

Component response rate variation underlies the stability of complex systems (revision notes)

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Effects of correlations interactions

If the off-diagonal elements of \mathbf{A} are sampled independently from an identical distribution, then $\max(\Re(\lambda))$ for $\mathbf{M} = \mathbf{A}$ can be estimated from five values¹. These values 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), and (5) the correlation of interaction strengths between components, M_{ij} and M_{ji} (ρ). When investigating the effect of varying component response rate $Var(\gamma)$ on stability by defining $\mathbf{M} = \gamma\mathbf{A}$, S remains unchanged. Further, values of γ_i were sampled such that $E[d]$ and $E[\mu]$ also remained unchanged (in practice, diagonal elements of \mathbf{M} were standardised so that mean values were identical before and after adding γ). What $Var(\gamma)$ does change is the variation in component interaction strengths, and ρ .

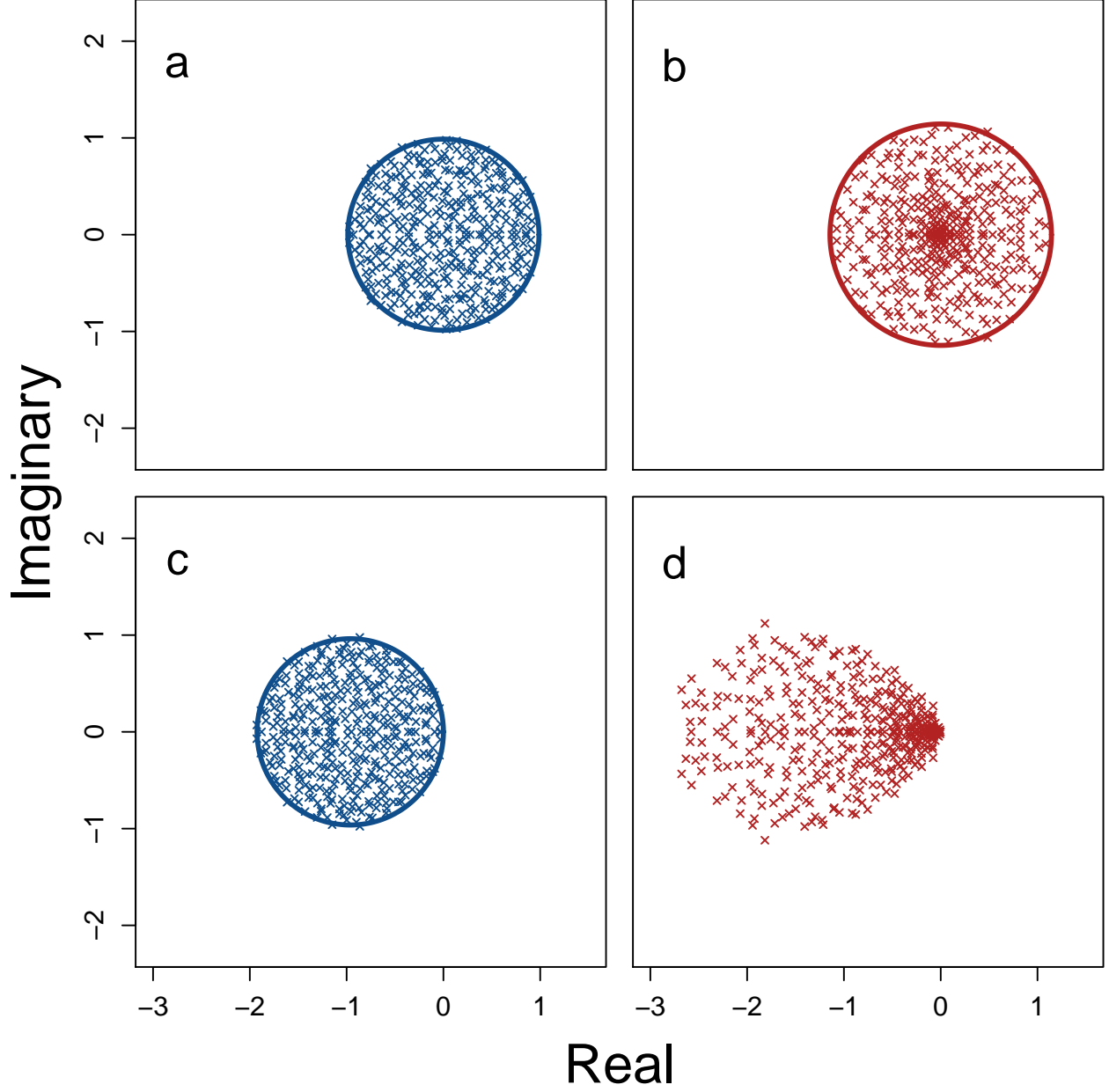
Introducing variation in γ increases the total variation in the system, making it more likely that $\mathbf{M} = \gamma\mathbf{A}$ is unstable. Variation of the off-diagonal elements in \mathbf{M} is described by the joint variation of two random variables (to simplify the notation, σ_M^2 and σ_A^2 refer to variances of off-diagonal elements only),

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

Note that in my simulations $E[\gamma_i] = 1$ and $E[A_{ij}] = 0$, so the above can be simplified,

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

The increase caused by σ_γ^2 can be visualised from the eigenvalue spectra of \mathbf{A} versus $\mathbf{M} = \gamma\mathbf{A}$. Given $d = 0$ and $C = 1$, the distribution of eigenvalues of \mathbf{M} and \mathbf{A} lie within a circle of a radius $\sigma_M^2 \sqrt{S}$ and $\sigma_A^2 \sqrt{S}$, respectively.



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23 The effect of γ does not necessarily result in a circular eigenvalue spectra of \mathbf{M} . In both panels of Figure 1,
 24 $S = 400$ and $\sigma_A = 1/\sqrt{S}$. In Figures 1a,b and 1c,d, $d = 0$ and $d = 1$, respectively, causing the eigenvalue
 25 spectra of \mathbf{A} to differ on the real axis (Figure a,c). Figure panels b and c show eigenvalue spectra after γ
 26 is included such that $M = \gamma A$, where elements of γ are drawn from a uniform distribution $\gamma \sim \mathcal{U}(0, 2)$. In
 27 both cases, $\sigma_A^2 = 0.05$ and $\sigma_\gamma^2 = 0.0031$. Nevertheless, the change in eigenvalue spectra caused by γ can affect
 28 $\max(\Re(\lambda))$ and therefore system stability.

29 Stability also decreases with increasing ρ such that $\max(\Re(\lambda)) \approx \sigma_M \sqrt{SC} (1 + \rho)$. Hence, when ρ values
 30 are negative, such as when \mathbf{M} models a predator-prey system in which M_{ij} and M_{ji} have opposing signs,
 31 stability is expected to increase². When elements of γ vary independently, the magnitude of ρ is decreased
 32 because σ_γ^2 increases the variance of M_{ij} without affecting the covariance between M_{ij} and M_{ji} ,

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

Because γ does not affect $\text{cov}(M_{ij}, M_{ji})$, the sign of ρ remains unchanged.

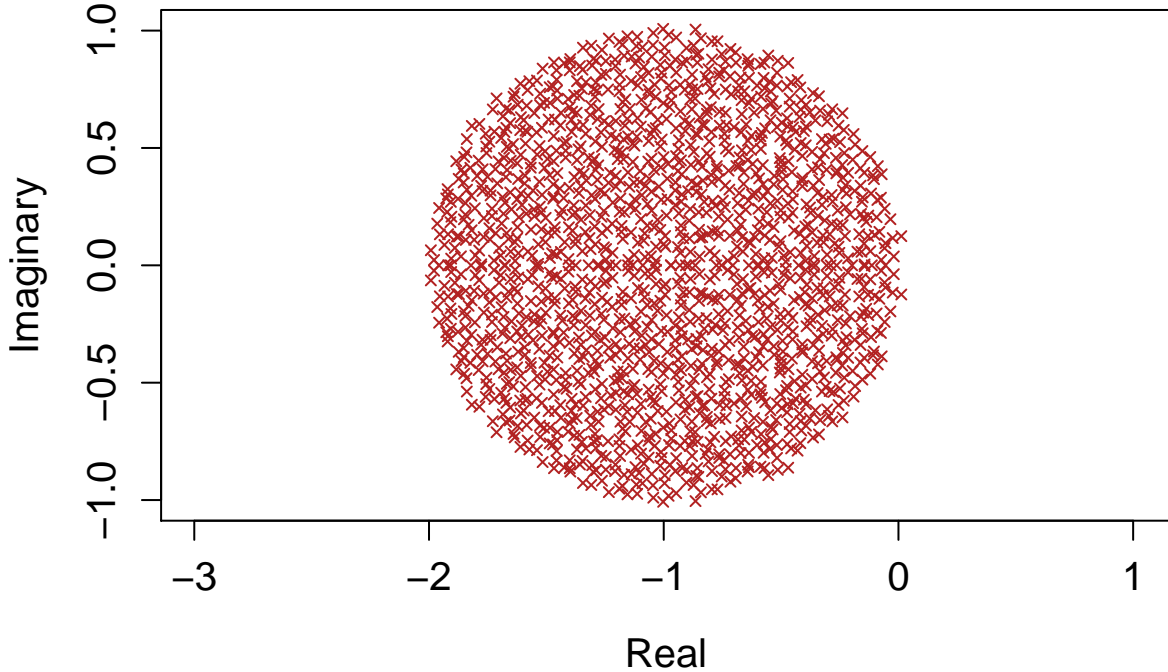
More down

The figure below shows the relationship between σ_γ and the radius of the circle in which eigenvalue spectra are contained given $S = 1024$, $C = 1$, and $\sigma_{\mathbf{A}} = 1/\sqrt{S}$. Values of γ were drawn from a uniform distribution $\gamma \sim \mathcal{U}(0, b)$ at increasing values of b so that $\sigma_\gamma = (1/12)b^2$ gradually increased.

Note that the correlation ρ adjusts the criteria for stability as follows³,

$$\sigma\sqrt{SC}(1 + \rho) < 1.$$

Given that diagonal values of \mathbf{M} are set to -1 , we can consider the relationship $S = 1600$, $C = 1$, and $\sigma = 1/40$. Under these parameter values, given $\rho = 0$, we know that $\sigma\sqrt{SC}(1 + \rho) = 1$. Hence, the expected value of $\max(\Re(\lambda)) = 0$



Hence, under the same set of parameters, we predict a linear effect of ρ on $\max(\Re(\lambda)) = 0$, such that $\max(\Re(\lambda)) = \rho$. Allesina and Tang note that ρ is defined as follows³,

$$\rho = \frac{E[M_{ij}M_{ji}] - E[M_{ij}]E[M_{ji}]}{\text{Var}[M_{ij}]}.$$

Since we define $\sigma = 1/\sqrt{S}$ and $C = 1$, $\sigma\sqrt{SC} = 1$, so the distribution of eigenvalues is circular with a radius of unity. Further, since we set $\text{diag}(\mathbf{M}) = -1$, we know that $E[\max(\Re(\lambda))] = 0$.

Gibbs et al.⁴ showed analytically that as $S \rightarrow \infty$, the effect of a diagonal matrix \mathbf{X} on the stability of $\mathbf{M} = \mathbf{X}\mathbf{A}$ becomes negligible. They also note that local stability of a random matrix can be predicted from simple moments affecting three parameters,

$$E_1 = \frac{1}{S(1-S)} \sum_{i \neq j} A_{ij},$$

$$E_2 = \frac{1}{S(1-S)} \sum_{i \neq j} A_{ij}^2 - E_1^2,$$

and,

$$E_c = \frac{1}{S(1-S)E_2^2} \sum_{i \neq j} A_{ij}A_{ji} - \frac{E_1^2}{E_2^2}.$$

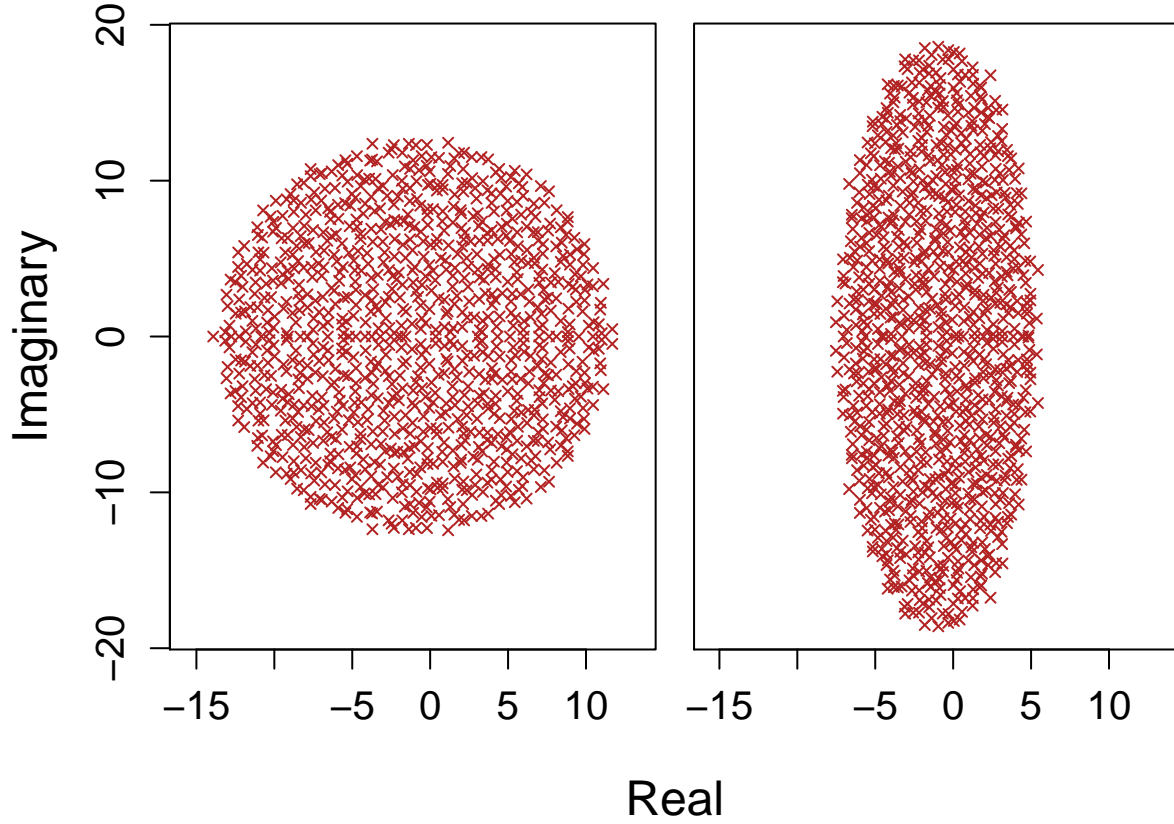
Note that given $\mu = 0$ and $C = 1$, $E_1 = 0$, while $E_2^2 = \text{Var}(A_{ij})$, and $E_c = \rho$. This suggests that my parameterisations should only be affected by $\text{Var}(A_{ij})$ and ρ . This does indeed appear to be the case if we restrict $\sigma = 1/\sqrt{S}$, where if $\rho = 0$, random matrices with γ have similar $E[\max(\Re(\lambda))]$ to those without. But the relationship between ρ and $E[\max(\Re(\lambda))]$ clearly differs when γ is included, and as S increases such that $\sigma > 1/\sqrt{S}$.

Hence, assuming high S and $\rho = 0$, we should not see an effect of γ on $E[\max(\Re(\lambda))]$. But there is clearly an effect of γ for nonzero ρ such that $\partial E[\max(\Re(\lambda))]/\partial \rho > 0$ and $\partial^2 E[\max(\Re(\lambda))]/\partial \rho^2 > 0$.

Note that, by definition, we have not changed $E[M_{ij}]$ with the addition of γ , since $E[\gamma_{ii}] = 1$. Elements of γ are pulled from a random uniform distribution between 0 and 2, meaning that no covariance should be induced between M_{ij} and M_{ji} .

Role of correlated matrices in stabilisation

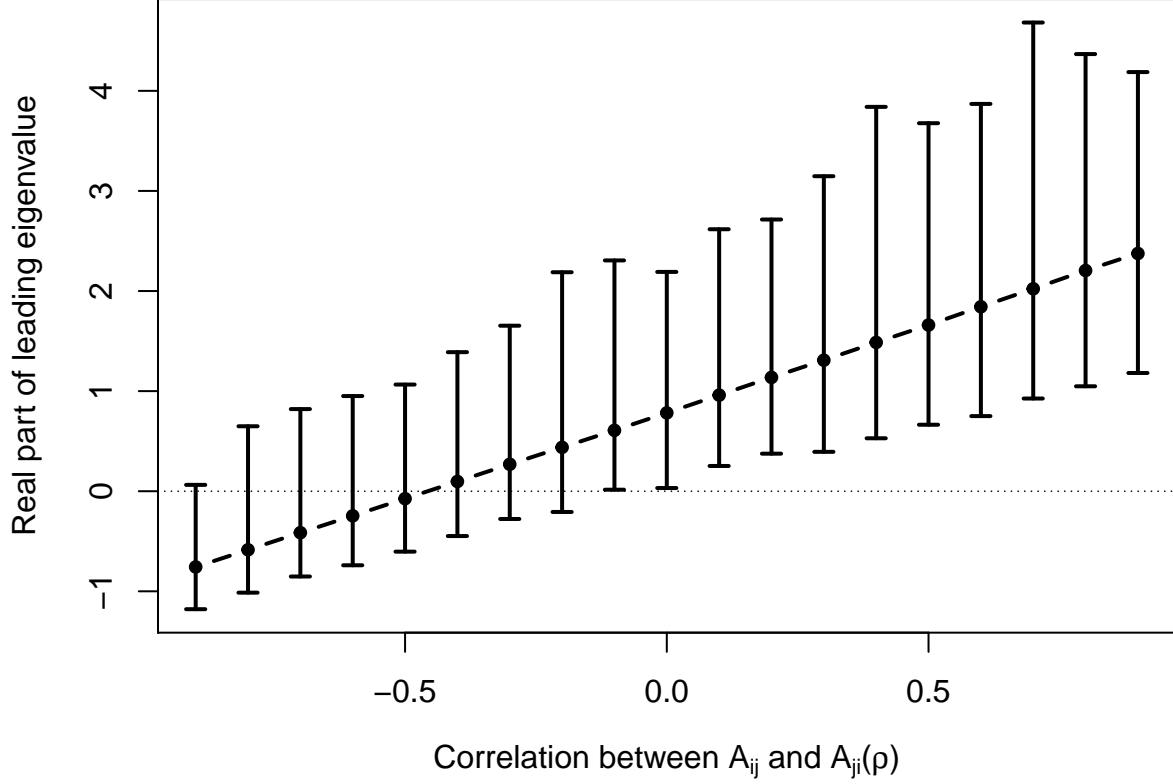
In complex systems represented by large random matrices, correlation between matrix elements A_{ij} and A_{ji} affects the distribution of eigenvalues and therefore local stability. As the correlation between matrix elements (ρ) decreases, the eigenvalue spectra changes such that more variation falls along the imaginary axis. The figure panels below compare a random matrix in which $\rho = 0$ (left) to one in which $\rho = -0.5$ (right). In both panels, complex systems include $S = 1000$ components, with diagonal elements of -1 and off-diagonal elements drawn from a normal distribution with a mean of $\mu = 0$ and standard deviation of $\sigma = 0.4$.



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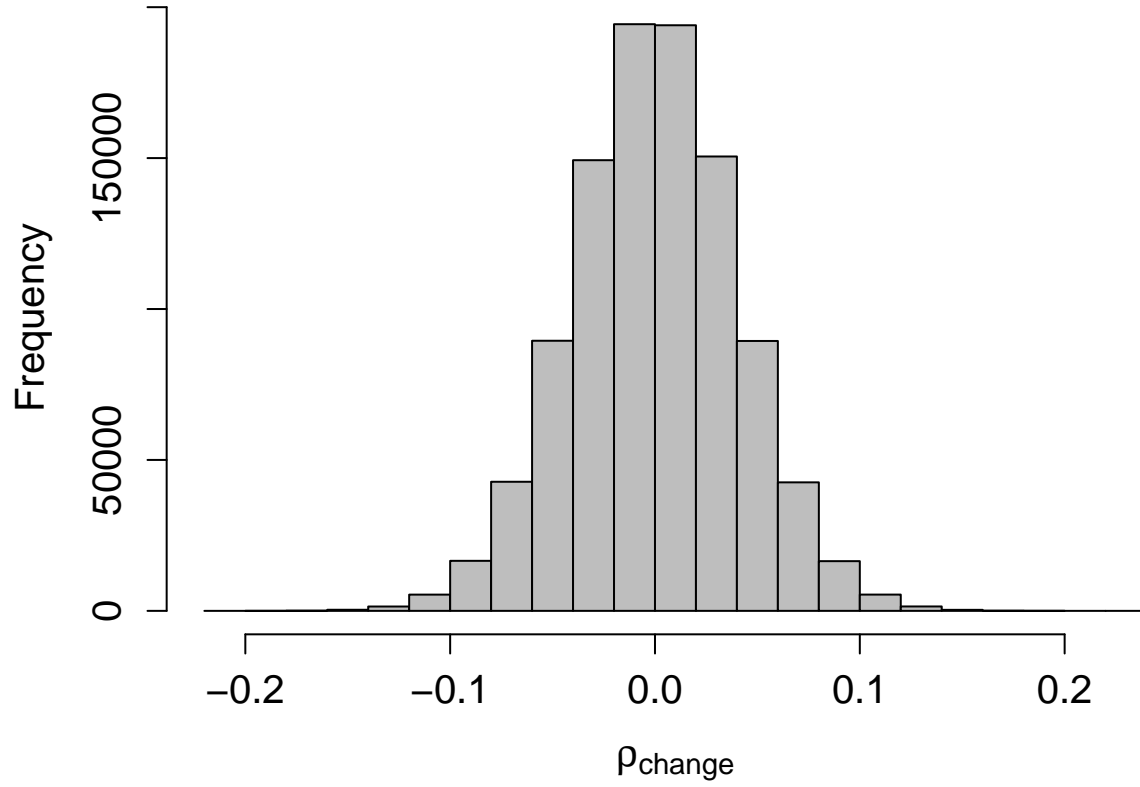
69 Because of this effect of ρ on the eigenvalue spectra, decreasing values of ρ will also tend to decrease the
70 rightmost eigenvalue of the matrix \mathbf{A} . This makes it more likely that the complex system represented by \mathbf{A}
71 is locally stable, as stability occurs when all real parts of eigenvalues are negative. Note that this elongation
72 along the imaginary axis is also characteristic of predator-prey communities (in which, by definition A_{ij} and
73 A_{ji} have opposing signs). Also note that as ρ increases such that $\rho > 0$, the same elongation happens along
74 the real axis, making random complex systems less likely to be stable.

75 A simple numerical analysis illustrates the linear relationship between ρ and the expected value of the real
76 part of the leading eigenvalue, $\max(\Re(\lambda))$. Below, I have run 10000 simulations across values of ρ from -0.9
77 to 0.9 for complex systems with $S = 25$ components. Error bars show 95% bootstrapped confidence intervals.



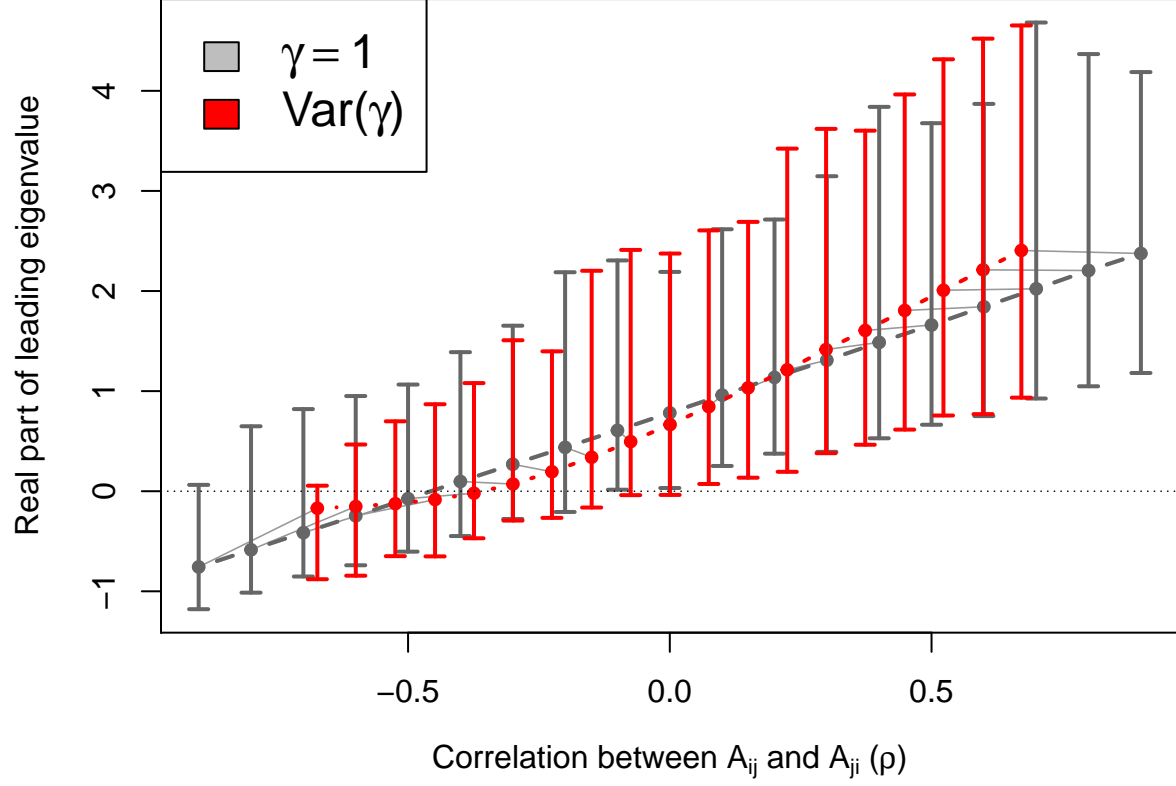
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79 In the main text, I demonstrated that when S is finite but system complexity $\sigma\sqrt{SC}$ is high (C defines the
80 connectance of \mathbf{A} , or the proportion of non-zero off-diagonal elements), variation in component response
81 rate γ often underlies system stability. In other words, highly complex systems that are observed to be
82 stable would typically not be if we removed the variation in their component response rates. Mathematically,
83 this means that by multiplying \mathbf{A} by a diagonal matrix γ with variable elements, the sign of $\max(\Re(\lambda))$ is
84 sometimes flipped from positive to negative in these finite systems of high complexity. Interestingly, this
85 increase in stability given $Var(\gamma) > 0$ is not necessarily caused by γ decreasing ρ . In fact, for $S = 25$, $\sigma = 0.4$,
86 and $C = 1$, random complex systems that are stabilised by γ typically have increased ρ values. Note that for
87 these parameter values, 1 million simulations found $\mathbf{M} = \gamma\mathbf{A}$ to be stable for 36 systems when all $\gamma_i = 1$, but
88 383 systems when $\gamma_i \sim \mathcal{U}(0, 2)$. Below shows the distribution of the difference in ρ between systems with
89 versus without $var(\gamma)$ for 1000000 stabilised systems; that is, $\rho_{change} = \rho_{var(\gamma)} - \rho_{\gamma=1}$.



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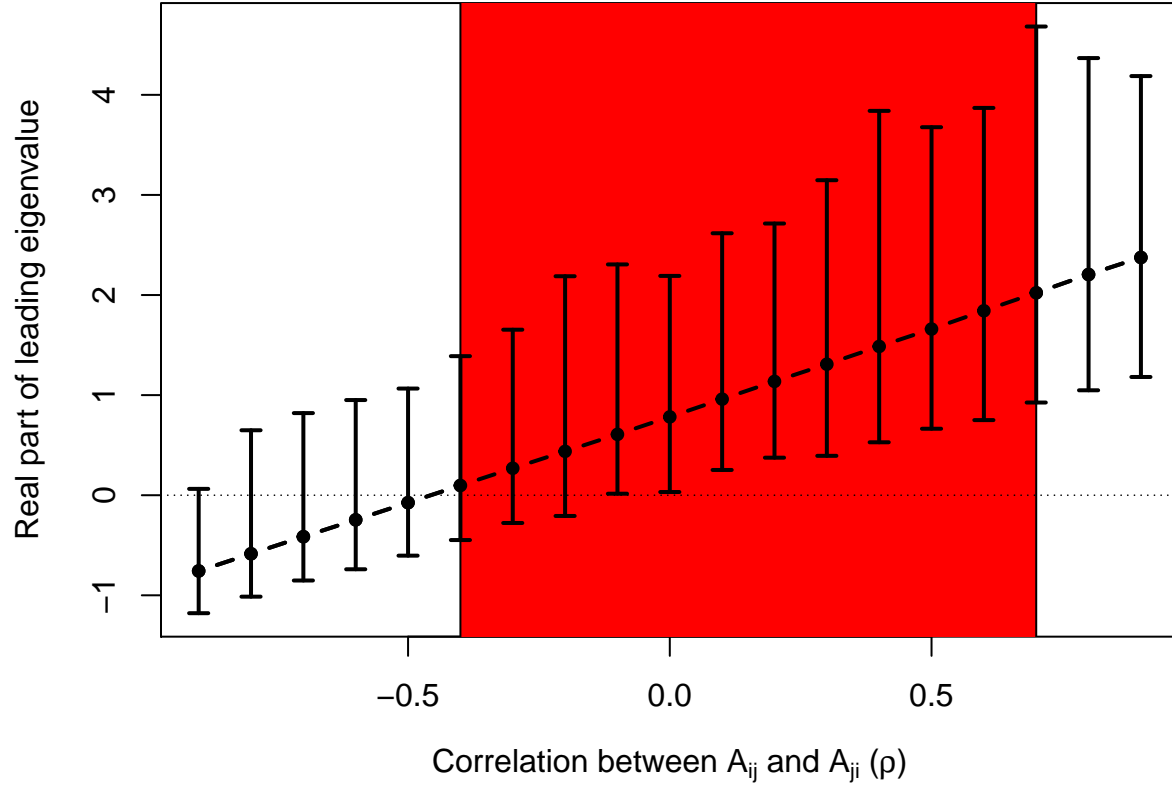
91 When \mathbf{A} was stabilised by $Var(\gamma)$, the change in ρ was normally distributed around 4.8394472×10^{-6} (95%
92 CIs: $-75.9050127 \times 10^{-6}$, $84.5804827 \times 10^{-6}$). Hence, decreasing the correlation between \mathbf{A}_{ij} and \mathbf{A}_{ji} was not
93 by itself the cause of stability. For a clearer picture of the effect of γ , it is useful to show the relationship
94 between ρ and $\max(\Re(\lambda))$ again as above, but this time also for how the relationship changes given $Var(\gamma)$.
95 That is, given $\mathbf{M} = \mathbf{A}$ in addition to $\mathbf{M} = \gamma\mathbf{A}$.



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97 Including $Var(\gamma)$ introduces a nonlinear relationship between ρ and $\max(\Re(\lambda))$. Points along the x-axis
 98 are spaced more closely together given $Var(\gamma)$ because $Var(\gamma)$ tends to decrease the absolute magnitude
 99 of ρ . Grey and red points centred on $\rho = 0$ represent the same simulations, before (grey) and after (red)
 100 including $Var(\gamma)$. Grey and red points to the left and right show decreasing and increasing simulated ρ
 101 values, respectively. Faint grey lines connect points for the same set of simulations, and where the red point
 102 is lower than the black point, the expected $\max(\Re(\lambda))$ was lower given $Var(\gamma)$.

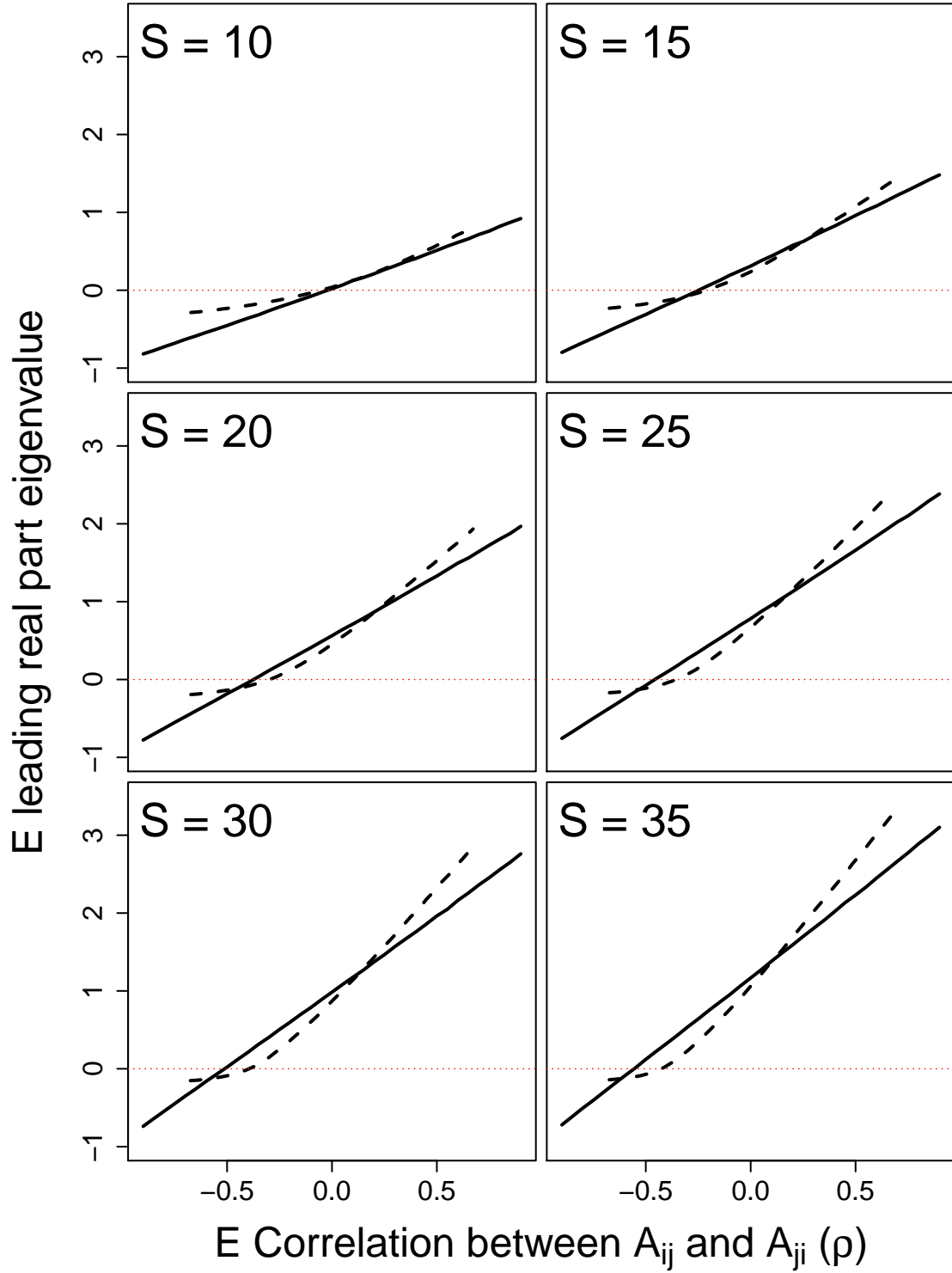
103 The region of ρ values for \mathbf{A} that would result in increased stability given $Var(\gamma)$ is highlighted with red
 104 shading below.



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106 In this red shaded region above, $\max(\Re(\lambda))$ is decreased by $Var(\gamma)$. The shaded region encompasses values of
 107 ρ between -0.4 and 0.7. But 1000000 simulated \mathbf{A} had values that ranged between -0.2642846 and 0.2668648,
 108 meaning that $\max(\Re(\lambda))$ was always expected to decrease given $Var(\gamma)$ even if $Var(\gamma)$ caused ρ to increase.

109 The curvature of the relationship between ρ and $\max(\Re(\lambda))$ is consistent across different values of S , as
 110 shown below. Including γ always results in a concave upward relationship between ρ and $\max(\Re(\lambda))$.



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112 In all panels above, the solid line shows the relationship between the expected ρ between \mathbf{A} elements A_{ij}
 113 and A_{ji} given no variation in component response rates (i.e., the diagonal matrix equals the identity matrix,
 114 $\gamma = \mathbf{I}$, so $\mathbf{M} = \mathbf{A}$). The dotted line shows the same relationship given variation in component response rates
 115 (i.e., the diagonal matrix contains elements drawn from a random uniform distribution between 0 and 2, so
 116 $\mathbf{M} = \gamma\mathbf{A}$).

References

1. Tang, S. & Allesina, S. Reactivity and stability of large ecosystems. *Frontiers in Ecology and Evolution* **2**, 1–8 (2014).
2. Allesina, S. & Tang, S. Stability criteria for complex ecosystems. *Nature* **483**, 205–208 (2012).
3. Allesina, S. & Tang, S. The stability–complexity relationship at age 40: a random matrix perspective. *Population Ecology* 63–75 (2015). doi:[10.1007/s10144-014-0471-0](https://doi.org/10.1007/s10144-014-0471-0)
4. Gibbs, T., Grilli, J., Rogers, T. & Allesina, S. The effect of population abundances on the stability of large random ecosystems. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics* **98**, 022410 (2018).