

# Component response rate variation drives stability in large complex systems

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The stability of a complex system generally decreases with increasing system size and interconnectivity, a counter-intuitive 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 show that when component response rates vary, the potential for system stability is markedly increased. Variation in  $\gamma$  becomes increasingly important as system size increases, such that the largest stable complex systems would be unstable if not for  $Var(\gamma)$ . My results reveal a previously unconsidered driver of system stability that is likely to be pervasive across all complex systems.

In 1972, May<sup>1</sup> 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  $(\sigma^2)^2$ . 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<sup>1-5</sup>, neurological<sup>6,7</sup>, biochemical<sup>8,9</sup>, and socio-economic<sup>10-13</sup> networks. As such, identifying general principles that

drive stability in complex systems is of wide-ranging importance.

Randomly assembled complex systems can be represented as large square matrices ( $M$ ) with  $S$  components (e.g., networks of species<sup>2</sup> or banks<sup>11</sup>). One element of such a matrix,  $M_{ij}$ , defines how component  $j$  affects component  $i$  in the system at a point of equilibrium<sup>2</sup>. 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  $\sigma^2$ ; 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 ( $\lambda$ ) of  $M$  are negative ( $\max(\Re(\lambda)) < 0$ )<sup>1,2</sup>. In a large system (high  $S$ ), eigenvalues are distributed uniformly<sup>14</sup> 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  $\sigma^2$  increase.

May's<sup>1,2</sup> stability criterion  $\sigma\sqrt{SC} < 1$  assumes that individual components respond to perturbations of the system at the same rate ( $\gamma$ ), 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 individuals, which might vary by orders of magnitude among species. Species with 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 has not been investigated in complex systems theory. Intuitively, variation in  $\gamma$  might be expected to decrease system stability by introducing a new source of variation into the system and thereby increasing  $\sigma$ . Here I show why, despite higher  $\sigma$ , complex systems in which  $\gamma$  varies are actually more likely to be stable, especially when  $S$  is high.

## Results

**Component response rates of random complex systems.** Rows in  $M$  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  $\gamma_i$ <sup>15</sup>. The distribution of  $\gamma$  over  $S$  components thereby models the distribution of component response rates. An instructive example compares one  $M$  where  $\gamma_i = 1$  for all  $i$  in  $S$  to the same  $M$  when half of  $\gamma_i = 1.95$  and half of  $\gamma_i = 0.05$ . This models one system in which  $\gamma$  is invariant and one in which  $\gamma$  varies, but systems are otherwise identical (note  $E[\gamma_i] = 1$  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  $\gamma_i$  to generate  $M$ . When  $\gamma_i = 1$ , eigenvalues of  $M$  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  $\gamma_i$  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  $\gamma = 1$ ) and all  $\Re(\lambda) < 0$ . The latter cluster has real components that have shifted to the right, but has a smaller radius. Overall, for 1 million randomly assembled  $M$ , 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  $\gamma$  can be observed by sampling  $\gamma_i$  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),  $E[\gamma] = 1$  when  $\gamma \sim \mathcal{U}(0, 2)$ , allowing comparison of  $M$  before and after variation in component response rate. Figure 2 shows a comparison of eigenvalue distributions given  $S = 1000$ ,  $C = 0.05$ , and  $\sigma = 0.4$ . As expected<sup>14</sup>, 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  $\gamma$  leads to a non-uniform distribution of eigenvalues, 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<sup>1,2</sup> threshold  $\sigma\sqrt{SC} < 1$ .

**Simulation of random M across S.** To investigate the effect of  $Var(\gamma)$  on system stability, I simulated random  $M$  matrices at  $\sigma = 0.4$  and  $C = 1$  across  $S$  ranging from 2-32. One million  $M$  were simulated for each  $S$ , and the stability of  $M$  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), and that the difference between the probabilities of observing a stable system increased with an increase in  $S$ ; i.e., the potential for  $Var(\gamma)$  to drive stability increased with system complexity. For the highest values of  $S$ , nearly all systems that were stable given  $Var(\gamma)$  would not have been stable given  $\gamma = 1$  (see Supplementary Information for full results).

**Targetted manipulation of  $\gamma$ .** To further investigate the potential of  $Var(\gamma)$  to be stabilising, I used a genetic algorithm (the space of possible  $\gamma$  values was too large to search exhaustively<sup>16</sup>). [Need a methods like sentence here](#). 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  $S \times S$   $M$  elements.

## Discussion

This suggests that the stability of large systems might be dependent upon variation in the response rate of their individual components, meaning that factors such as generation time (in ecological networks), transaction speed (in economic networks), or communication speed (in social networks) needs to be considered when investigating the stability of complex systems. *Cite 17 here?*

It is important to point out that  $Var(\gamma)$  is not stabilising per se; that is, adding variation in  $\gamma$  to a particular system  $M$  does not necessarily increase the probability that the system will be stable (see Supplementary Information). Rather, systems that are observed to be stable are more likely to vary in  $\gamma$ , and for this  $Var(\gamma)$

to be critical to their stability. This is caused by the shift in the distribution of eigenvalues that occurs by introducing  $Var(\gamma)$  (Fig. 1b, 2b), which can sometimes result in all  $\Re(\lambda) < 0$  but might also increase  $\Re(\lambda)$  values.

I have focused broadly on random complex systems, but it is also worthwhile to consider more restricted interactions such as those of specific ecological networks<sup>2</sup>. These include systems in which all interactions are negative (competitive networks), positive (mutualist networks), or  $i$  and  $j$  pairs have opposing signs (predator-prey networks). In general, competitive and mutualist networks tend to be destabilising, and predator-prey network tend to be stabilising<sup>18</sup>. When  $Var(\gamma)$  is applied to each, the proportion of stable competitive and predator-prey networks increases, but the proportion of stable mutualist networks does not (see Supplementary Information). Additionally, when each component of  $M$  is interpreted as a unique species and given a random intrinsic growth rate<sup>19</sup>, feasibility is not increased by  $Var(\gamma)$ , suggesting that variation in species generation time might be unlikely to drive stability in purely multi-species networks (see Supplementary Information).

Hence, managing the response rates of system components in a targetted way can potentially facilitate the stabilisation of complex systems through a reduction in dimensionality.

My results show that complex systems are more likely to be stable when the response rates of system components vary. These results are broadly applicable to understanding stability of complex networks in 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 a vector of potentially evolving traits ( $\mathbf{x}$ )<sup>15</sup>. 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  $\mathbf{x}$ ,

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

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

118 In the above,  $f_i$  and  $g_j$  are functions that define the effects of all species densities and trait values on the  
 119 density of a species  $i$  and the value of trait  $j$ , respectively. Patel et al. were interested in stability when  
 120 the evolution of traits was relatively slow or fast in comparison with the change in species densities<sup>15</sup>, and  
 121 this is modulated in the above by the scalar  $\epsilon$ . The value of  $\epsilon$  thereby determines the timescale separation  
 122 between ecology and evolution, with high  $\epsilon$  modelling relatively fast evolution and low  $\epsilon$  modelling relative  
 123 slow evolution<sup>15</sup>.

124 I use the same principle that Patel et al. use to modulate the relative rate of evolution to modulate rates of  
 125 component responses for  $S$  components. Following May<sup>1,20</sup>, the value of a component  $i$  at time  $t$  ( $v_i(t)$ ) is  
 126 affected by the value of  $j$  ( $v_j(t)$ ) and  $j$ 's marginal effect on  $i$  ( $m_{ij}$ ), and by  $i$ 's response rate ( $\gamma_i$ ),

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

127 In matrix notation<sup>20</sup>,

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

128 In the above,  $\gamma$  is a diagonal matrix in which elements correspond to individual component response rates.  
 129 Therefore,  $\gamma \mathbf{M}$  modulates the values of components and can be analysed using the techniques of May<sup>1,20</sup>.

130 **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  $M$ . This is technically impossible because  $\gamma_i$  can take any real value between 0-2, but even rounding  $\gamma$  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>16</sup>. In this case, the practical solution is finding vectors of  $\gamma$  that decrease the most positive real eigenvalue of  $M$ . The genetic algorithm below 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 (in the below, this “giving up” criteria is met when 20 generations pass, or if the fitness increase from one generation to the next is below a certain criteria).

For each of 40000 random  $M$  ( $\sigma = 0.4$ ,  $C = 1$ ), the genetic algorithm initialised 1000 different sets of  $\gamma \sim \mathcal{U}(0, 2)$  values of size  $S$ . Eigenanalysis was performed on  $M$  using each set of  $\gamma$  values, and the 20 sets with the lowest  $\max(\Re(\lambda))$  each produced 50 clonal offspring with subsequent mutation and crossover between the resulting new population of 1000  $\gamma$  sets. The genetic algorithm terminated if a stable  $M$  was found, 20 generations occurred, or a convergence criteria of minimum fitness increase between generations was satisfied.

The while loop in `rand_mat_ga` continues until either `iter` generations have occurred, a solution  $\gamma$  vector is found that results in all  $\Re(\lambda) < 0$ , or some criteria of minimum fitness increase is observed (by default, `converg = 0.01`). Within the genetic algorithm,  $\gamma$  values are mutated, crossover occurs between  $\gamma$  vectors, and selection occurs in each generation such that the 20  $\gamma$  vectors that produce the lowest maximum  $\Re(\lambda)$  are allowed to have 50 offspring each. In mutation, any  $\gamma_i$  values that mutate below zero are multiplied by  $-1$ , and any values that mutate above 2 are set to 2. Note also that if a solution is found, then one such  $\gamma$  vector causing stability is printed to a file.

**System feasibility.** For complex systems in which individual system components ( $S$ ) represent the density of some tangible quantity, it is important to consider the feasibility of the system. Feasible equilibria assume that the values of all system components are positive at equilibrium<sup>5,19,21</sup>. This is of particular interest

for ecological communities because population density cannot take negative values, meaning that ecological systems need to be feasible for stability to be biologically realistic<sup>19</sup>. Consequently, the use of random matrices and traditional stability criteria for making inferences in theoretical analyses of species networks has recently been criticised<sup>19</sup>. While the key results in the main text 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  $M$ . This analysis reveals that feasibility is not affected by  $Var(\gamma)$ , meaning that for pure interacting species networks, variation in component response time (i.e., species generation time) does not affect stability at biologically realistic species densities. Nevertheless, ecological interactions do not exist in isolation in empirical systems, but instead interact with evolutionary<sup>15</sup>, abiotic, or social-economic systems. The relevance of  $\gamma$  for complex system stability presented in the main text should therefore not be ignored in the broader context of ecological communities.

Dougoud et al.<sup>19</sup> define the following feasibility criteria for ecological systems characterised by  $S$  interacting species with varying densities.

$$x^* = -(\theta I + (CS)^{-\delta} A)^{-1} r.$$

In the above,  $x^*$  is the vector of species abundances at equilibrium (for feasibility, all values in  $x^*$  must be positive). The matrix  $I$  is the identity matrix (1s on the diagonal, 0s on the off-diagonal elements), and the value  $\theta$  is strength of intraspecific competition (diagonal elements). As I have done elsewhere, diagonal values are set to  $-1$ , so  $\theta = -1$ . The variable  $C$  is the inter-connectivity (i.e., ‘connectance’) of the community, which was set to  $C = 1$  throughout the manuscript and supplemental information, except [where otherwise noted](#). The variable  $\delta$  is a normalisation parameter that modulates the strength of interactions ( $\sigma$  in the main text), which are held in  $A$ . In the main text, implicitly,  $\delta = 0$  underlying strong interactions. Hence, the whole  $(CS)^{-\delta} = 1$ , so in the above, a diagonal matrix of -1s ( $\theta I$ ) is added to  $A$ , 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>19</sup> by  $\frac{\sigma}{(CS)^{-\delta}} \sqrt{SC} < -1$ , and hence  $(CS)^{-\delta} = 1$  for the randomly simulated systems in the



main text and supplemental information). The above criteria is therefore reduced to the below; note that the  
 parenthetical in both equations produces an  $M$  matrix as used throughout the main text and supplemental  
 information,

$$x^* = -(\theta I + A)^{-1} r.$$

To check the feasibility criteria, I therefore inverted  $M = (\theta I + A)$  and multiplied elements by -1, then  
 multiplied the resulting matrix by the vector of population growth rates  $r$ . Feasibility is satisfied if all of the  
 elements of the resulting vector are positive.

The population growth rate for an individual species  $i$  is sampled from a normal distribution of  $r_i \sim \mathcal{N}(0, 0.4^2)$ .

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**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  $\gamma$  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.

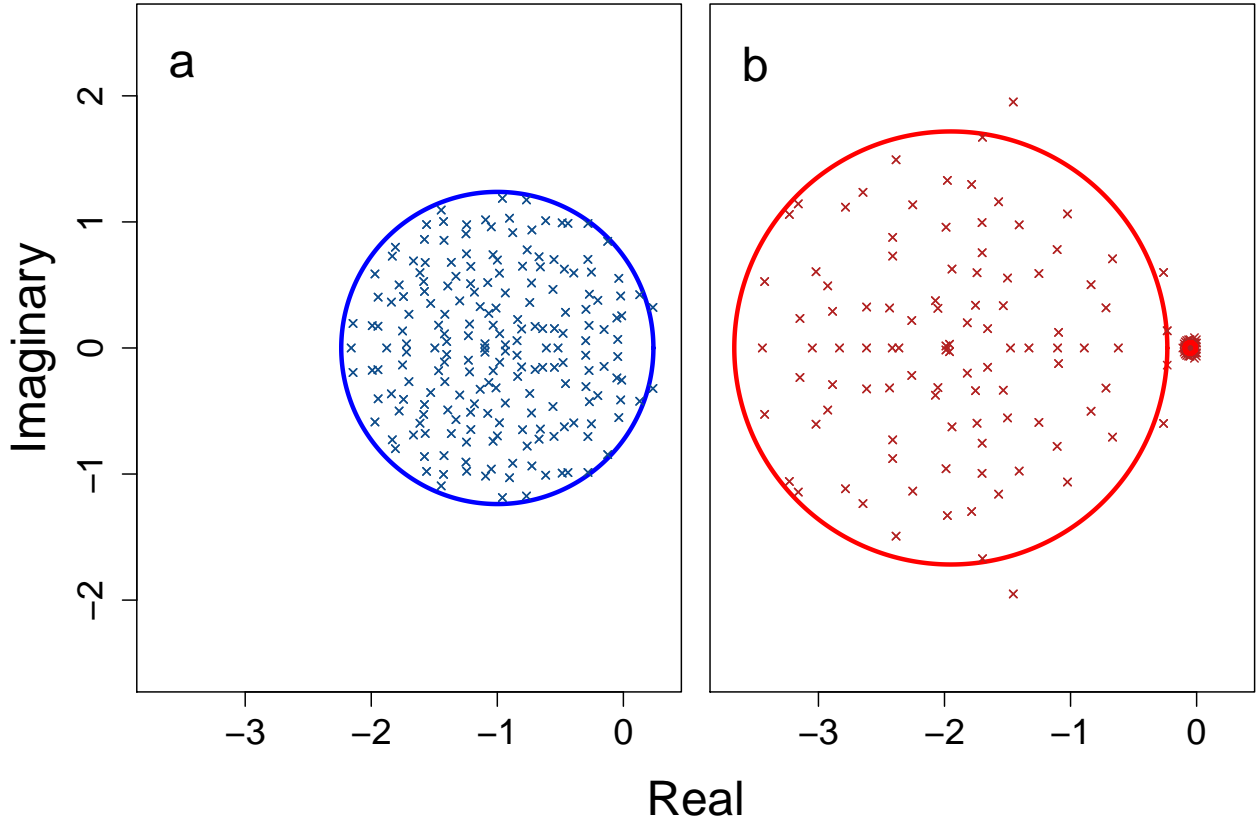
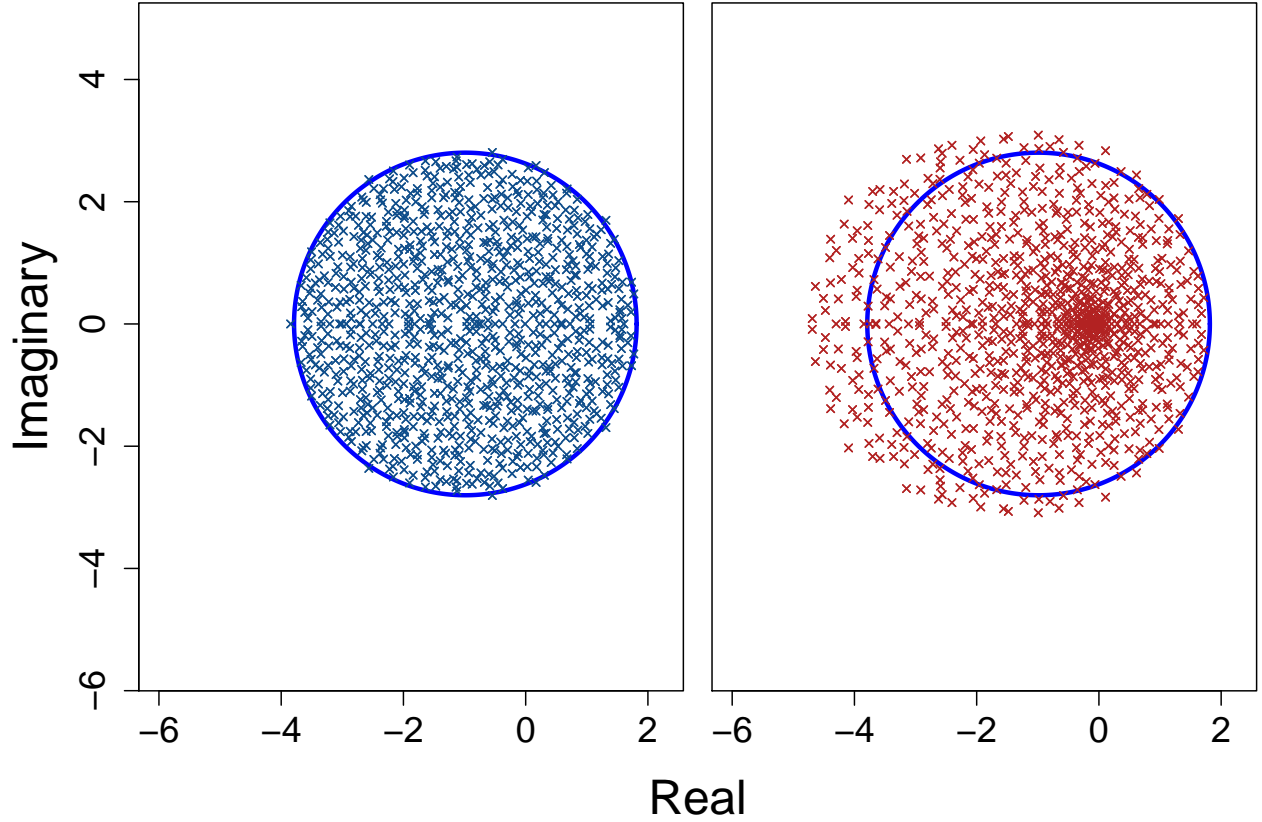


Figure 2: Distributions of eigenvalues before (a) and after (b) introducing variation in component response rate ( $\gamma$ ) in complex systems. Each panel show the same system where  $S = 1000$ ,  $C = 0.05$ , and  $\sigma = 0.4$ . **a.** Eigenvalues plotted in the absence of  $Var(\gamma)$  where  $E[\gamma] = 1$ , versus **b.** eigenvalues plotted given  $\gamma \sim \mathcal{U}(0, 2)$ , which increases the variance of interaction strengths ( $\sigma^2$ ) 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 0.718 and 0.728 for a and b, respectively.



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

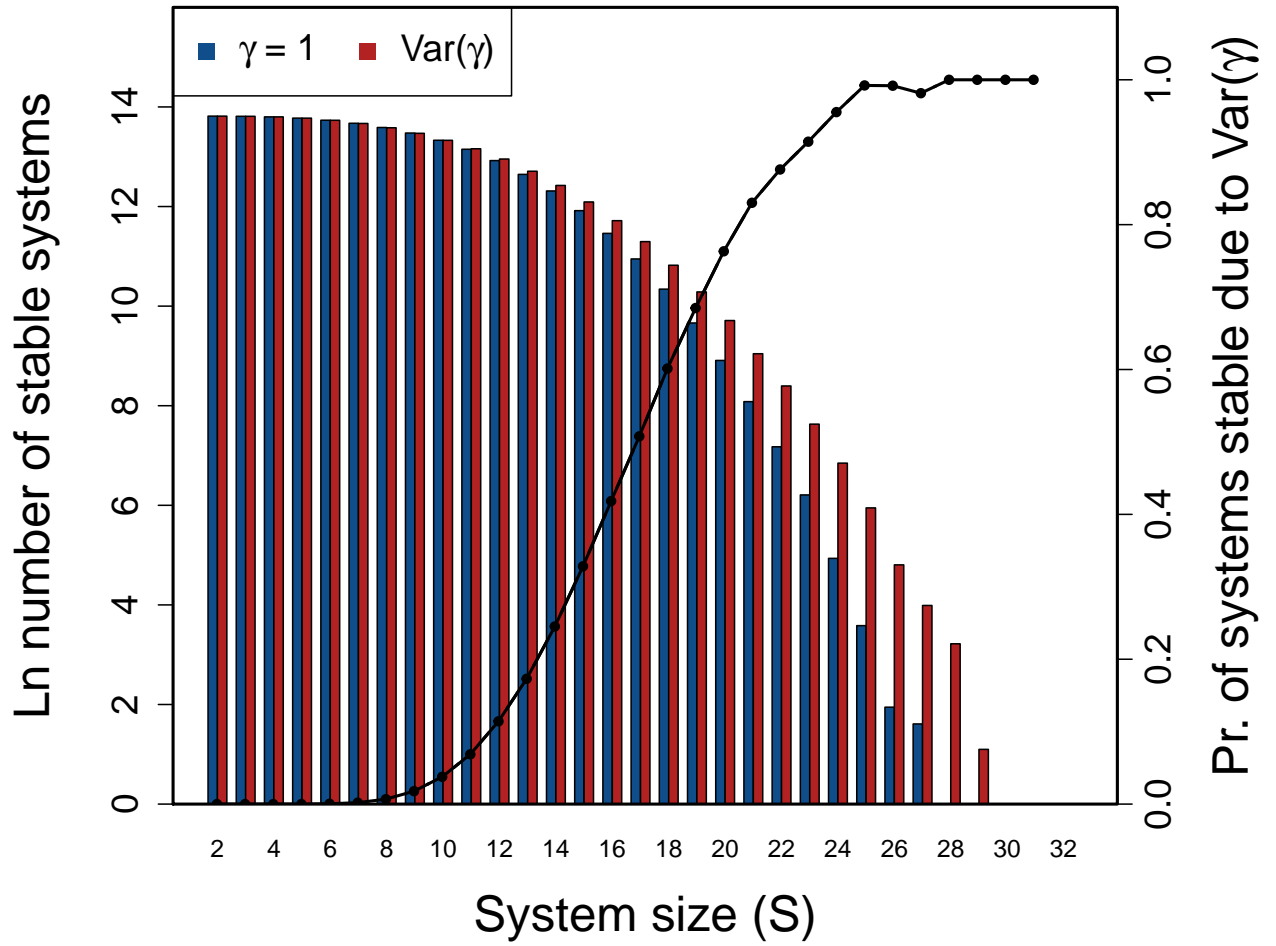


Figure 4: Stability of large complex systems given  $\gamma = 1$  versus targetted  $Var(\gamma)$ . The ln number of systems that are stable across different system sizes ( $S$ , max  $S = 40$ ) for  $C = 1$ , and the proportion of systems wherein a targetted search of  $\gamma$  values successfully 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 targetted to increase stability, but would not be stable if  $Var(\gamma) = 0$ .

