

Stability criteria for complex ecosystems

Stefano Allesina^{1,2} & Si Tang¹

Forty years ago, May proved^{1,2} that sufficiently large or complex ecological networks have a probability of persisting that is close to zero, contrary to previous expectations^{3–5}. May analysed large networks in which species interact at random^{1,2,6}. However, in natural systems pairs of species have well-defined interactions (for example predator–prey, mutualistic or competitive). Here we extend May's results to these relationships and find remarkable differences between predator–prey interactions, which are stabilizing, and mutualistic and competitive interactions, which are destabilizing. We provide analytic stability criteria for all cases. We use the criteria to prove that, counterintuitively, the probability of stability for predator–prey networks decreases when a realistic food web structure is imposed^{7,8} or if there is a large preponderance of weak interactions^{9,10}. Similarly, stability is negatively affected by nestedness^{11–14} in bipartite mutualistic networks. These results are found by separating the contribution of network structure and interaction strengths to stability. Stable predator–prey networks can be arbitrarily large and complex, provided that predator–prey pairs are tightly coupled. The stability criteria are widely applicable, because they hold for any system of differential equations.

May's theorem deals with community matrices^{1,2,6} M , of size $S \times S$, where S is the number of species. M_{ij} describes the effect that species j has on i around a feasible equilibrium point (that is, species have positive densities) of an unspecified dynamical system describing the species' densities through time.

In May's work^{1,2}, the diagonal coefficients are -1 , and the off-diagonal coefficients are drawn from a distribution with mean 0 and variance σ^2 with probability C and are 0 otherwise. For these matrices, the probability of stability is close to 0 whenever the 'complexity' $\sigma\sqrt{SC} > 1$. Local stability measures the tendency of the system to return to equilibrium after perturbations. In unstable systems, even infinitesimal perturbations cause the system to move away from equilibrium, potentially leading to the loss of species. Thus, it should be extremely improbable to observe rich (large S) or highly connected (large C) persistent ecosystems^{1,2}. Mathematically, an equilibrium point is stable if all the eigenvalues of the community matrix have negative real parts^{1,2,6}.

Local stability can only describe the behaviour of the system around an equilibrium point, whereas natural systems are believed to operate far from a steady state^{5,15}. However, methods based on local stability are well suited to the study of large systems^{1,16,17}, whose empirical parameterization would be unfeasible. Moreover, the methods are general, so that they can be applied to any system of differential equations.

May's matrices have random structure: each pair of species interacts with the same probability. However, this randomness translates, for large S , into fixed interaction frequencies, so that these matrices follow a precise mixture of interaction types. For example, in May's matrices predator–prey interactions are twice as frequent as mutualistic ones (Supplementary Table 1). Here we extend May's work to different types of interaction, starting from the random case.

Suppose that two species j and i interact with probability C , and that the interaction strength is drawn from a distribution: M_{ij} takes the value of a random variable X with mean $\mathbb{E}(X) = 0$ and variance

$\text{Var}(X) = \sigma^2$. The diagonal elements of the community matrix, representing self-regulation, are set to $-d$. For large systems, the eigenvalues are contained in a circle¹⁸ in the complex plane (Fig. 1 and Supplementary Information). The circle is centred at $(-d, 0)$ and the radius is $\sigma\sqrt{SC}$. In stable systems, the whole circle is contained in the left half-plane (that is, all eigenvalues have negative real parts). Thus, the system is stable when the radius is smaller than d : $\sqrt{SC} < \theta = d/\sigma$.

In predator–prey networks, interactions come in pairs with opposite signs: whenever $M_{ij} > 0$, then $M_{ji} < 0$. With probability C , we sample one interaction strength from the distribution of $|X|$ and the other from $-|X|$, whereas with probability $(1 - C)$ both are zero. The eigenvalues of large predator–prey matrices are contained in a vertically stretched ellipse¹⁹, centred at $(-d, 0)$, with horizontal radius $\sigma\sqrt{SC}(1 - \mathbb{E}^2(|X|)/\sigma^2)$ and thus the stability criterion is $\sqrt{SC} < \theta/(1 - \mathbb{E}^2(|X|)/\sigma^2)$ (Fig. 1 and Supplementary Information).

When we constrain M_{ij} and M_{ji} to have the same sign, and thus impose a mixture of competition and mutualism with equal probability, the eigenvalues are enclosed in a horizontally stretched ellipse¹⁹ and the criterion becomes $\sqrt{SC} < \theta/(1 + \mathbb{E}^2(|X|)/\sigma^2)$ (Fig. 1 and Supplementary Information).

Take $C = 0.1$, $X \sim N(0, 1/4)$ (that is, X follows a normal distribution with mean 0 and variance 1/4), and $d = 1$. The criterion becomes $\sqrt{SC} < 2$ for random matrices, and is violated whenever $S \geq 41$. For predator–prey we find $\sqrt{SC} < 2\pi/(\pi - 2)$ (violated for $S \geq 303$) and for the mixture of competition and mutualism $\sqrt{SC} < 2\pi/(\pi + 2)$ (violated for $S \geq 15$). Since $\mathbb{E}(|X|)/\sigma > 0$ for any distribution of X , the stability criteria form a strict hierarchy in which the mixture matrices are the least likely to be stable, the random matrices are intermediate, and the predator–prey matrices are the most likely to be stable (Fig. 2 and Table 1). Considerations based on qualitative stability² and numerical simulations¹⁶ are consistent with this hierarchy.

In the three cases above, the mean interaction strength is zero, and the coefficients come from the same distribution. In fact we can shuffle the interaction strengths, thereby transforming a network of one type into another: the difference in stability is driven exclusively by the arrangement of the coefficients in pairs with random, opposite and same signs, respectively. This feature allows us to further derive the stability criteria for all intermediate cases by using linear combinations of the three cases above (Supplementary Information).

Two ecologically important cases, however, cannot produce a mean interaction strength of zero. In mutualistic networks all interactions are positive, whereas in competitive networks they are negative. In these cases, for large systems, all the eigenvalues except one (equal to the row sum) are contained in an ellipse (Fig. 3 and Supplementary Figs 1 and 2). In mutualistic networks in which all interaction pairs are positive and drawn from the distribution of $|X|$ independently with probability C , the stability criterion becomes $(S - 1)C\mathbb{E}(|X|)/\sigma < \theta$ (that is, row sum < 0 ; Supplementary Information). For competitive matrices, in which interaction pairs are drawn from the distribution of $-|X|$ with probability C , the criterion is

$$\sqrt{SC}(1 + (1 - 2C)\mathbb{E}^2(|X|)/\sigma^2) / \sqrt{1 - C\mathbb{E}^2(|X|)/\sigma^2 + C\mathbb{E}(|X|)/\sigma} < \theta$$

¹Department of Ecology and Evolution, University of Chicago, 1101 East 57th Street, Chicago, Illinois 60637, USA. ²Computation Institute, University of Chicago, 5735 South Ellis Avenue, Chicago, Illinois 60637, USA.

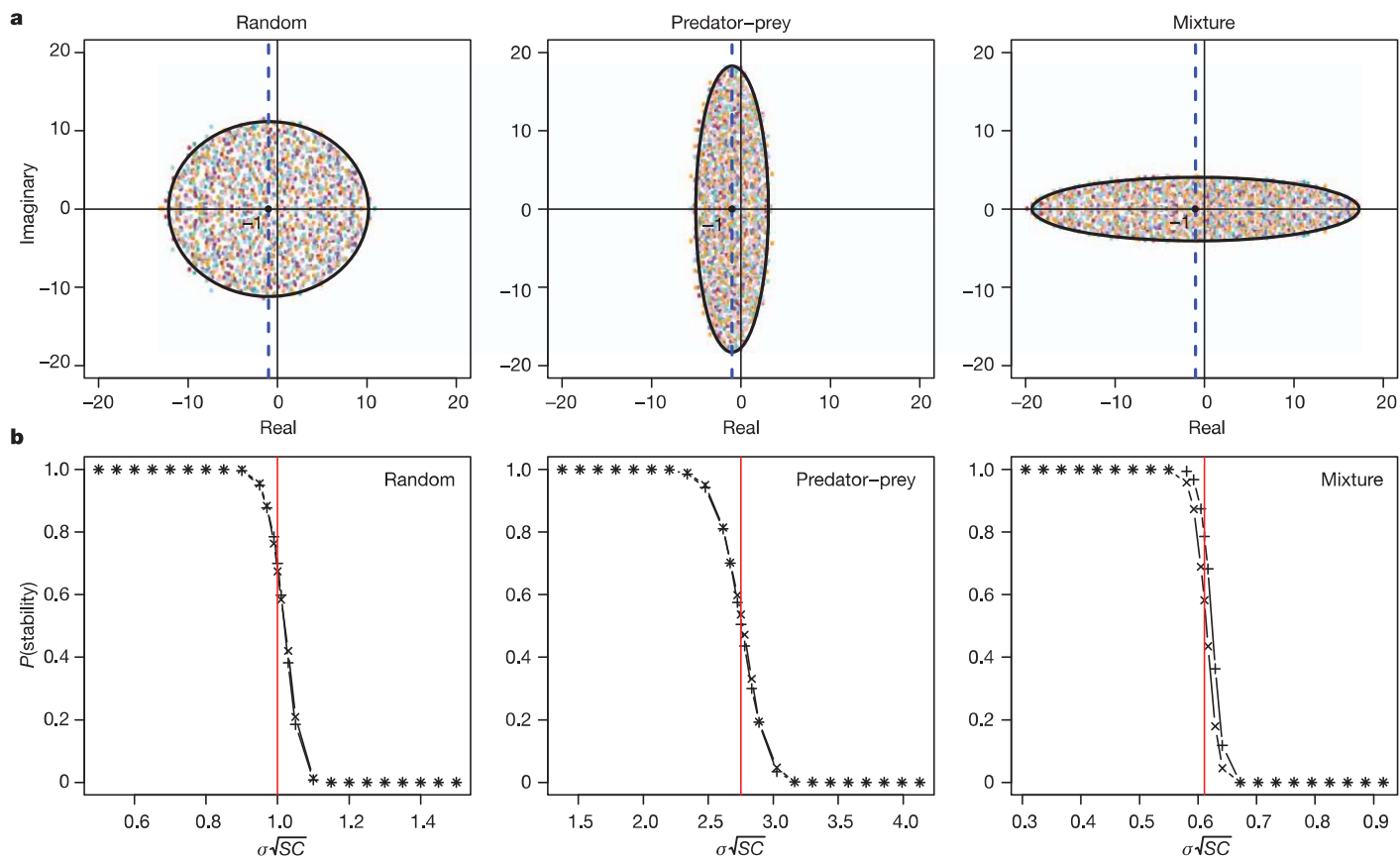


Figure 1 | Distributions of the eigenvalues and corresponding stability profiles. **a**, For $X \sim N(0, \sigma^2)$, $S = 250$, $C = 0.25$ and $\sigma = 1$, we plot the eigenvalues of 10 matrices (colours) with $-d = -1$ on the diagonal and off-diagonal elements, following the random, predator-prey or mixture prescriptions. The black ellipses are derived analytically in the text. **b**, Numerical simulations for the corresponding stability profiles. For the random case, starting from $S = 250$, $C = 0.5$, $\sigma = 0.1$ and $d = 1$, we

systematically varied C (crosses) or σ (plus signs) to obtain $\sigma\sqrt{SC}$ spanning $[0.5, \dots, 1.0, \dots, 1.5]$ of the critical value for stability (indicated in red, 1 in the case of random matrices). The profiles were obtained by computing the probability of stability out of 1,000 matrices. The predator-prey case is as the random but with $\sigma = 0.5$ and critical value $\pi/(\pi - 2)$. The mixture case is as the random but with critical value $\pi/(\pi + 2)$. In all cases, the phase transition between stability and instability is accurately predicted by our derivation.

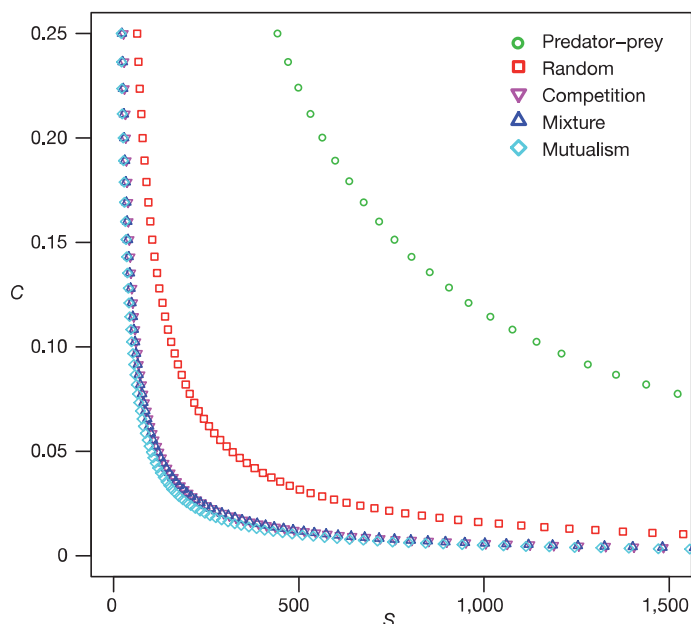


Figure 2 | Stability criteria for different types of interaction. We fixed $\theta = d/\sigma = 4$, and for a given connectance C we solved for the largest integer S that satisfies the stability criterion for each type of interactions. Combinations of S and C below each curve lead to stable matrices with a probability close to 1. The interaction types form a strict hierarchy from mutualism (most unlikely to be stable) to predator-prey (most likely to be stable).

(Supplementary Information). In both cases, stability decreases rapidly with higher complexity, and mutualistic matrices are less likely to be stable than their competitive counterpart (Fig. 2 and Table 1).

Having derived the stability criteria, we want to assess the effect of imposing realistic food web structure within the predator-prey case. It is believed that realistic food web structures should improve stability^{7,8,17}. In community matrices of food webs, producers have positive columns and negative rows, with the opposite for top predators. To test whether these variations affect stability, we plotted the eigenvalues for predator-prey webs in which interactions are arranged, following the cascade²⁰ and niche²¹ models. Imposing realistic structures results in eigenvalues with larger real parts than the corresponding unstructured predator-prey case (Supplementary Information and Supplementary Fig. 3). Thus, the cascade and niche models produce networks that are less likely to be stable than their unstructured predator-prey counterpart, with the niche model having a larger discrepancy: imposing realistic food web structure hampers stability.

Similarly, we measured the effect of realistic structures on mutualistic networks. Several published mutualistic networks are bipartite^{11–14}: there are two types of node (for example plants and pollinators), and interactions occur exclusively between different types. In addition, bipartite mutualistic networks tend to be nested¹¹: the interactions of the specialists form a subset of those of the generalists. Nestedness is believed to beget stability^{12–14}. We plotted the eigenvalues for these two types of structure and compared the results with those obtained for the unstructured mutualistic case (Fig. 3, Supplementary Information and Supplementary Fig. 4). As stated above, stability in mutualistic networks is determined by the row sum. The bipartite case yields row sums that,

Table 1 | Stability criteria for different types of interaction and network structure

Interaction	Stability criterion	$S_{\max}(C, \theta)$		
		(0.1, 2.0)	(0.1, 4.0)	(0.2, 4.0)
Nested mutualism	$(S-1)C\sqrt{\frac{2}{\pi}} < \theta$	9	28	18
Mutualism		16 (15)	41 (51)	22 (20)
Bipartite mutualism	$\sqrt{SC} < \frac{\theta\pi}{\pi+2}$	17	41	23
Mixture		17 (14)	58 (59)	33 (29)
Competition	$\sqrt{SC}\left(1 + \frac{2-2C}{\pi-2C}\right)\sqrt{\frac{\pi-2C}{\pi}} + C\sqrt{\frac{2}{\pi}} < \theta$	17 (15)	62 (63)	38 (33)
Random		50 (40)	168 (160)	88 (80)
Niche predator–prey	$\sqrt{SC} < \theta$	149	461	245
Cascade predator–prey		298	1,134	535
Predator–prey		314 (302)	1,201 (1,211)	603 (605)

In all cases, the criterion is derived for large $S \times S$ matrices with $X \sim N(0, \sigma^2)$ (and thus $\mathbb{E}(|X|) = \sigma\sqrt{2/\pi}$), connectance C and $\theta = d/\sigma$. Numerical simulations report, for a given combination of C and θ , the largest S (S_{\max}) yielding a probability of stability ≥ 0.5 (computed using 1,000 matrices). In parenthesis are the analytical predictions.

for large S , are equal to the unstructured case. Accordingly, we did not find a discrepancy in stability for the bipartite case. However, in nested structures some rows and columns have sums that are larger than average (generalist plants and animals). Consequently, nested matrices are inherently less likely to be stable than unstructured ones. These findings are confirmed by numerical simulations. Using the same method, we found that asymmetric coupling of interaction strengths (where each large M_{ij} is coupled with a small M_{ji}), contrary to current expectations²², does not influence stability in mutualistic networks (Supplementary Information and Supplementary Fig. 5).

We have considered how the arrangement of the interactions affects stability, and have found several counterintuitive results. These results can be accounted for by the fact that we provide a very conservative test for the effects of structure on stability (Supplementary Information). We now assess the role of the magnitude of interaction strengths. In fact, our findings extend to any distribution of coefficient strengths (Supplementary Information).

Typically, ecologists have regarded σ as the ‘average interaction strength’^{1,2}. However, σ does not provide information on weak interactions^{9,10,17}: we can have the same σ for two distributions with distinct shapes, and thus different proportions of weak and strong interactions (Supplementary Information). We analyse how the shape of the distribution affects stability for fixed S , C , d and σ . If the distribution contains many weak interactions, the expected magnitude $\mathbb{E}(|X|) \approx 0$. In contrast, if weak interactions are rare, $\mathbb{E}(|X|) \approx \sigma$. In the predator–prey systems, lowering $\mathbb{E}(|X|)$ decreases $\theta/(1 - \mathbb{E}^2(|X|)/\sigma^2)$ and thus

hampers stability. We conclude that weak interactions, contrary to current beliefs^{9,10,17}, can destabilize predator–prey systems. Weakening the interactions shifts $\mathbb{E}(|X|)$ closer to zero and therefore makes predator–prey systems closer to their random counterpart. With the same argument, weak interactions can stabilize the mixture of competition and mutualism case and have no effect on random networks. Variability in interaction strengths was previously found to be detrimental for stability in large food webs²³ and competitive networks¹⁷.

For example, consider a uniform distribution $X \sim U[-\sigma\sqrt{3}, \sigma\sqrt{3}]$ and contrast it with the normal case $X \sim N(0, \sigma^2)$. Both parameterizations lead to $\mathbb{E}(X) = 0$ and $\text{Var}(X) = \sigma^2$. In the uniform case, $\mathbb{E}(|X|) = \sigma\sqrt{3}/2 \approx 0.866\sigma$, whereas in the normal case $\mathbb{E}(|X|) = \sigma\sqrt{2/\pi} \approx 0.798\sigma$. This means that the uniform distribution, on average, leads to stronger interactions than the corresponding normal case. In turn, this has a large effect on stability: the criterion for the predator–prey case becomes $\sqrt{SC} < 4\theta$ for the uniform distribution, whereas it is $\sqrt{SC} < \pi/(\pi-2)\theta \approx 2.75\theta$ for the normal case. The random case is unaffected by the choice of the distribution ($\sqrt{SC} < \theta$), whereas in the mixture of competition and mutualism we have $\sqrt{SC} < 4\theta/7 \approx 0.571\theta$ for the uniform distribution and $\sqrt{SC} < \pi\theta/(\pi+2) \approx 0.61\theta$ for the normal case. These considerations extend to any choice of distribution for the interaction strengths (Supplementary Information and Supplementary Figs 6 and 7): weak interactions, all other things being equal, are destabilizing for food webs, stabilizing for mutualistic and competitive networks (and their mixture), and have no effect on random networks.

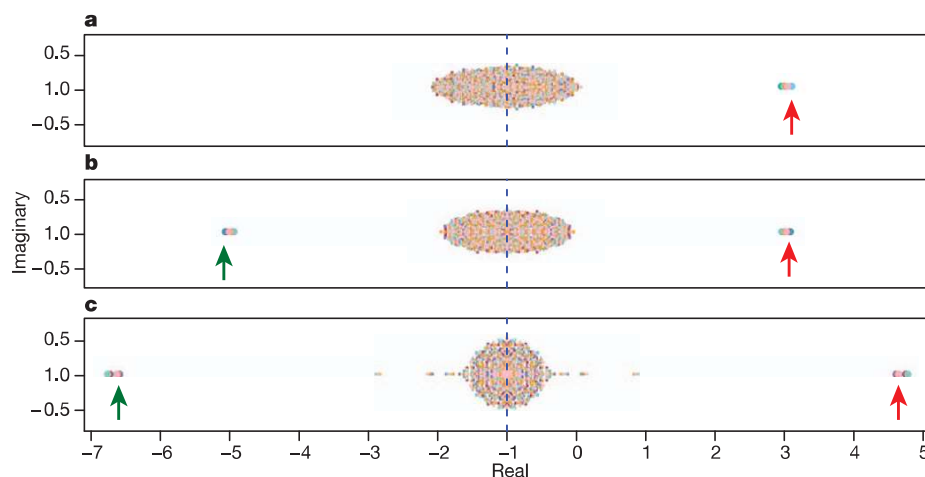


Figure 3 | Distribution of the eigenvalues for the three types of mutualism. **a**, Unstructured mutualism. **b**, Bipartite mutualism. **c**, Nested and bipartite mutualism. In all cases, $S = 250$, $\sigma = 0.1$, $C = 0.2$ and $d = 1$. Note that the bipartite case does produce extreme negative real eigenvalues (green arrow) coupled with positive ones, but the row sum (and thus the rightmost eigenvalue,

red arrow) is equal to that of the unstructured mutualistic case. The nested matrices, in which generalist species yield (on average) larger row and column sums, have larger rightmost eigenvalues. Thus, highly nested matrices are less likely than the other two cases to be stable.

We have derived stability criteria for unstructured networks in which species interact at random, in predator–prey, mutualistic, and competitive pairs. These results hold for arbitrary diagonal values and arbitrary distribution of interaction strengths (Supplementary Information). Our analysis shows that, all other things being equal, weak interactions can be either stabilizing or destabilizing depending on the type of interactions between species. In predator–prey systems, realistic structure and weak interactions are detrimental for stability. However, in natural food webs, which seem to persist in time, weak interactions are preponderant²⁴. The persistence of these networks might be explained by the interplay between their structure and weak interactions, even though each would be destabilizing if taken in isolation. For example, as suggested previously², generalist predators could have weak interactions with their numerous prey, reducing the effect of the realistic structure and driving the system closer to the unstructured case.

Predator–prey systems differ markedly from the other cases studied here. Suppose that a network is unstable. The system can be stabilized either by lowering C , S or σ (decreasing its complexity), or by increasing the self-regulation d . This is in line with May's argument: large and highly interconnected systems are difficult to stabilize. For random networks, reducing complexity is the only way to stabilize the system. However, in the other cases, networks can be stabilized by altering the distribution of interaction strengths; by modifying the parameters of the system we can typically change the distribution of the off-diagonal elements without altering the diagonal ones (Supplementary Information). For competition, mutualism and their mixture, stability is achievable by decreasing the average interaction strength $\mathbb{E}(|X|)$, which is akin to lowering complexity. On the contrary, predator–prey networks can be stabilized by increasing the strength of interaction $\mathbb{E}(|X|)$, and thus the coupling between predators and prey. Predator–prey systems are therefore the only ones that can potentially elude May's conclusions^{1,2} and support an arbitrarily large, complex and stable ecological network.

Our results show that the ubiquity of consumer–resource relationships in nature could be due to their intrinsic dynamical properties. These findings are not limited to ecological networks, but instead hold for any system of differential equations resting at an equilibrium point.

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