

# Component response rate variation underlies the stability of complex systems

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## Abstract

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 ( $\gamma$ ) of randomly generated complex systems. I use numerical simulations to show that when component response rates vary, the potential for system stability is markedly increased. These results are robust to common network structures, including small-world and scale-free networks, and cascade food webs. Variation in  $\gamma$  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.

## 19 Introduction

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

28 Randomly assembled complex systems can be represented as large square matrices ( $\mathbf{M}$ ) with  $S$  components  
29 (e.g., networks of species<sup>2</sup> or banks<sup>11</sup>). One element of such a matrix,  $M_{ij}$ , defines how component  $j$   
30 affects component  $i$  in the system at a point of equilibrium<sup>2</sup>. Off-diagonal elements ( $i \neq j$ ) therefore define  
31 interactions between components, while diagonal elements ( $i = j$ ) define component self-regulation ( $d$ , e.g.,  
32 carrying capacity in ecological communities). Traditionally, off-diagonal elements are assigned non-zero values  
33 with a probability  $C$ , which are sampled from a distribution with variance  $\sigma_M^2$ ; diagonal elements are set to  
34  $d = -1$ <sup>1,2,4</sup>. Local system stability is assessed using eigenanalysis, with the system being stable if the real  
35 parts of all eigenvalues ( $\lambda$ ) of  $\mathbf{M}$  are negative ( $\max(\Re(\lambda)) < 0$ )<sup>1,2</sup>. In a large system (high  $S$ ), eigenvalues are  
36 distributed uniformly<sup>14</sup> within a circle centred at  $\Re = -1$  (the mean value of diagonal elements) and  $\Im = 0$ ,  
37 with a radius of  $\sigma_M\sqrt{SC}$ <sup>1,2,4</sup> (Figs 1a and 2a). Local stability of randomly assembled systems therefore  
38 becomes increasingly unlikely as  $S$ ,  $C$ , and  $\sigma_M$  increase.

39 May’s<sup>1,2</sup> stability criterion  $\sigma_M\sqrt{SC} < 1$  assumes that the expected response rates ( $\gamma$ ) of individual components  
40 to perturbations of the system are identical, but this is highly unlikely in any complex system. In ecological  
41 communities, for example, the rate at which population density changes following perturbation will depend  
42 on the generation time of organisms, which might vary by orders of magnitude among species. Species with  
43 short generation times will respond quickly (high  $\gamma$ ) to perturbations relative to species with long generation

times (low  $\gamma$ ). 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  $\gamma$  ( $\sigma_\gamma^2$ ) might be expected to decrease system stability by introducing a new source of variation into the system and thereby increasing  $\sigma_M$ . Here I show that, despite higher  $\sigma_M$ , realistic complex systems (such that  $S$  is high but finite) are actually more likely to be stable if their individual component response rates vary. My results are robust across commonly observed network structures, including random<sup>1</sup>, small-world<sup>15</sup>, scale-free<sup>16</sup>, cascade food web<sup>17</sup> networks.

## Results

**Component response rates of random complex systems.** Complex systems  $\mathbf{M}$  are built from two matrices, one modelling component interactions ( $\mathbf{A}$ ), and second modelling component response rates ( $\gamma$ ). Both  $\mathbf{A}$  and  $\gamma$  are square  $S \times S$  matrices. Rows in  $\mathbf{A}$  define how a given component  $i$  is affected by each component  $j$  in the system, including itself (where  $i = j$ ). Off-diagonal elements of  $\mathbf{A}$  are independent and identically distributed (i.i.d), and diagonal elements are set to  $A_{ii} = -1$  as in May<sup>1</sup>. Diagonal elements of  $\gamma$  are positive, and off-diagonal elements are set to zero (i.e.  $\gamma$  is a diagonal matrix with positive support). The distribution of  $\gamma$  over  $S$  components thereby models the distribution of component response rates. The dynamics of the entire system  $\mathbf{M}$  can be defined as follows<sup>18</sup>,

$$M = \gamma A. \tag{1}$$

Equation 1 thereby serves as a null model to investigate how variation in component response rate ( $\sigma_\gamma$ ) affects complex systems. In the absence of such variation ( $\sigma_\gamma = 0$ ),  $\gamma$  is set to the identity matrix (diagonal elements all equal 1) and  $\mathbf{M} = \mathbf{A}$ . Under these conditions, eigenvalues of  $\mathbf{M}$  are distributed uniformly<sup>14</sup> in a circle centred at  $(-d, 0)$  with a radius of  $\sigma_M \sqrt{SC}$ <sup>1</sup> (Figure 1a).

**Effect of  $\sigma_\gamma^2$  on  $\mathbf{M}$  (co)variation.** The value of  $\max(\Re(\lambda))$ , and therefore system stability, can be estimated from five properties of  $\mathbf{M}$ <sup>19</sup>. These properties include (1) system size ( $S$ ), (2) mean self-regulation of components ( $d$ ), (3) mean interaction strength between components ( $\mu$ ), (4) the standard deviation between component interaction strengths ( $\sigma_M$ ), and (5) the correlation of interaction strengths between components,  $M_{ij}$  and  $M_{ji}$  ( $\rho$ ). Positive  $\sigma_\gamma$  does not change  $S$ , nor does it necessarily change  $E[d]$  or  $E[\mu]$ . What  $\sigma_\gamma$  does change is the total variation in component interaction strengths ( $\sigma_M$ ), and  $\rho$ . Introducing variation in  $\gamma$  increases the total variation in the system. Variation of the off-diagonal elements in  $\mathbf{M}$  is described by the joint variation of two random variables,

$$\sigma_M^2 = \sigma_A^2 \sigma_\gamma^2 + \sigma_A^2 E[\gamma_i]^2 + \sigma_\gamma^2 E[A_{ij}]^2. \quad (2)$$

Given  $E[\gamma_i] = 1$  and  $E[A_{ij}] = 0$ , equation 2 can be simplified,

$$\sigma_M^2 = \sigma_A^2 (1 + \sigma_\gamma^2). \quad (3)$$

The increase caused by  $\sigma_\gamma^2$  can be visualised from the eigenvalue spectra of  $\mathbf{A}$  versus  $\mathbf{M} = \gamma\mathbf{A}$  (Figure 1). Given  $d = 0$  and  $C = 1$ , the distribution of eigenvalues of  $\mathbf{A}$  and  $\mathbf{M}$  lie within a circle of a radius  $\sigma_A\sqrt{S}$  and  $\sigma_M\sqrt{S}$ , respectively (Figure 1a vs. 1b). If  $d \neq 0$ , positive  $\sigma_\gamma^2$  changes the distribution of eigenvalues<sup>20-22</sup>, potentially affecting stability (Figure 1c vs. 1d).

Given  $\sigma_\gamma^2 = 0$ ,  $\max(\Re(\lambda))$  decrease linearly with  $\rho$  such that<sup>23</sup>,

$$\max(\Re(\lambda)) \approx \sigma_M \sqrt{SC} (1 + \rho). \quad (4)$$

If  $\rho < 0$ , such as when  $\mathbf{M}$  models a predator-prey system in which  $M_{ij}$  and  $M_{ji}$  have opposing signs, stability increases<sup>2</sup>. If diagonal elements of  $\gamma$  vary independently, the magnitude of  $\rho$  is decreased because  $\sigma_\gamma^2$  increases

the variance of  $M_{ij}$  without affecting the expected covariance between  $M_{ij}$  and  $M_{ji}$ ,

$$\rho = \frac{\text{cov}(M_{ij}, M_{ji})}{\sigma_A^2(1 + \sigma_\gamma^2)}. \quad (5)$$

Nevertheless, numerical simulations reveal that  $\sigma_\gamma^2 > 0$  results in a nonlinear relationship between  $\rho$  and  $\max(\Re(\lambda))$ , which can sometimes increase the stability of the system.

**Numerical simulations of random  $\mathbf{M}$  with and without  $\sigma_\gamma$ .** I used numerical simulations to isolate the effect of  $\sigma_\gamma$  on system stability by comparing the same  $\mathbf{M} = \gamma\mathbf{A}$  given  $\sigma_\gamma > 0$  versus  $\sigma_\gamma = 0$  across a range of parameter combinations. Values of  $\gamma_{ii}$  were sampled from a uniform distribution where  $\gamma \sim \mathcal{U}(0, 2)$  (see Supplementary Information for other distributions, which give similar results). For  $\sigma_\gamma = 0$ , diagonal elements were standardised to the mean value of sampled  $\gamma_{ii}$  so that  $E[d]$  of  $\mathbf{M}$  were identical.

#### **Simulation of random $\mathbf{M}$ across $\rho$**

**Simulation of random  $\mathbf{M}$  across  $S$ .** To investigate the effect of  $\text{Var}(\gamma)$  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  $\text{Var}(\gamma)$  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  $\text{Var}(\gamma)$  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  $\text{Var}(\gamma)$  would not have been stable given  $\gamma = 1$ .

**Targeted manipulation of  $\gamma$ .** To further investigate the potential of  $\text{Var}(\gamma)$  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  $\gamma$  values leading to stability in a complex system) is too large to search exhaustively<sup>24</sup>. Generations of selection on  $\gamma$  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  $\gamma$  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  $S$   $\gamma$  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<sup>5,25,26</sup>. 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 realistic<sup>25</sup>. 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 communities<sup>2</sup> (e.g., competitive, mutualist, predator-prey; see Supplementary Information). I emphasise that  $\gamma$  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.<sup>27</sup> (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.

## 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's<sup>1</sup> 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.

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.

My focus is distinct from Gibbs et al.<sup>21</sup>, who applied the same mathematical framework to investigate how a diagonal matrix  $\mathbf{X}$  (equivalent to  $\gamma$  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.<sup>21</sup> 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  $\sigma$  and increased  $S$  to thereby increase total system complexity (see Supplemental Information for results simulated across  $\sigma$  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.

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<sup>5,22,25,27</sup> 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 systems<sup>18</sup>, 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  $\gamma$  has been investigated<sup>20</sup> and recently applied to questions concerning species density and feasibility<sup>21,22</sup>, but  $\gamma$  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 ( $\gamma$ ).** 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



178 a vector of potentially evolving traits ( $\mathbf{x}$ )<sup>18</sup>. For any species  $i$  or trait  $j$ , change in species density ( $N_i$ ) or  
 179 trait value ( $x_j$ ) with time ( $t$ ) is a function of the vectors  $\mathbf{N}$  and  $\mathbf{x}$ ,

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

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

180 In the above,  $f_i$  and  $g_j$  are functions that define the effects of all species densities and trait values on the  
 181 density of a species  $i$  and the value of trait  $j$ , respectively. Patel et al. were interested in stability when  
 182 the evolution of traits was relatively slow or fast in comparison with the change in species densities<sup>18</sup>, and  
 183 this is modulated in the above by the scalar  $\epsilon$ . The value of  $\epsilon$  thereby determines the timescale separation  
 184 between ecology and evolution, with high  $\epsilon$  modelling relatively fast evolution and low  $\epsilon$  modelling relative  
 185 slow evolution<sup>18</sup>.

186 I use the same principle that Patel et al. use to modulate the relative rate of evolution to modulate rates of  
 187 component responses for  $S$  components. Following May<sup>1,28</sup>, the value of a component  $i$  at time  $t$  ( $v_i(t)$ ) is  
 188 affected by the value of  $j$  ( $v_j(t)$ ) and  $j$ 's marginal effect on  $i$  ( $a_{ij}$ ), and by  $i$ 's response rate ( $\gamma_i$ ),

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

189 In matrix notation<sup>28</sup>,

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

190 In the above,  $\gamma$  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<sup>1,20,28</sup>. 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  $\gamma$ , especially at high  $S$ . Variation in  $\gamma$  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  $\gamma$  vectors would be evaluated for each unique  $\mathbf{M} = \gamma\mathbf{A}$ . This is technically impossible because  $\gamma_i$  can take any real value between 0-2, but even rounding  $\gamma_i$  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 evolution<sup>24</sup>. In this case, the practical solution is finding vectors of  $\gamma$  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  $\gamma$  vectors and allowing this population to evolve through a process of mutation, crossover (swapping  $\gamma_i$  values between vectors), selection, and reproduction until either a  $\gamma$  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  $\gamma$  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  $\gamma$  vector, and the 20  $\gamma$  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  $\gamma$  vectors. Mutation of each  $\gamma_i$  in a  $\gamma$  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  $\gamma_i$  (any  $\gamma_i$  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  $\gamma$  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  $\gamma_i$  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  $\gamma$  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.<sup>25</sup> 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  $\theta$  is the strength of intraspecific competition (diagonal elements). Diagonal values are set to  $-1$ , so  $\theta = -1$ . The variable  $\delta$  is a normalisation parameter that modulates the strength of interactions ( $\sigma$ ) for  $\mathbf{J}$ . Implicitly, here  $\delta = 0$  underlying strong interactions. Hence,  $(CS)^{-\delta} = 1$ , so in the above, a diagonal matrix of -1s ( $\theta \mathbf{I}$ ) 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's<sup>1</sup> stability criterion<sup>25</sup> 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 below (see also<sup>27</sup>),

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

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.

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**Supplementary Information:** Full tables of stability results for simulations across different system size ( $S$ )

values, ecological community types, connectance ( $C$ ) values, interaction strengths ( $\sigma$ ), and  $\gamma$  distributions are provided as supplementary material. An additional table also shows results for how feasibility changes across  $S$ . All code and simulation outputs are publicly available as part of the RandomMatrixStability package on GitHub (<https://github.com/bradduthie/RandomMatrixStability>).

**Additional Information:** The author declares no competing interests. All work was carried out by A. Bradley Duthie, and all code and data are accessible on [GitHub](#).

## 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. Watts, D. J. & Strogatz, S. H. Collective dynamics of ‘small world’ networks. *Nature* **393**, 440–442 (1998).

16. Albert, R. & Barabási, A. L. Statistical mechanics of complex networks. *Reviews of Modern Physics* **74**, 47–97 (2002).

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

18. Patel, S., Cortez, M. H. & Schreiber, S. J. Partitioning the effects of eco-evolutionary feedbacks on community stability. *American Naturalist* **191**, 1–29 (2018).

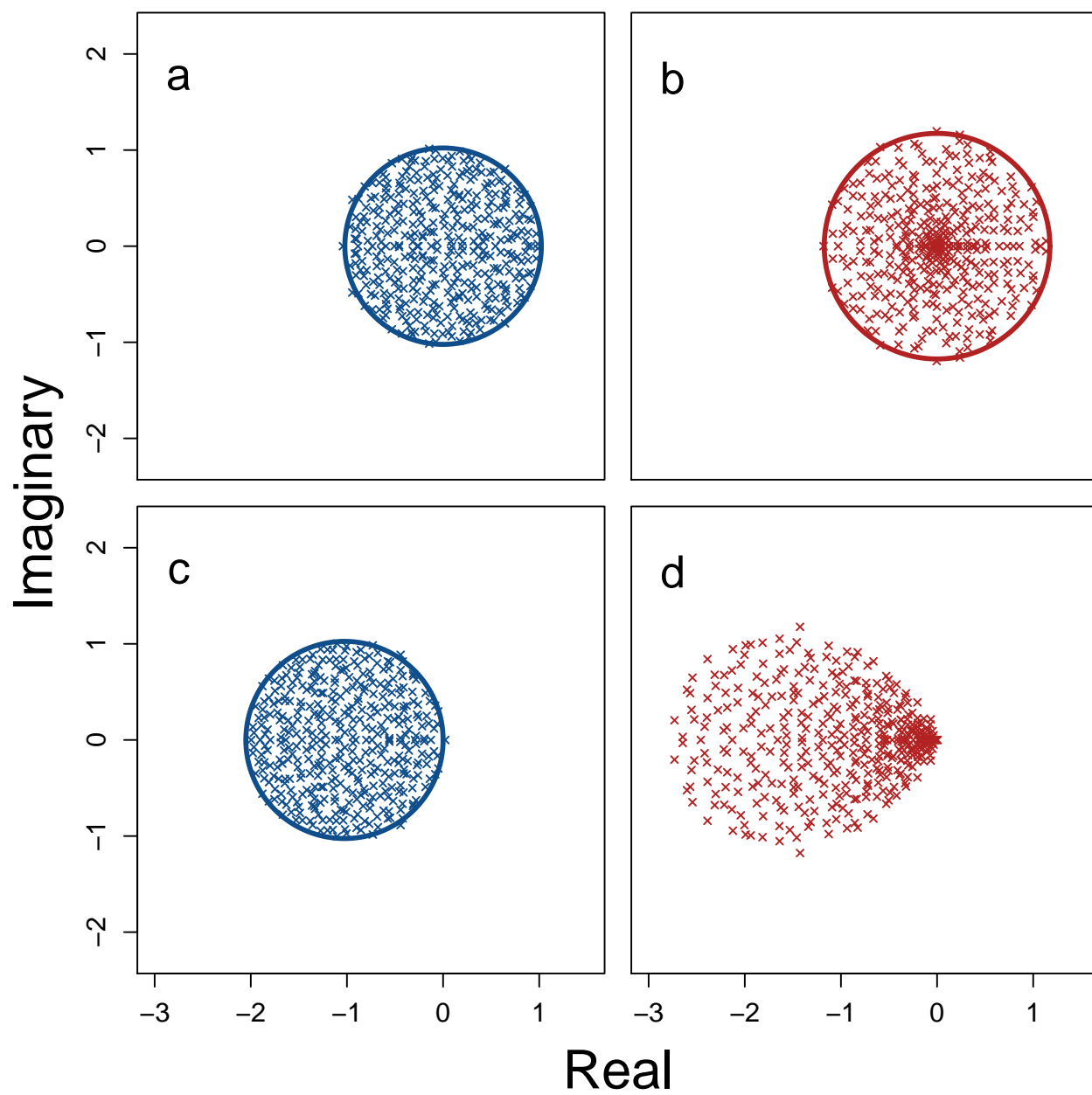
19. Tang, S. & Allesina, S. Reactivity and stability of large ecosystems. *Frontiers in Ecology and Evolution* **2**, 1–8 (2014).

20. 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).

21. Gibbs, T., Grilli, J., Rogers, T. & Allesina, S. The effect of population abundances on the stability of

- 279 large random ecosystems. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics* **98**, 022410  
280 (2018).
- 281 22. Stone, L. The feasibility and stability of large complex biological networks: a random matrix approach.  
282 *Scientific Reports* **8**, 8246 (2018).
- 283 23. Tang, S., Pawar, S. & Allesina, S. Correlation between interaction strengths drives stability in large  
284 ecological networks. **17**, 1094–1100 (2014).
- 285 24. Hamblin, S. On the practical usage of genetic algorithms in ecology and evolution. *Methods in Ecology*  
286 *and Evolution* **4**, 184–194 (2013).
- 287 25. Dougoud, M., Vinckenbosch, L., Rohr, R., Bersier, L.-F. & Mazza, C. The feasibility of equilibria in  
288 large ecosystems: a primary but neglected concept in the complexity-stability debate. *PLOS Computational*  
289 *Biology* **14**, e1005988 (2018).
- 290 26. Song, C. & Saavedra, S. Will a small randomly assembled community be feasible and stable? *Ecology* **99**,  
291 743–751 (2018).
- 292 27. Serván, C. A., Capitán, J. A., Grilli, J., Morrison, K. E. & Allesina, S. Coexistence of many species in  
293 random ecosystems. *Nature Ecology and Evolution* **2**, 1237–1242 (2018).
- 294 28. May, R. M. Qualitative stability in model ecosystems. *Ecology* **54**, 638–641 (1973).

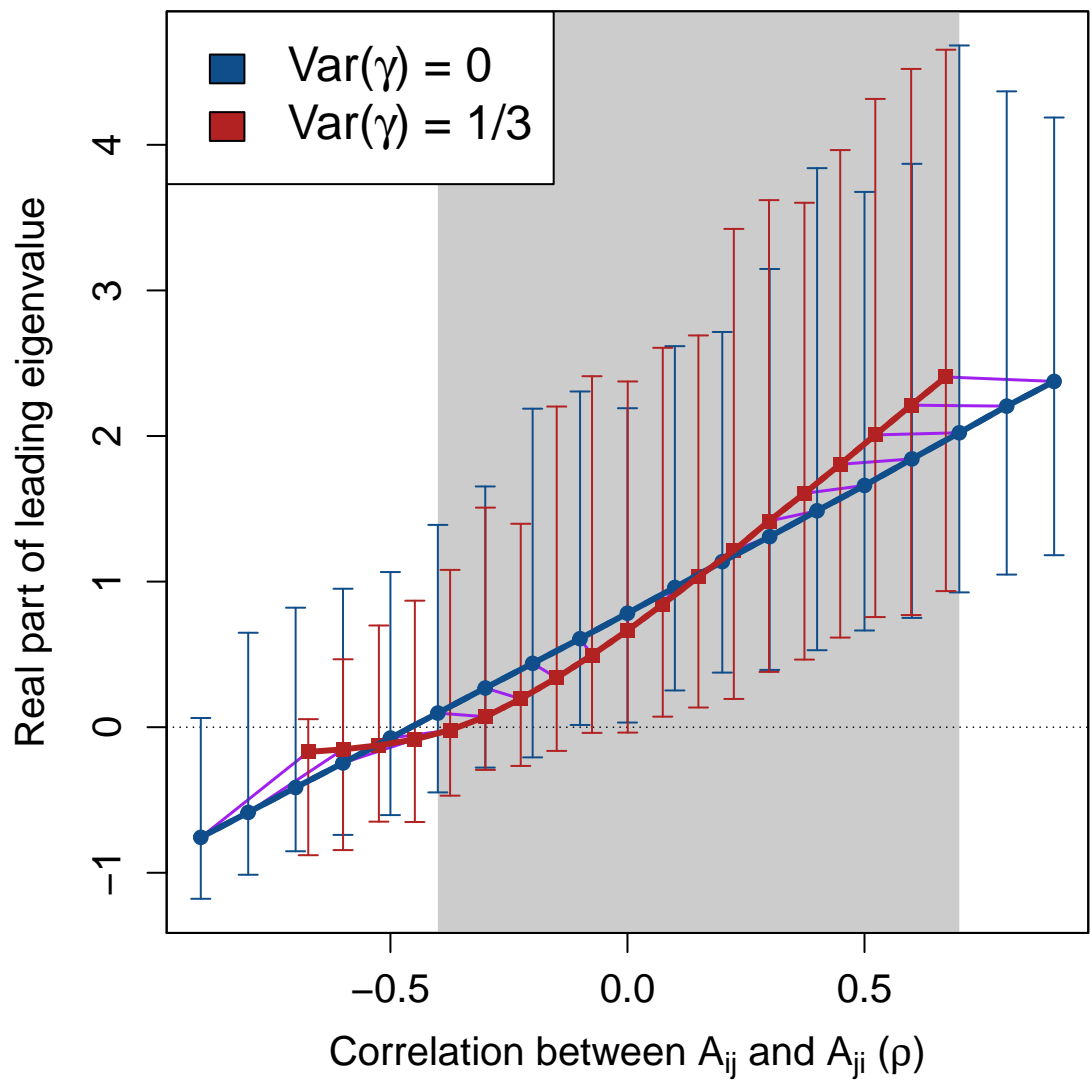
295 **Figure 1: Eigenvalue distributions of random complex systems.** Each panel shows the real (x-axis)  
 296 and imaginary (y-axis) parts of  $S = 400$  eigenvalues from random  $S \times S$  matrices. **(a)** A system represented  
 297 by a matrix  $\mathbf{A}$ , in which all elements are sampled from a normal distribution with  $\mu = 0$  and  $\sigma_A = 1/\sqrt{S}$ .  
 298 Points are uniformly distributed within a circle centred at the origin with a radius of  $\sigma_A\sqrt{S} = 1$ . **(b)** The  
 299 same system after including variation in the response rates of  $S$  components, represented by the diagonal  
 300 matrix  $\gamma$ , such that  $\mathbf{M} = \gamma\mathbf{A}$ . Elements of  $\gamma$  are randomly sampled from a uniform distribution of  $\min = 0$   
 301 and  $\max = 2$ . Eigenvalues of  $\mathbf{M}$  are distributed non-uniformly within a circle centred at the origin with a  
 302 radius of  $\sqrt{\sigma_A^2(1 + \sigma_\gamma^2)S} \approx 1.17$ . **(c)** A different random system  $\mathbf{A}$  constructed from the same parameters  
 303 as in **a**, except with diagonal values of  $-1$ . **(d)** The same system **c** after including variation in component  
 304 response rates, sampled from  $\mathcal{U}(0, 2)$  as in **b**.



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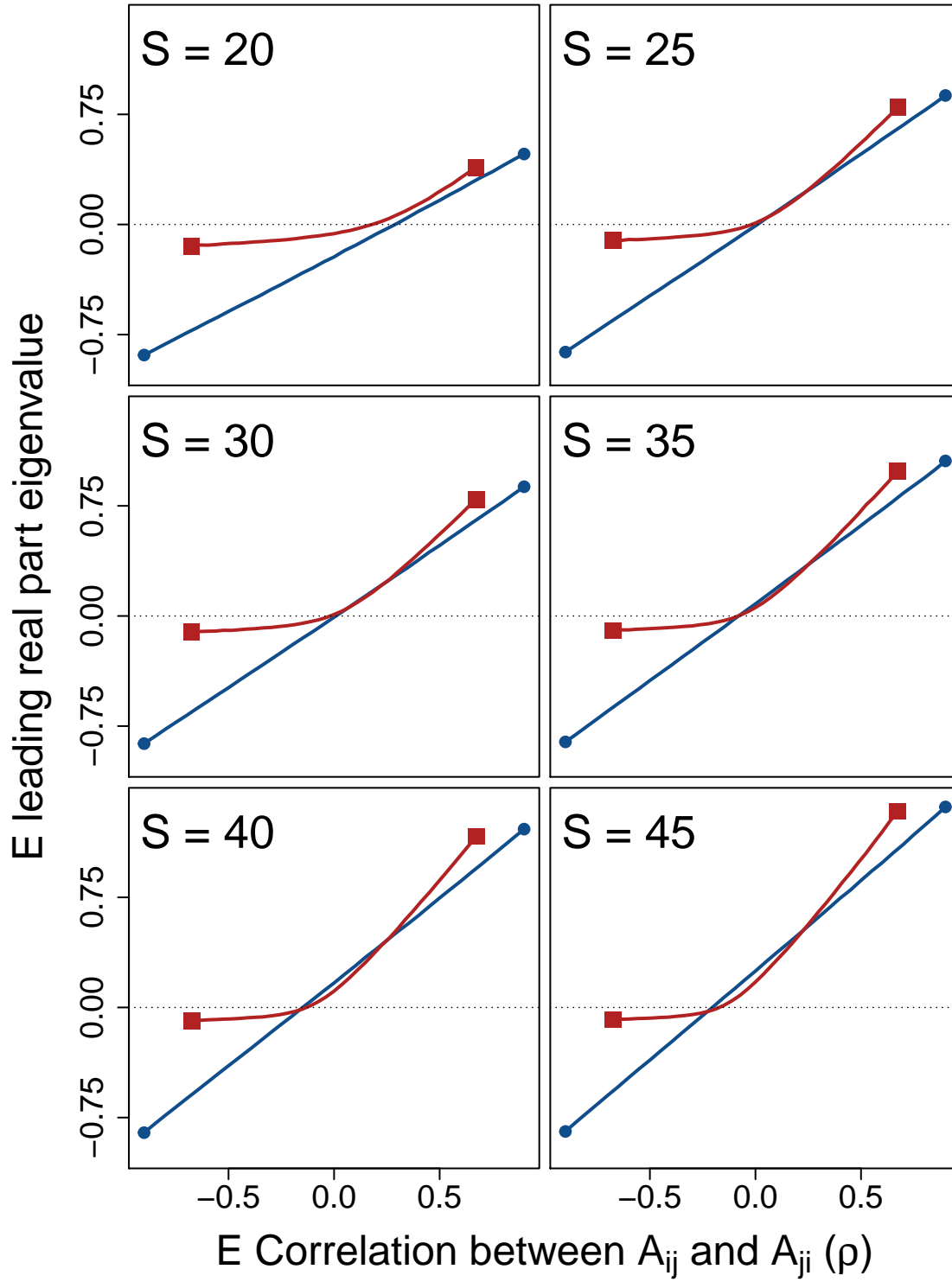


306 Figure 2: Insert a new caption here.



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308 Figure 3: Insert a new caption here.



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Figure 4: Stability of large complex systems with and without variation in component response rate ( $\gamma$ ). 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  $\gamma$  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  $\gamma$  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  $\text{Var}(\gamma) = 0$ .

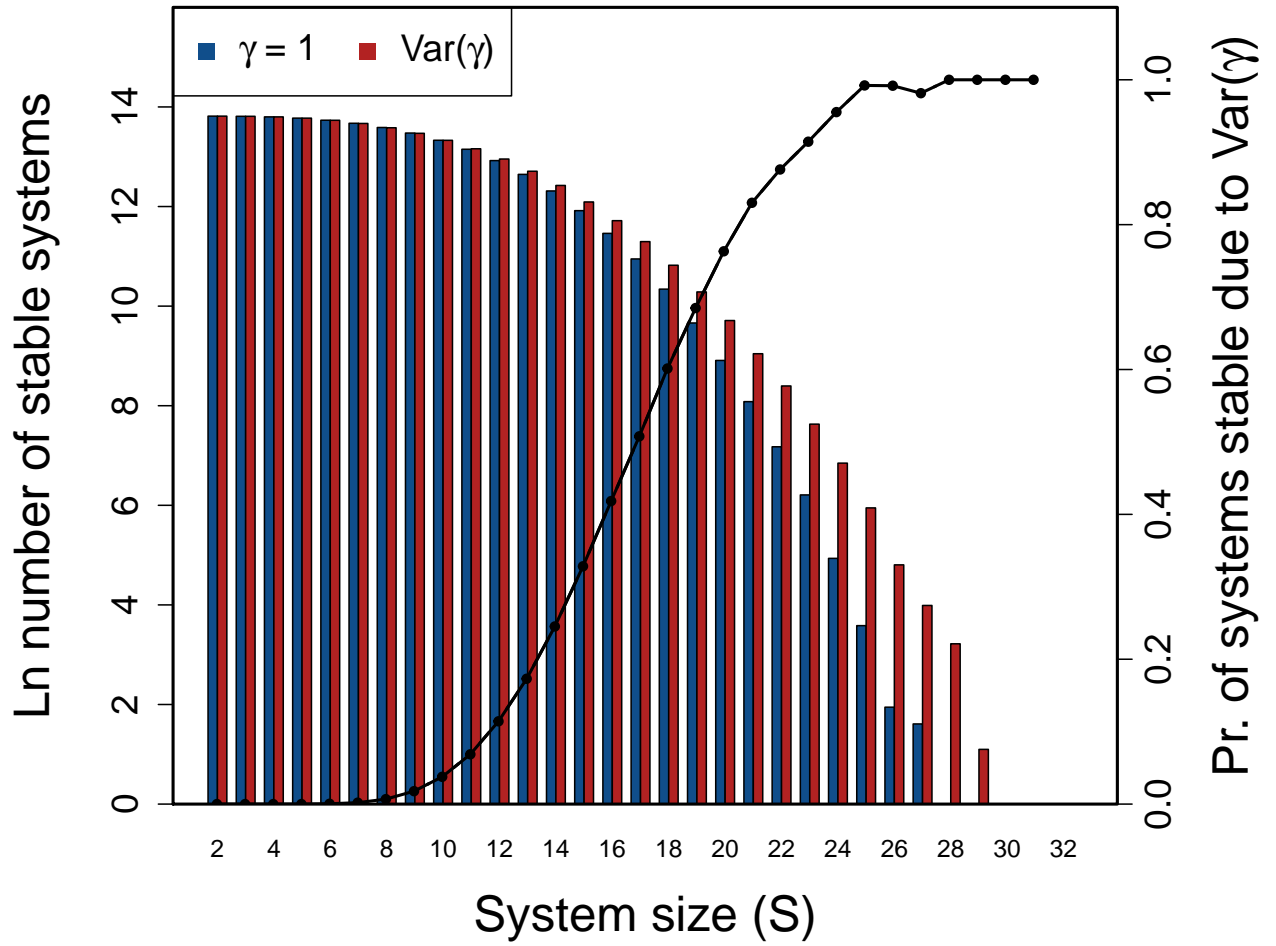


Figure 5: Stability of large complex systems given  $\gamma = 1$  versus targeted  $Var(\gamma)$ . The ln number of systems that are stable across different system sizes ( $S$ , max  $S = 40$ ) for  $C = 1$ , and the proportion of systems wherein a targeted search of  $\gamma$  values successfully resulted in system stability. For each  $S$ , 100000 complex systems are randomly generated. Stability of each complex system is tested given variation in  $\gamma$  using a genetic algorithm to maximise the effect of  $\gamma$  values on increasing stability, as compared to stability in an otherwise identical system in which  $\gamma$  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  $Var(\gamma) = 0$ .

