbf{n}^* are positive. The matrix \mathbf{I} is the identity matrix, and the value θ is the strength of intraspecific competition (diagonal elements). Diagonal values are set to -1 , so $\theta = -1$. The variable δ is a normalisation parameter that modulates the strength of interactions (σ) for \mathbf{J} . Implicitly, here $\delta = 0$ underlying strong interactions. Hence, $(CS)^{-\delta} = 1$, so in the above, a diagonal matrix of -1 s ($\theta\mathbf{I}$) is added to \mathbf{J} , which has a diagonal of all zeros and an off-diagonal affecting species interactions (i.e., the expression $(CS)^{-\delta}$ relates to May's¹ stability criterion²⁰ by $\frac{\sigma}{(CS)^{-\delta}}\sqrt{SC} < 1$, and hence for my purposes $(CS)^{-\delta} = 1$). Given $\mathbf{A} = \theta\mathbf{I} + \mathbf{J}$, the above criteria is therefore reduced to the below²²,

$$\mathbf{n}^* = -\mathbf{A}^{-1}\mathbf{r}.$$

To check the feasibility criteria for $\mathbf{M} = \gamma\mathbf{A}$, I therefore evaluated $-\mathbf{M}^{-1}\mathbf{r}$ (\mathbf{r} elements were sampled i.i.d. from $r_i \sim \mathcal{N}(0, 0.4^2)$). Feasibility is satisfied if all of the elements of the resulting vector are positive.

Acknowledgements: I am supported by a Leverhulme Trust Early Career Fellowship (ECF-2016-376). Conversations with L. Bussière and N. Bunnefeld, and comments from J. J. Cusack and I. L. Jones, improved the quality of this work.

References

1. May, R. M. Will a large complex system be stable? *Nature* **238**, 413–414 (1972).
2. Allesina, S. & Tang, S. Stability criteria for complex ecosystems. *Nature* **483**, 205–208 (2012).
3. Mougi, A. & Kondoh, M. Diversity of interaction types and ecological community stability. *Science* **337**, 349–351 (2012).
4. Allesina, S. *et al.* Predicting the stability of large structured food webs. *Nature Communications* **6**, 7842 (2015).
5. Grilli, J. *et al.* Feasibility and coexistence of large ecological communities. *Nature Communications* **8**, (2017).
6. Gray, R. T. & Robinson, P. A. Stability and synchronization of random brain networks with a distribution of connection strengths. *Neurocomputing* **71**, 1373–1387 (2008).
7. Gray, R. T. & Robinson, P. A. Stability of random brain networks with excitatory and inhibitory connections. *Neurocomputing* **72**, 1849–1858 (2009).
8. Rosenfeld, S. Patterns of stochastic behavior in dynamically unstable high-dimensional biochemical networks. *Gene Regulation and Systems Biology* **3**, 1–10 (2009).
9. MacArthur, B. D., Sanchez-Garcia, R. J. & Ma’ayan, A. Microdynamics and criticality of adaptive regulatory networks. *Physics Review Letters* **104**, 168701 (2010).
10. May, R. M., Levin, S. A. & Sugihara, G. Complex systems: Ecology for bankers. *Nature* **451**, 893–895 (2008).
11. Haldane, A. G. & May, R. M. Systemic risk in banking ecosystems. *Nature* **469**, 351–355 (2011).
12. Suweis, S. & D’Odorico, P. Early warning signs in social-ecological networks. *PLoS ONE* **9**, (2014).
13. Bardoscia, M., Battiston, S., Caccioli, F. & Caldarelli, G. Pathways towards instability in financial networks. *Nature Communications* **8**, 1–7 (2017).
14. Tao, T. & Vu, V. Random matrices: Universality of ESDs and the circular law. *Annals of Probability* **38**, 2023–2065 (2010).
15. Patel, S., Cortez, M. H. & Schreiber, S. J. Partitioning the effects of eco-evolutionary feedbacks on community stability. *American Naturalist* **191**, 1–29 (2018).
16. Ahmadian, Y., Fumarola, F. & Miller, K. D. Properties of networks with partially structured and partially random connectivity. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics* **91**, 012820 (2015).
17. Gibbs, T., Grilli, J., Rogers, T. & Allesina, S. The effect of population abundances on the stability of large random ecosystems. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics* **98**, 022410 (2018).
18. Stone, L. The feasibility and stability of large complex biological networks: a random matrix approach. *Scientific Reports* **8**, 8246 (2018).
19. Hamblin, S. On the practical usage of genetic algorithms in ecology and evolution. *Methods in Ecology and Evolution* **4**, 184–194 (2013).
20. Dougoud, M., Vinckenbosch, L., Rohr, R., Bersier, L.-F. & Mazza, C. The feasibility of equilibria in large ecosystems: a primary but neglected concept in the complexity-stability debate. *PLOS Computational Biology* **14**, e1005988 (2018).
21. Song, C. & Saavedra, S. Will a small randomly assembled community be feasible and stable? *Ecology* **99**, 743–751 (2018).
22. Serván, C. A., Capitán, J. A., Grilli, J., Morrison, K. E. & Allesina, S. Coexistence of many species in

random ecosystems. *Nature Ecology and Evolution* **2**, 1237–1242 (2018).

23. May, R. M. Qualitative stability in model ecosystems. *Ecology* **54**, 638–641 (1973).

This Supplementary information supports the manuscript “Component response rate variation drives stability in large complex systems” with additional analyses to support its conclusions. All text, code, and data underlying this manuscript are publicly available on [GitHub](#) as part of the RandomMatrixStability R package.

The [RandomMatrixStability package](#) includes all functions and tools for recreating the text, this Supplementary information, and running all code; additional documentation is also provided for package functions. The RandomMatrixStability package is available on [GitHub](#); to download it, the [devtools](#) library is needed.

```
install.packages("devtools");
library(devtools);
```

The code below installs the RandomMatrixStability package using devtools.

```
install_github("bradduthie/RandomMatrixStability");
```

Supplementary Information table of contents

- [Stability across increasing \$S\$](#)
- [Stability given targeted manipulation of \$\gamma\$ \(genetic algorithm\)](#)
- [Stability of ecological networks](#)
 - [Competitor networks](#)
 - [Mutualist networks](#)
 - [Predator-prey networks](#)
- [Sensitivity of connectance \(\$C\$ \) values](#)
 - [C = 0.3](#)
 - [C = 0.5](#)
 - [C = 0.7](#)
 - [C = 0.9](#)
- [Large networks of \$C = 0.05\$ across \$S\$ and \$\sigma\$](#)
 - [σ = 0.3](#)
 - [σ = 0.4](#)
 - [σ = 0.5](#)
 - [σ = 0.6](#)
- [Sensitivity of distribution of \$\gamma\$](#)
- [Feasibility of complex systems](#)
- [Consistency with Gibbs et al. \(2018\)](#)

Stability across increasing S

Figure 3 of the main text reports the number of stable random complex systems found over 1 million iterations. The table below shows the results for all simulations of random \mathbf{M} matrices at $\sigma = 0.4$ and $C = 1$ given a range of $S = \{2, 3, \dots, 49, 50\}$. In this table, the A0 refers to matrices where $\gamma = 1$, while A1 refers to matrices after $Var(\gamma)$ is added and $\gamma \sim \mathcal{U}(0, 2)$. Each row summarises data for a given S over 1 million randomly simulated \mathbf{M} (A0 and A1). The column A0_unstable shows the number of A0 matrices that are unstable, and the column A0_stable shows the number of A0 matrices that are stable (these two columns sum to 1 million). Similarly, the column A1_unstable shows the number of A1 matrices that are unstable and A1_stable shows the number that are stable. The columns A1_stabilised and A1_destabilised show how many A0 matrices were stabilised or destabilised, respectively, by $Var(\gamma)$.

S	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	293	999707	293	999707	0	0
3	3602	996398	3609	996391	0	7
4	14937	985063	15008	984992	0	71
5	39289	960711	39783	960217	36	530
6	78845	921155	80207	919793	389	1751
7	133764	866236	136904	863096	1679	4819
8	204112	795888	208241	791759	5391	9520
9	288041	711959	291775	708225	12619	16353
10	384024	615976	384931	615069	23153	24060
11	485975	514025	481019	518981	35681	30725
12	590453	409547	577439	422561	48302	35288
13	689643	310357	669440	330560	57194	36991
14	777496	222504	751433	248567	60959	34896
15	850159	149841	821613	178387	58567	30021
16	905057	94943	877481	122519	51255	23679
17	943192	56808	919536	80464	40854	17198
18	969018	30982	949944	50056	30102	11028
19	984301	15699	970703	29297	20065	6467
20	992601	7399	983507	16493	12587	3493
21	996765	3235	991532	8468	7030	1797
22	998693	1307	995567	4433	3884	758
23	999503	497	997941	2059	1883	321
24	999861	139	999059	941	899	97
25	999964	36	999617	383	380	33
26	999993	7	999878	122	121	6
27	999995	5	999946	54	53	4
28	1000000	0	999975	25	25	0
29	1000000	0	999997	3	3	0
30	1000000	0	999999	1	1	0
31	1000000	0	999999	1	1	0
32	1000000	0	1000000	0	0	0
33	1000000	0	1000000	0	0	0
34	1000000	0	1000000	0	0	0
35	1000000	0	1000000	0	0	0
36	1000000	0	1000000	0	0	0
37	1000000	0	1000000	0	0	0
38	1000000	0	1000000	0	0	0
39	1000000	0	1000000	0	0	0
40	1000000	0	1000000	0	0	0
41	1000000	0	1000000	0	0	0
42	1000000	0	1000000	0	0	0
43	1000000	0	1000000	0	0	0
44	1000000	0	1000000	0	0	0
45	1000000	0	1000000	0	0	0
46	1000000	0	1000000	0	0	0
47	1000000	0	1000000	0	0	0
48	1000000	0	1000000	0	0	0
49	1000000	0	1000000	0	0	0
50	1000000	0	1000000	0	0	0

Overall, the ratio of stable A1 matrices to stable A0 matrices found is greater than 1 whenever $S > 10$ (compare column 5 to column 3), and this ratio increases with increasing S (column 1). Hence, more randomly

created complex systems (\mathbf{M}) are stable given variation in γ than when $\gamma = 1$. Note that feasibility results were omitted for the table above, but are [reported below](#).

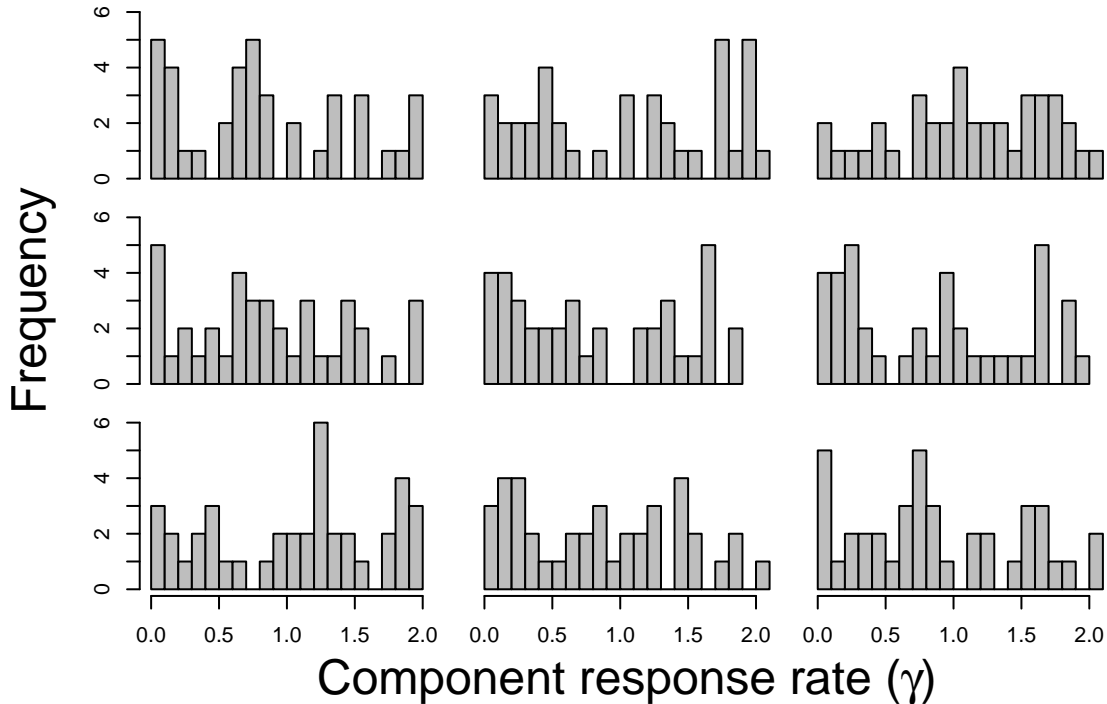
Stability given targeted manipulation of γ (genetic algorithm)

Figure 4 of the main text reports the number of stable random complex systems found over 100000 using the genetic algorithm to maximise stability with a vector γ . Stability results for 100000 \mathbf{M} for each S from 2-40 are shown below. Results for A0 indicate systems in which $\gamma = 1$, while A1 refers to systems in which the genetic algorithm searched for a set of γ values that stabilised the system.

S	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	26	99974	26	99974	0	0
3	358	99642	358	99642	0	0
4	1505	98495	1505	98495	0	0
5	3995	96005	3982	96018	13	0
6	8060	91940	7956	92044	104	0
7	13420	86580	12953	87047	468	1
8	20518	79482	18940	81060	1578	0
9	28939	71061	25148	74852	3793	2
10	38241	61759	30915	69085	7327	1
11	48682	51318	36398	63602	12286	2
12	58752	41248	40710	59290	18043	1
13	68888	31112	44600	55400	24289	1
14	77651	22349	47528	52472	30124	1
15	84912	15088	49971	50029	34942	1
16	90451	9549	52274	47726	38178	1
17	94332	5668	54124	45876	40209	1
18	96968	3032	55831	44169	41139	2
19	98384	1616	58079	41921	40305	0
20	99269	731	60181	39819	39088	0
21	99677	323	63338	36662	36339	0
22	99854	146	66350	33650	33504	0
23	99947	53	70478	29522	29469	0
24	99983	17	74121	25879	25862	0
25	99991	9	78364	21636	21627	0
26	99999	1	82635	17365	17364	0
27	100000	0	86433	13567	13567	0
28	100000	0	89951	10049	10049	0
29	100000	0	92716	7284	7284	0
30	100000	0	95171	4829	4829	0
31	100000	0	96844	3156	3156	0
32	100000	0	98128	1872	1872	0
33	100000	0	98941	1059	1059	0
34	100000	0	99358	642	642	0
35	100000	0	99702	298	298	0
36	100000	0	99856	144	144	0
37	100000	0	99921	79	79	0
38	100000	0	99970	30	30	0
39	100000	0	99989	11	11	0
40	100000	0	99994	6	6	0

The distributions of nine γ vectors from the highest S values are shown below. This comparison shows the high number of stable \mathbf{M} that can be produced through a targeted search of γ values, and suggests that many otherwise unstable systems could potentially be stabilised by an informed manipulation of their component response times. Such a possibility might conceivably reduce the dimensionality of problems involving stability in social-ecological or economic systems.

Distributions of γ values in vectors for the highest values of S are shown below.



The distribution of γ values found by the genetic algorithm is uniform. A uniform distribution was used to initialise γ values, so there is therefore no evidence that a particular distribution of γ is likely to be found to stabilise a matrix \mathbf{M} .

Stability of ecological networks

While the foundational work of May¹ applies broadly to complex networks, much attention has been given specifically to ecological networks of interacting species. In these networks, the matrix \mathbf{A} is interpreted as a community matrix and each row and column is interpreted as a single species. The per capita effect that the density of any species i has on the population dynamics of species j is found in A_{ij} , meaning that \mathbf{A} holds the effects of pair-wise interactions between S species^{2,3}. While May's original work¹ considered only randomly assembled communities, recent work has specifically looked at more restricted ecological communities including competitive networks (all off-diagonal elements of \mathbf{A} are negative), mutualist networks (all off-diagonal elements of \mathbf{A} are positive), and predator-prey networks (for any pair of i and j , the effect of i on j is negative and j on i is positive, or vice versa)^{2,3}. In general, competitor and mutualist networks tend to be unstable, while predator-prey networks tend to be highly stabilising².

I investigated competitor, mutualist, and predator-prey networks following Allesina et al.². To create these networks, I first generated a random matrix \mathbf{A} , then changed the elements of \mathbf{A} accordingly. If \mathbf{A} was a competitive network, then the sign of any positive off-diagonal elements was reversed to be negative. If \mathbf{A} was a mutualist network, then the sign of any positive off-diagonal elements was reversed to be positive. And if \mathbf{A} was a predator-prey network, then all i and j pairs of elements were checked; any pairs of the same sign were changed so that one was negative and the other was positive.

The number of stable $\mathbf{M} = \gamma\mathbf{A}$ systems was estimated [exactly as it was](#) in the main text for random matrices for values of S from 2 to 50 (100 in the case of the relatively more stable predator-prey interactions), except that only 100000 random \mathbf{M} were generated instead of 1 million.

The following tables for restricted ecological communities can therefore be compared with the random \mathbf{M} [results above](#) (but note that counts from systems with comparable probabilities of stability will be an order of magnitude lower in the tables below due to the smaller number of \mathbf{M} matrices generated). As with the [results above](#), in the tables below, **A0** refers to matrices when $\gamma = 1$ and **A1** refers to matrices after $Var(\gamma)$ is added. The column **A0_unstable** shows the number of A0 matrices that are unstable, and the column **A0_stable** shows the number of A0 matrices that are stable (these two columns sum to 100000). Similarly, the column **A1_unstable** shows the number of A1 matrices that are unstable and **A1_stable** shows the number that are stable. The columns **A1_stabilised** and **A1_destabilised** show how many A0 matrices were stabilised or destabilised, respectively, by $Var(\gamma)$.

Competition

Results for competitor interaction networks are shown below

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	48	99952	48	99952	0	0
3	229	99771	231	99769	0	2
4	701	99299	704	99296	0	3
5	1579	98421	1587	98413	0	8
6	3218	96782	3253	96747	6	41
7	5519	94481	5619	94381	23	123
8	9062	90938	9237	90763	77	252
9	13436	86564	13729	86271	230	523
10	18911	81089	19303	80697	505	897
11	25594	74406	25961	74039	1011	1378
12	33207	66793	33382	66618	1724	1899
13	41160	58840	41089	58911	2655	2584
14	50575	49425	49894	50106	3777	3096
15	59250	40750	57892	42108	4824	3466
16	67811	32189	65740	34260	5634	3563
17	75483	24517	73056	26944	5943	3516
18	82551	17449	79878	20122	5780	3107
19	88030	11970	85204	14796	5417	2591
20	92254	7746	89766	10234	4544	2056
21	95233	4767	93002	6998	3695	1464
22	97317	2683	95451	4549	2803	937
23	98508	1492	97122	2878	1991	605
24	99240	760	98407	1593	1216	383
25	99669	331	99082	918	739	152
26	99871	129	99490	510	452	71
27	99938	62	99732	268	240	34
28	99985	15	99888	112	108	11
29	99990	10	99951	49	46	7
30	100000	0	99981	19	19	0
31	100000	0	99993	7	7	0
32	100000	0	99996	4	4	0
33	100000	0	99998	2	2	0
34	100000	0	100000	0	0	0
...
50	100000	0	100000	0	0	0

Mutualism

Results for mutualist interaction networks are shown below

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	56	99944	56	99944	0	0
3	3301	96699	3301	96699	0	0
4	34446	65554	34446	65554	0	0
5	86520	13480	86520	13480	0	0
6	99683	317	99683	317	0	0
7	99998	2	99998	2	0	0
8	100000	0	100000	0	0	0
9	100000	0	100000	0	0	0
10	100000	0	100000	0	0	0
11	100000	0	100000	0	0	0
12	100000	0	100000	0	0	0
...
50	100000	0	100000	0	0	0

Predator-prey

Results for predator-prey interaction networks are shown below

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	0	100000	0	100000	0	0
3	0	100000	0	100000	0	0
4	0	100000	0	100000	0	0
5	1	99999	1	99999	0	0
6	4	99996	4	99996	0	0
7	2	99998	2	99998	0	0
8	5	99995	5	99995	0	0
9	20	99980	21	99979	0	1
10	20	99980	22	99978	0	2
11	38	99962	39	99961	0	1
12	64	99936	66	99934	0	2
13	87	99913	91	99909	0	4
14	157	99843	159	99841	0	2
15	215	99785	227	99773	0	12
16	293	99707	310	99690	0	17
17	383	99617	408	99592	0	25
18	443	99557	473	99527	3	33
19	642	99358	675	99325	4	37
20	836	99164	887	99113	7	58
21	1006	98994	1058	98942	10	62
22	1153	98847	1228	98772	20	95
23	1501	98499	1593	98407	30	122
24	1841	98159	1996	98004	40	195
25	2146	97854	2316	97684	58	228
26	2643	97357	2809	97191	119	285
27	3034	96966	3258	96742	158	382
28	3690	96310	3928	96072	201	439
29	4257	95743	4532	95468	290	565
30	4964	95036	5221	94779	424	681

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
31	5627	94373	5978	94022	452	803
32	6543	93457	6891	93109	666	1014
33	7425	92575	7777	92223	818	1170
34	8540	91460	8841	91159	1071	1372
35	9526	90474	9842	90158	1337	1653
36	10617	89383	10891	89109	1624	1898
37	12344	87656	12508	87492	2021	2185
38	13675	86325	13877	86123	2442	2644
39	15264	84736	15349	84651	2870	2955
40	17026	82974	17053	82947	3363	3390
41	18768	81232	18614	81386	3905	3751
42	20791	79209	20470	79530	4579	4258
43	23150	76850	22754	77246	5217	4821
44	25449	74551	24184	75816	6285	5020
45	27702	72298	26464	73536	6754	5516
46	30525	69475	28966	71034	7646	6087
47	32832	67168	31125	68875	8487	6780
48	36152	63848	33865	66135	9479	7192
49	38714	61286	36242	63758	10125	7653
50	41628	58372	38508	61492	11036	7916
51	44483	55517	41023	58977	11704	8244
52	48134	51866	44287	55713	12573	8726
53	51138	48862	46721	53279	13223	8806
54	54261	45739	49559	50441	13757	9055
55	57647	42353	52403	47597	14324	9080
56	60630	39370	55293	44707	14669	9332
57	63647	36353	57787	42213	15103	9243
58	66961	33039	60439	39561	15450	8928
59	69968	30032	63708	36292	15246	8986
60	72838	27162	66270	33730	15177	8609
61	75609	24391	68873	31127	15006	8270
62	77999	22001	71318	28682	14538	7857
63	80616	19384	73517	26483	14510	7411
64	83089	16911	76209	23791	13784	6904
65	85150	14850	78086	21914	13412	6348
66	86908	13092	80437	19563	12477	6006
67	88671	11329	82379	17621	11718	5426
68	90537	9463	84483	15517	10878	4824
69	91969	8031	86233	13767	10033	4297
70	93181	6819	87914	12086	9070	3803
71	94330	5670	89200	10800	8401	3271
72	95324	4676	90833	9167	7359	2868
73	96143	3857	91805	8195	6726	2388
74	96959	3041	93065	6935	5900	2006
75	97543	2457	93987	6013	5222	1666
76	97969	2031	94900	5100	4481	1412
77	98497	1503	95756	4244	3809	1068
78	98744	1256	96442	3558	3269	967
79	99045	955	96942	3058	2837	734
80	99276	724	97528	2472	2329	581
81	99481	519	97996	2004	1894	409
82	99556	444	98321	1679	1597	362

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
83	99691	309	98722	1278	1227	258
84	99752	248	98943	1057	1015	206
85	99833	167	99144	856	837	148
86	99895	105	99346	654	642	93
87	99925	75	99461	539	530	66
88	99945	55	99566	434	428	49
89	99976	24	99675	325	324	23
90	99977	23	99756	244	243	22
91	99982	18	99839	161	155	12
92	99988	12	99865	135	135	12
93	99994	6	99885	115	115	6
94	99993	7	99911	89	88	6
95	99998	2	99953	47	47	2
96	99999	1	99965	35	35	1
97	99999	1	99979	21	21	1
98	100000	0	99973	27	27	0
99	100000	0	99984	16	16	0
100	100000	0	99989	11	11	0

Overall, as expected², predator-prey communities are relatively stable while mutualist communities are highly unstable. But interestingly, while $Var(\gamma)$ stabilises predator-prey and competitor communities, it does not stabilise mutualist communities. This is unsurprising because purely mutualist communities are characterised by a very positive² leading $\Re(\lambda)$, and it is highly unlikely that $Var(\gamma)$ alone will shift all real parts of eigenvalues to negative values.

Sensitivity of connectance (C) values

In the main text, for simplicity, I assumed connectance values of $C = 1$, meaning that all off-diagonal elements of a matrix \mathbf{M} were potentially nonzero and sampled from a normal distribution $\mathcal{N}(0, \sigma^2)$ where $\sigma = 0.4$. Here I present four tables showing the number of stable communities given $C = \{0.3, 0.5, 0.7, 0.9\}$. In all cases, uniform variation in component response rate ($\gamma \sim \mathcal{U}(0, 2)$) led to a higher number of stable communities than when γ did not vary ($\gamma = 1$). In contrast to the main text, 100000 rather than 1 million \mathbf{M} were simulated. As with the results on [stability with increasing S](#) shown above, in the tables below **A0** refers to matrices when $\gamma = 1$, and **A1** refers to matrices after $Var(\gamma)$ is added. The column **A0_unstable** shows the number of **A0** matrices that are unstable, and the column **A0_stable** shows the number of **A0** matrices that are stable (these two columns sum to 100000). Similarly, the column **A1_unstable** shows the number of **A1** matrices that are unstable and **A1_stable** shows the number that are stable. The columns **A1_stabilised** and **A1_destabilised** show how many **A0** matrices were stabilised or destabilised, respectively, by $Var(\gamma)$.

Connectance $C = 0.3$

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised	A0_infeasible
2	5	99995	5	99995	0	0	75110
3	6	99994	6	99994	0	0	87526
4	24	99976	24	99976	0	0	93713
5	59	99941	59	99941	0	0	96929
6	98	99902	98	99902	0	0	98492
7	160	99840	161	99839	0	1	99243
8	290	99710	293	99707	0	3	99582
9	430	99570	434	99566	0	4	99821

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised	A0_infeasible
10	648	99352	653	99347	1	6	99895
11	946	99054	957	99043	0	11	99945
12	1392	98608	1415	98585	4	27	99978
13	2032	97968	2065	97935	5	38	99987
14	2627	97373	2688	97312	10	71	99988
15	3588	96412	3647	96353	35	94	99996
16	5019	94981	5124	94876	51	156	99998
17	6512	93488	6673	93327	79	240	99999
18	8444	91556	8600	91400	165	321	100000
19	10416	89584	10667	89333	244	495	100000
20	13254	86746	13477	86523	425	648	100000
21	16248	83752	16481	83519	642	875	100000
22	19497	80503	19719	80281	929	1151	100000
23	23654	76346	23776	76224	1368	1490	100000
24	28485	71515	28389	71611	1914	1818	100000
25	32774	67226	32483	67517	2428	2137	100000
26	38126	61874	37411	62589	3221	2506	100000
27	43435	56565	42418	57582	3828	2811	100000
28	49333	50667	47840	52160	4565	3072	100000
29	55389	44611	53381	46619	5329	3321	100000
30	60826	39174	58388	41612	5918	3480	100000
31	66820	33180	64043	35957	6345	3568	100000
32	72190	27810	69036	30964	6685	3531	100000
33	77053	22947	73587	26413	6826	3360	100000
34	81816	18184	78157	21843	6673	3014	100000
35	85651	14349	82041	17959	6383	2773	100000
36	88985	11015	85657	14343	5721	2393	100000
37	92072	7928	88805	11195	5180	1913	100000
38	94329	5671	91444	8556	4451	1566	100000
39	95912	4088	93295	6705	3804	1187	100000
40	97232	2768	95201	4799	2967	936	100000
41	98179	1821	96506	3494	2356	683	100000
42	98826	1174	97489	2511	1786	449	100000
43	99275	725	98312	1688	1251	288	100000
44	99583	417	98872	1128	903	192	100000
45	99776	224	99339	661	576	139	100000
46	99865	135	99518	482	413	66	100000
47	99938	62	99744	256	226	32	100000
48	99956	44	99824	176	151	19	100000
49	99980	20	99914	86	85	19	100000
50	99993	7	99950	50	46	3	100000
51	99998	2	99971	29	28	1	100000
52	99998	2	99986	14	14	2	100000
53	99999	1	99992	8	7	0	100000
54	100000	0	99997	3	3	0	100000
55	100000	0	99999	1	1	0	100000
56	100000	0	99998	2	2	0	100000
57	100000	0	99999	1	1	0	100000
58	100000	0	100000	0	0	0	100000
...
100	100000	0	100000	0	0	0	100000

Connectance C = 0.5

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised	A0_infeasible
2	7	99993	7	99993	0	0	74863
3	32	99968	32	99968	0	0	87434
4	122	99878	122	99878	0	0	93761
5	320	99680	321	99679	0	1	96830
6	667	99333	673	99327	0	6	98481
7	1233	98767	1252	98748	0	19	99187
8	2123	97877	2156	97844	3	36	99654
9	3415	96585	3471	96529	16	72	99816
10	5349	94651	5450	94550	30	131	99900
11	7990	92010	8185	91815	81	276	99958
12	11073	88927	11301	88699	219	447	99973
13	14971	85029	15204	84796	445	678	99986
14	19754	80246	19992	80008	764	1002	99991
15	25020	74980	25239	74761	1185	1404	99996
16	30860	69140	30938	69062	1902	1980	99999
17	37844	62156	37562	62438	2758	2476	100000
18	44909	55091	44251	55749	3595	2937	99999
19	52322	47678	51011	48989	4573	3262	99999
20	60150	39850	58295	41705	5382	3527	100000
21	67147	32853	64895	35105	5925	3673	100000
22	74177	25823	71358	28642	6310	3491	100000
23	80297	19703	77034	22966	6507	3244	100000
24	85372	14628	82039	17961	6209	2876	100000
25	89719	10281	86539	13461	5562	2382	100000
26	92947	7053	90141	9859	4707	1901	100000
27	95436	4564	92950	7050	3844	1358	100000
28	97196	2804	95171	4829	2999	974	100000
29	98300	1700	96842	3158	2115	657	100000
30	99103	897	98033	1967	1466	396	100000
31	99502	498	98665	1335	1068	231	100000
32	99745	255	99185	815	696	136	100000
33	99881	119	99572	428	375	66	100000
34	99955	45	99788	212	191	24	100000
35	99979	21	99900	100	95	16	100000
36	99995	5	99950	50	50	5	100000
37	99997	3	99970	30	28	1	100000
38	99998	2	99986	14	13	1	100000
39	99999	1	99991	9	9	1	100000
40	100000	0	100000	0	0	0	100000
41	100000	0	99999	1	1	0	100000
42	100000	0	99999	1	1	0	100000
43	100000	0	100000	0	0	0	100000
...
50	100000	0	100000	0	0	0	100000

Connectance C = 0.7

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised	A0_infeasible
2	7	99993	7	99993	0	0	75160

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised	A0_infeasible
3	106	99894	106	99894	0	0	87447
4	395	99605	397	99603	0	2	93849
5	1117	98883	1123	98877	0	6	96827
6	2346	97654	2367	97633	6	27	98402
7	4314	95686	4388	95612	16	90	99218
8	7327	92673	7456	92544	61	190	99611
9	11514	88486	11792	88208	150	428	99808
10	16247	83753	16584	83416	415	752	99904
11	22481	77519	22759	77241	884	1162	99952
12	29459	70541	29729	70271	1548	1818	99977
13	37631	62369	37567	62433	2419	2355	99984
14	46317	53683	45696	54304	3548	2927	99995
15	54945	45055	53695	46305	4671	3421	99994
16	63683	36317	61643	38357	5567	3527	99999
17	72004	27996	69375	30625	6124	3495	100000
18	79220	20780	76158	23842	6413	3351	100000
19	85286	14714	82283	17717	5982	2979	99999
20	90240	9760	87181	12819	5398	2339	100000
21	93676	6324	91077	8923	4468	1869	100000
22	96203	3797	94045	5955	3425	1267	100000
23	97866	2134	96161	3839	2496	791	100000
24	98842	1158	97633	2367	1713	504	100000
25	99433	567	98630	1370	1079	276	100000
26	99760	240	99259	741	655	154	100000
27	99895	105	99576	424	377	58	100000
28	99950	50	99790	210	194	34	100000
29	99981	19	99915	85	80	14	100000
30	99994	6	99952	48	47	5	100000
31	99998	2	99972	28	28	2	100000
32	99999	1	99992	8	8	1	100000
33	100000	0	99997	3	3	0	100000
34	100000	0	99999	1	1	0	100000
35	100000	0	100000	0	0	0	100000
...
50	100000	0	100000	0	0	0	100000

Connectance C = 0.9

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised	A0_infeasible
2	14	99986	14	99986	0	0	75187
3	240	99760	240	99760	0	0	87443
4	1008	98992	1016	98984	0	8	93795
5	2708	97292	2729	97271	2	23	96814
6	5669	94331	5755	94245	13	99	98439
7	9848	90152	10057	89943	91	300	99208
8	15903	84097	16201	83799	336	634	99603
9	22707	77293	23110	76890	765	1168	99803
10	30796	69204	31122	68878	1526	1852	99909
11	40224	59776	40082	59918	2649	2507	99951
12	49934	50066	49288	50712	3773	3127	99977
13	60138	39862	58803	41197	4984	3649	99986

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised	A0_infeasible
14	69100	30900	67110	32890	5755	3765	99995
15	77607	22393	74884	25116	6273	3550	100000
16	84663	15337	81780	18220	5975	3092	100000
17	90075	9925	87290	12710	5209	2424	100000
18	93944	6056	91419	8581	4271	1746	100000
19	96650	3350	94530	5470	3287	1167	99999
20	98160	1840	96698	3302	2191	729	100000
21	99111	889	98133	1867	1389	411	100000
22	99588	412	98905	1095	903	220	100000
23	99837	163	99480	520	452	95	100000
24	99932	68	99744	256	228	40	100000
25	99976	24	99863	137	133	20	100000
26	99995	5	99950	50	49	4	100000
27	99996	4	99986	14	13	3	100000
28	100000	0	99993	7	7	0	100000
29	100000	0	99996	4	4	0	100000
30	100000	0	99998	2	2	0	100000
31	100000	0	100000	0	0	0	100000
...
50	100000	0	100000	0	0	0	100000

Sensitivity of interaction strength (σ) values

Results below show stability results given varying interaction strengths (σ) for $C = 0.05$ (note that system size S values are larger and increase by 10 with increasing rows). In the tables below (as [above](#)), A0 and A1 refers to matrices for $\gamma = 1$ and $Var(\gamma)$, respectively.

Interaction strength $\sigma = 0.3$

S	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
10	0	100000	0	100000	0	0
20	0	100000	0	100000	0	0
30	0	100000	0	100000	0	0
40	0	100000	0	100000	0	0
50	0	100000	0	100000	0	0
60	2	99998	2	99998	0	0
70	4	99996	4	99996	0	0
80	6	99994	6	99994	0	0
90	5	99995	5	99995	0	0
100	11	99989	11	99989	0	0
110	12	99988	13	99987	0	1
120	23	99977	23	99977	0	0
130	40	99960	40	99960	0	0
140	62	99938	65	99935	0	3
150	162	99838	165	99835	0	3
160	325	99675	329	99671	2	6
170	829	99171	851	99149	6	28
180	1817	98183	1860	98140	31	74
190	3927	96073	3989	96011	143	205
200	8084	91916	8048	91952	557	521

S	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
210	15558	84442	15147	84853	1534	1123
220	26848	73152	25342	74658	3625	2119
230	43386	56614	39535	60465	6992	3141
240	62734	37266	56684	43316	9815	3765
250	80128	19872	73080	26920	10128	3080
260	92206	7794	86619	13381	7490	1903
270	97946	2054	94824	5176	3797	675
280	99659	341	98534	1466	1265	140
290	99962	38	99696	304	281	15
300	99994	6	99964	36	34	4

Interaction strength $\sigma = 0.4$

S	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
10	3	99997	3	99997	0	0
20	15	99985	15	99985	0	0
30	48	99952	48	99952	0	0
40	85	99915	85	99915	0	0
50	163	99837	163	99837	0	0
60	280	99720	282	99718	0	2
70	561	99439	566	99434	3	8
80	1009	98991	1029	98971	6	26
90	2126	97874	2175	97825	31	80
100	4580	95420	4653	95347	142	215
110	9540	90460	9632	90368	465	557
120	19090	80910	18668	81332	1676	1254
130	35047	64953	33220	66780	4172	2345
140	56411	43589	52439	47561	7297	3325
150	78003	21997	72574	27426	8477	3048
160	92678	7322	88438	11562	5901	1661
170	98614	1386	96670	3330	2397	453
180	99839	161	99418	582	499	78
190	99990	10	99945	55	52	7
200	100000	0	99995	5	5	0
210	100000	0	100000	0	0	0
...
300	100000	0	100000	0	0	0

Interaction strength $\sigma = 0.5$

S	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
10	36	99964	36	99964	0	0
20	195	99805	195	99805	0	0
30	519	99481	523	99477	0	4
40	1096	98904	1101	98899	2	7
50	2375	97625	2397	97603	9	31
60	4898	95102	4968	95032	83	153
70	10841	89159	10916	89084	432	507
80	22281	77719	21988	78012	1622	1329
90	42010	57990	39998	60002	4458	2446

S	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
100	67289	32711	63098	36902	7153	2962
110	88137	11863	84023	15977	6108	1994
120	97678	2322	95557	4443	2740	619
130	99795	205	99304	696	578	87
140	99989	11	99948	52	49	8
150	100000	0	100000	0	0	0
...
300	100000	0	100000	0	0	0

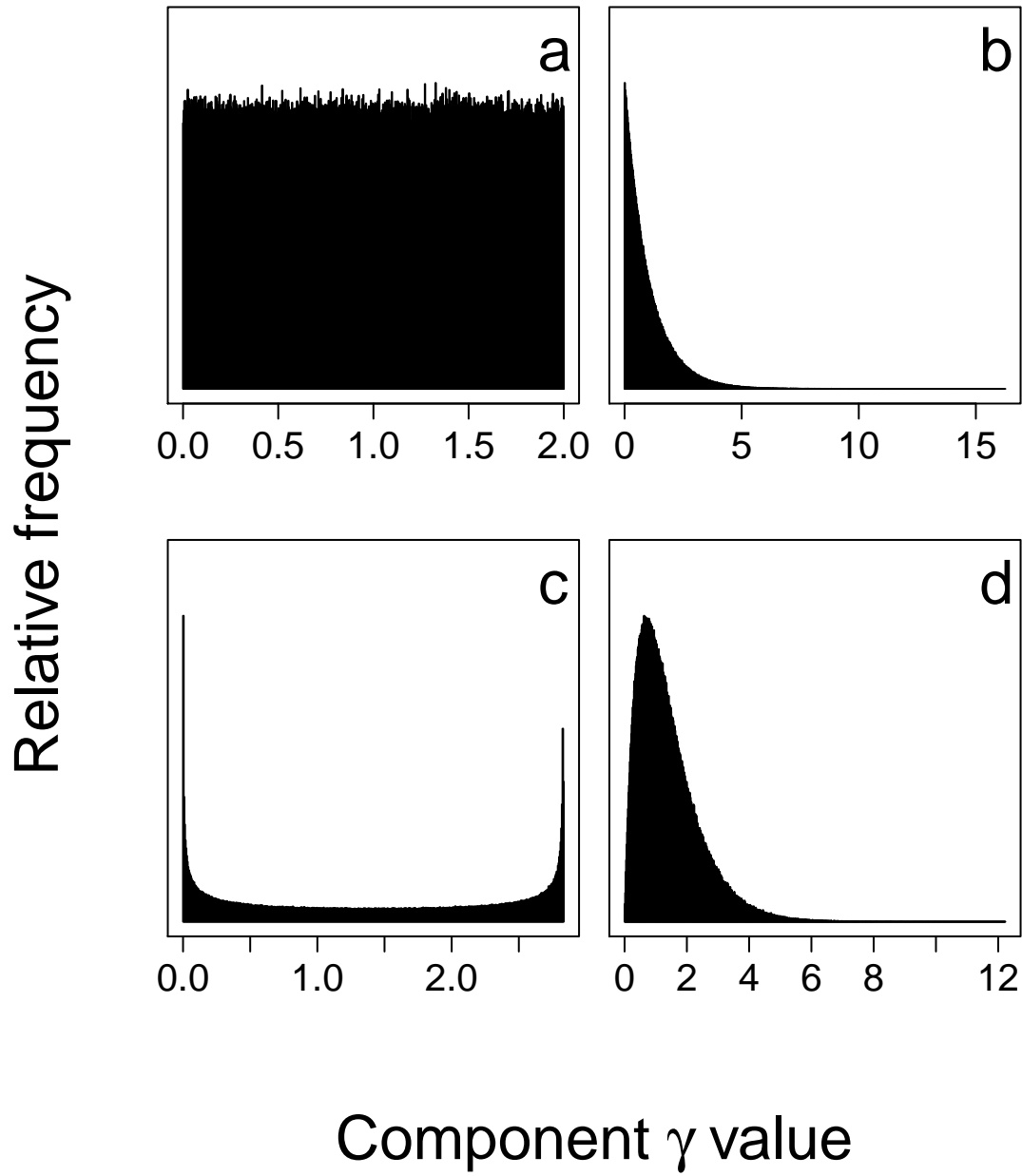
Interaction strength $\sigma = 0.6$

S	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
10	162	99838	162	99838	0	0
20	798	99202	799	99201	0	1
30	2273	97727	2289	97711	6	22
40	5259	94741	5298	94702	70	109
50	12084	87916	12054	87946	446	416
60	26072	73928	25511	74489	1810	1249
70	50121	49879	47747	52253	4748	2374
80	77806	22194	73810	26190	6421	2425
90	94862	5138	92069	7931	3842	1049
100	99527	473	98822	1178	870	165
110	99984	16	99912	88	80	8
120	100000	0	99998	2	2	0
130	100000	0	100000	0	0	0
...
300	100000	0	100000	0	0	0

Sensitivity of distribution of γ

In the main text, I considered a uniform distribution of component response rates $\gamma \sim \mathcal{U}(0, 2)$. The number of unstable and stable \mathbf{M} matrices are reported in [a table above](#) across different values of S . Here I show complementary results for three different distributions including an exponential, beta, and gamma distribution of γ values. The shape of these distributions is shown in the figure below.

Distributions of component response rate (γ) values in complex systems. The stabilities of simulated complex systems with these γ distributions are compared to otherwise identical complex systems with a fixed component response rate of $\gamma = 1$ across different system sizes (S ; i.e., component numbers) given a unit γ standard deviation ($\sigma_\gamma = 1$) for b-d. Distributions are as follows: (a) uniform, (b) exponential, (c) beta ($\alpha = 0.5$ and $\beta = 0.5$), and (d) gamma ($k = 2$ and $\theta = 2$). Each panel shows 1 million randomly generated γ values.



The same 100000 \mathbf{M} matrices were used to investigate stability when applying each of these different distributions of γ values. The table below shows the number of \mathbf{M} that were unstable ($_unst$) and stable ($_stbl$) for the exponential (Exp), beta, and gamma distributions.

S	Exp_unst	Exp_stbl	beta_unst	beta_stbl	gamma_unst	gamma_stbl
2	30	99970	30	99970	30	99970
3	355	99645	355	99645	355	99645
4	1506	98494	1512	98488	1516	98484
5	3930	96070	3971	96029	4006	95994
6	7738	92262	7844	92156	7918	92082
7	13606	86394	13889	86111	13990	86010
8	20535	79465	21002	78998	21114	78886
9	28614	71386	29060	70940	29110	70890

S	Exp_unst	Exp_stbl	beta_unst	beta_stbl	gamma_unst	gamma_stbl
10	38375	61625	38388	61612	38441	61559
11	48616	51384	48211	51789	47957	52043
12	59254	40746	58025	41975	57473	42527
13	68816	31184	66753	33247	66127	33873
14	77721	22279	75149	24851	74222	25778
15	84842	15158	82030	17970	81040	18960
16	90365	9635	87809	12191	86600	13400
17	94171	5829	91756	8244	90668	9332
18	96978	3022	94977	5023	94176	5824
19	98376	1624	97018	2982	96268	3732
20	99218	782	98357	1643	97765	2235
21	99678	322	99124	876	98746	1254
22	99864	136	99599	401	99323	677
23	99954	46	99783	217	99668	332
24	99978	22	99920	80	99821	179
25	99996	4	99967	33	99911	89
26	99999	1	99979	21	99960	40
27	99999	1	99990	10	99983	17
28	100000	0	99999	1	99991	9
29	100000	0	99999	1	99999	1
30	100000	0	100000	0	100000	0
31	100000	0	100000	0	99999	1
32	100000	0	100000	0	100000	0
...
50	100000	0	100000	0	100000	0

In comparison to the uniform distribution (a), proportionally fewer random systems are found with the exponential distribution (b), while more are found with the beta (c) and gamma (d) distributions.

Feasibility of complex systems

When feasibility was evaluated with and without variation in γ , there was no increase in stability for \mathbf{M} where γ varied as compared to where $\gamma = 1$. Results below illustrate this result, which was general to all other simulations performed.

S	A0_infeasible	A0_feasible	A1_infeasible	A1_feasible	A1_made_feasible	A1_made_infeasible
2	749978	250022	749942	250058	35552	35516
3	874519	125481	874296	125704	36803	36580
4	937192	62808	937215	62785	26440	26463
5	968776	31224	968639	31361	16319	16182
6	984313	15687	984463	15537	9006	9156
7	992149	7851	992161	7839	4991	5003
8	996124	3876	996103	3897	2644	2623
9	998014	1986	998027	1973	1361	1374
10	999031	969	999040	960	698	707
11	999546	454	999514	486	377	345
12	999764	236	999792	208	160	188
13	999883	117	999865	135	105	87
14	999938	62	999945	55	40	47

S	A0_infeasible	A0_feasible	A1_infeasible	A1_feasible	A1_made_feasible	A1_made_infeasible
15	999971	29	999964	36	31	24
16	999988	12	999991	9	8	11
17	999996	4	999991	9	8	3
18	999997	3	999999	1	1	3
19	999998	2	999997	3	3	2
20	1000000	0	999999	1	1	0
21	1000000	0	1000000	0	0	0
22	999999	1	1000000	0	0	1
23	1000000	0	1000000	0	0	0
24	1000000	0	1000000	0	0	0
25	1000000	0	1000000	0	0	0
26	1000000	0	1000000	0	0	0
27	1000000	0	1000000	0	0	0
28	1000000	0	1000000	0	0	0
29	1000000	0	1000000	0	0	0
30	1000000	0	1000000	0	0	0
31	1000000	0	1000000	0	0	0
32	1000000	0	1000000	0	0	0
33	1000000	0	1000000	0	0	0
34	1000000	0	1000000	0	0	0
35	1000000	0	1000000	0	0	0
36	1000000	0	1000000	0	0	0
37	1000000	0	1000000	0	0	0
38	1000000	0	1000000	0	0	0
39	1000000	0	1000000	0	0	0
40	1000000	0	1000000	0	0	0
41	1000000	0	1000000	0	0	0
42	1000000	0	1000000	0	0	0
43	1000000	0	1000000	0	0	0
44	1000000	0	1000000	0	0	0
45	1000000	0	1000000	0	0	0
46	1000000	0	1000000	0	0	0
47	1000000	0	1000000	0	0	0
48	1000000	0	1000000	0	0	0
49	1000000	0	1000000	0	0	0
50	1000000	0	1000000	0	0	0

Hence, in general, $Var(\gamma)$ does not appear to affect feasibility in pure species interaction networks⁴.

Consistency with Gibbs et al. (2018)

The question that I address in the main text is distinct from that of Gibbs et al.⁵, who focused instead on the effect of a diagonal matrix of biological species densities \mathbf{X} on a community matrix \mathbf{M} given a species interaction matrix \mathbf{A} . This is modelled as below,

$$\mathbf{M} = \mathbf{XA}.$$

Mathematically, the above is identical to my model in the main text where the system \mathbf{M} is defined by component interaction strengths \mathbf{A} and individual component response rates γ ,

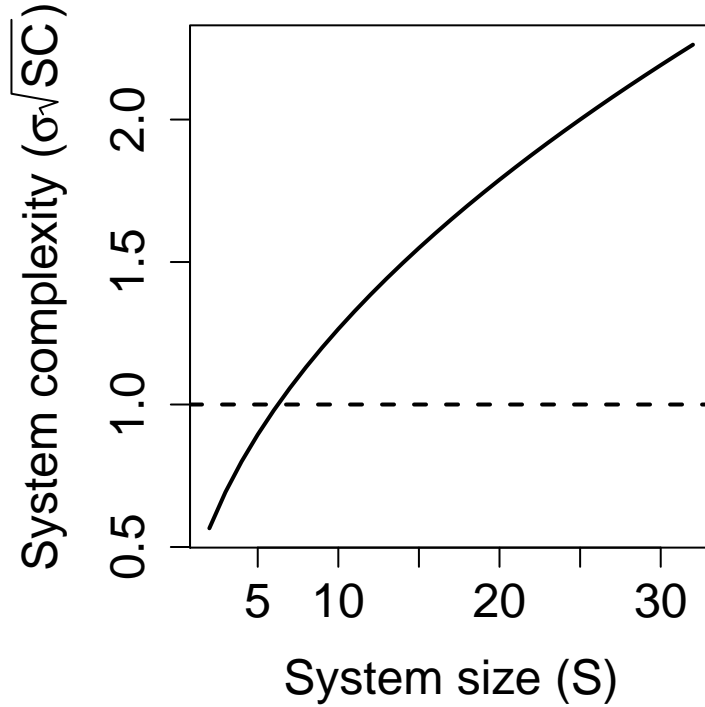
$$\mathbf{M} = \gamma \mathbf{A}.$$

I focused on the probability of observing a stable versus unstable system given variation in γ as system complexity ($\sigma\sqrt{SC}$) increased. I increased system complexity by holding C and σ constant and incrementally increasing S to obtain numerical results. In contrast, Gibbs et al.⁵ applied analytical techniques to instead focus on a different question concerning the effect of γ on the stability of \mathbf{M} given \mathbf{A} as $S \rightarrow \infty$, with σ scaled so that $\sigma = 1/\sqrt{S}$. Under such scaling, Gibbs et al.⁵ showed that the effect of γ on stability should decrease exponentially as S increases, which I demonstrate below by running simulations in which $\sigma = 1/\sqrt{S}$.

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	3111	96889	3111	96889	0	0
3	5203	94797	5237	94763	1	35
4	6743	93257	6818	93182	6	81
5	7889	92111	8005	91995	20	136
6	8834	91166	8991	91009	55	212
7	9885	90115	10072	89928	81	268
8	10516	89484	10764	89236	108	356
9	11135	88865	11383	88617	145	393
10	11819	88181	12095	87905	181	457
11	12414	87586	12700	87300	213	499
12	12865	87135	13136	86864	283	554
13	13530	86470	13836	86164	324	630
14	13745	86255	14042	85958	362	659
15	14401	85599	14720	85280	387	706
16	14793	85207	15123	84877	428	758
17	15004	84996	15356	84644	444	796
18	15361	84639	15735	84265	472	846
19	16062	83938	16303	83697	592	833
20	15814	84186	16184	83816	566	936
21	16171	83829	16492	83508	640	961
22	16671	83329	17049	82951	641	1019
23	17000	83000	17291	82709	718	1009
24	17411	82589	17666	82334	765	1020
25	17414	82586	17742	82258	783	1111
26	17697	82303	18027	81973	806	1136
27	18010	81990	18316	81684	880	1186
28	18584	81416	18735	81265	1008	1159
29	18401	81599	18572	81428	942	1113
30	18497	81503	18754	81246	952	1209
31	18744	81256	18942	81058	991	1189
32	18936	81064	19194	80806	1022	1280
33	19174	80826	19346	80654	1113	1285
34	19477	80523	19632	80368	1120	1275
35	19659	80341	19777	80223	1206	1324
36	19883	80117	19929	80071	1275	1321
37	20275	79725	20348	79652	1308	1381
38	20067	79933	20190	79810	1275	1398
39	20416	79584	20516	79484	1340	1440
40	20370	79630	20489	79511	1359	1478
41	20295	79705	20430	79570	1382	1517
42	20767	79233	20839	79161	1418	1490
43	20688	79312	20705	79295	1471	1488
44	21049	78951	21028	78972	1555	1534

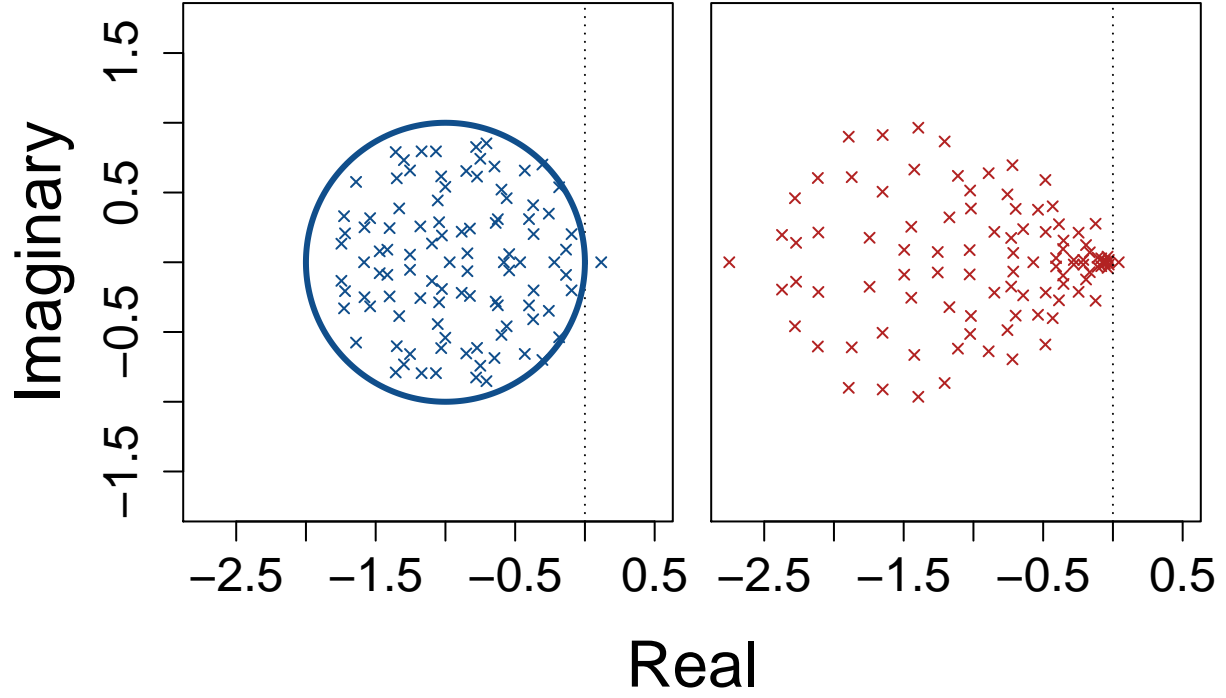
N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
45	21114	78886	21034	78966	1572	1492
46	21163	78837	21195	78805	1463	1495
47	21373	78627	21353	78647	1535	1515
48	21338	78662	21285	78715	1632	1579
49	21547	78453	21566	78434	1575	1594
50	21738	78262	21633	78367	1636	1531
51	21967	78033	21892	78108	1698	1623

Above table results can be compared to those of the [main results](#). Note that 100000 (not 1 million), simulations are run to confirm consistency with Gibbs et al.⁵. The difference between my model and Gibbs et al.⁵ is that in the latter, $\sigma\sqrt{SC} = 1$ remains constant with increasing S . In the former, $\sigma\sqrt{SC}$ increases with S , so the expected complexity of the system also increases accordingly. Consequently, for the scaled σ in the table above, systems are not more likely to be stabilised by γ as S increases, consistent with Gibbs et al.⁵. Note that overall stability does decrease with increasing S due to the increased density of eigenvalues (see below).

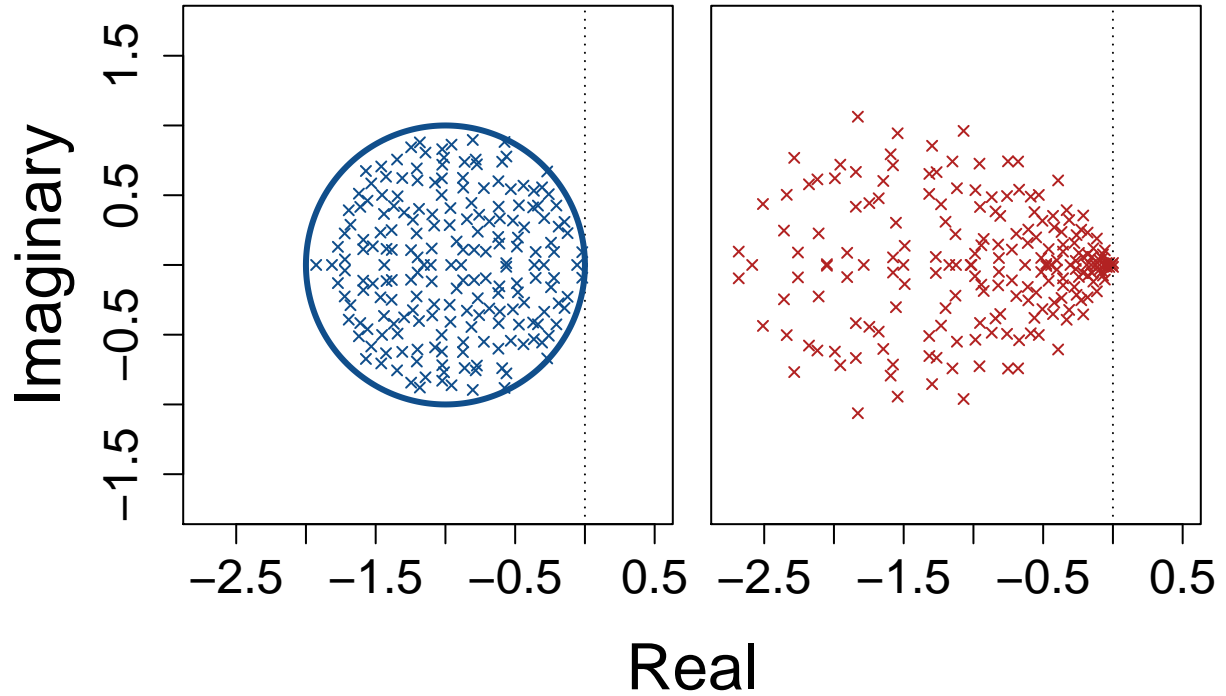


Complexity as a function of S in the main text (solid) versus in Gibbs et al.⁵ (dashed).

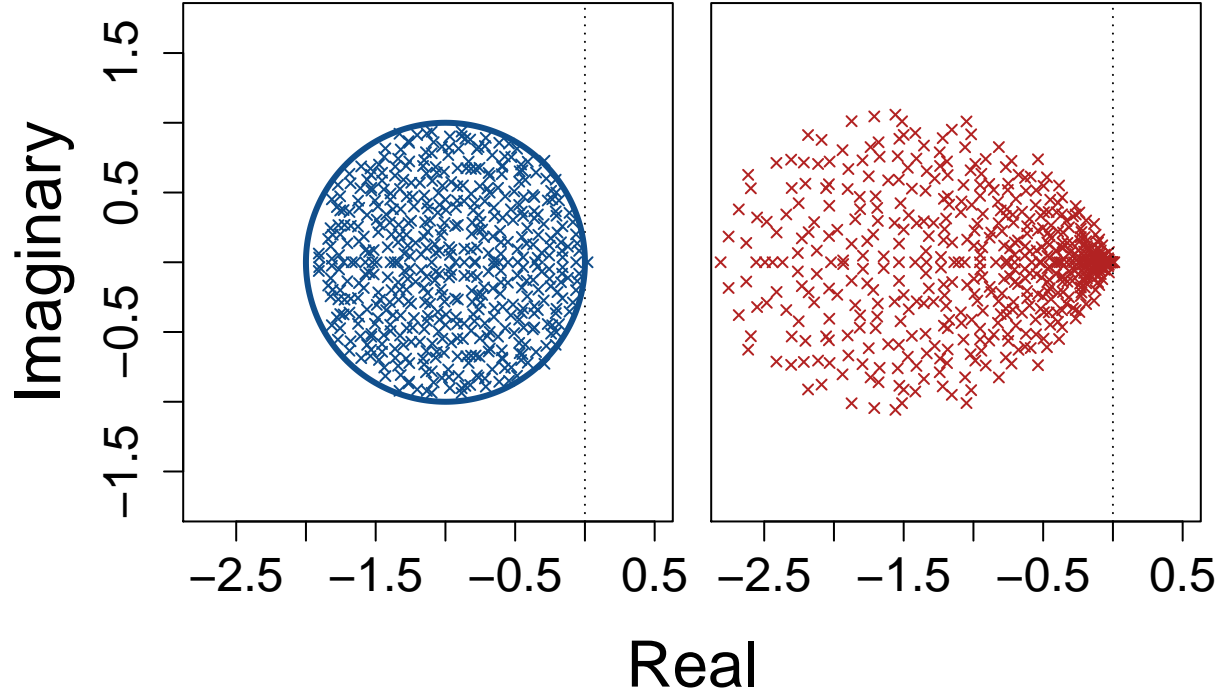
When the complexity is scaled to $\sigma\sqrt{SC} = 1$, an increase in S increases the eigenvalue density within a circle with a unit radius centred at $(-1, 0)$ on the complex plane. As $S \rightarrow \infty$, this circle becomes increasingly saturated. Gibbs et al.⁵ showed that a diagonal matrix γ will have an exponentially decreasing effect on stability with increasing S . Increasing S is visualised below, first with a system size $S = 100$.



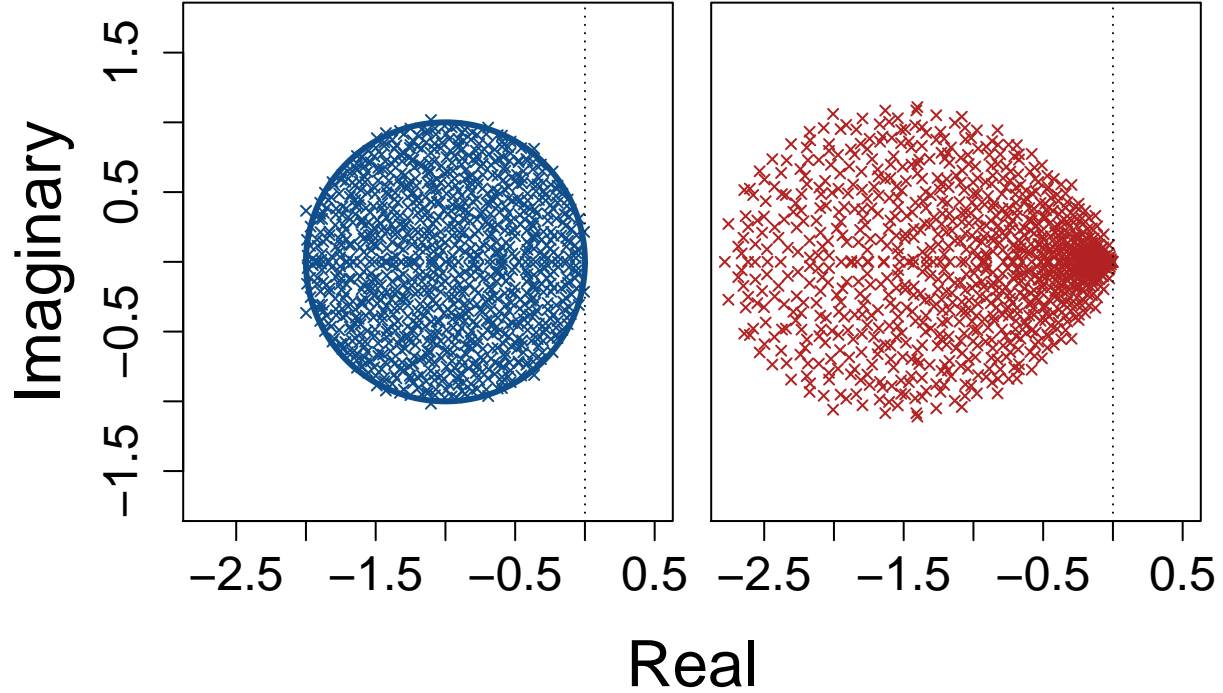
The left panel above shows the distribution of eigenvalues; the blue ellipse shows the unit radius within which eigenvalues are expected to be contained. The right panel shows how eigenvalue distributions change given $\gamma \sim \mathcal{U}(0, 2)$. The vertical dotted line shows the threshold of stability, $\Re = 0$. Increasing to $S = 200$, the scaling $\sigma = 1/\sqrt{S}$ maintains the expected distribution of eigenvalues but increases eigenvalue density.



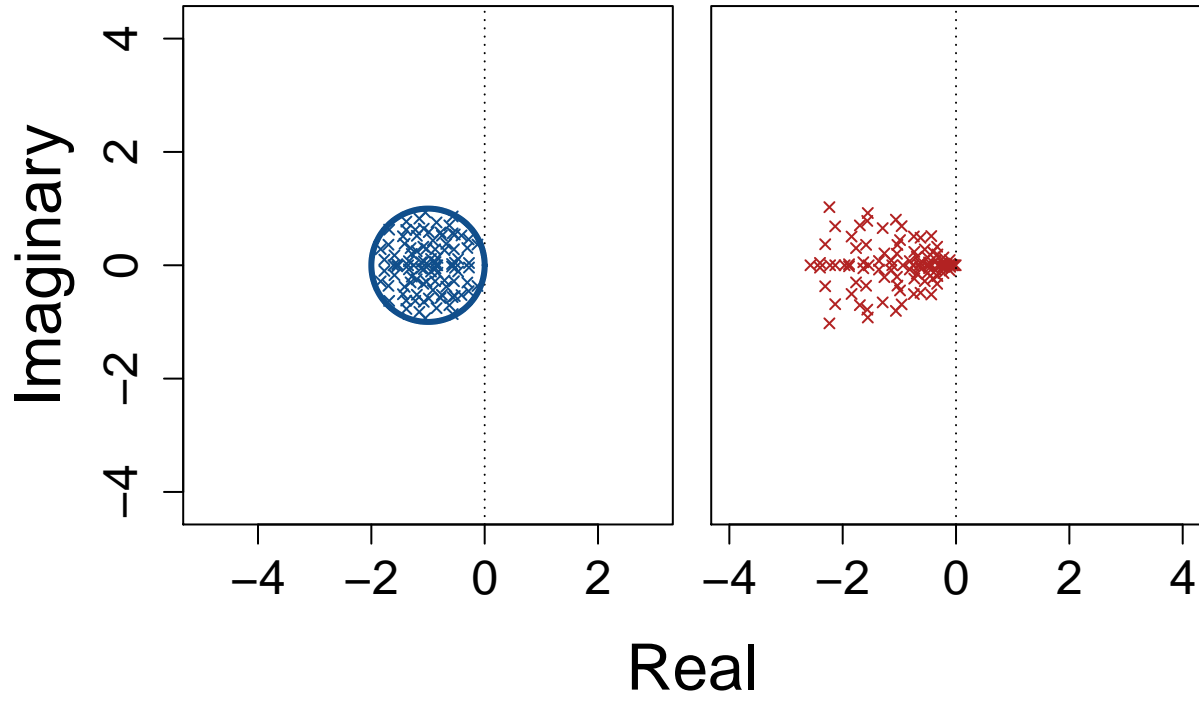
We can increase the system size to $S = 500$ and see the corresponding increase in eigenvalue density.



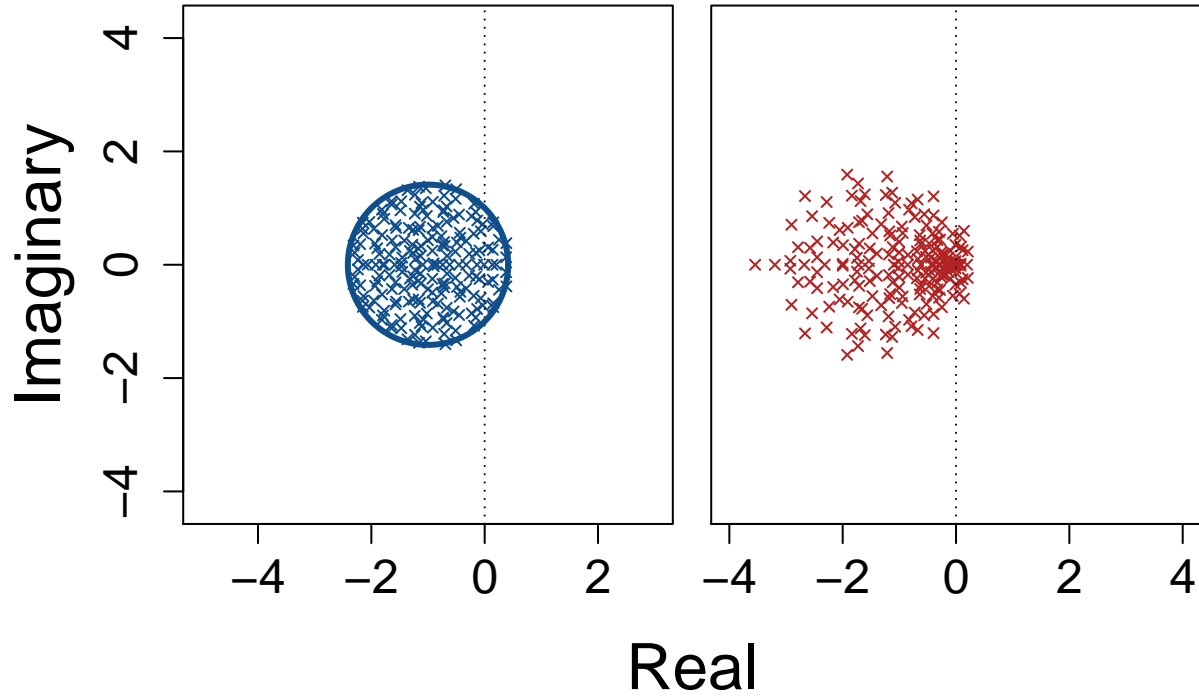
Finally, below shows a increase in system size to $S = 1000$.



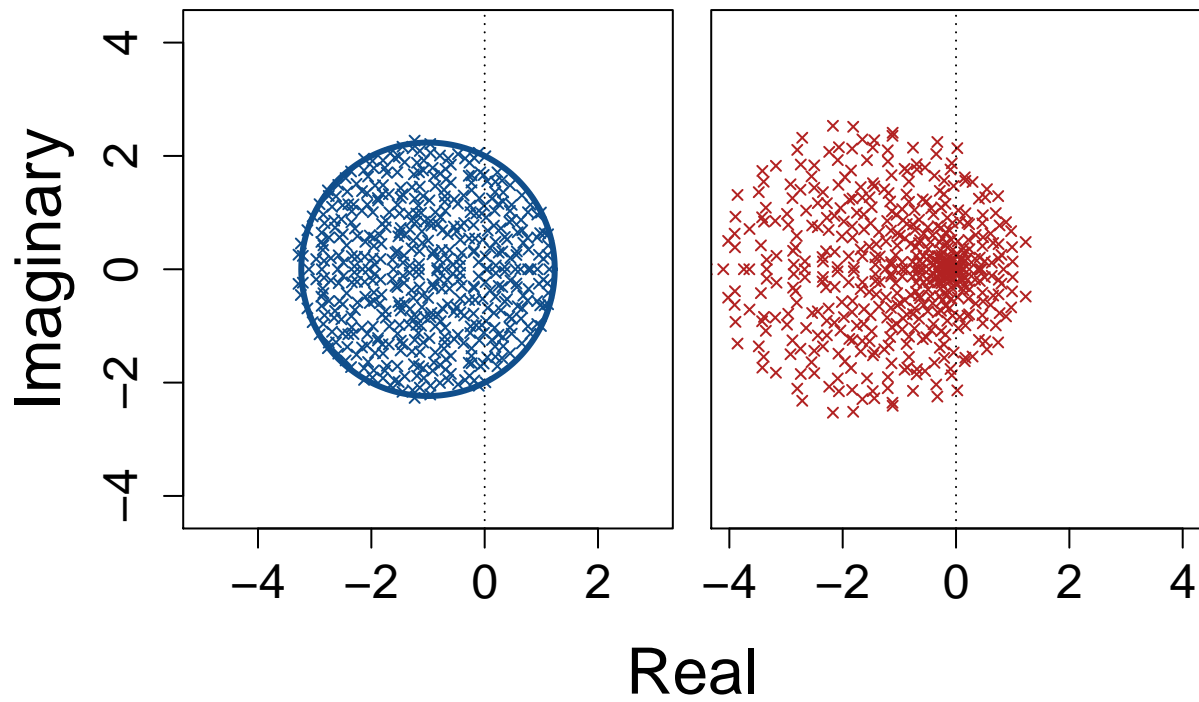
In contrast, in the model of the main text, the complexity of system is not scaled to $\sigma\sqrt{SC} = 1$. Rather, the density of eigenvalues within a circle centred at $(-1, 0)$ with a radius $\sigma\sqrt{SC}$ is held constant such that there are $S/\pi(\sigma\sqrt{SC})^2$ eigenvalues per unit area of the circle. As S increases, so does the expected complexity of the system, but the density of eigenvalues remains finite causing error around this expectation. Below shows a system where $S = 100$, $C = 0.0625$, and $\sigma = 0.4$, where $\sigma\sqrt{SC} = 1$ (identical to the first example distribution above in which $S = 100$ and $\sigma = 1/\sqrt{S}$).



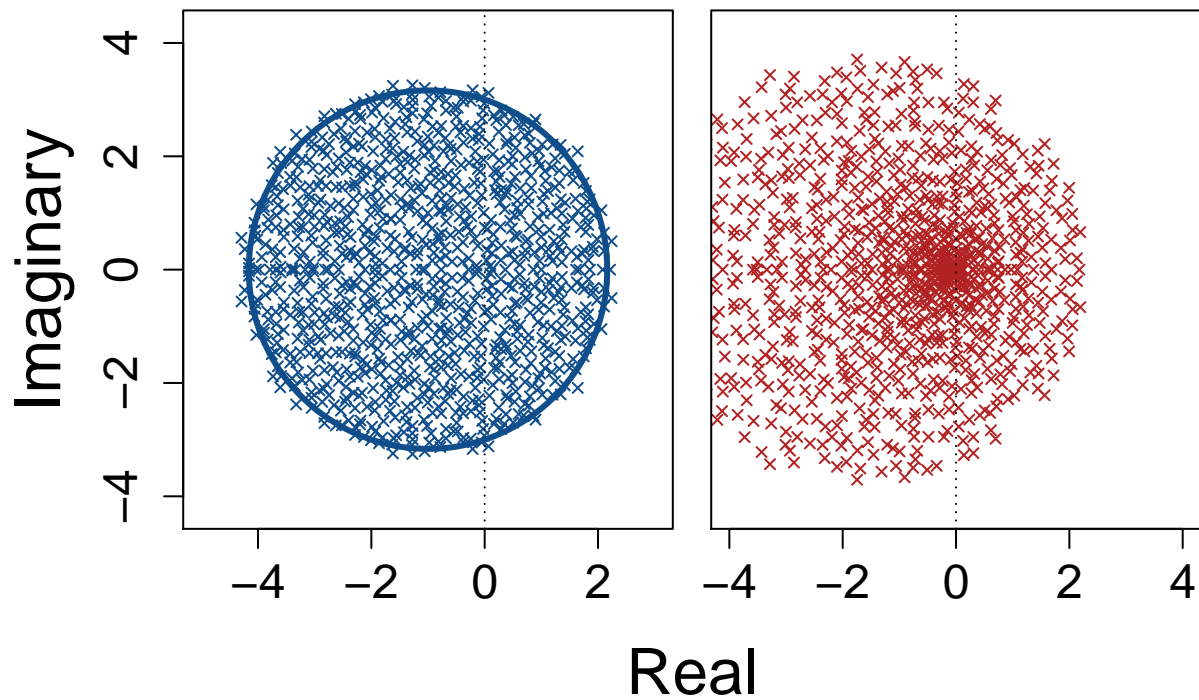
Now when S is increased to 200 while keeping $C = 0.0625$ and $\sigma = 0.4$, the area of the circle within which eigenvalues are contained increases to keep the density of eigenvalues constant.



Note that the expected distribution of eigenvalues increases so that the threshold $\Re = 0$ is exceeded. Below, system size is increased to $S = 500$.



Finally, $S = 1000$ is shown below. Again, the density of eigenvalues per unit remains constant at ca 2, but the system has increased in complexity such that some real components of eigenvalues are almost assured to be greater than zero.



References

1. May, R. M. Will a large complex system be stable? *Nature* **238**, 413–414 (1972).
2. Allesina, S. & Tang, S. Stability criteria for complex ecosystems. *Nature* **483**, 205–208 (2012).
3. Allesina, S. *et al.* Predicting the stability of large structured food webs. *Nature Communications* **6**, 7842 (2015).
4. Serván, C. A., Capitán, J. A., Grilli, J., Morrison, K. E. & Allesina, S. Coexistence of many species in random ecosystems. *Nature Ecology and Evolution* **2**, 1237–1242 (2018).
5. Gibbs, T., Grilli, J., Rogers, T. & Allesina, S. The effect of population abundances on the stability of large random ecosystems. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics* **98**, 022410 (2018).