

Component response rate variation underlies the stability of complex systems

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

In 1972, May¹ first demonstrated that randomly assembled systems of sufficient complexity are almost inevitably unstable given infinitesimally small perturbations. Complexity in this case is defined by the size of the system (i.e., the number of potentially interacting components; S), its connectance (i.e., the probability that one component will interact with another; C), and the variance of interaction strengths (σ^2)². May's finding that the probability of local stability falls to near zero given a sufficiently high threshold of $\sigma\sqrt{SC}$ is broadly relevant for understanding the dynamics and persistence of systems such as ecological¹⁻⁵, neurological^{6,7}, biochemical^{8,9}, and socio-economic¹⁰⁻¹³ networks. As such, identifying general principles that affect stability in complex systems is of wide-ranging importance.

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

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

Results

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

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

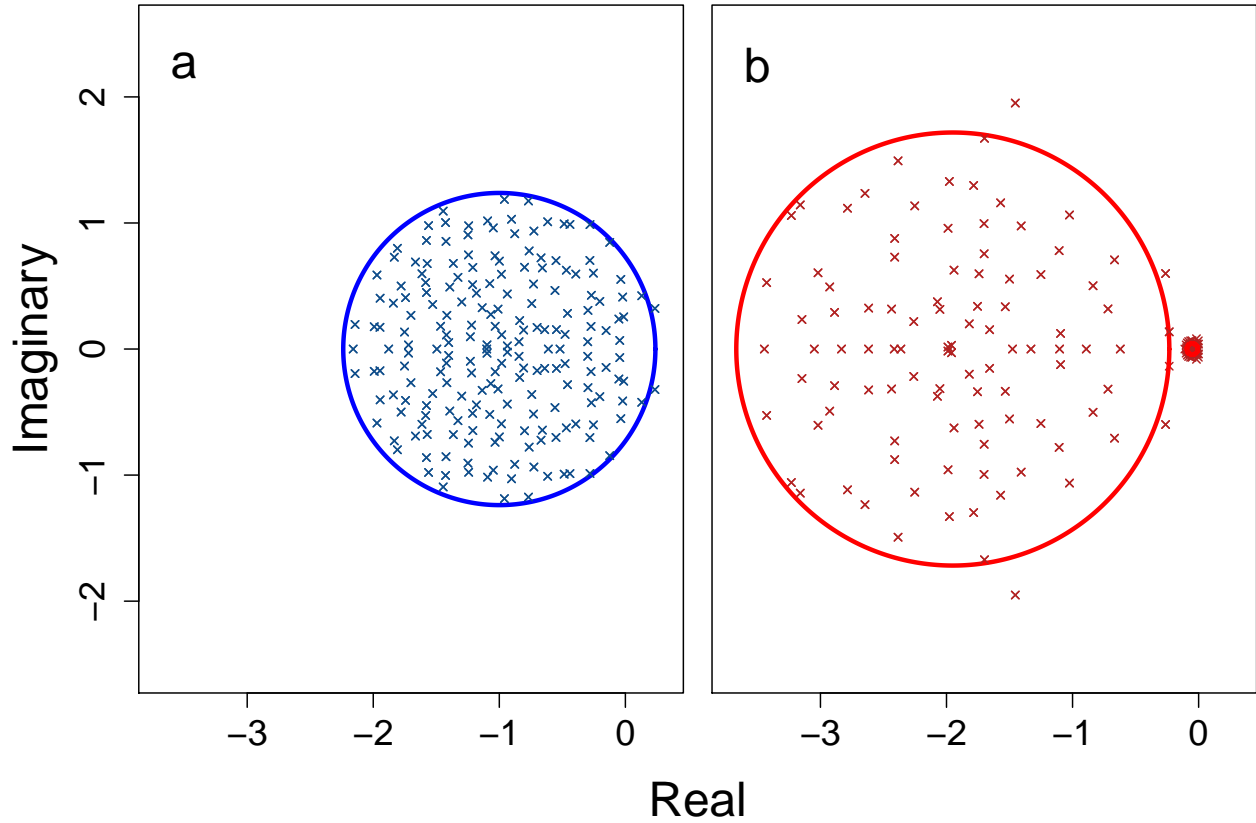
Simulation of random \mathbf{M} across S . To investigate the effect of $Var(\gamma)$ on stability across systems of varying complexity, I simulated random \mathbf{M} matrices at $\sigma = 0.4$ and $C = 1$ across $S = \{2, 3, \dots, 49, 50\}$. One million \mathbf{M} were simulated for each S , and the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

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

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

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

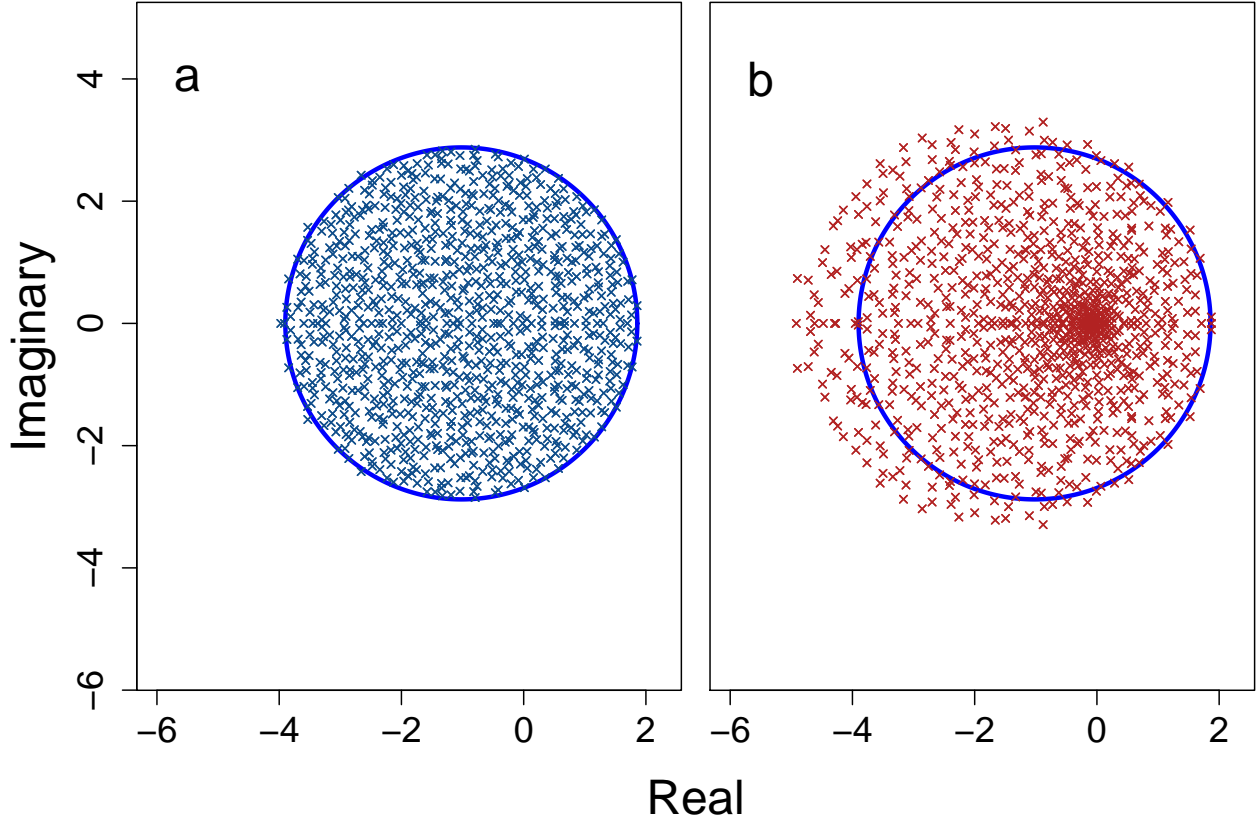
Figure 1: Example distribution of eigenvalues before (a) and after (b) separating a randomly generated complex system into fast ($\gamma = 1.95$) and slow ($\gamma = 0.05$) component response rates. Each panel shows the same system where $S = 200$, $C = 0.05$, and $\sigma = 0.4$, and in each case $E[\gamma]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



Discussion

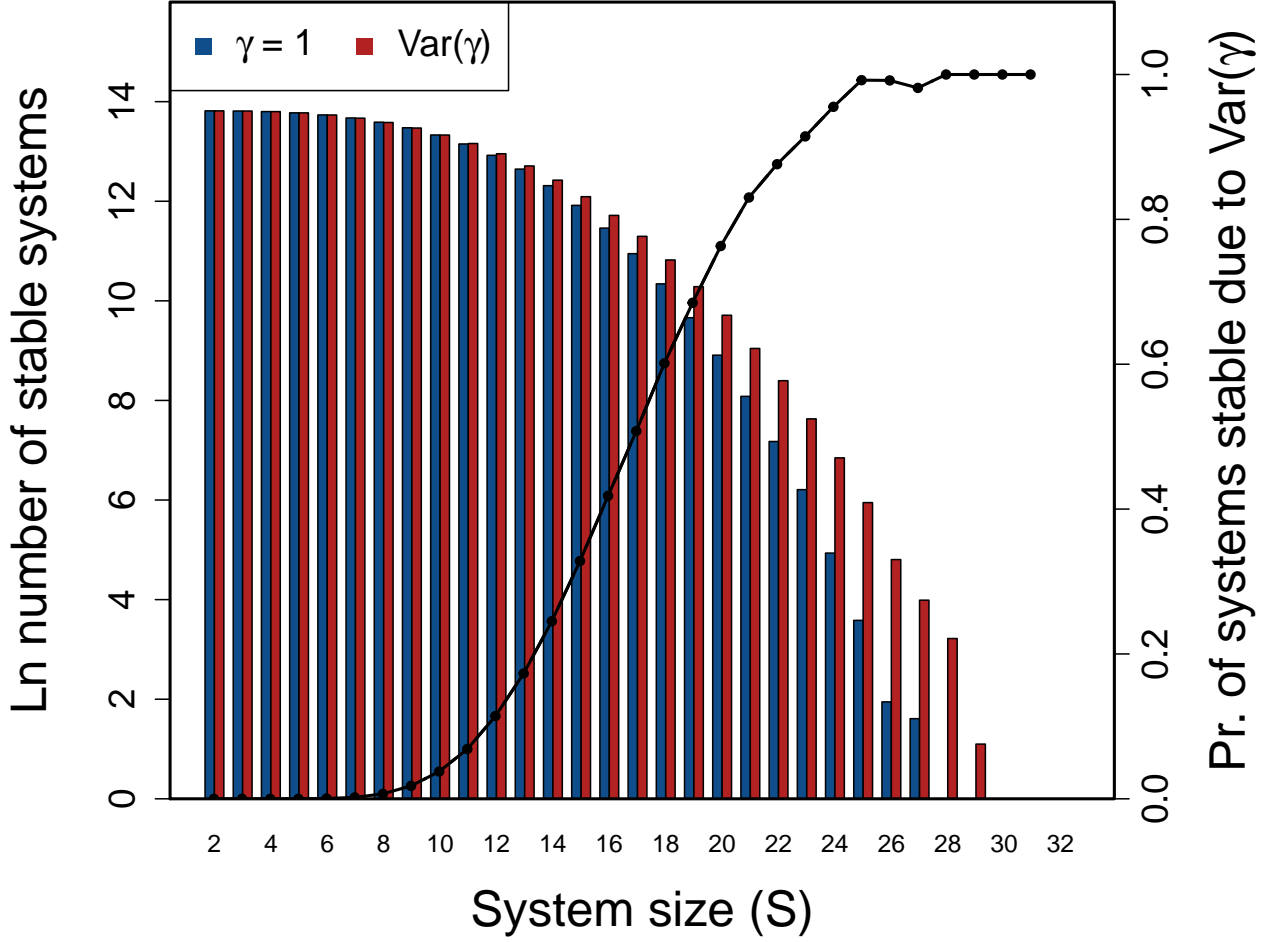
I have shown that the stability of complex systems might often be contingent upon variation in the response rates of their individual components, meaning that factors such as rate of trait evolution (in biological networks), transaction speed (in economic networks), or communication speed (in social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

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



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

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

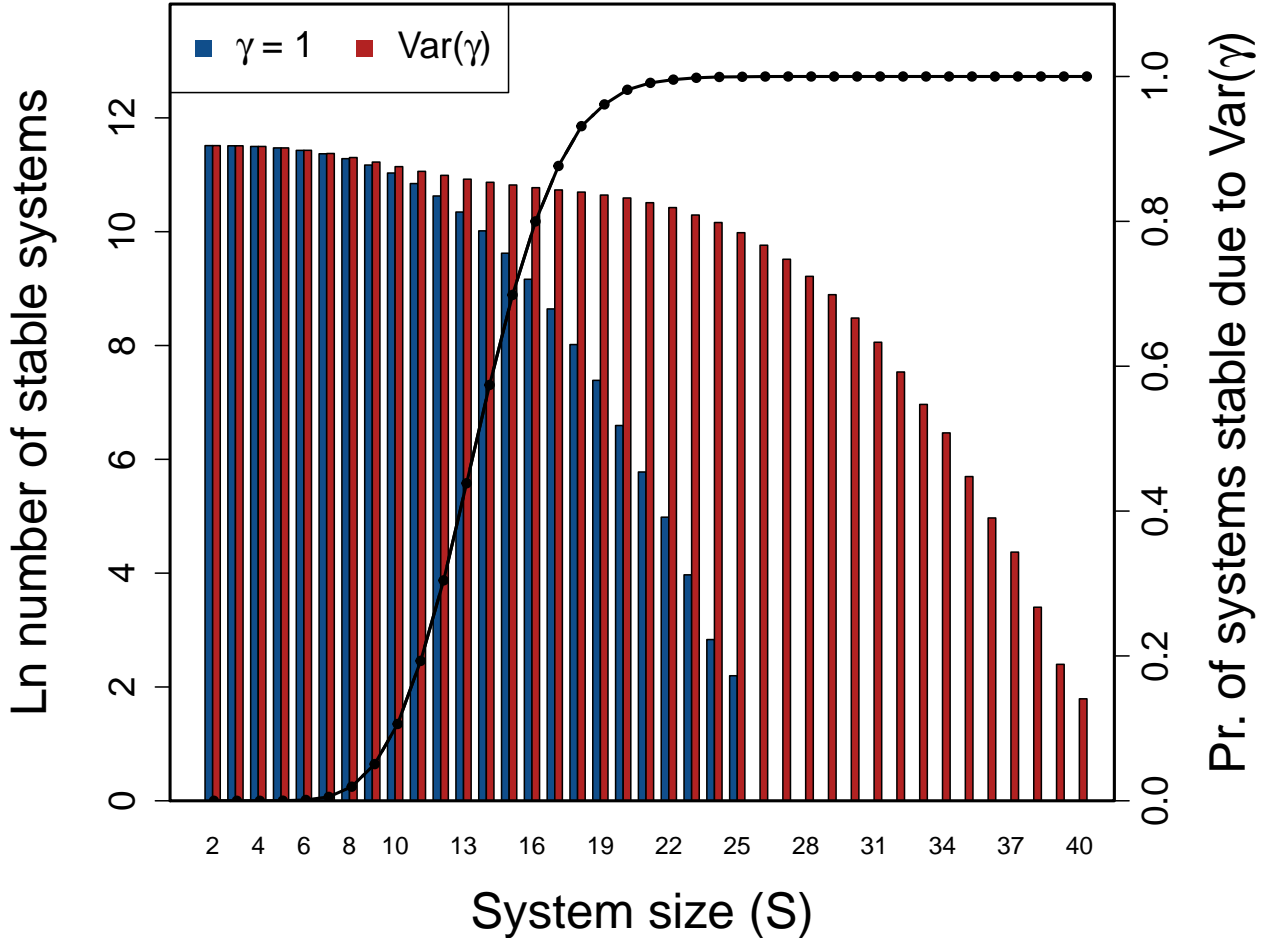


My focus is distinct from Gibbs et al.¹⁷, who applied the same mathematical framework to investigate how a diagonal matrix \mathbf{X} (equivalent to γ in my model) affects the stability of a community matrix \mathbf{M} given an interaction matrix \mathbf{A} within a generalised Lotka-Volterra model, where $\mathbf{M} = \mathbf{XA}$. Gibbs et al.¹⁷ analytically demonstrated that the effect of \mathbf{X} on system stability decreases exponentially as system size becomes arbitrarily large ($S \rightarrow \infty$). 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, $\sigma\sqrt{SC}$ (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.

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



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

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

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

Methods

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

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

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

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

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

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

In matrix notation²³,

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

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

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

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

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

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

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

In the above, \mathbf{n}^* is the vector of species densities at equilibrium. Feasibility is satisfied if all elements in \mathbf{n}^* are positive. The matrix \mathbf{I} is the identity matrix, and the value θ is the strength of intraspecific competition (diagonal elements). Diagonal values are set to -1 , so $\theta = -1$. The variable δ is a normalisation parameter that modulates the strength of interactions (σ) for \mathbf{J} . Implicitly, here $\delta = 0$ underlying strong interactions. Hence, $(CS)^{-\delta} = 1$, so in the above, a diagonal matrix of -1 s ($\theta\mathbf{I}$) is added to \mathbf{J} , which has a diagonal of all zeros and an off-diagonal affecting species interactions (i.e., the expression $(CS)^{-\delta}$ relates to May's¹ stability criterion²⁰ by $\frac{\sigma}{(CS)^{-\delta}}\sqrt{SC} < 1$, and hence for my purposes $(CS)^{-\delta} = 1$). Given $\mathbf{A} = \theta\mathbf{I} + \mathbf{J}$, the above criteria is therefore reduced to the below (see also²²),

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

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

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

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

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

The code below installs the `RandomMatrixStability` package using `devtools`.

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

While downloading this package is recommended, all relevant code is also reproduced below with explanation, so it is possible to recreate all analyses using only this Supplementary Information.

Supplementary Information table of contents

- [Further explanation of \$\gamma\$](#)
- [Code and simulations underlying Fig. 1](#)
- [Code and simulations underlying Fig. 2](#)
- [Stability across increasing \$S\$](#)
- [Stability of ecological networks](#)
 - [Competitor networks](#)
 - [Mutualist networks](#)
 - [Predator-prey networks](#)
- [Different connectance \(\$C\$ \) values](#)
 - $C = 0.3$
 - $C = 0.5$
 - $C = 0.7$
 - $C = 0.9$
- [Different distributions of \$\gamma\$](#)
- [Genetic algorithm](#)
- [Feasibility of complex systems](#)

Further explanation of γ

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

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

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 densities¹, 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 evolution¹.

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^{2,3}, 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 (m_{ij}), and by i 's response rate (γ_i),

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

In matrix notation³,

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

In the above, γ is a diagonal matrix in which elements correspond to individual component response rates. Therefore, $\gamma \mathbf{M}$ modulates the values of components and can be analysed using the techniques of May^{2,3}.

Code and simulations underlying Fig. 1

The sample M used for the eigenvalue distributions in Fig. 1 of the text is available on [GitHub](#), and was produced by running the following function.

```
find_bgamma <- function(S = 200, C = 0.05, Osd = 0.4, iters = 10000){
  while(iters > 0){
    A_dat <- rnorm(n = S * S, mean = 0, sd = Osd);
    A_mat <- matrix(data = A_dat, nrow = S);
    C_dat <- rbinom(n = S * S, size = 1, prob = C);
    C_mat <- matrix(data = C_dat, nrow = S, ncol = S);
    A_mat <- A_mat * C_mat;
    gammas <- c(rep(1.95, S/2), rep(0.05, S/2))
    mu_gam <- mean(gammas);
    diag(A_mat) <- -1;
    A1 <- gammas * A_mat;
    A0 <- mu_gam * A_mat;
    A0_e <- eigen(A0)$values;
    A0_r <- Re(A0_e);
    A0_i <- Im(A0_e);
    A1_e <- eigen(A1)$values;
    A1_r <- Re(A1_e);
    A1_i <- Im(A1_e);
    if(max(A0_r) >= 0 & max(A1_r) < 0){
```

```

        return(list(A0 = A0, A1 = A1));
      break;
    }
    print(its);
    its <- its - 1;
  }
}

```

The above `find_bgamma` function terminates when a matrix M is found that is not stable when all component response rates are set to $\gamma = 1$, but is stable when half of component response rates are 1.95 and half are 0.05. The function is used to illustrate the concept of how fast versus slow component responses can cause a system to become stable. Simulations were run for `iter = 1000000`, but terminated once an acceptable $A0$ and $A1$ were found. The code below plots the eigenvalue distributions of $A0$ and $A1$ in panels **a** and **b**, respectively. The plot itself can be recreated with the function and code below.

```

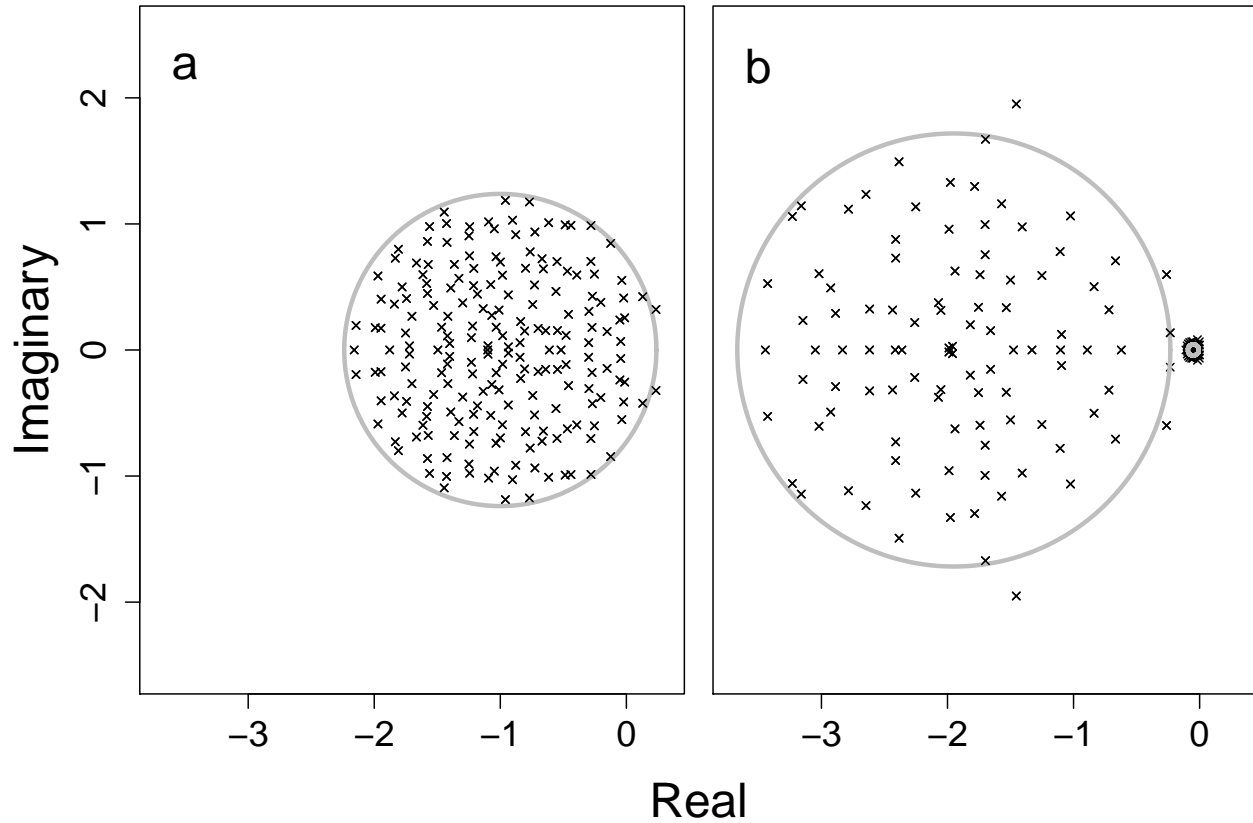
A0 <- as.matrix(A0[, -1]);
A1 <- as.matrix(A1[, -1]);
plot_Fig_1 <- function(A0, A1){
  S_val <- dim(A0)[1];
  A0_e <- eigen(A0)$values;
  A0_r <- Re(A0_e);
  A0_i <- Im(A0_e);
  A1_e <- eigen(A1)$values;
  A1_r <- Re(A1_e);
  A1_i <- Im(A1_e);
  A0_vm <- A0;
  diag(A0_vm) <- NA;
  A0vec <- as.vector(t(A0_vm));
  A0vec <- A0vec[is.na(A0vec) == FALSE];
  A1_vm <- A1;
  diag(A1_vm) <- NA;
  A1vec <- as.vector(t(A1_vm));
  A1vec <- A1vec[is.na(A1vec) == FALSE];
  fhalf <- 1:(0.5*length(A1vec));
  shalf <- (0.5*length(A1vec)+1):length(A1vec);
  par(mfrow = c(1, 2), mar = c(0.5, 0.5, 0.5, 0.5), oma = c(5, 5, 0, 0));
  plot(A0_r, A0_i, xlim = c(-3.7, 0.3), ylim = c(-2, 2), pch = 4, cex = 0.7,
       xlab = "", ylab = "", cex.lab = 1.5, cex.axis = 1.5, asp = 1);
  vl <- seq(from = 0, to = 2*pi, by = 0.001);
  A0x0 <- sqrt(S_val) * sd(A0vec) * cos(vl) + mean(diag(A0));
  A0y0 <- sqrt(S_val) * sd(A0vec) * sin(vl);
  text(x = -3.5, y = 2.25, labels = "a", cex = 2);
  points(x = A0x0, y = A0y0, type = "l", lwd = 3, col = "grey");
  points(A0_r, A0_i, pch = 4, cex = 0.7);
  plot(A1_r, A1_i, xlim = c(-3.7, 0.3), ylim = c(-2, 2), pch = 4, cex = 0.7,
       xlab = "", ylab = "", cex.lab = 1.5, cex.axis = 1.5, asp = 1,
       col = "black", yaxt = "n");
  vl <- seq(from = 0, to = 2*pi, by = 0.001);
  A0x1a <- sqrt(0.5*S_val) * sd(A1vec[fhalf]) * cos(vl) + mean(diag(A1)[1:(0.5*S_val)]);
  A0y1a <- sqrt(S_val) * sd(A1vec[fhalf]) * sin(vl);
  points(x = A0x1a, y = A0y1a, type = "l", lwd = 3, col = "grey");
  A0x1b <- sqrt(0.5*S_val) * sd(A1vec[shalf]) * cos(vl) +
    mean( diag(A1)[( 0.5*S_val) + 1 ):S_val );
  A0y1b <- sqrt(0.5*S_val) * sd(A1vec[shalf]) * sin(vl);

```

```

points(x = A0x1b, y = A0y1b, type = "l", lwd = 3, col = "grey");
points(A1_r[1:S_val], A1_i[1:S_val], pch = 4, cex = 0.7);
text(x = -3.5, y = 2.25, labels = "b", cex = 2);
mtext(side = 1, "Real", outer = TRUE, line = 3, cex = 2);
mtext(side = 2, "Imaginary", outer = TRUE, line = 2.5, cex = 2);
}
plot_Fig_1(A0 = A0, A1 = A1);

```



To find out how frequently M was stable given that all $\gamma = 1$ versus $\gamma = \{1.95, 0.05\}$, the function below was created.

```

stab_bgamma <- function(S = 200, C = 0.05, Osd = 0.4, iters = 10000){
  res <- matrix(data = 0, nrow = iters, ncol = 2);
  A0_count <- 0;
  A1_count <- 0;
  while(iters > 0){
    A_dat <- rnorm(n = S * S, mean = 0, sd = Osd);
    A_mat <- matrix(data = A_dat, nrow = S);
    C_dat <- rbinom(n = S * S, size = 1, prob = C);
    C_mat <- matrix(data = C_dat, nrow = S, ncol = S);
    A_mat <- A_mat * C_mat;
    gammas <- c(rep(1.95, S/2), rep(0.05, S/2))
    mu_gam <- mean(gammas);
    diag(A_mat) <- -1;
    A1 <- gammas * A_mat;
    A0 <- mu_gam * A_mat;
    A0_e <- eigen(A0)$values;
    A0_r <- Re(A0_e);
  }
}

```

```

    A0_i  <- Im(A0_e);
    A1_e  <- eigen(A1)$values;
    A1_r  <- Re(A1_e);
    A1_i  <- Im(A1_e);
    if(max(A0_r) < 0){
      res[s, 1] <- 1;
      A0_count  <- A0_count + 1;
    }
    if(max(A1_r) < 0){
      res[s, 2] <- 1;
      A1_count  <- A1_count + 1;
    }
    print(c(s, A0_count, A1_count));
    s <- s + 1;
  }
  return(res);
}

```

The above functions produced the `bi_pr_st` data.

```

bi_pr_st <- read.csv("sim_results/bi_gamma/bi_pr_st.csv");
pr_st    <- bi_pr_st[, -1];

```

The function `stab_bgamma` was run for `iters = 1000000`, and the resulting matrix `ress` was returned. Each row of `ress` represents a single M given $\gamma = 1$ (column 1) versus $\gamma = \{1.95, 0.05\}$ (column 2). Values of 0 indicate that M was found to be unstable (at least one real component of its eigenvalues greater than or equal to zero), whereas values of 1 indicate that M was found to be stable (all real components of eigenvalues are negative). The frequencies of stable M were 1 given $\gamma = 1$ and 32 given $\gamma = \{1.95, 0.05\}$, as reported in the main text and legend of Fig. 1 (raw data are [available on GitHub](#)).

Code and simulations underlying Fig. 2

Figure 2 of the main text shows eigenvalue distributions in a system where $S = 1000$, $C = 1$, and $\sigma = 0.4$. Eigenvalues can be reproduced using the code below for when $\gamma = 1$ (panel a) and $\gamma \sim \mathcal{U}(0, 2)$ (panel b). The function below reproduces the figure.

```

plot_Fig_2 <- function(){
  A_comp <- NULL;
  A_dat <- rnorm(n = 1000000, mean = 0, sd = 0.4);
  A_mat <- matrix(data = A_dat, nrow = 1000);
  C_dat <- rbinom(n = 1000 * 1000, size = 1, prob = 1);
  C_mat <- matrix(data = C_dat, nrow = 1000, ncol = 1000);
  A_mat <- A_mat * C_mat;
  gammas <- runif(n = 1000, min = 0, max = 2);
  mu_gam <- mean(gammas);
  diag(A_mat) <- -1;
  A1 <- gammas * A_mat;
  A0 <- mu_gam * A_mat;
  A0_e <- eigen(A0)$values;
  A0_r <- Re(A0_e);
  A0_i <- Im(A0_e);
  A1_e <- eigen(A1)$values;
  A1_r <- Re(A1_e);

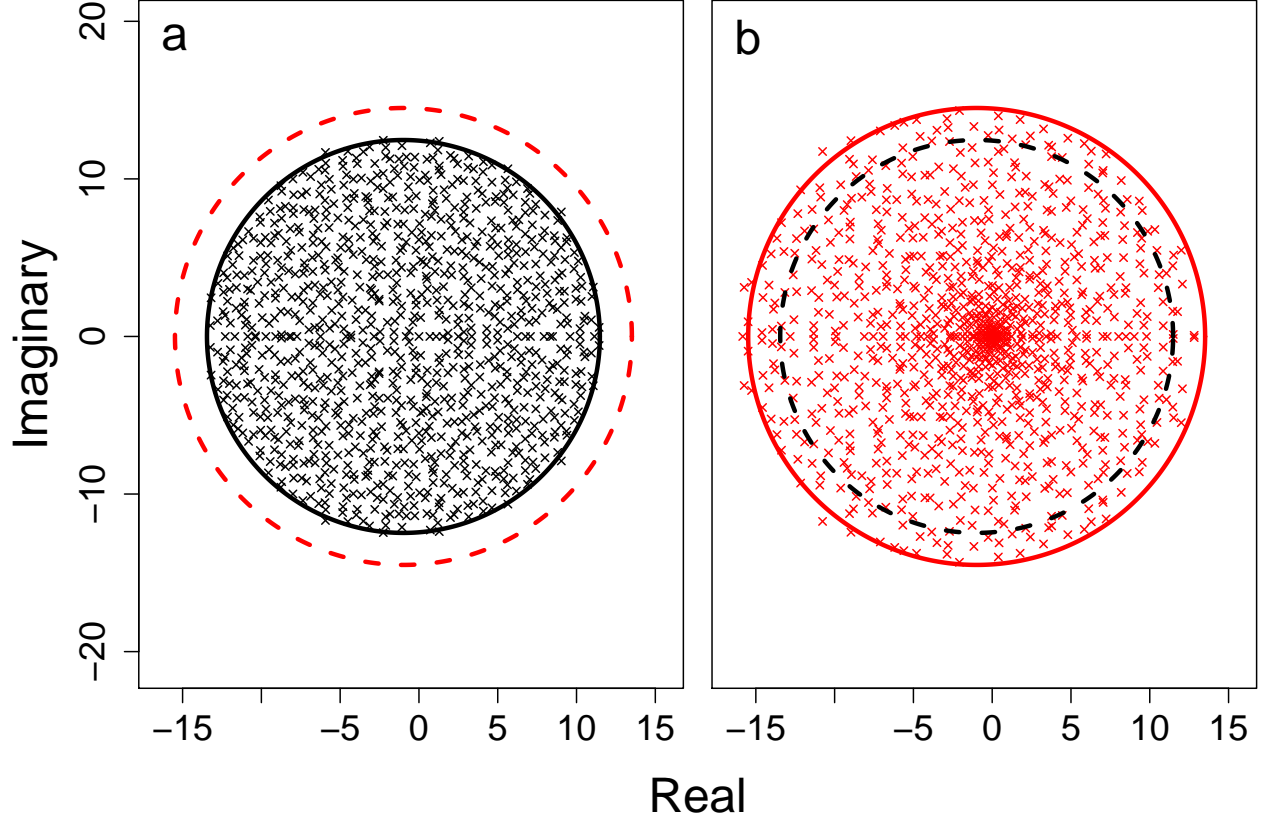
```



```

A1_i    <- Im(A1_e);
A0_vm   <- A0;
diag(A0_vm) <- NA;
A0vec   <- as.vector(A0_vm);
A0vec   <- A0vec[is.na(A0vec) == FALSE];
A1_vm   <- A1;
diag(A1_vm) <- NA;
A1vec   <- as.vector(A1_vm);
A1vec   <- A1vec[is.na(A1vec) == FALSE];
par(mfrow = c(1, 2), mar = c(0.5, 0.5, 0.5, 0.5), oma = c(5, 5, 0, 0));
plot(A0_r, A0_i, xlim = c(-16.5, 15.5), ylim = c(-16.5, 15.5), pch = 4,
     cex = 0.7, xlab = "", ylab = "", cex.lab = 1.5, cex.axis = 1.5,
     asp = 1);
v1 <- seq(from = 0, to = 2*pi, by = 0.001);
x0 <- sqrt(1000) * sd(A0vec) * cos(v1) + mean(diag(A0));
y0 <- sqrt(1000) * sd(A0vec) * sin(v1);
x1 <- sqrt(1000) * sd(A1vec) * cos(v1) + mean(diag(A1));
y1 <- sqrt(1000) * sd(A1vec) * sin(v1);
text(x = -15.5, y = 19, labels = "a", cex = 2);
points(x = x0, y = y0, type = "l", lwd = 3);
points(x = x1, y = y1, type = "l", col = "red", lwd = 3, lty = "dashed");
plot(A1_r, A1_i, xlim = c(-16.5, 15.5), ylim = c(-16.5, 15.5), pch = 4, cex = 0.7,
     xlab = "", ylab = "", cex.lab = 1.5, cex.axis = 1.5, asp = 1, col = "red",
     yaxt = "n");
text(x = -15.5, y = 19, labels = "b", cex = 2);
points(x = x1, y = y1, type = "l", col = "red", lwd = 3)
points(x = x0, y = y0, type = "l", lwd = 3, lty = "dashed");
mtext(side = 1, "Real", outer = TRUE, line = 3, cex = 2);
mtext(side = 2, "Imaginary", outer = TRUE, line = 2.5, cex = 2);
}
plot_Fig_2();

```



Stability across increasing S

Figure 3 of the main text reports the number of stable random complex systems found over 1 million iterations. The data used to make this figure are read into R below.

```
dat <- read.csv(file = "sim_results/C_1/random_all.csv");
dat <- dat[,-1]; # Extra row-indicating column removed
```

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

S	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	293	999707	293	999707	0	0
3	3602	996398	3609	996391	0	7
4	14937	985063	15008	984992	0	71
5	39289	960711	39783	960217	36	530
6	78845	921155	80207	919793	389	1751
7	133764	866236	136904	863096	1679	4819
8	204112	795888	208241	791759	5391	9520
9	288041	711959	291775	708225	12619	16353

S	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
10	384024	615976	384931	615069	23153	24060
11	485975	514025	481019	518981	35681	30725
12	590453	409547	577439	422561	48302	35288
13	689643	310357	669440	330560	57194	36991
14	777496	222504	751433	248567	60959	34896
15	850159	149841	821613	178387	58567	30021
16	905057	94943	877481	122519	51255	23679
17	943192	56808	919536	80464	40854	17198
18	969018	30982	949944	50056	30102	11028
19	984301	15699	970703	29297	20065	6467
20	992601	7399	983507	16493	12587	3493
21	996765	3235	991532	8468	7030	1797
22	998693	1307	995567	4433	3884	758
23	999503	497	997941	2059	1883	321
24	999861	139	999059	941	899	97
25	999964	36	999617	383	380	33
26	999993	7	999878	122	121	6
27	999995	5	999946	54	53	4
28	1000000	0	999975	25	25	0
29	1000000	0	999997	3	3	0
30	1000000	0	999999	1	1	0
31	1000000	0	999999	1	1	0
32	1000000	0	1000000	0	0	0
33	1000000	0	1000000	0	0	0
34	1000000	0	1000000	0	0	0
35	1000000	0	1000000	0	0	0
36	1000000	0	1000000	0	0	0
37	1000000	0	1000000	0	0	0
38	1000000	0	1000000	0	0	0
39	1000000	0	1000000	0	0	0
40	1000000	0	1000000	0	0	0
41	1000000	0	1000000	0	0	0
42	1000000	0	1000000	0	0	0
43	1000000	0	1000000	0	0	0
44	1000000	0	1000000	0	0	0
45	1000000	0	1000000	0	0	0
46	1000000	0	1000000	0	0	0
47	1000000	0	1000000	0	0	0
48	1000000	0	1000000	0	0	0
49	1000000	0	1000000	0	0	0
50	1000000	0	1000000	0	0	0

Overall, the ratio of stable **A1** matrices to stable **A0** matrices found is greater than 1 (compare column 5 to column 3), and this ratio increases with increasing S (column 1). Hence, more randomly created complex systems (M) are generated given variation in γ than when $\gamma = 1$. The results underlying this table were produced with the `rand_gen_var` function below.

```
rand_gen_var <- function(max_sp, iters, int_type = 0, rmx = 0.4, C = 1){
  tot_res <- NULL;
  fea_res <- NULL;
  for(i in 2:max_sp){
    iter      <- iters;
```

```

tot_res[[i-1]] <- matrix(data = 0, nrow = iter, ncol = 7);
fea_res[[i-1]] <- matrix(data = 0, nrow = iter, ncol = 7);
while(iter > 0){
  r_vec    <- rnorm(n = i, mean = 0, sd = rmx);
  A0_dat   <- rnorm(n = i * i, mean = 0, sd = 0.4);
  A0       <- matrix(data = A0_dat, nrow = i, ncol = i);
  A0       <- species_interactions(mat = A0, type = int_type);
  C_dat    <- rbinom(n = i * i, size = 1, prob = C);
  C_mat    <- matrix(data = C_dat, nrow = i, ncol = i);
  A0       <- A0 * C_mat;
  diag(A0) <- -1;
  gam1     <- runif(n = i, min = 0, max = 2);
  A1       <- A0 * gam1;
  A0       <- A0 * mean(gam1);
  A0_stb   <- max(Re(eigen(A0)$values)) < 0;
  A1_stb   <- max(Re(eigen(A1)$values)) < 0;
  A0_fea   <- min(-1*solve(A0) %*% r_vec) > 0;
  A1_fea   <- min(-1*solve(A1) %*% r_vec) > 0;
  if(A0_stb == TRUE){
    tot_res[[i-1]][iter, 1] <- 1;
  }
  if(A1_stb == TRUE){
    tot_res[[i-1]][iter, 2] <- 1;
  }
  if(A0_fea == TRUE){
    fea_res[[i-1]][iter, 1] <- 1;
  }
  if(A1_fea == TRUE){
    fea_res[[i-1]][iter, 2] <- 1;
  }
  iter    <- iter - 1;
}
print(i);
}
all_res <- summarise_randmat(tot_res = tot_res, fea_res = fea_res);
return(all_res);
}

```

The above function calls the two functions `species_interactions` and `summarise_randmat`, which are provided below.

```

species_interactions <- function(mat, type = 0){
  if(type == 1){
    mat[mat > 0] <- -1*mat[mat > 0];
  }
  if(type == 2){
    mat[mat < 0] <- -1*mat[mat < 0];
  }
  if(type == 3){
    for(i in 1:dim(mat)[1]){
      for(j in 1:dim(mat)[2]){
        if(mat[i, j] * mat[j, i] > 0){
          mat[j, i] <- -1 * mat[j, i];
        }
      }
    }
  }
}

```

```

    }
  }
}
return(mat);
}

summarise_randmat <- function(tot_res, fea_res){
  sims <- length(tot_res);
  all_res <- matrix(data = 0, nrow = sims, ncol = 13);
  for(i in 1:sims){
    all_res[i, 1] <- i + 1;
    # Stable and unstable
    all_res[i, 2] <- sum(tot_res[[i]][,1] == FALSE);
    all_res[i, 3] <- sum(tot_res[[i]][,1] == TRUE);
    all_res[i, 4] <- sum(tot_res[[i]][,2] == FALSE);
    all_res[i, 5] <- sum(tot_res[[i]][,2] == TRUE);
    # Stabilised and destabilised
    all_res[i, 6] <- sum(tot_res[[i]][,1] == FALSE &
                        tot_res[[i]][,2] == TRUE);
    all_res[i, 7] <- sum(tot_res[[i]][,1] == TRUE &
                        tot_res[[i]][,2] == FALSE);
    # Feasible and infeasible
    all_res[i, 8] <- sum(fea_res[[i]][,1] == FALSE);
    all_res[i, 9] <- sum(fea_res[[i]][,1] == TRUE);
    all_res[i, 10] <- sum(fea_res[[i]][,2] == FALSE);
    all_res[i, 11] <- sum(fea_res[[i]][,2] == TRUE);
    # Feased and defeased
    all_res[i, 12] <- sum(fea_res[[i]][,1] == FALSE &
                        fea_res[[i]][,2] == TRUE);
    all_res[i, 13] <- sum(fea_res[[i]][,1] == TRUE &
                        fea_res[[i]][,2] == FALSE);
  }
  cnames <- c("N", "A0_unstable", "A0_stable", "A1_unstable", "A1_stable",
              "A1_stabilised", "A1_destabilised", "A0_infeasible",
              "A0_feasible", "A1_infeasible", "A1_feasible",
              "A1_made_feasible", "A1_made_infeasible");
  colnames(all_res) <- cnames;
  return(all_res);
}

```

Note that feasibility results were omitted for the table above, but are [reported below](#).

Stability of ecological networks

While the foundational work of May¹ applies broadly to complex networks, much attention has been given specifically to ecological networks of interacting species. In these networks, the matrix M is interpreted as a community matrix and each row and column is interpreted as a single species. The effect that the density of any species i has on the population dynamics of species j is found in M_{ij} , meaning that M holds the effects of pair-wise interactions between S species²⁻⁴. While May's original work¹ considered only randomly assembled communities, recent work has specifically looked at more restricted ecological communities including competitive networks (all off-diagonal elements of M are negative), mutualist networks (all off-diagonal elements of M are positive), and predator-prey networks (for any pair of i and j , the effect of

i on j is negative and j on i is positive, or vice versa)²⁻⁵. In general, competitor and mutualist networks tend to be unstable, while predator-prey networks tend to be highly stabilising.

I investigated competitor, mutualist, and predator-prey networks following Allesina et al.². To create these networks, I first generated a random matrix M , then changed the elements of M accordingly. If M was a competitive network, then the sign of any positive off-diagonal elements was reversed to be negative. If M was a mutualist network, then the sign of any positive off-diagonal elements was reversed to be positive. And if M was a predator-prey network, then all i and j pairs of elements were checked; any pairs of the same sign were changed so that one was negative and the other was positive. The `species_interaction` function used to do this is below.

```
species_interactions <- function(mat, type = 0){
  if(type == 1){
    mat[mat > 0] <- -1*mat[mat > 0];
  }
  if(type == 2){
    mat[mat < 0] <- -1*mat[mat < 0];
  }
  if(type == 3){
    for(i in 1:dim(mat)[1]){
      for(j in 1:dim(mat)[2]){
        if(mat[i, j] * mat[j, i] > 0){
          mat[j, i] <- -1 * mat[j, i];
        }
      }
    }
  }
  return(mat);
} # Note: -1 values are added in the diagonal later
```

This function was applied to all created matrices M , then the number of stable M matrices was estimated exactly as it was in the main text for random matrices for values of S from 2 to 50 (100 in the case of the relatively more stable predator-prey interactions), except that only 100000 random M were generated instead of 1 million. This produced the data set below.

```
cdata <- read.csv(file = "sim_results/ecology/competition_C_1.csv");
mdat <- read.csv(file = "sim_results/ecology/mutualism_C_1.csv");
pdat <- read.csv(file = "sim_results/ecology/pred-prey_C_1.csv");
```

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

Competition

Results for competitor interaction networks are shown below

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised
2	48	99952	48	99952	0
3	229	99771	231	99769	0

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

Mutualism

Results for mutualist interaction networks are shown below

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

Predator-prey

Results for predator-prey interaction networks are shown below

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised
2	0	100000	0	100000	0
3	0	100000	0	100000	0
4	0	100000	0	100000	0
5	1	99999	1	99999	0
6	4	99996	4	99996	0
7	2	99998	2	99998	0
8	5	99995	5	99995	0
9	20	99980	21	99979	0
10	20	99980	22	99978	0
11	38	99962	39	99961	0
12	64	99936	66	99934	0
13	87	99913	91	99909	0
14	157	99843	159	99841	0
15	215	99785	227	99773	0
16	293	99707	310	99690	0
17	383	99617	408	99592	0
18	443	99557	473	99527	3
19	642	99358	675	99325	4
20	836	99164	887	99113	7
21	1006	98994	1058	98942	10
22	1153	98847	1228	98772	20
23	1501	98499	1593	98407	30
24	1841	98159	1996	98004	40
25	2146	97854	2316	97684	58
26	2643	97357	2809	97191	119
27	3034	96966	3258	96742	158
28	3690	96310	3928	96072	201
29	4257	95743	4532	95468	290
30	4964	95036	5221	94779	424
31	5627	94373	5978	94022	452
32	6543	93457	6891	93109	666
33	7425	92575	7777	92223	818
34	8540	91460	8841	91159	1071
35	9526	90474	9842	90158	1337
36	10617	89383	10891	89109	1624
37	12344	87656	12508	87492	2021
38	13675	86325	13877	86123	2442
39	15264	84736	15349	84651	2870
40	17026	82974	17053	82947	3363
41	18768	81232	18614	81386	3905
42	20791	79209	20470	79530	4579
43	23150	76850	22754	77246	5217
44	25449	74551	24184	75816	6285
45	27702	72298	26464	73536	6754
46	30525	69475	28966	71034	7646
47	32832	67168	31125	68875	8487
48	36152	63848	33865	66135	9479
49	38714	61286	36242	63758	10125
50	41628	58372	38508	61492	11036

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised
51	44483	55517	41023	58977	11704
52	48134	51866	44287	55713	12573
53	51138	48862	46721	53279	13223
54	54261	45739	49559	50441	13757
55	57647	42353	52403	47597	14324
56	60630	39370	55293	44707	14669
57	63647	36353	57787	42213	15103
58	66961	33039	60439	39561	15450
59	69968	30032	63708	36292	15246
60	72838	27162	66270	33730	15177
61	75609	24391	68873	31127	15006
62	77999	22001	71318	28682	14538
63	80616	19384	73517	26483	14510
64	83089	16911	76209	23791	13784
65	85150	14850	78086	21914	13412
66	86908	13092	80437	19563	12477
67	88671	11329	82379	17621	11718
68	90537	9463	84483	15517	10878
69	91969	8031	86233	13767	10033
70	93181	6819	87914	12086	9070
71	94330	5670	89200	10800	8401
72	95324	4676	90833	9167	7359
73	96143	3857	91805	8195	6726
74	96959	3041	93065	6935	5900
75	97543	2457	93987	6013	5222
76	97969	2031	94900	5100	4481
77	98497	1503	95756	4244	3809
78	98744	1256	96442	3558	3269
79	99045	955	96942	3058	2837
80	99276	724	97528	2472	2329
81	99481	519	97996	2004	1894
82	99556	444	98321	1679	1597
83	99691	309	98722	1278	1227
84	99752	248	98943	1057	1015
85	99833	167	99144	856	837
86	99895	105	99346	654	642
87	99925	75	99461	539	530
88	99945	55	99566	434	428
89	99976	24	99675	325	324
90	99977	23	99756	244	243
91	99982	18	99839	161	155
92	99988	12	99865	135	135
93	99994	6	99885	115	115
94	99993	7	99911	89	88
95	99998	2	99953	47	47
96	99999	1	99965	35	35
97	99999	1	99979	21	21
98	100000	0	99973	27	27
99	100000	0	99984	16	16
100	100000	0	99989	11	11

Overall, as expected², predator-prey communities are relatively stable while mutualist communities are highly

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

Different connectance (C) values

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

All data reported below for various values of C are accessible using the below.

```
C3dat <- read.csv(file = "sim_results/C_other/rand_c-0pt3.csv");
C5dat <- read.csv(file = "sim_results/C_other/rand_c-0pt5.csv");
C7dat <- read.csv(file = "sim_results/C_other/rand_c-0pt7.csv");
C9dat <- read.csv(file = "sim_results/C_other/rand_c-0pt9.csv");
```

These objects **C3dat**, **C5dat**, **C7dat**, and **C9dat** include the results for $C = 0.3$, $C = 0.5$, $C = 0.7$, and $C = 0.9$, respectively.

Connectance $C = 0.3$

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	5	99995	5	99995	0	0
3	6	99994	6	99994	0	0
4	24	99976	24	99976	0	0
5	59	99941	59	99941	0	0
6	98	99902	98	99902	0	0
7	160	99840	161	99839	0	1
8	290	99710	293	99707	0	3
9	430	99570	434	99566	0	4
10	648	99352	653	99347	1	6
11	946	99054	957	99043	0	11
12	1392	98608	1415	98585	4	27
13	2032	97968	2065	97935	5	38
14	2627	97373	2688	97312	10	71
15	3588	96412	3647	96353	35	94
16	5019	94981	5124	94876	51	156
17	6512	93488	6673	93327	79	240
18	8444	91556	8600	91400	165	321
19	10416	89584	10667	89333	244	495
20	13254	86746	13477	86523	425	648
21	16248	83752	16481	83519	642	875
22	19497	80503	19719	80281	929	1151
23	23654	76346	23776	76224	1368	1490

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
24	28485	71515	28389	71611	1914	1818
25	32774	67226	32483	67517	2428	2137
26	38126	61874	37411	62589	3221	2506
27	43435	56565	42418	57582	3828	2811
28	49333	50667	47840	52160	4565	3072
29	55389	44611	53381	46619	5329	3321
30	60826	39174	58388	41612	5918	3480
31	66820	33180	64043	35957	6345	3568
32	72190	27810	69036	30964	6685	3531
33	77053	22947	73587	26413	6826	3360
34	81816	18184	78157	21843	6673	3014
35	85651	14349	82041	17959	6383	2773
36	88985	11015	85657	14343	5721	2393
37	92072	7928	88805	11195	5180	1913
38	94329	5671	91444	8556	4451	1566
39	95912	4088	93295	6705	3804	1187
40	97232	2768	95201	4799	2967	936
41	98179	1821	96506	3494	2356	683
42	98826	1174	97489	2511	1786	449
43	99275	725	98312	1688	1251	288
44	99583	417	98872	1128	903	192
45	99776	224	99339	661	576	139
46	99865	135	99518	482	413	66
47	99938	62	99744	256	226	32
48	99956	44	99824	176	151	19
49	99980	20	99914	86	85	19
50	99993	7	99950	50	46	3
51	99998	2	99971	29	28	1
52	99998	2	99986	14	14	2
53	99999	1	99992	8	7	0
54	100000	0	99997	3	3	0
55	100000	0	99999	1	1	0
56	100000	0	99998	2	2	0
57	100000	0	99999	1	1	0
58	100000	0	100000	0	0	0
...
100	100000	0	100000	0	0	0

Connectance $C = 0.5$

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	7	99993	7	99993	0	0
3	32	99968	32	99968	0	0
4	122	99878	122	99878	0	0
5	320	99680	321	99679	0	1
6	667	99333	673	99327	0	6
7	1233	98767	1252	98748	0	19
8	2123	97877	2156	97844	3	36
9	3415	96585	3471	96529	16	72
10	5349	94651	5450	94550	30	131
11	7990	92010	8185	91815	81	276

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
12	11073	88927	11301	88699	219	447
13	14971	85029	15204	84796	445	678
14	19754	80246	19992	80008	764	1002
15	25020	74980	25239	74761	1185	1404
16	30860	69140	30938	69062	1902	1980
17	37844	62156	37562	62438	2758	2476
18	44909	55091	44251	55749	3595	2937
19	52322	47678	51011	48989	4573	3262
20	60150	39850	58295	41705	5382	3527
21	67147	32853	64895	35105	5925	3673
22	74177	25823	71358	28642	6310	3491
23	80297	19703	77034	22966	6507	3244
24	85372	14628	82039	17961	6209	2876
25	89719	10281	86539	13461	5562	2382
26	92947	7053	90141	9859	4707	1901
27	95436	4564	92950	7050	3844	1358
28	97196	2804	95171	4829	2999	974
29	98300	1700	96842	3158	2115	657
30	99103	897	98033	1967	1466	396
31	99502	498	98665	1335	1068	231
32	99745	255	99185	815	696	136
33	99881	119	99572	428	375	66
34	99955	45	99788	212	191	24
35	99979	21	99900	100	95	16
36	99995	5	99950	50	50	5
37	99997	3	99970	30	28	1
38	99998	2	99986	14	13	1
39	99999	1	99991	9	9	1
40	100000	0	100000	0	0	0
41	100000	0	99999	1	1	0
42	100000	0	99999	1	1	0
43	100000	0	100000	0	0	0
...
50	100000	0	100000	0	0	0

Connectance $C = 0.7$

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	7	99993	7	99993	0	0
3	106	99894	106	99894	0	0
4	395	99605	397	99603	0	2
5	1117	98883	1123	98877	0	6
6	2346	97654	2367	97633	6	27
7	4314	95686	4388	95612	16	90
8	7327	92673	7456	92544	61	190
9	11514	88486	11792	88208	150	428
10	16247	83753	16584	83416	415	752
11	22481	77519	22759	77241	884	1162
12	29459	70541	29729	70271	1548	1818
13	37631	62369	37567	62433	2419	2355
14	46317	53683	45696	54304	3548	2927

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
15	54945	45055	53695	46305	4671	3421
16	63683	36317	61643	38357	5567	3527
17	72004	27996	69375	30625	6124	3495
18	79220	20780	76158	23842	6413	3351
19	85286	14714	82283	17717	5982	2979
20	90240	9760	87181	12819	5398	2339
21	93676	6324	91077	8923	4468	1869
22	96203	3797	94045	5955	3425	1267
23	97866	2134	96161	3839	2496	791
24	98842	1158	97633	2367	1713	504
25	99433	567	98630	1370	1079	276
26	99760	240	99259	741	655	154
27	99895	105	99576	424	377	58
28	99950	50	99790	210	194	34
29	99981	19	99915	85	80	14
30	99994	6	99952	48	47	5
31	99998	2	99972	28	28	2
32	99999	1	99992	8	8	1
33	100000	0	99997	3	3	0
34	100000	0	99999	1	1	0
35	100000	0	100000	0	0	0
...
50	100000	0	100000	0	0	0

Connectance $C = 0.9$

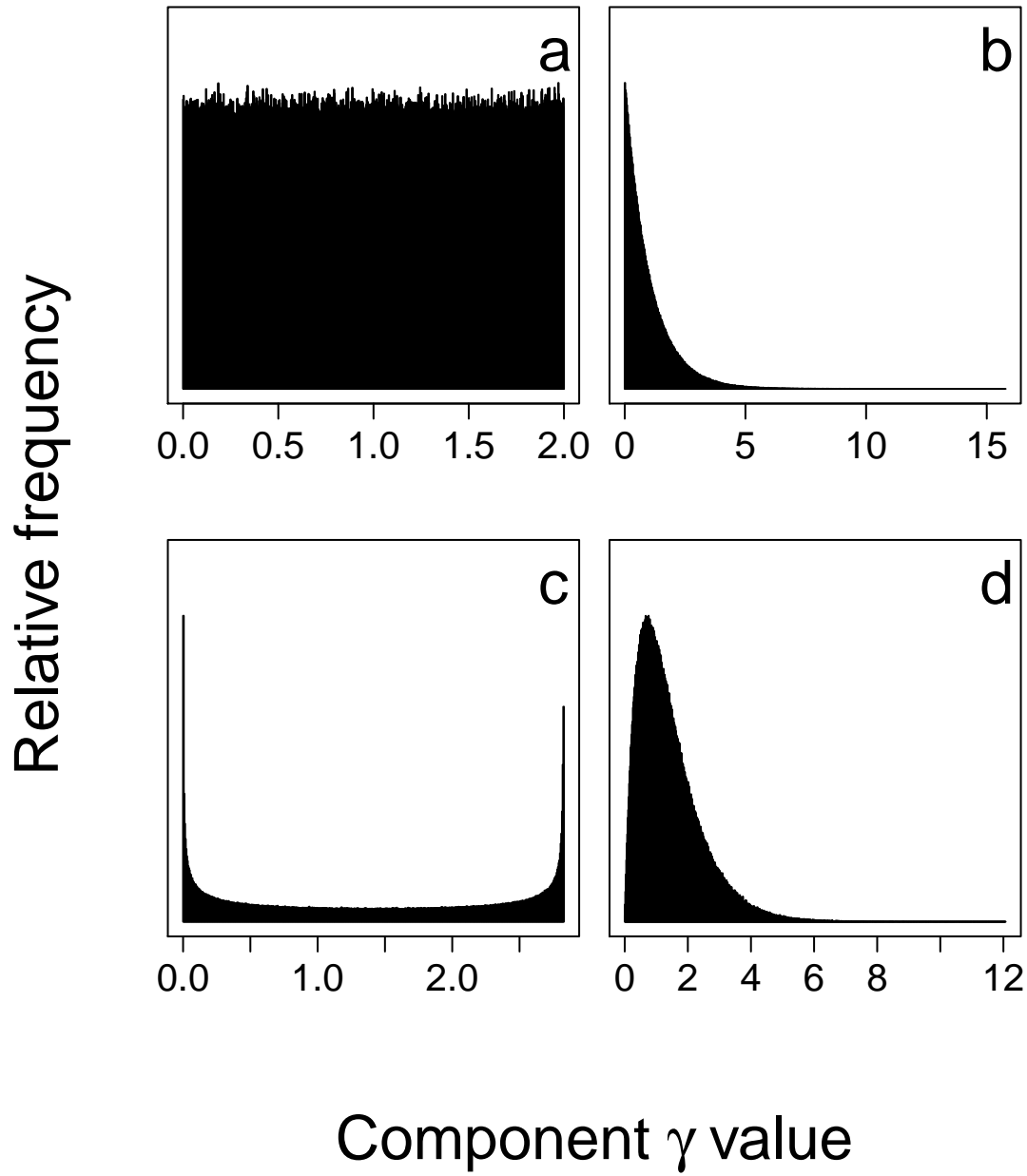
N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	14	99986	14	99986	0	0
3	240	99760	240	99760	0	0
4	1008	98992	1016	98984	0	8
5	2708	97292	2729	97271	2	23
6	5669	94331	5755	94245	13	99
7	9848	90152	10057	89943	91	300
8	15903	84097	16201	83799	336	634
9	22707	77293	23110	76890	765	1168
10	30796	69204	31122	68878	1526	1852
11	40224	59776	40082	59918	2649	2507
12	49934	50066	49288	50712	3773	3127
13	60138	39862	58803	41197	4984	3649
14	69100	30900	67110	32890	5755	3765
15	77607	22393	74884	25116	6273	3550
16	84663	15337	81780	18220	5975	3092
17	90075	9925	87290	12710	5209	2424
18	93944	6056	91419	8581	4271	1746
19	96650	3350	94530	5470	3287	1167
20	98160	1840	96698	3302	2191	729
21	99111	889	98133	1867	1389	411
22	99588	412	98905	1095	903	220
23	99837	163	99480	520	452	95
24	99932	68	99744	256	228	40
25	99976	24	99863	137	133	20

N	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
26	99995	5	99950	50	49	4
27	99996	4	99986	14	13	3
28	100000	0	99993	7	7	0
29	100000	0	99996	4	4	0
30	100000	0	99998	2	2	0
31	100000	0	100000	0	0	0
...
50	100000	0	100000	0	0	0

Different distributions of γ

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

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



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

```
fourdists <- read.csv(file = "sim_results/different_distr/four_distr_rand.csv");
kable(fourdists);
```

S	Exp_unst	Exp_stbl	beta_unst	beta_stbl	gamma_unst	gamma_stbl
2	30	99970	30	99970	30	99970
3	355	99645	355	99645	355	99645
4	1506	98494	1512	98488	1516	98484
5	3930	96070	3971	96029	4006	95994
6	7738	92262	7844	92156	7918	92082

S	Exp_unst	Exp_stbl	beta_unst	beta_stbl	gamma_unst	gamma_stbl
7	13606	86394	13889	86111	13990	86010
8	20535	79465	21002	78998	21114	78886
9	28614	71386	29060	70940	29110	70890
10	38375	61625	38388	61612	38441	61559
11	48616	51384	48211	51789	47957	52043
12	59254	40746	58025	41975	57473	42527
13	68816	31184	66753	33247	66127	33873
14	77721	22279	75149	24851	74222	25778
15	84842	15158	82030	17970	81040	18960
16	90365	9635	87809	12191	86600	13400
17	94171	5829	91756	8244	90668	9332
18	96978	3022	94977	5023	94176	5824
19	98376	1624	97018	2982	96268	3732
20	99218	782	98357	1643	97765	2235
21	99678	322	99124	876	98746	1254
22	99864	136	99599	401	99323	677
23	99954	46	99783	217	99668	332
24	99978	22	99920	80	99821	179
25	99996	4	99967	33	99911	89
26	99999	1	99979	21	99960	40
27	99999	1	99990	10	99983	17
28	100000	0	99999	1	99991	9
29	100000	0	99999	1	99999	1
30	100000	0	100000	0	100000	0
31	100000	0	100000	0	99999	1
32	100000	0	100000	0	100000	0
...
50	100000	0	100000	0	100000	0

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

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 M . This is technically impossible because γ_i can take any real value between 0-2, but even rounding γ 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 evolution⁶. In this case, the practical solution is finding vectors of γ that decrease the most positive real eigenvalue of M . The genetic algorithm below achieves this by initialising a large population of 1000 different potential γ vectors and allowing this population to evolve through a process of mutation, crossover (swapping γ_i values between vectors), selection, and reproduction until either a γ vector is found where all $\Re(\lambda) < 0$ or some “giving up” criteria is met (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). The genetic algorithm relies on five functions. The first outer function `Evo_rand_gen_var` runs all of the simulations (`max_sp` refers to the maximum S value simulated, and `iters` refers to the number of M to try for each S).

```
Evo_rand_gen_var <- function(max_sp, iters, int_type = 0, rmx = 0.4, C = 1){
  tot_res <- NULL;
```

```

fea_res <- NULL;
for(i in 2:max_sp){
  nn      <- i;
  A1_stt  <- 0;
  A2_stt  <- 0;
  A1_fet  <- 0;
  A2_fet  <- 0;
  iter    <- iters;
  tot_res[[i-1]] <- matrix(data = 0, nrow = iter, ncol = 3);
  fea_res[[i-1]] <- matrix(data = 0, nrow = iter, ncol = 2);
  while(iter > 0){
    r_vec    <- rnorm(n = i, mean = 0, sd = rmx);
    A0_dat   <- rnorm(n = i * i, mean = 0, sd = 0.4);
    A0       <- matrix(data = A0_dat, nrow = i, ncol = i);
    A0       <- species_interactions(mat = A0, type = int_type);
    C_dat    <- rbinom(n = i * i, size = 1, prob = C);
    C_mat    <- matrix(data = C_dat, nrow = i, ncol = i);
    A0       <- A0 * C_mat;
    diag(A0) <- -1;
    gam1     <- runif(n = i, min = 0, max = 2);
    A1       <- A0 * gam1;
    A0_stb   <- max(Re(eigen(A0)$values)) < 0;
    A1_stb   <- rand_mat_ga(A1);
    A0_fea   <- min(-1*solve(A0) %*% r_vec) > 0;
    A1_fea   <- min(-1*solve(A1) %*% r_vec) > 0;
    if(A0_stb == TRUE){
      tot_res[[i-1]][iter, 1] <- 1;
    }
    if(A1_stb == TRUE){
      tot_res[[i-1]][iter, 2] <- 1;
    }
    if(A0_fea == TRUE){
      fea_res[[i-1]][iter, 1] <- 1;
    }
    if(A1_fea == TRUE){
      fea_res[[i-1]][iter, 2] <- 1;
    }
    iter     <- iter - 1;
  }
  print(i);
}
all_res <- summarise_randmat(tot_res = tot_res, fea_res = fea_res);
return(all_res);
}

```

Note that `Evo_rand_gen_var` calls three custom sub-functions, `species_interactions`, `rand_mat_ga`, and `summarise_randmat`. The first simply allows for non-random interactions between components (e.g., modelling [ecological interactions](#) of random, competition, mutualism, or predator-prey).

```

species_interactions <- function(mat, type = 0){
  if(type == 1){
    mat[mat > 0] <- -1*mat[mat > 0];
  }
  if(type == 2){

```

```

    mat[mat < 0] <- -1*mat[mat < 0];
  }
  if(type == 3){
    for(i in 1:dim(mat)[1]){
      for(j in 1:dim(mat)[2]){
        if(mat[i, j] * mat[j, i] > 0){
          mat[j, i] <- -1 * mat[j, i];
        }
      }
    }
  }
  return(mat);
}

```

The sub-function `rand_mat_ga` does the work of the genetic algorithm, searching for γ vectors that are stabilising.

```

rand_mat_ga <- function(A1, max_it = 20, converg = 0.01){
  nn      <- dim(A1)[1];
  rind     <- runif(n = nn*1000, min = 0, max = 1);
  inds     <- matrix(data = rind, nrow = 1000, ncol = nn);
  lastf    <- -10;
  ccrit    <- 10;
  find_st  <- 0;
  iter     <- max_it;
  while(iter > 0 & find_st < 1 & ccrit > converg){
    ivar    <- rep(x = 0, length = dim(inds)[1]);
    ifit    <- rep(x = 0, length = dim(inds)[1]);
    isst    <- rep(x = 0, length = dim(inds)[1]);
    for(i in 1:dim(inds)[1]){
      ifit[i] <- -1*max(Re(eigen(inds[i,]*A1)$values));
      ivar[i] <- var(inds[i,]);
      isst[i] <- max(Re(eigen(inds[i,]*A1)$values)) < 0;
    }
    most_fit <- order(ifit, decreasing = TRUE)[1:20];
    parents <- inds[most_fit,];
    new_gen <- matrix(data = t(parents), nrow = 1000, ncol = nn,
                      byrow = TRUE);
    mu_dat  <- rbinom(n = nn*1000, size = 1, prob = 0.2);
    mu_dat2 <- rnorm(n = nn*1000, mean = 0, sd = 0.02);
    mu_dat2[mu_dat2 < 0] <- -mu_dat2[mu_dat2 < 0];
    mu_dat2[mu_dat2 > 2] <- 2;
    mu_dat3 <- mu_dat * mu_dat2;
    mu_mat  <- matrix(data = mu_dat3, nrow = 1000, ncol = nn);
    new_gen <- new_gen + mu_mat;
    new_gen <- crossover(inds = new_gen, pr = 0.1);
    inds    <- new_gen;
    find_st <- max(isst);
    newf    <- mean(ifit);
    ccrit    <- newf - lastf;
    lastf    <- newf;
    iter     <- iter - 1;
  }
  if(find_st == 1){

```

```

    s_row <- which(isst == 1)[1];
    writt <- c(nn, inds[s_row,]);
    cat(writt, file = "evo_out.txt", append = TRUE);
    cat("\n", file = "evo_out.txt", append = TRUE);
  }
  return(find_st);
}

```

The while loop in `rand_mat_ga` continues until either `iter` generations have occurred, a solution γ 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, γ values are mutated, crossover occurs between γ vectors, and selection occurs in each generation such that the 20 γ vectors that produce the lowest maximum $\Re(\lambda)$ are allowed to have 50 offspring each. In mutation, any γ_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 γ vector causing stability is printed to a file.

Crossover occurs in the `crossover` function below.

```

crossover <- function(inds, pr = 0.1){
  crossed <- floor(dim(inds)[1] * pr);
  cross1 <- sample(x = 1:dim(inds)[1], size = crossed);
  cross2 <- sample(x = 1:dim(inds)[1], size = crossed);
  for(i in 1:length(cross1)){
    fromv <- sample(x = 1:dim(inds)[2], size = 1);
    tov <- sample(x = 1:dim(inds)[2], size = 1);
    temp <- inds[cross1[i],fromv:tov];
    inds[cross1[i],fromv:tov] <- inds[cross2[i],fromv:tov];
    inds[cross2[i],fromv:tov] <- temp;
  }
  return(inds);
}

```

After all M are simulated in `Evo_rand_gen_var`, the `summarise_randmat` formats the data into a table.

```

summarise_randmat <- function(tot_res, fea_res){
  sims <- length(tot_res);
  all_res <- matrix(data = 0, nrow = sims, ncol = 7);
  for(i in 1:sims){
    A0_unst <- tot_res[[i]][,1] == FALSE;
    A0_stbl <- tot_res[[i]][,1] == TRUE;
    A1_unst <- tot_res[[i]][,2] == FALSE;
    A1_stbl <- tot_res[[i]][,2] == TRUE;
    stabled <- tot_res[[i]][,1] == FALSE & tot_res[[i]][,2] == TRUE;
    unstabled <- tot_res[[i]][,1] == TRUE & tot_res[[i]][,2] == FALSE;
    all_res[i, 1] <- i + 1;
    all_res[i, 2] <- sum(A0_unst);
    all_res[i, 3] <- sum(A0_stbl);
    all_res[i, 4] <- sum(A1_unst);
    all_res[i, 5] <- sum(A1_stbl);
    all_res[i, 6] <- sum(stabled);
    all_res[i, 7] <- sum(unstabled);
  }
  colnames(all_res) <- c("N", "A0_unstable", "A0_stable", "A1_unstable",
    "A1_stable", "A1_stabilised", "A1_destabilised");
  return(all_res);
}

```

}

Stability results for 40000 M for each S from 2-40 are shown below. Results for A0 indicate systems in which $\gamma = 1$, while A1 refers to systems in which the genetic algorithm searched for a set of γ values that stabilised the system.

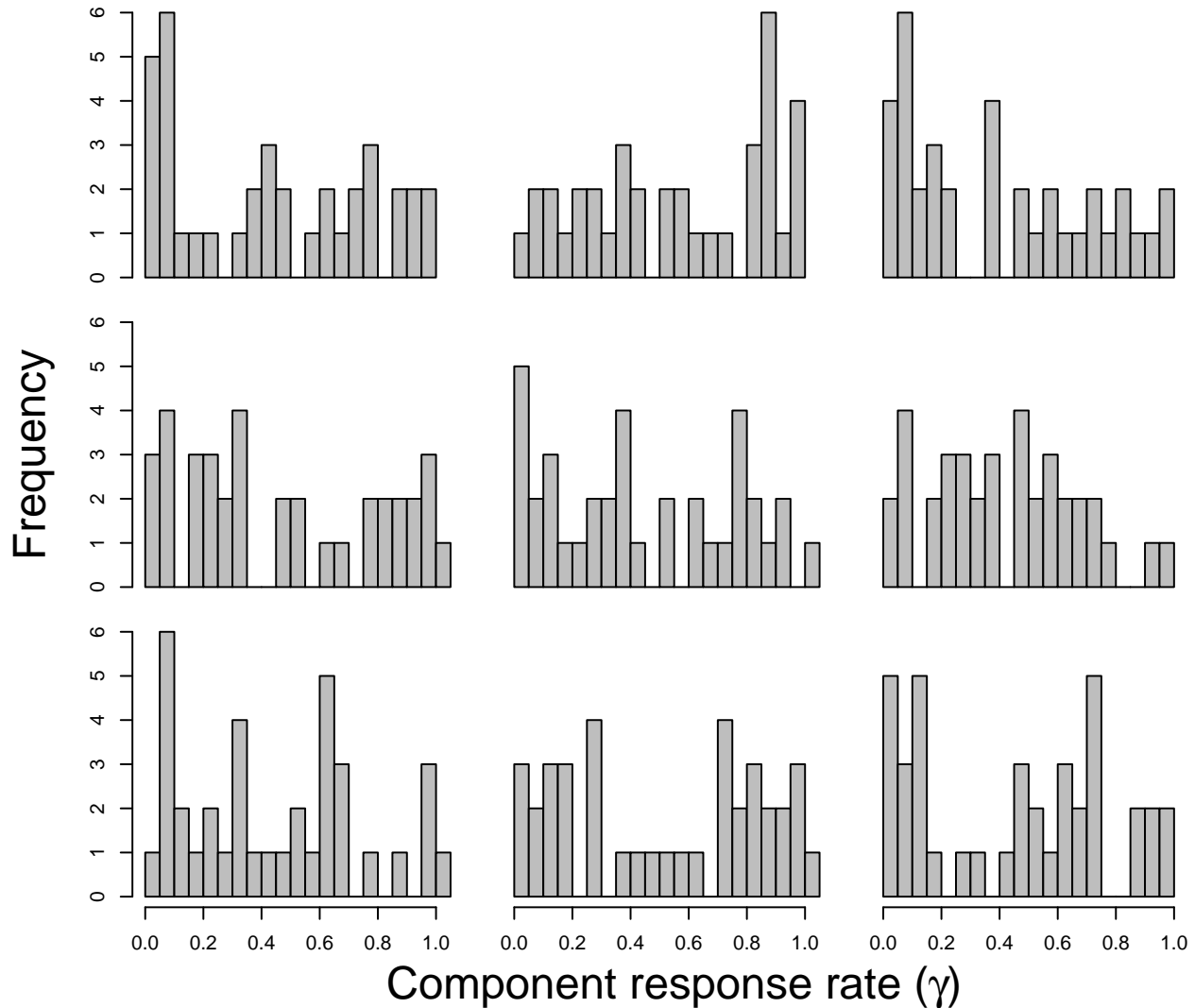
S	A0_unstable	A0_stable	A1_unstable	A1_stable	A1_stabilised	A1_destabilised
2	13	39987	13	39987	0	0
3	157	39843	157	39843	0	0
4	563	39437	563	39437	0	0
5	1588	38412	1581	38419	7	0
6	3268	36732	3219	36781	49	0
7	5370	34630	5196	34804	175	1
8	8231	31769	7604	32396	627	0
9	11704	28296	10181	29819	1523	0
10	15215	24785	12303	27697	2912	0
11	19529	20471	14599	25401	4930	0
12	23480	16520	16210	23790	7270	0
13	27570	12430	17800	22200	9770	0
14	31096	8904	18899	21101	12198	1
15	34036	5964	19948	20052	14089	1
16	36231	3769	21000	19000	15231	0
17	37737	2263	21693	18307	16044	0
18	38808	1192	22291	17709	16518	1
19	39391	609	23221	16779	16170	0
20	39711	289	23943	16057	15768	0
21	39867	133	25361	14639	14506	0
22	39950	50	26584	13416	13366	0
23	39982	18	28162	11838	11820	0
24	39994	6	29660	10340	10334	0
25	39997	3	31405	8595	8592	0
26	39999	1	33057	6943	6942	0
27	40000	0	34602	5398	5398	0
28	40000	0	35957	4043	4043	0
29	40000	0	37154	2846	2846	0
30	40000	0	38104	1896	1896	0
31	40000	0	38722	1278	1278	0
32	40000	0	39259	741	741	0
33	40000	0	39551	449	449	0
34	40000	0	39742	258	258	0
35	40000	0	39879	121	121	0
36	40000	0	39929	71	71	0
37	40000	0	39967	33	33	0
38	40000	0	39989	11	11	0
39	40000	0	39994	6	6	0
40	40000	0	39996	4	4	0

The distributions of nine γ vectors from the highest S values are shown below. Recall that 1 million random matrices were generated for the less computationally intense task of [comparing](#) M when $\gamma = 1$ versus when $\gamma \sim \mathcal{U}(0, 2)$, so it is more informative to compare stability in column 5 above with column 3 above. **This comparison shows the high number of stable M that can be produced through a targetted search of γ values, and suggests that many otherwise unstable systems could potentially be**

stabilised by an informed manipulation of their component response times. Such a possibility might conceivably reduce the dimensionality of problems involving stability in social-ecological or economic systems.

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

```
evo_out <- scan(file = "sim_results/evolved/evo_out.txt");
plot_evo_out(evo_out);
```



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

Feasibility of complex systems

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^{7–9}. 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 realistic⁸. Consequently, the use of random matrices and traditional stability

criteria for making inferences in theoretical analyses of species networks has recently been criticised⁸. 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 evolutionary¹⁰, 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.

Dougoud et al.⁸ 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 θ 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 connectance of the community, which was set to $C = 1$ throughout the manuscript and supplemental information, except [where otherwise noted](#). The variable δ is a normalisation parameter that modulates the strength of interactions (σ 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 (θI) 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's¹ stability criterion⁸ by $\frac{\sigma}{(CS)^{-\delta}} \sqrt{SC} < -1$, and hence $(CS)^{-\delta} = 1$ for the randomly simulated systems in the main text and Supplementary 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 $r_i \sim \mathcal{N}(0, 0.4^2)$, as shown in the `rand_gen_var` function in [blue section](#) on “Stability across increasing S ” above. Hence, each component i of the complex system M is assumed to be a species with a growth rate of r_i . Note that negative intrinsic growth rates are not unrealistic, and will occur in obligate mutualists in the absence of a partner.

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

S	A0_infeasible	A0_feasible	A1_infeasible	A1_feasible	A1_made_feasible	A1_made_infeasible
2	749978	250022	749942	250058	35552	35516
3	874519	125481	874296	125704	36803	36580
4	937192	62808	937215	62785	26440	26463
5	968776	31224	968639	31361	16319	16182
6	984313	15687	984463	15537	9006	9156
7	992149	7851	992161	7839	4991	5003
8	996124	3876	996103	3897	2644	2623
9	998014	1986	998027	1973	1361	1374
10	999031	969	999040	960	698	707
11	999546	454	999514	486	377	345

S	A0_infeasible	A0_feasible	A1_infeasible	A1_feasible	A1_made_feasible	A1_made_infeasible
12	999764	236	999792	208	160	188
13	999883	117	999865	135	105	87
14	999938	62	999945	55	40	47
15	999971	29	999964	36	31	24
16	999988	12	999991	9	8	11
17	999996	4	999991	9	8	3
18	999997	3	999999	1	1	3
19	999998	2	999997	3	3	2
20	1000000	0	999999	1	1	0
21	1000000	0	1000000	0	0	0
22	999999	1	1000000	0	0	1
23	1000000	0	1000000	0	0	0
24	1000000	0	1000000	0	0	0
25	1000000	0	1000000	0	0	0
26	1000000	0	1000000	0	0	0
27	1000000	0	1000000	0	0	0
28	1000000	0	1000000	0	0	0
29	1000000	0	1000000	0	0	0
30	1000000	0	1000000	0	0	0
31	1000000	0	1000000	0	0	0
32	1000000	0	1000000	0	0	0
33	1000000	0	1000000	0	0	0
34	1000000	0	1000000	0	0	0
35	1000000	0	1000000	0	0	0
36	1000000	0	1000000	0	0	0
37	1000000	0	1000000	0	0	0
38	1000000	0	1000000	0	0	0
39	1000000	0	1000000	0	0	0
40	1000000	0	1000000	0	0	0
41	1000000	0	1000000	0	0	0
42	1000000	0	1000000	0	0	0
43	1000000	0	1000000	0	0	0
44	1000000	0	1000000	0	0	0
45	1000000	0	1000000	0	0	0
46	1000000	0	1000000	0	0	0
47	1000000	0	1000000	0	0	0
48	1000000	0	1000000	0	0	0
49	1000000	0	1000000	0	0	0
50	1000000	0	1000000	0	0	0

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

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