Component response rate variation drives stability in large complex systems

A. Bradley Duthie (alexander.duthie@stir.ac.uk)

Biological and Environmental Sciences, University of Stirling, Stirling, UK, FK9 4LA

The stability of a complex system generally decreases with increasing system size and inter-connectivity, 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 (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 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[1] 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

1

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

23 Randomly assembled complex systems can be represented as large square matrices ($\mathbf{M}$) with S components

24 (e.g., networks of species[2] or banks[11]). One element of such a matrix, M_{ij}, defines how component j

25 affects component i in the system at a point of equilibrium[2]. Off-diagonal elements ($i \neq j$) therefore define

26 interactions between components, while diagonal elements ($i = j$) define component self-regulation (e.g.,

27 carrying capacity in ecological communities). Traditionally, off-diagonal elements are assigned non-zero values

28 with a probability C, which are sampled from a distribution with variance σ^2; diagonal elements are set

29 to -1[1,2,4]. Local system stability is assessed using eigenanalysis, with the system being stable if the real

30 parts of all eigenvalues (λ) of $\mathbf{M}$ are negative ($\max(\Re(\lambda)) < 0$)[1,2]. In a large system (high S), eigenvalues

31 are distributed uniformly[14] within a circle centred at $\Re = -1$ (the mean value of diagonal elements) and

32 $\Im = 0$, with a radius of $\sigma\sqrt{SC}$[1,2,4] (Figs 1a and 2a). Local stability of randomly assembled systems therefore

33 becomes increasingly unlikely as S, C, and σ^2 increase.

34 May's[1,2] stability criterion $\sigma\sqrt{SC} < 1$ assumes that individual components respond to perturbations of the

35 system at the same rate (γ), but this is highly unlikely in any complex system. In ecological communities, for

36 example, the rate at which population density changes following perturbation will depend on the generation

37 time of individuals, which might vary by orders of magnitude among species. Species with short generation

38 times will respond quickly (high γ) to perturbations relative to species with long generation times (low γ).

39 Similarly, the speed at which individual banks respond to perturbations in financial networks, or individuals

40 or institutions respond to perturbations in complex social networks, is likely to vary. The effect of such

41 variance has not been investigated in complex systems theory. Intuitively, variation in γ might be expected

42 to decrease system stability by introducing a new source of variation into the system and thereby increasing

43 σ. Here I show why, despite higher σ, complex systems in which γ varies are actually more likely to be stable,

44 especially when S is high.

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 $E[\gamma_i] = 1$ 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 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 $\gamma = 1$) 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 $\mathbf{M}$, 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), $E[\gamma] = 1$ 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 expected[14], 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

3

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 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).

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 large complex system) is too large to search exhaustively[19]. Selection on γ value combinations to minimise $\max\left(\Re(\lambda)\right)$ demonstrated the potential for $Var(\gamma)$ to increase system stability. Across $S = \{2, 3, ..., 39, 40\}$, 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 $S \times S$ **M** elements.

System feasibility given Var(γ) 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. Feasibile equilibria assume that the values of all system components are positive at equilibrium[5,20,21]. 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[20]. While my key 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 **M** tested for stability, and additionally for specific types of ecological

4

97 communities[2] (e.g., competitive, mutualist, predator-prey; see Supplementary Information). Feasibility was

98 unaffected by $Var(\gamma)$, meaning that for pure interacting species networks, variation in component response

99 time (i.e., species generation time) does not affect stability at biologically realistic species densities.

Discussion

101 This suggests that the stability of large systems might be dependent upon variation in the response rate of

102 their individual components, meaning that factors such as generation time (in ecological networks), transaction

103 speed (in economic networks), or communication speed (in social networks) needs to be considered when

104 investigating the stability of complex systems. *Cite 16 here*?

105 It is important to point out that $Var(\gamma)$ is not stabilising per se; that is, adding variation in γ to a particular

106 system $\mathbf{M}$ does not necessarily increase the probability that the system will be stable (see Supplementary

107 Information). Rather, systems that are observed to be stable are more likely to vary in γ, and for this $Var(\gamma)$

108 to be critical to their stability. This is caused by the shift in the distribution of eigenvalues that occurs by

109 introducing $Var(\gamma)$ (Fig. 1b, 2b), which can sometimes result in all $\Re(\lambda) < 0$ but might also increase $\Re(\lambda)$

110 values.

111 I have focused broadly on random complex systems, but it is also worthwhile to consider more restricted

112 interactions such as those of specific ecological networks[2]. These include systems in which all interactions

113 are negative (competitive networks), positive (mutualist networks), or i and j pairs have opposing signs

114 (predator-prey networks). In general, competitive and mutualist networks tend to be destabilising, and

115 predator-prey network tend to be stabilising[22]. When $Var(\gamma)$ is applied to each, the proportion of stable

116 competitive and predator-prey networks increases, but the proportion of stable mutualist networks does

117 not (see Supplementary Information). Additionally, when each component of $\mathbf{M}$ is interpreted as a unique

118 species and given a random intrinsic growth rate[20], feasibility is not increased by $Var(\gamma)$, suggesting that

119 variation in species generation time might be unlikely to drive stability in purely multi-species networks (see

120 Supplementary Information).

5

Nevertheless, ecological interactions do not exist in isolation in empirical systems, but instead interact with evolutionary[15], abiotic, or social-economic systems. The relevance of γ for complex system stability presented in the main text should therefore not be ignored in the broader context of ecological communities.

Hence, managing the response rates of system components in a targeted 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 (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 densities[15], 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

6

₁₃₉ slow evolution[15].

₁₄₀ I use the same principle that Patel et al. use to modulate the relative rate of evolution to modulate rates of

₁₄₁ component responses for S components. Following May[1,23], the value of a component i at time t $(v_i(t))$ is

₁₄₂ 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),

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

₁₄₃ In matrix notation[23],

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

₁₄₄ In the above, γ is a diagonal matrix in which elements correspond to individual component response rates.

₁₄₅ Therefore, $\mathbf{M} = \gamma \mathbf{A}$ modulates the values of components and can be analysed using the techniques of

₁₄₆ May[1,16,23].

₁₄₇ **Genetic algorithm**. Ideally, to investigate the potential of $Var(\gamma)$ for increasing the proportion of stable

₁₄₈ complex systems, the search space of all possible γ vectors would be evaluated for each unique $\mathbf{M} = \gamma \mathbf{A}$.

₁₄₉ This is technically impossible because γ_i can take any real value between 0-2, but even rounding γ_i to

₁₅₀ reasonable values would result in a search space too large to practically explore. Under these conditions,

₁₅₁ genetic algorithms are highly useful tools for finding practical solutions by mimicking the process of biological

₁₅₂ evolution[19]. In this case, the practical solution is finding vectors of γ that decrease the most positive real

₁₅₃ eigenvalue of $\mathbf{M}$. The genetic algorithm used achieves this by initialising a large population of 1000 different

₁₅₄ potential γ vectors and allowing this population to evolve through a process of mutation, crossover (swaping

₁₅₅ γ_i values between vectors), selection, and reproduction until either a γ vector is found where all $\Re(\lambda) < 0$ or

₁₅₆ some "giving up" critiera is met.

₁₅₇ For each $S = \{2, 3, ..., 39, 40\}$, the genetic algorithm was run for 100000 random $\mathbf{M}$ $(\sigma = 0.4, C = 1)$, where

158 $\mathbf{M} = \gamma \mathbf{A}$. The genetic algorithm was initialised with a populatoin of 1000 different γ vectors with elements

159 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

160 20 γ vectors resulting in $\mathbf{M}$ with the lowest $\max(\Re(\lambda))$ each produced 50 clonal offspring with subsequent

161 random mutation and crossover between the resulting new population of 1000 γ vectors (any γ_i values that

162 mutated below zero were multiplied by -1, and any values that mutated above 2 were set to 2). The genetic

163 algorithm terminated if a stable $\mathbf{M}$ was found, 20 generations occurred, or if the mean γ fitness increase

164 between generations was less than 0.01 (where fitness was defined as $W_\gamma = -\max(\Re(\lambda))$ for $\mathbf{M}$).

165 **System feasibility**. Dougoud et al.[20] define the following feasibility criteria for ecological systems charac-

166 terised by S interacting species with varying densities in a classical Lotka-Volterra model,

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

167 In the above, $\mathbf{x}^*$ is the vector of species abundances at equilibrium (feasibility is satisfied if all values in $\mathbf{x}^*$

168 are positive). The matrix $\mathbf{I}$ is the identity matrix, and the value θ is strength of intraspecific competition

169 (diagonal elements). Diagonal values are set to -1, so $\theta = -1$. The variable δ is a normalisation parameter

170 that modulates the strength of interactions (σ) for $\mathbf{J}$. Implicitly, here $\delta = 0$ underlying strong interactions.

171 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

172 zeros and an off-diagonal affecting species interactions (i.e., the expression $(CS)^{-\delta}$ relates to May's[1] stability

173 criterion[20] 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

174 criteria is therefore reduced to the below,

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

175 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.

176 from $r_i \sim \mathcal{N}(0, 0.4^2)$). Feasibility is satisfied if all of the elements of the resulting vector are positive.

Supplementary Information: Full tables of stability results for simulations across different system size (S) values, ecological community types, connectance (C) values, interaction strengths (σ), and γ 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).

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. *arXiv* (2017).

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*

219 *and Evolution* **4,** 184–194 (2013).

220 20. Dougoud, M., Vinckenbosch, L., Rohr, R., Bersier, L.-F. & Mazza, C. The feasibility of equilibria in

221 large ecosystems: a primary but neglected concept in the complexity-stability debate. *PLOS Computational*

222 *Biology* **14,** e1005988 (2018).

223 21. Song, C. & Saavedra, S. Will a small randomly assembled community be feasible and stable? *Ecology* **99,**

224 743–751 (2018).

225 22. Allesina, S. & Levine, J. M. A competitive network theory of species diversity. *Proceedings of the National*

226 *Academy of Sciences of the United States of America* **108,** 5638–5642 (2011).

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

11

228 **Figure 1: Example distribution of eigenvalues before (a) and after (b) separating a randomly**

229 **generated complex system into fast ($\gamma = 1.95$) and slow ($\gamma = 0.05$) component response rates.**

230 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.,

231 only the distribution of γ differs between panels). **a.** Eigenvalues plotted when all $\gamma = 1$; distributions of

232 points are uniformly distributed within the blue circle with a radius of $\sigma\sqrt{SC} = 1.238$ centred at -1 on

233 the real axis. **b.** Eigenvalues plotted when half $\gamma = 1.95$ and half $\gamma = 0.05$; distributions of points can be

234 partitioned into one large circle centred at $\gamma = -1.95$ and one small circle centred at $\gamma = -0.05$. In a, the

235 maximum real eigenvalue $\max(\Re(\lambda)) = 0.2344871$, while in b $\max(\Re(\lambda))$ = -0.0002273135, meaning that

236 the complex system in b but not a is stable because in b $\max(\Re(\lambda)) < 0$. In 1 million randomly generated

237 complex systems under the same parameter values, 1 was stable when $\gamma = 1$ while 32 were stable when

238 $\gamma = \{1.95, 0.05\}$. Overall, complex systems that are separated into fast versus slow components tend to be

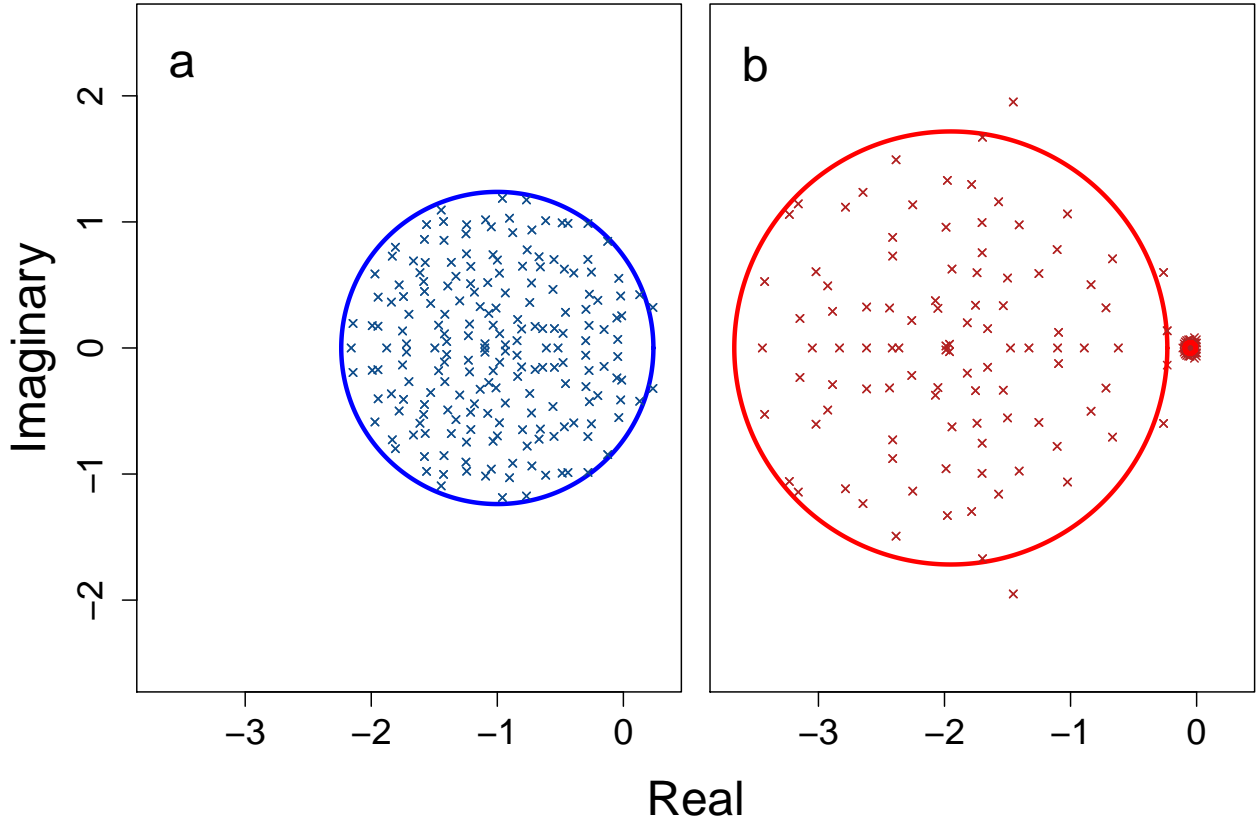239 more stable than otherwise identical systems with identical component response rates.

240

12

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 elipses in both panels show the circle centred on the distribution in panel a. Proportions of $\Re(\lambda) < 0$ are 0.721 and 0.735 for a and b, respectively.
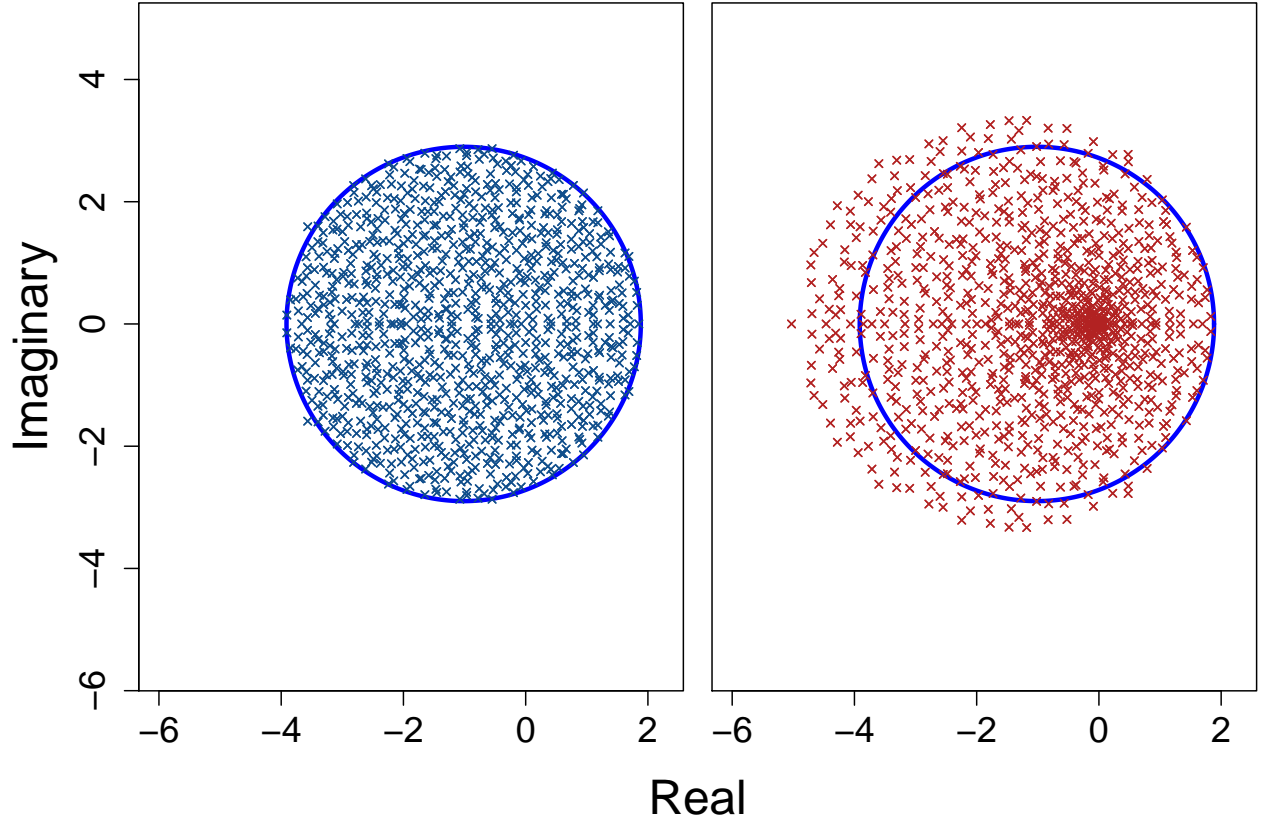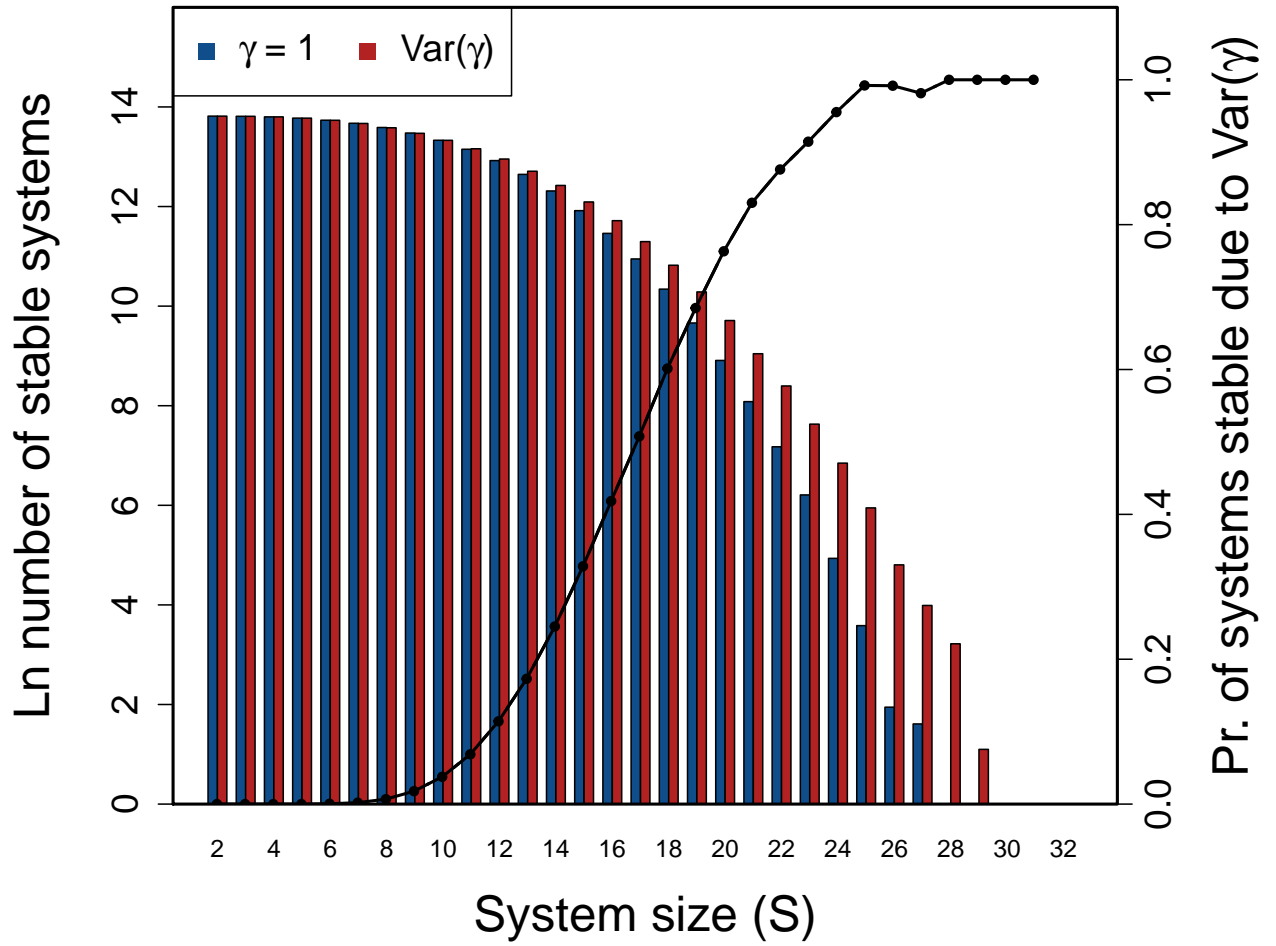
Figure 3: Stability of large complex systems with and without variation in component response
rate (γ). The ln number of systems that are stable across different system sizes (S) given $C = 1$, and the
proportion of systems in which variation in γ is critical for system stability. For each S, 1 million 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 $Var(\gamma)$ 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 $Var(\gamma)$, respectively. The black line shows the proportion of systems that are stable
when $Var(\gamma) > 0$, but would be unstable if $Var(\gamma) = 0$.

14

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 $Var(\gamma) = 0$.