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 (γ) 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 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 $Var(\gamma)$. My results therefore reveal a previously unconsidered aspect of system stability that is likely to be pervasive across all realistic complex systems.

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Introduction

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 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 species[2] or banks[11]). One element of such a matrix, M_{ij}, defines how component j affects component i in the system at a point of equilibrium[2]. Off-diagonal elements ($i \neq j$) therefore define interactions between components, while diagonal elements ($i = j$) define component self-regulation (d, 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_M^2; diagonal elements are set to $d = -1$[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 uniformly[14] within a circle centred at $\Re = -1$ (the mean value of diagonal elements) and $\Im = 0$, with a radius of $\sigma_M\sqrt{SC}$[1,2,4] (Figs 1a and 2a). Local stability of randomly assembled systems therefore becomes increasingly unlikely as S, C, and σ_M increase.

May's[1,2] stability criterion $\sigma_M\sqrt{SC} < 1$ 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

44 times (low γ). Similarly, the speed at which individual banks respond to perturbations in financial networks,

45 or individuals or institutions respond to perturbations in complex social networks, is likely to vary. The

46 effect of such variance on stability has not been investigated in complex systems theory. Intuitively, variation

47 in γ (σ_γ^2) might be expected to decrease system stability by introducing a new source of variation into the

48 system and thereby increasing σ_M. Here I show that, despite higher σ_M, realistic complex systems (such

49 that S is high but finite) are actually more likely to be stable if their individual component response rates

50 vary. My results are robust across commonly observed network structures, including random[1], small-world[15],

51 scale-free[16], cascade food web[17] networks.

Results

53 **Component response rates of random complex systems**. Complex systems $\mathbf{M}$ are built from two

54 matrices, one modelling component interactions ($\mathbf{A}$), and second modelling component response rates (γ).

55 Both $\mathbf{A}$ and γ are square $S \times S$ matrices. Rows in $\mathbf{A}$ define how a given component i is affected by each

56 component j in the system, including itself (where $i = j$). Off-diagonal elments of $\mathbf{A}$ are independent and

57 identically distributed (i.i.d), and diagonal elements are set to $A_{ii} = -1$ as in May[1]. Diagonal elements of

58 γ are positive, and off-diagonal elements are set to zero (i.e. γ is a diagonal matrix with positive support).

59 The distribution of γ over S components thereby models the distribution of component response rates. The

60 dynamics of the entire system $\mathbf{M}$ can be defined as follows[18],

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

61 Equation 1 thereby serves as a null model to investigate how variation in component response rate (σ_γ)

62 affects complex systems. In the absence of such variation ($\sigma_\gamma = 0$), γ is set to the identity matrix (diagonal

63 elements all equal 1) and $\mathbf{M} = \mathbf{A}$. Under these conditions, eigenvalues of $\mathbf{M}$ are distributed uniformly[14] in a

64 circle centred at $(-d, 0)$ with a radius of $\sigma_M \sqrt{SC}$[1] (Figure 1a).

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Effect of σ_γ^2 on M (co)variation. The value of $\max(\Re(\lambda))$, and therefore system stability, can be estimated from five properties of $\mathbf{M}$[19]. These properties include (1) system size (S), (2) mean self-regulation of components (d), (3) mean interaction strength between components (μ), (4) the standard deviation between component interaction strengths (σ_M), and (5) the correlation of interaction strengths between components, M_{ij} and M_{ji} (ρ). Positive σ_γ does not change S, nor does it necessarily change $E[d]$ or $E[\mu]$. What σ_γ does change is the total variation in component interaction strengths (σ_M), and ρ. Introducing variation in γ 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,

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

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

$$\sigma_M^2 = \sigma_A^2 (1 + \sigma_\gamma^2). \tag{3}$$

The increase caused by σ_γ^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 σ_γ^2 changes the distribution of eigenvalues[20–22], potentially affecting stability (Figure 1c vs. 1d).

Given $\sigma_\gamma^2 = 0$, $\max(\Re(\lambda))$ decrease linearly with ρ such that[23],

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

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[2]. If diagonal elements of γ vary independently, the magnitude of ρ is decreased because σ_γ^2 increases

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81   the variance of M_{ij} without affecting the expected covariance between M_{ij} and M_{ji}.

82   **Numerical simulations of random M with and without σ_γ^2.** I used numerical simulations and

83   eigenanalysis to test how variation in γ affects stability in random matrices with known properties, comparing

84   the stability of **A** versus $\mathbf{M} = \gamma \mathbf{A}$. Values of γ were sampled from a uniform distribution where $\gamma_i \sim \mathcal{U}(0, 2)$

85   and $\sigma_\gamma^2 = 1/3$ (see Supplementary Information for other distributions, which give similar results). Diagonal

86   elements of simulated **A** were standardised to the mean value of sampled γ so that $E[d]$ of **M** and **M** were

87   guaranteed to be identical. Here I focus on the effect of γ across values of ρ, and for increasing system sizes

88   (S) in random and structured networks. By increasing S, the objective is to determine the effect of γ as

89   system complexity increases toward the boundary at which stability is realistic for a finite system.

90   **Simulation of random M across ρ**

91   Ten thousand numerical simulations of **M** revealed that $\sigma_\gamma^2 > 0$ results in a nonlinear relationship between

92   ρ and $\max(\Re(\lambda))$, which can sometimes increase the stability of the system. Figure 2 shows a comparison

93   of $\max(\Re(\lambda))$ across ρ values when $\sigma_\gamma^2 = 0$ versus $\sigma_\gamma^2 = 1/3$ given $S = 25$ and $\sigma = 0.4$. For $-0.4 \le \rho \le 0.7$

94   (shaded region of Figure 2), expected $\max(\Re(\lambda))$ was lower given $\sigma_\gamma^2 = 1/3$. For $\rho \ge -0.1$, the range of

95    $\max(\Re(\lambda))$ values observed given $\sigma_\gamma^2 = 1/3$ also had a lower bound, which included negative values for

96    $\rho = -0.1$ and $\rho = 0$. Hence, across a wide range of system correlations, variation in the response rate of

97   system components had a stabilising effect.

98   The stabilising effect of σ_γ^2 across ρ increased with increasing S. Figure 3 shows 10000 numerical simulations

99   of **M** for $\sigma_\gamma^2 = 0$ versus $\sigma_\gamma^2 = 1/3$ across increasing S given $\sigma = 0.2$ (σ has been lowered here to better

100   illustrate the effect of S; note that now given $S = 25$, $1 = \sigma\sqrt{SC}$). For relatively small systems ($S \le 25$),

101   positive σ_γ^2 never decreased the expected $\max(\Re(\lambda))$. But as S increased, the curvilinear relationship between

102   ρ and $\max(\Re(\lambda))$ resulted in **M** with lower expected $\max(\Re(\lambda))$ for low magnitudes of ρ. In turn, as S

103   increased, and systems became more complex, positive σ_γ^2 increased the proportion of numerical simulations

104   that were observed to be stable (see below).

105   **Simulation of random 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 $S = \{2, 3, ..., 49, 50\}$. 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 exhaustively[24]. Generations of selection on γ value combinations to minimise $\max(\Re(\lambda))$ demonstrated the potential for $Var(\gamma)$ to increase system stability. Across $S = \{2, 3, ..., 39, 40\}$, 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(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. Feasibilility assumes that values of all components are positive at equilibrium[5,25,26]. 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[25]. 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[2] (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

132 such as expected generation time. Feasibility was unaffected by $Var(\gamma)$ and instead occurred with a fixed

133 probability of $1/2^S$, consistent with a recent proof by Serván et al.[27] (see Supplementary Information). Hence,

134 for pure interacting species networks, variation in component response rate (i.e., species generation time)

135 does not affect stability at biologically realistic species densities.

Discussion

137 I have shown that the stability of complex systems might often be contigent upon variation in the response

138 rates of their individual components, meaning that factors such as rate of trait evolution (in biological

139 networks), transaction speed (in economic networks), or communication speed (in social networks) need

140 to be considered when investigating the stability of complex systems. Variation in component response

141 rate is more likely to be critical for stability in systems that are especially complex, and it can ultimately

142 increase the probability that system stability is observed above that predicted by May's[1] classically derived

143 $\sigma\sqrt{SC}$ criterion. The logic outlined here is general, and potentially applies to any complex system in which

144 individual system components can vary in their reaction rates to system perturbation.

145 It is important to recognise that variation in component response rate is not stabilising per se; that is, adding

146 variation in component response rates to a particular system does not increase the probability that the system

147 will be stable. Rather, highly complex systems that are observed to be stable are more likely to have varying

148 component response rates, and for this variation to be critical to their stability (Fig. 3). This is caused by

149 the shift to a non-uniform distribution of eigenvalues that occurs by introducing $Var(\gamma)$ (Fig. 1b, 2b), which

150 can sometimes cause all of the real components of the eigenvalues of the system matrix to become negative,

151 but might also increase the real components of eigenvalues.

152 My focus is distinct from Gibbs et al.[21], who applied the same mathematical framework to investigate

153 how a diagonal matrix $\mathbf{X}$ (equivalent to γ in my model) affects the stability of a community matrix $\mathbf{M}$

154 given an interaction matrix $\mathbf{A}$ within a generalised Lotka-Volterra model, where $\mathbf{M} = \mathbf{XA}$. Gibbs et al.[21]

155 analytically demonstrated that the effect of $\mathbf{X}$ on system stability decreases exponentially as system size

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becomes arbitrarily large ($S \to \infty$) 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 Supplemental 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.

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[5,22,25,27] 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[18], 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 investigated[20] and recently applied to questions concerning species density and feasibility[21,22], 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 ($\mathbf{x}$)[18]. 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[18], 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 evolution[18].

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[1,28], 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 notation[28],

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

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[1,20,28]. 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 evolution[24]. 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

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₂₂₁ some "giving up" critiera is met.

₂₂₂ For each $S = \{2, 3, ..., 39, 40\}$, the genetic algorithm was run for 100000 random $\mathbf{M}$ ($\sigma = 0.4$, $C = 1$). The

₂₂₃ genetic algorithm was initialised with a population of 1000 different γ vectors with elements sampled i.i.d

₂₂₄ from $\gamma_i \sim \mathcal{U}(0, 2)$. Eigenanalysis was performed on the $\mathbf{M}$ resulting from each γ vector, and the 20 γ

₂₂₅ vectors resulting in $\mathbf{M}$ with the lowest $\max{(\Re(\lambda))}$ each produced 50 clonal offspring with subsequent random

₂₂₆ mutation and crossover between the resulting new generation of 1000 γ vectors. Mutation of each γ_i in a

₂₂₇ γ vector occurred with a probability of 0.2, resulting in a mutation effect of size $\mathcal{N}(0, 0.02)$ being added

₂₂₈ to generate the newly mutated γ_i (any γ_i values that mutated below zero were multiplied by -1, and any

₂₂₉ values that mutated above 2 were set to 2). Crossover occurred between two sets of 100 γ vectors paired in

₂₃₀ each generation; vectors were randomly sampled with replacement among but not within sets. Vector pairs

₂₃₁ selected for crossover swapped all elements between and including two γ_i randomly selected with replacement

₂₃₂ (this allowed for reversal of vector element positions during crossover; e.g., $\{\gamma_4, \gamma_5, \gamma_6, \gamma_7\} \rightarrow \{\gamma_7, \gamma_6, \gamma_5, \gamma_4\}$).

₂₃₃ The genetic algorithm terminated if a stable $\mathbf{M}$ was found, 20 generations occurred, or if the mean γ fitness

₂₃₄ increase between generations was less than 0.01 (where fitness was defined as $W_\gamma = -\max{(\Re(\lambda))}$ for $\mathbf{M}$).

₂₃₅ **System feasibility**. Dougoud et al.[25] identify the following feasibility criteria for ecological systems

₂₃₆ characterised by S interacting species with varying densities in a generalised Lotka-Volterra model,

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

₂₃₇ In the above, $\mathbf{n}^*$ is the vector of species densities at equilibrium. Feasibility is satisfied if all elements in $\mathbf{n}^*$

₂₃₈ are positive. The matrix $\mathbf{I}$ is the identity matrix, and the value θ is the strength of intraspecific competition

₂₃₉ (diagonal elements). Diagonal values are set to -1, so $\theta = -1$. The variable δ is a normalisation parameter

₂₄₀ that modulates the strength of interactions (σ) for $\mathbf{J}$. Implicitly, here $\delta = 0$ underlying strong interactions.

₂₄₁ 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

₂₄₂ zeros and an off-diagonal affecting species interactions (i.e., the expression $(CS)^{-\delta}$ relates to May's[1] stability

₂₄₃ criterion[25] 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[27]),

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

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.

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).

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Figure 1: Eigenvalue distributions of random complex systems. Each panel shows the real (x-axis) and imaginary (y-axis) parts of $S = 400$ eigenvalues from random $S \times S$ matrices. (**a**) A system represented by a matrix $\mathbf{A}$, in which all elements are sampled from a normal distribution with $\mu = 0$ and $\sigma_A = 1/\sqrt{S}$. Points are uniformly distributed within a circle centred at the origin with a radius of $\sigma_A\sqrt{S} = 1$. (**b**) The same system after including variation in the response rates of S components, represented by the diagonal matrix γ, such that $\mathbf{M} = \gamma\mathbf{A}$. Elements of γ are randomly sampled from a uniform distribution from $\min = 0$ to $\max = 2$. Eigenvalues of $\mathbf{M}$ are then distributed non-uniformly within a circle centred at the origin with a 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 as in **a**, except with diagonal values of -1. (**d**) The same system **c** after including variation in component response rates, sampled from $\mathcal{U}(0, 2)$ as in **b**.
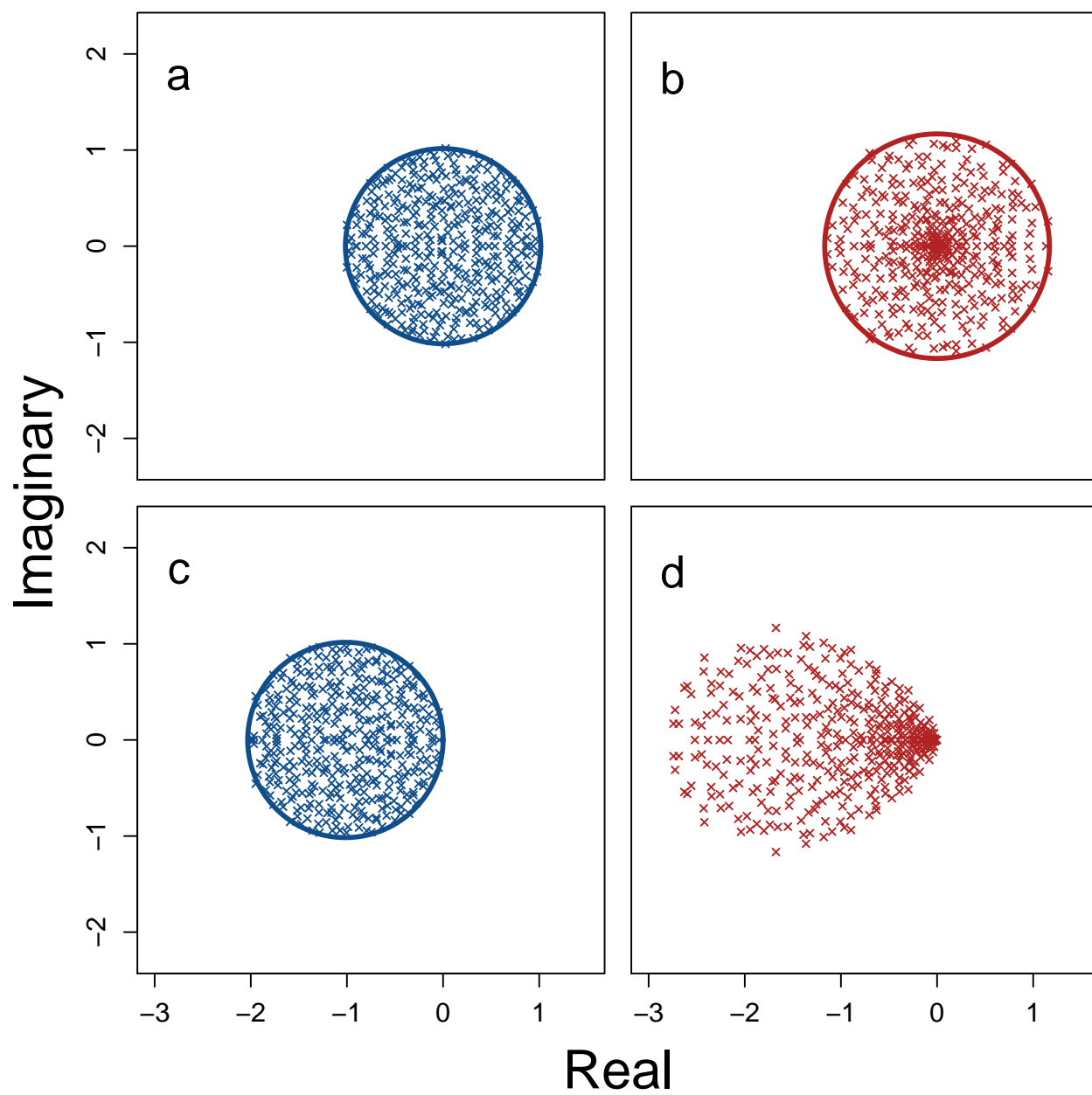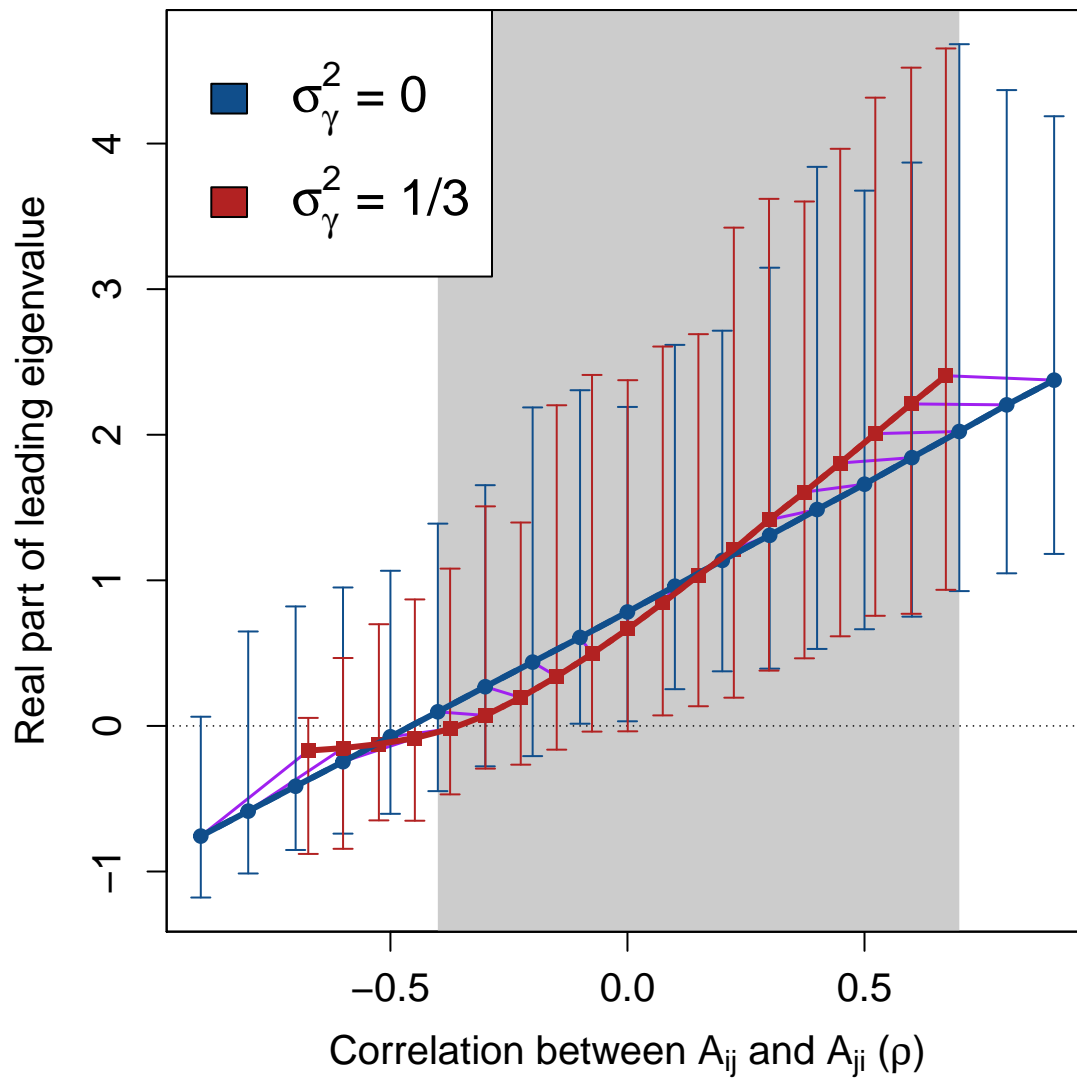
Figure 2: Complex system correlation versus stability with and without variation in component

response rates. Each point represents 10000 replicate numerical simulations of a random complex system

$\mathbf{M} = \gamma \mathbf{A}$ with a fixed correlation between off-diagonal elements A_{ij} and A_{ji} (ρ, x-axis). Where real parts

of eigenvalues of $\mathbf{M}$ are negative (y-axis), $\mathbf{M}$ is stable (black dotted line). Blue circles show systems in the

absence of variation in component response rates ($\sigma_\gamma^2 = 0$). Red squares show systems in which $\sigma_\gamma^2 = 1/3$.

Arrows show the range of real parts of leading eigenvalues observed. Because γ decreases the magnitude of ρ,

purple lines are included to link replicate simulations before (blue circles) and after (red squares) including γ.

The range of ρ values in which γ decreases the mean real part of the leading eigenvalue is indicated with

grey shading. In all simulations, system size and connectence were set to $S = 25$ and $C = 1$, respectively.

Off-diagonal elements of $\mathbf{A}$ were randomly sampled from $A_{ij} \sim \mathcal{N}(0, 0.4)$, and diagonal elements were set to

-1. Elements of γ were sampled, $\gamma_i \sim \mathcal{U}(0, 2)$.

Figure 3: System correlation versus stability across different system sizes. In each panel, 10000

random complex systems $\mathbf{M} = \gamma\mathbf{A}$ are simulated for each correlation $\rho = \{-0.90, -0.85, ..., 0.85, 0.90\}$

between off-diagonal elements A_{ij} and A_{ji}. Lines show the expected real part of the leading eigenvalues

of $\mathbf{M}$ (red squares; $\sigma_\gamma^2 = 1/3$) versus $\mathbf{A}$ (blue circles; $\sigma_\gamma^2 = 0$) across ρ, where negative values (below the

dotted black line) indicate system stability. Differences between lines thereby show the effect of component

response rate variation (γ) on system stability across system correlations and sizes (S). For all simulations,

system connectance was $C = 1$. Off-diagonal elements of $\mathbf{A}$ were randomly sampled from $A_{ij} \sim \mathcal{N}(0, 0.2)$,

and diagonal elements were set to -1. Elements of γ were sampled such that $\gamma_i \sim \mathcal{U}(0, 2)$, so $\sigma_\gamma^2 = 1/3$.
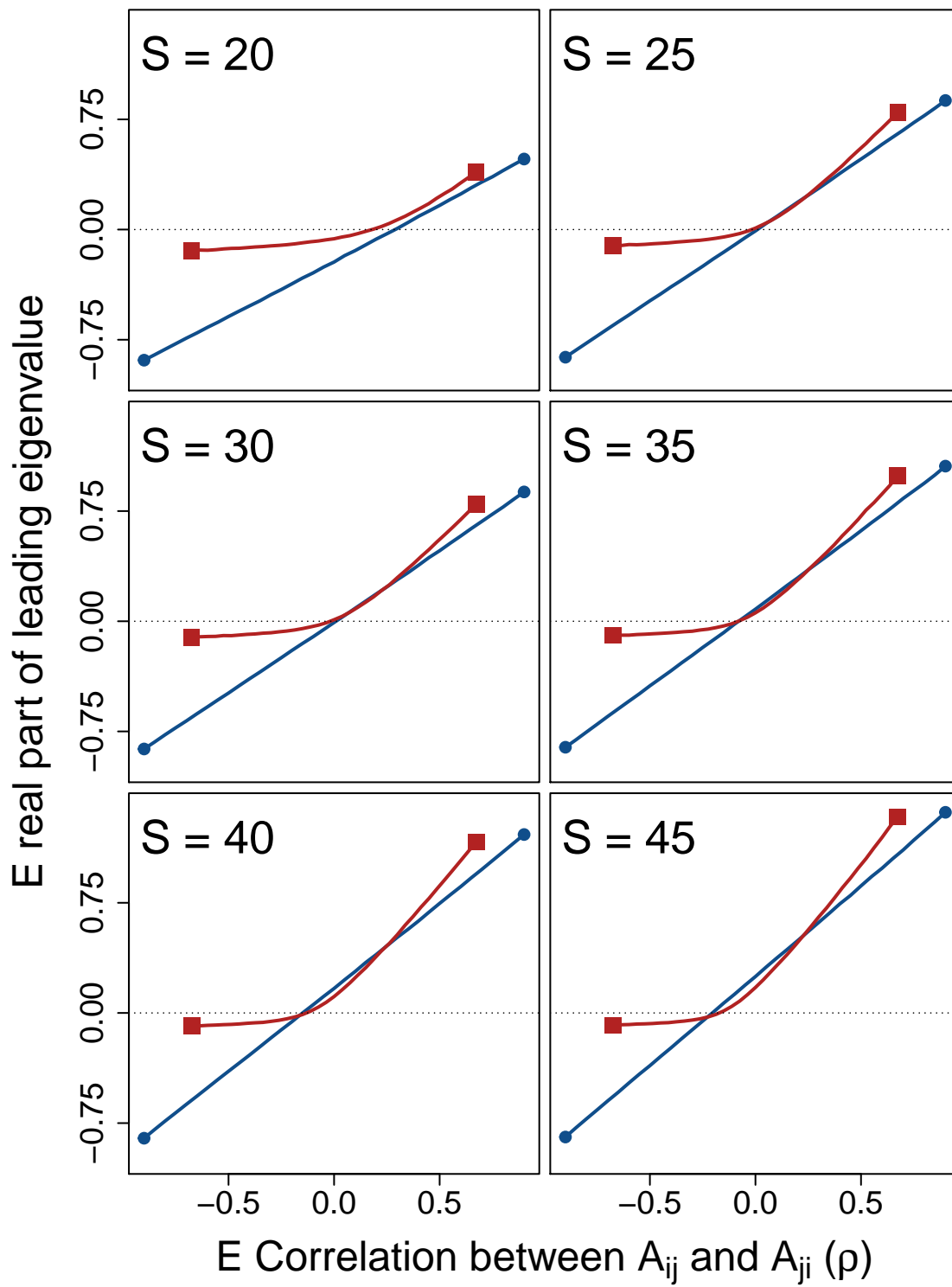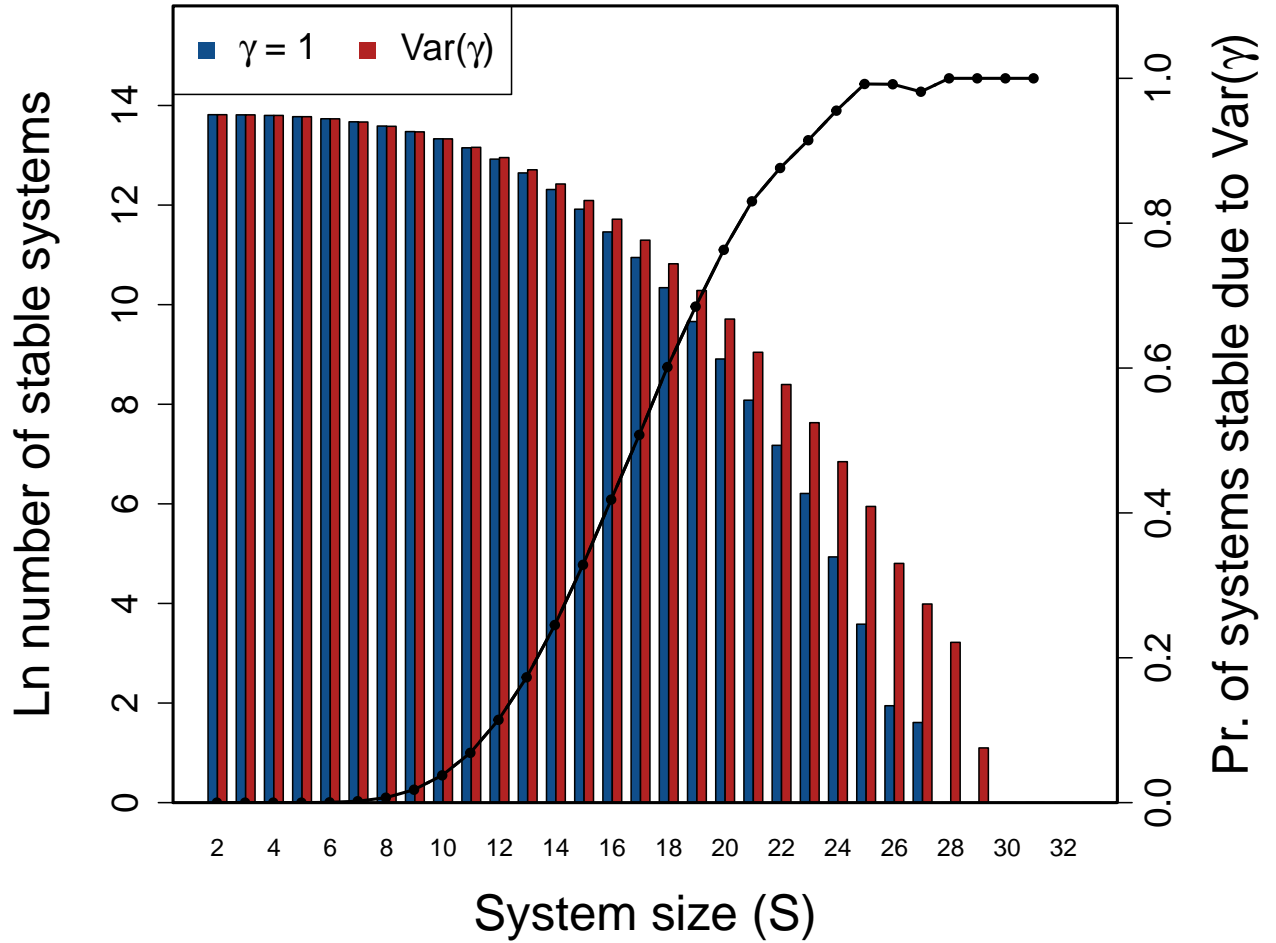
Figure 4: Stability of large complex systems with and without variation in component response

rate (γ). The ln number of systems that are stable across different system sizes ($S = \{2, 3, ..., 49, 50\}$) 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 $\sigma_\gamma^2 > 0$ 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 σ_γ^2, respectively. The black line shows the proportion of systems that

are stable when $\sigma_\gamma^2 > 0$, but would be unstable if $\sigma_\gamma^2 = 0$.

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