

Stability criteria for complex ecosystems [☆]

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Abstract

Forty years ago, Robert May questioned a central belief in ecology by proving that sufficiently large or complex ecological networks have probability of persisting close to zero. To prove this point, he analyzed large networks in which species interact at random. However, in natural systems pairs of species have well-defined interactions (e.g., predator-prey, mutualistic or competitive). Here we extend May's results to these relationships and find remarkable differences between predator-prey interactions, which increase stability, and mutualistic and competitive, which are destabilizing. We provide analytic stability criteria for all cases. These results have broad applicability in ecology. For example, we show that, surprisingly, the probability of stability for predator-prey networks is decreased when we impose realistic food web structure or we introduce a large preponderance of weak interactions. Similarly, stability is negatively impacted by nestedness in bipartite mutualistic networks.

May showed mathematically that large and complex ecosystems are inherently unstable [1, 2]. This contribution has been one of the main drivers of theoretical ecology ever since [3, 4, 5], as it clashed with the prevailing belief of ecologists that large, highly complex ecosystems (such as those observed empirically) were more stable than simpler ones (found in extreme environments and disturbed ecosystems) [6, 7].

May's theorem deals with a particular type of community matrix [8, 1, 2] M , of size $S \times S$ (S is the number of species in the system). The matrix M describes the effect a species j (column) has on species i (row) around the equilibrium point of an unspecified dynamical system describing the density of the species through time.

The diagonal coefficients of M are all -1 , while the off-diagonal coefficients are drawn from a normal distribution $N(0, \sigma^2)$ with probability C and are 0 otherwise. For large S , May proved that the probability of stability is close to 0 whenever the “complexity” $K = \sigma\sqrt{SC} > 1$. Local stability measures the tendency of the system to return to equilibrium after small perturbations. In unstable systems, even infinitesimal perturbations will make the system move away from the equilibrium state, potentially resulting in the loss of species. Thus, it should be extremely improbable to observe rich (large S) or highly connected (large C) ecosystems persisting through time. Mathematically, an equilibrium point is stable if all the eigenvalues of the corresponding community matrix have negative real part.

The networks described by these matrices have random structure: each pair of species interacts with a given probability. However, this randomness translates, for large S , into fixed interaction frequencies, so that when we are constructing the matrices above, we are following a precise mixture of interaction types. We can classify interactions types according to the signs of the ordered pair (M_{ij}, M_{ji}) (effect of j on i and vice versa), and compute their expected frequencies in a large random matrix. For the pair $(0, 0)$: non-interacting, the expected frequency is $(1 - C)^2$; $(+, 0)$ or $(0, +)$: commensalism, $C(1 - C)$; $(-, 0)$ or $(0, -)$: amensalism, $C(1 - C)$; $(-, -)$: competition, $C^2/4$; $(+, +)$: mutualism, $C^2/4$; $(+, -)$ or $(-, +)$: predator-prey, $C^2/2$.

Here we show how the criterion for stability changes when we impose a specific type of interaction between species. We start with predator-prey matrices, which are like random matrices but with the constraint that if $M_{ij} > 0$, then $M_{ji} < 0$: the interaction is beneficial for one species and detrimental for the other. Numerical simulations showed that these matrices are more stable than random ones [9]. This is confirmed by our results, as we find that the stability criterion becomes $K < \pi/(\pi - 2) \approx 2.75$. Thus, stable predator-prey systems can be much larger and more

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complex than random ones. For example, for $\sigma = 0.5$, $C = 0.1$, the stability criterion is violated for $S = 40$ in the random case, but $S = 304$ for the predator-prey case.

It should be noted that the mean of the off-diagonal coefficients $\overline{M_{ij}}$ is 0 in both cases. In fact, both random and predator-prey matrices will have (on average) the same number of positive and negative coefficients, and with the same magnitude. The only difference between the matrices is that in the predator-prey case, coefficients are arranged in pairs, such that one is negative and the other is positive. However, this arrangement modifies the expected interaction strength product for two interacting species $\overline{M_{ij}M_{ji}}$ (i.e., the expectation is taken over all the pairs in which M_{ij} or M_{ji} are $\neq 0$), which is 0 in the random case, but $-\sigma^2/2/\pi$ in the predator-prey case. Thus, the difference in stability arises from having negative $\overline{M_{ij}M_{ji}}$. This is confirmed by showing that the mean eigenvalue $\overline{\lambda} = -1$ in both cases (the trace being $-S$), while the variance [10] (for large S) is $\text{Var}(\lambda) = 0$ in the random case and $\text{Var}(\lambda) = (S - 1)C\overline{M_{ij}M_{ji}}$ in the predator-prey case. Note that the variance can be negative given that the eigenvalues can be complex conjugate. Having negative variance means that the variance of the imaginary part of the eigenvalues is larger than that of the real part. If the stability is driven by having negative $\overline{M_{ij}M_{ji}}$, reversing its sign should decrease stability.

The matrices yielding the opposite sign for $\overline{M_{ij}M_{ji}}$, compared to the predator-prey case, are those in which pairs of species interact as mutualists or competitors, and for each pair the interaction type is assigned at random. In these matrices, we still have $\overline{M_{ij}} = 0$, but now $\overline{M_{ij}M_{ji}} = \sigma^2/2/\pi$. Accordingly, the stability criterion becomes $K < \pi/(\pi + 2) \approx 0.61$: this mixture of competition and mutualism leads to a large decrease in stability. For $\sigma = 0.5$, $C = 0.1$ the criterion is violated for $S = 15$.

We derived these criteria for stability in the following way. Consider a random, $S \times S$ matrix, A , whose elements are all Gaussian with mean $\overline{A_{ij}} = 0$, mean square value $\overline{A_{ij}^2} = 1/S$, and mean interaction strength product $\overline{A_{ij}A_{ji}} = \tau/S$. For $S \rightarrow \infty$, the eigenvalues of A , $\lambda = x + iy$, are uniformly distributed in the ellipse $(x/a)^2 + (y/b)^2 \leq 1$, with $a = (1 + \tau)$ and $b = (1 - \tau)$ [11].

To obtain the community matrices we are interested in, rescale the matrix A : $\sigma\sqrt{S}A = M$. Thus, the elements M_{ij} have the following properties: $\overline{M_{ij}} = 0$, $\overline{M_{ij}^2} = \sigma^2$, and $\overline{M_{ij}M_{ji}} = \tau\sigma^2$. For large S , the eigenvalues of M are approximately uniformly distributed in an ellipse with $a = \sigma\sqrt{S}(1 + \tau)$ and $b = \sigma\sqrt{S}(1 - \tau)$.

The value of τ can be derived for all the types of matrices illustrated above. In the random case, $\overline{M_{ij}M_{ji}} = \tau\sigma^2 = 0$, and thus $a = b = \sigma\sqrt{S}$ (i.e., the eigenvalues are distributed in a circle). For the predator-prey case, the expectation for the product $\overline{M_{ij}M_{ji}}$ is $-\sigma^2/2/\pi$: the expectation for the product of two independent, identically distributed half-normal random variables, with a negative sign accounting for the opposite signs of the coefficients. Thus, $\overline{M_{ij}M_{ji}} = \tau\sigma^2 = -\sigma^2/2/\pi$, leading to $\tau = -2/\pi$, $a = \sigma\sqrt{S}(1 - 2/\pi)$ and $b = \sigma\sqrt{S}(1 + 2/\pi)$. Similarly, for the mixture of competition and mutualism we have $\overline{M_{ij}M_{ji}} = \tau\sigma^2 = \sigma^2/2/\pi$ and thus $\tau = 2/\pi$.

These results hold for completely connected matrices, with ellipses centered at $(0, 0)$. Setting the diagonal coefficients to $-d$ centers the ellipses at $(-d, 0)$ (for May's results, $d = 1$). For stable matrices, the ellipses must be fully contained in the left half-plane ($a < d$), as the real part of all eigenvalues must be negative to attain stability. Accordingly, the stability criteria for fully connected matrices are: random, $\sigma\sqrt{S} < d$; predator-prey, $\sigma\sqrt{S}(1 - 2/\pi) < d$; mixture of competition and mutualism, $\sigma\sqrt{S}(1 + 2/\pi) < d$. To account for general connectance, $C < 1$, we follow May [1, 2] and include it under the square root, obtaining the stability criteria in Table 1.

We have confirmed these results by plotting the density of the eigenvalues in the complex plane (Figure 1, top): even for matrices of moderate size (50 species or more), the approximation is very accurate. To show the sharpness of the transition from high to low probability of stability, we performed extensive numerical simulations (Figure 1, bottom).

In all the above cases, $\overline{M_{ij}} = 0$, and the expected row (column) sum is also 0. What happens if we relax these constraints? The most extreme case is that of mutualism ($M_{ii} = -d$, whereas M_{ji}, M_{ij} are drawn from $|N(0, \sigma^2)|$ with probability C and zero otherwise), in which the mean coefficient is $\overline{M_{ij}} = \sigma\sqrt{2/\pi}$ and the expected row (column) sum is $R = (S - 1)C\overline{M_{ij}} - d$. In these matrices, we find an extreme, real eigenvalue $\lambda^P = R$, while the remaining eigenvalues (for $C = 1$) are arranged in a circle centered at $(-d - C\overline{M_{ij}}, 0)$ (Figure 2, top). Numerical simulations suggest that the radius of this circle is approximately $K\pi/(2 + \pi)$. Because for mutualism the stability is determined exclusively by $\lambda^P = R$, the criterion becomes $R < 0$, which is equivalent to diagonal dominance [12]. Therefore, in this type of matrix the fact that interactions are arranged in pairs does not influence stability. For the competition case, the situation is reversed (Figure 2, bottom): we find an extreme negative eigenvalue

Interaction	Stability Criterion	S_{\max}		
		$(C, \sigma, d) = (0.33, 0.1, 0.25)$	$(0.25, 0.2, 1.0)$	$(0.25, 0.5, 2.0)$
Nested Mut.		8	20	16
Mutualism	$\sigma(S - 1)C < \frac{d}{\sqrt{\frac{2}{\pi}}}$	8 (8.5)	23 (24)	18 (19.05)
Bipartite Mut.		9	24	19
Mixture	$\sigma\sqrt{SC} < \frac{d\pi}{\pi+2}$	11 (7)	28 (23.9)	41 (37.3)
Competition	$\sigma \left(\frac{\sqrt{S}\pi}{2+\pi} + \sqrt{\frac{2}{\pi}} \right) < d$	12	33	50
Random	$\sigma\sqrt{SC} < d$	26 (18.9)	72 (64)	109 (100)
Niche Pred.-Prey		75	202	295
Cascade Pred.-Prey		125	417	649
Predator-Prey	$\sigma\sqrt{SC} < \frac{d\pi}{\pi-2}$	148 (143.4)	482 (484.7)	745 (757.3)

Table 1: Stability criteria for different types of interactions and network structures. In all cases, the criteria hold for large, $S \times S$ Gaussian matrices with connectance C and diagonal coefficients $-d$. The elements of the matrix have mean square σ^2 . The competition criterion holds for $C = 1$. Numerical simulations report, for a given combination of parameters, the largest S yielding probability of stability ≥ 0.5 (computed using 1000 matrices). In parenthesis the analytical predictions.

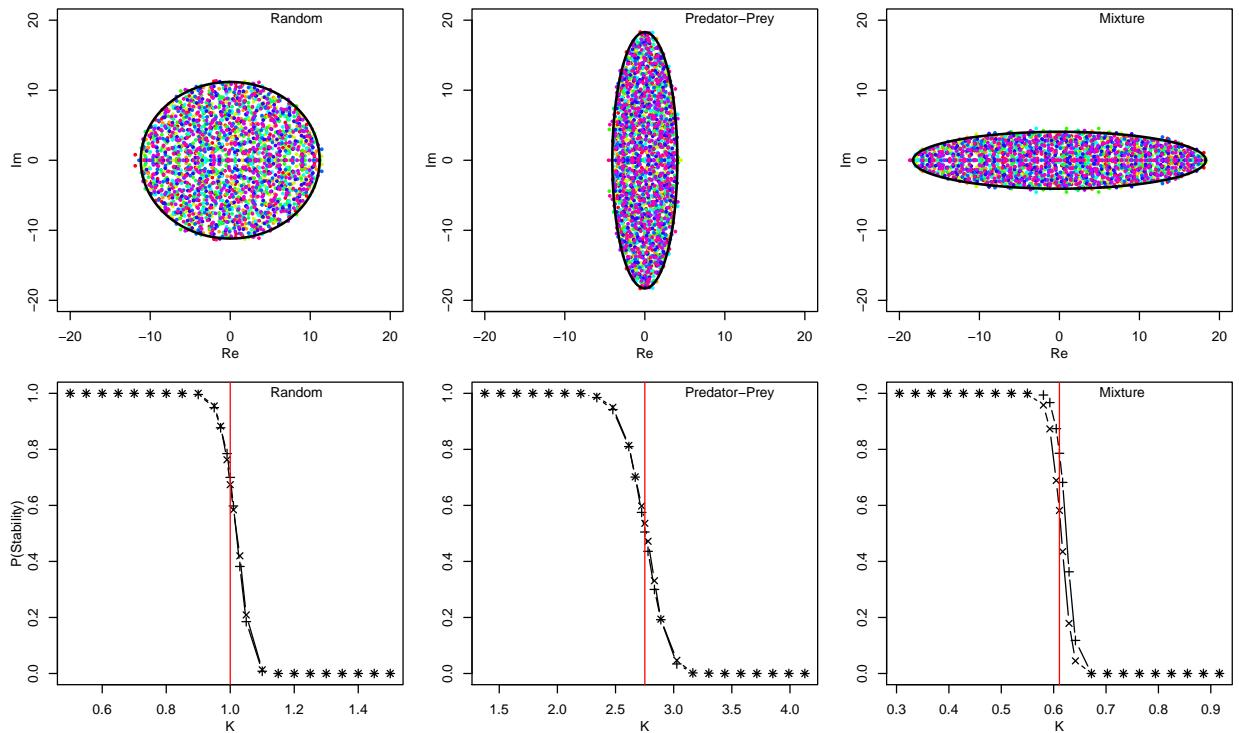


Figure 1: Top: Distribution of the eigenvalues for random, predator-prey and mixture of competition and mutualism matrices. For $S = 250$, $C = 0.25$ and $\sigma = 1$, we plot the eigenvalues of 10 matrices (colors) with 0 on the diagonal and off-diagonal elements following the random, predator prey or mixture prescriptions. The black ellipses are derived analytically in the text. Bottom: Corresponding stability profiles. For the random case, starting from $S = 250$, $C = 0.5$, $\sigma = 0.1$ and $d = 1$, we systematically varied C (\times) or σ (+) in order obtain $K = \sigma\sqrt{SC}$ 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 computing the probability of stability out of 1000 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 $\pi/(\pi + 2)$.

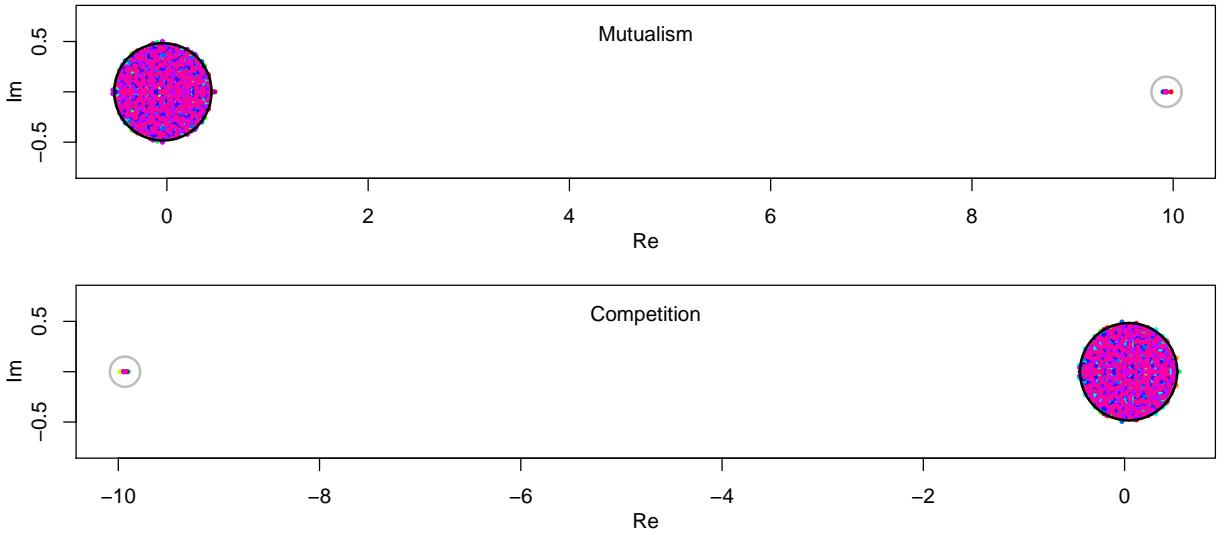


Figure 2: Distribution of the eigenvalues for mutualism and competition, obtained from 10 matrices (colors), with $S = 250$, $C = 1$, $\sigma = 0.05$ and $d = 0$. In both cases we observe an extreme, real eigenvalue whose value equals the row-sum in the matrices (circled in gray). The remaining eigenvalues, for $C = 1$, are contained in a circle of radius $\sigma\sqrt{SC\pi}/(2 + \pi)$.

$\lambda^N = R = -(S - 1)C\bar{M}_{ij} - d$, and the others are contained (for $C = 1$), in a circle centered in $(-d + C\bar{M}_{ij}, 0)$ with a radius of $K\pi/(2 + \pi)$. The maximum eigenvalue is at the very right edge of the circle, so that we can derive a stability criterion only for $C = 1$: $\sigma(\sqrt{S}\pi/(2 + \pi) + \sqrt{2/\pi}) < d$. For the general case in which $C < 1$, the non-extreme eigenvalues are approximately contained in an ellipse, but we have not found an exact expression for general C .

Returning to the predator-prey case, we assess the effect of imposing realistic food web structure. In community matrices describing food webs, we expect producers to have positive columns and negative rows, with the converse for top predators. These variations are likely to move some eigenvalues “vertically” in the complex plane (as the large row and column sums have opposite signs). To test this hypothesis, we plotted the eigenvalues for predator-prey webs in which interactions are arranged following the cascade [13] and niche [14] models (Appendix). Although these models cannot fully reproduce food web structure [14, 15, 16], they are widely used to simulate food webs (e.g., [17, 18]). It is generally believed that including realistic food web structure should increase stability (e.g., [19, 20]).

In both cases, we find several extreme eigenvalues with large imaginary part (Figure 3). Because the eigenvalues of these matrices must have the same mean and variance [10] observed in the unstructured predator-prey case, we observe a distortion of the ellipses, yielding larger real parts than expected. Thus, cascade and niche models should produce networks that are less stable than their unstructured predator-prey counterpart, with the niche model having a larger discrepancy. These considerations are confirmed by numerical experiments (Figure 3). We conclude that, surprisingly, imposing realistic food web structure hampers stability.

In the same spirit, we measured the effect realistic structures produce in mutualistic networks. Several published mutualistic networks are bipartite [21, 22, 23, 24]: there are two types of nodes (e.g., plants and pollinators), and interactions occur exclusively between different types. Also, bipartite mutualistic networks tend to be nested [21]: the interactions of the specialists are subset of those of the generalists. Nestedness is believed to beget stability [22, 23, 24]. We drew the eigenvalues for these two types of structure (bipartite, bipartite and nested Appendix, Figure 4), and contrasted the results with those obtained for the unstructured mutualistic case. We observed several large real eigenvalues as in the unstructured mutualistic case, but now for each positive eigenvalue we found an equally large negative one (Figure 4). The bipartite case yields row sums that are substantially similar to the unstructured case. Accordingly, we do not expect a large discrepancy in stability. However, given that nested structures will yield (on average), larger maximum row/column sum (associated with the generalist plants and animals), nested structures are inherently less stable than unstructured ones. These results are confirmed by numerical simulations (Figure 5).

We have so far considered how the arrangement of the interaction coefficients affects stability, we now assess the role of interaction strength distributions. We have extracted coefficients from normal (or half-normal) distributions, where the majority of interactions are close to 0 and thus “weak”. These “weak interactions” are thought to contribute considerably to the stability and persistence of natural systems [25, 26]. To examine their effect, we extended our analysis to the cases in which the absolute value of each coefficient is taken either from a uniform or a gamma distribution, parametrized such that $\overline{M_{ij}} = 0$ and $\overline{M_{ij}^2} = \sigma^2$ (as in the normal case) (Appendix). Note that the different distributions represent different frequencies of weak interactions. Therefore, changing the distribution impacts $\overline{M_{ij}M_{ji}}$, which, compared to the random case, has to be negative to increase stability and positive to depress stability. When weak interactions are preponderant, $\overline{M_{ij}M_{ji}}$ is expected to be smaller in magnitude. Therefore, weak interactions should increase the stability for mutualistic and competitive systems, but decrease the stability of predator-prey matrices and have no effect in the random case. This argument is matched by analytical and numerical results (Appendix), showing that, contrary to the current belief, weak interactions can be destabilizing.

To summarize the stability properties of the various matrices, we performed numerical simulations for all the types of networks and with three parametrizations (Table 1). We searched for the largest S yielding a probability of stability ≥ 0.5 (measured using 1000 matrices). In all cases, S increases when moving from nested mutualism to predator-prey.

We have shown that arrangement into signed pairs of interactions has large impact on stability. For example, the random, mixture and predator-prey matrices contain basically the same coefficients, and the large difference in stability is driven exclusively by their arrangement (pairs with random signs, pairs with same sign and pairs with opposite signs, respectively). This is consistent with the fact that the variance of the eigenvalues is driven by the mean product between nonzero pairs $\overline{M_{ij}M_{ji}}$.

Mutualism, competition, and their mixture, although yielding the same pairwise mean product, and the same mean and variance of the eigenvalues, have very different stability properties: increasing the fraction of competitive interactions increases stability. In these cases the stability is driven by higher moments of the eigenvalue distribution. We conjecture that the stability properties in these matrices are thus influenced by products of three or more coefficients at a time. For example, the product of three competitive interactions would yield a different sign from that of three mutualistic interactions, potentially accounting for the difference in stability.

Surprisingly, imposing realistic structure to the interaction networks appears to be detrimental for stability both in the predator-prey and the mutualistic cases. This does necessarily mean that more realistic networks should be less stable, as in our comparisons all the coefficients have (in absolute value) the same expectation, while this is not the case in natural systems (e.g., generalist species will have typically lower values for each interaction compared to specialists). However, we can safely assert that realistic structure alone is not contributing to stability: an increase in stability can be observed only if there is an interplay between the network structure and the interaction strengths. The fact that interaction strengths are a major determinant of stability is confirmed by our analysis showing that weak interactions can be either stabilizing or destabilizing depending on the type of interaction between species.

We have shown that simply plotting the density of the eigenvalues provides qualitative insight into the stability of the systems. Using this graphical method, the effect of any type of network structure can be readily analyzed.

Finally, we have found a consistent “stability hierarchy” spanning mutualism to predator-prey. Predator-prey interactions enable the stable coexistence of networks as large and complex as those observed empirically.

Our results are not limited to the stability of ecological (or biological) systems. The criteria, in fact, hold for any system of differential equations resting at an equilibrium point.

References

- [1] R.M. May, *Nature* **238**, 413 (1972).
- [2] R.M. May, *Stability and complexity in model ecosystems* (Princeton Univ Pr, 2001).
- [3] S.L. Pimm, *Nature* **307**, 321 (1984).
- [4] K.S. McCann, *Nature* **405**, 228 (2000).
- [5] J.M. Montoya, S.L. Pimm, R.V. Solé, *Nature* **442**, 259 (2006).
- [6] R. MacArthur, *Ecology* **36**, 533 (1955).
- [7] C.S. Elton, *Animal ecology* (Univ Chicago Pr, 2001).
- [8] R. Levins, *Evolution in changing environments: some theoretical explorations* (Princeton Univ Pr, 1968).
- [9] S. Allesina, M. Pascual, *Theor. Ecol.* **1**, 55 (2008).

- [10] J. Jorgensen, A.M.K. Rossignol, C.J. Puccia, R. Levins, P.A. Rossignol, *Ecology* **81**, 2928 (2000).
- [11] H.J. Sommers, A. Crisanti, H. Sompolinsky, Y. Stein, *Phys. Rev. Lett.* **60**, 1895 (1988).
- [12] R.S. Varga, *Geršgorin and His Circles* (Springer-Verlag, Berlin, 2004).
- [13] J.E. Cohen, F. Briand, C.M. Newman, Z.J. Palka, *Community food webs: data and theory* (Springer, 1990).
- [14] R.J. Williams, N.D. Martinez, *Nature* **404**, 180 (2000).
- [15] M.F. Cattin, L.F. Bersier, C. Banašek-Richter, R. Baltensperger, J.P. Gabriel, *Nature* **427**, 835 (2004).
- [16] S. Allesina, D. Alonso, M. Pascual, *Science* **320**, 658 (2008).
- [17] X. Chen, J.E. Cohen, *Proc. Roy. Soc. B* **268**, 869 (2001).
- [18] N.D. Martinez, R.J. Williams, J.A. Dunne, *Ecological networks: linking structure to dynamics in food webs* pp. 163–185 (2006).
- [19] S.J. McNaughton, *Nature* **274**, 251 (1978).
- [20] P. Yodzis, *Nature* **289**, 674 (1981).
- [21] J. Bascompte, P. Jordano, C.J. Melián, J.M. Olesen, *Proc. Natl Acad. Sci. USA* **100**, 9383 (2003).
- [22] T. Okuyama, J.N. Holland, *Ecol. lett.* **11**, 208 (2008).
- [23] U. Bastolla, *et al.*, *Nature* **458**, 1018 (2009).
- [24] E. Thébault, C. Fontaine, *Science* **329**, 853 (2010).
- [25] K. McCann, A. Hastings, G.R. Huxel, *Nature* **395**, 794 (1998).
- [26] M. Emmerson, J.M. Yearsley, *Proc. Roy. Soc. B* **271**, 397 (2004).
- [27] Thanks to A. Eklof, R.M. May, P. Staniczenko for comments. Research supported by NSF EF # 0827493.

Appendix

Construction of the community matrices

In the main text we analyze different types of matrices. Here we detail how the matrices were constructed. In all cases, the parameters are: S , number of species; C , desired level of connectance; σ , standard deviation of the normal distribution from which coefficients are drawn; $-d$ value of the diagonal coefficients. For each matrix, we also report the expected mean and variance for the eigenvalues.

Random Matrices

In the random case, we construct the matrices in the following way: i) for each coefficient M_{ij} , $i \neq j$, we draw a random value X from an uniform distribution $U[0, 1]$. If the value is $X \leq C$, we draw the coefficient M_{ij} from a normal $N(0, \sigma^2)$. Otherwise ($X > C$), $M_{ij} = 0$. ii) All $M_{ii} = -d$. For these matrices, the eigenvalues have $\bar{\lambda} = -d$ and $\text{Var}(\lambda) = 0$.

Predator-Prey Matrices

i) For each coefficient M_{ij} , $j > i$, we draw a random value X from $U[0, 1]$. ii) If the value is $X \leq C$, we draw a second random value Y from $U[0, 1]$. If this new random value is $Y \leq 0.5$, we draw M_{ij} from an half-normal distribution $|N(0, \sigma^2)|$ and M_{ji} from a negative half-normal $-|N(0, \sigma^2)|$, while if $Y > 0.5$ we do the opposite. iii) If $X > C$, we assign 0 to both coefficients. iv) All $M_{ii} = -d$. For predator-prey, $\bar{\lambda} = -d$ and $\text{Var}(\lambda) = -(S-1)C\sigma^2/2/\pi$.

Mixture of Competition and Mutualism Matrices

i) For each coefficient M_{ij} , $j > i$, we draw a random value X from $U[0, 1]$. ii) If the value is $X \leq C$, we draw a second random value Y from $U[0, 1]$. If this new random value is $Y \leq 0.5$, we draw M_{ij} and M_{ji} from an half-normal $|N(0, \sigma^2)|$, while if $Y > 0.5$ we draw both coefficients from a negative half-normal distribution. iii) If $X > C$, we assign 0 to both coefficients. iv) All $M_{ii} = -d$. For this mixture, $\bar{\lambda} = -d$ and $\text{Var}(\lambda) = (S-1)C\sigma^2/2/\pi$.

Mutualism Matrices

i) For each coefficient M_{ij} , $j > i$, we draw a random value X from $U[0, 1]$. If the value is $X \leq C$, we draw both M_{ij} and M_{ji} from an half-normal $|N(0, \sigma^2)|$. Otherwise, we assign 0 to both coefficients. ii) All $M_{ii} = -d$. For mutualism, $\bar{\lambda} = -d$ and $\text{Var}(\lambda) = (S-1)C\sigma^2/2/\pi$.

Competition Matrices

i) For each coefficient M_{ij} , $j > i$, we draw a random value X from $U[0, 1]$. If the value is $X \leq C$, we draw both M_{ij} and M_{ji} from a negative half-normal $-|N(0, \sigma^2)|$. Otherwise, we assign 0 to both coefficients. ii) All $M_{ii} = -d$. For competition, $\bar{\lambda} = -d$ and $\text{Var}(\lambda) = (S-1)C\sigma^2/2/\pi$.

Cascade Predator-Prey Matrices

In the cascade model [13], species are ordered and each species has a fixed probability of preying upon the preceding species. The produced networks do not contain cycles, although cycles are observed in empirical networks [14]. In the cascade model, the species with highest ranking functions as a top predator, while that with the lowest ranking as a producer. Accordingly, the highest ranked has positive column and negative row, while the opposite is true for the lowest ranked.

The matrix construction algorithm is: i) For each coefficient M_{ij} , $j > i$, we draw a random value X from $U[0, 1]$. If the value is $X \leq C$, we draw the coefficient M_{ij} from an half-normal $|N(0, \sigma^2)|$ and the coefficient M_{ji} from a negative half-normal $-|N(0, \sigma^2)|$. Otherwise, we assign 0 to both coefficients. ii) All $M_{ii} = -d$. For the cascade model, $\bar{\lambda} = -d$ and $\text{Var}(\lambda) = -(S-1)C\sigma^2/2/\pi$.

Niche Predator-Prey Matrices

The niche model [14] allows for trophic cycles and cannibalism. The species are ordered (each one being assigned a “niche value”, η_i). A “niche radius”, r_i , proportional to η_i , is drawn for each species along with a “niche center” c_i . Each species i preys upon all the species whose η_j are included in the range $[c_i - r_i/2, c_i + r_i/2]$. The produced networks are interval (i.e., each predator preys upon consecutive species). Empirical networks, however, are not perfectly interval [14, 15, 16].

To generate the matrices, we first produced an adjacency matrix A , using the niche model ($A_{ij} = 1$ if i is a prey of j). Then we obtained a “sign matrix” $S = -A + A^t$. Finally, M_{ij} is obtained multiplying X_{ij} taken from an half-normal distribution $|N(0, \sigma^2)|$ by S_{ij} . The diagonal elements are set to $-d$. For the niche model, $\bar{\lambda} = -d$ and $\text{Var}(\lambda) = -(S-1)C\sigma^2/2/\pi$.

Mutualistic Bipartite Matrices

For the bipartite case, we divided the species in two group of equal size ($S/2$, when S is even). For each M_{ij} where i belongs to the first group and j to the second, we draw M_{ij} and M_{ji} from an half-normal distribution $|N(0, \sigma^2)|$ with probability $C' = 2C(S-1)/S$ (so that the expected connectance is matched). The diagonal is $-d$. For the bipartite mutualistic model, $\bar{\lambda} = -d$ and $\text{Var}(\lambda) = (S-1)C\sigma^2/2/\pi$.

Mutualistic Nested Matrices

Nestedness is a property of the incidence matrix B (typically rectangular) in which the row are the species belonging to the first group (e.g., plants) and the rows those in the second group (e.g., pollinators). Say that to match the desired connectance C in the matrix M , we want to arrange L links in B . We arrange the links in the following way: First, to guarantee connectedness, i) we fill the first row; ii) we fill the first column; iii) We arrange the subsequent links so that the matrix is perfectly nested. For example (using a squared incidence matrix), say that B is 6×6 :

$$B = \begin{bmatrix} \mathbf{1,1} & \mathbf{1,2} & \mathbf{1,3} & \mathbf{1,4} & \mathbf{1,5} & \mathbf{1,6} \\ \mathbf{2,1} & \mathbf{2,2} & \mathbf{2,3} & \mathbf{2,4} & \mathbf{2,5} & 2,6 \\ \mathbf{3,1} & \mathbf{3,2} & \mathbf{3,3} & 3,4 & 3,5 & 3,6 \\ \mathbf{4,1} & \mathbf{4,2} & 4,3 & 4,4 & 4,5 & 4,6 \\ \mathbf{5,1} & 5,2 & 5,3 & 5,4 & 5,5 & 5,6 \\ \mathbf{6,1} & 6,2 & 6,3 & 6,4 & 6,5 & 6,6 \end{bmatrix}$$

and suppose we want to include 17 links. First, we fill the first row $(1, 1)$ to $(1, 6)$, so that we placed 6 links. The next five links are used to fill the first column $(2, 1)$ to $(6, 1)$. Finally, the last six links are placed in $(2, 2)$, $(2, 3)$, $(3, 2)$, $(2, 4)$, $(3, 3)$, etc. Note that the sum of the x and y coordinates for the links is growing. In fact, ordering the potential link by their coordinate sums, and giving precedence to those with smaller row number in case of ties, guarantees the maintenance of perfect nestedness. This is the filling algorithm we used in the simulations. Once we obtain B , we use it (along with its transpose), to determine the interactions in the matrix M . All the nonzero values of M_{ij} are taken from the half-normal $|N(0, \sigma^2)|$. The diagonal is $-d$. For the bipartite nested mutualistic model, $\bar{\lambda} = -d$ and $\text{Var}(\lambda) = (S-1)C\sigma^2/2/\pi$.

Different Distributions and Weak Interactions

The goal of this section is to investigate whether our findings are robust to changes in the distribution of interaction strengths and to assess the role weak interactions play for stability. In the main text, we deal with normal (or half-normal) distributions. Here, we consider uniform distributions and gamma distributions with different shapes.

To measure how preponderant “weak interactions” are in a distribution of interaction strengths, we take the expectation for the absolute value. For example, for a normal distribution, define X as a random variable taken from the distribution $|N(0, \sigma^2)|$. The expectation for X is $E[X] = \sigma\sqrt{2/\pi} \approx 0.798\sigma$ (as we saw in the main text).

Before we can examine the other distributions, we have to parametrize them in such a way that $\overline{M_{ij}} = 0$ and $\overline{M_{ij}^2} = \sigma^2$. In this way, we are satisfying the conditions we stated in the main text, and we are considering distributions of interaction strengths with the same mean and variance.

We start from a uniform distribution $U[0, \theta]$. We will sample positive coefficients from the distribution and negative coefficients reversing the sign. Thus, the interaction strengths (for the nonzero terms) are distributed uniformly in

$U[-\theta, \theta]$. Clearly, the distribution satisfies $\overline{M_{ij}} = 0$. When $\theta = \sigma\sqrt{3}$, the variance $\overline{M_{ij}^2} = \frac{4}{12}\theta^2\sigma^2 = \sigma^2$. With such a parametrization, the expected interaction is $E[X] = \sigma\sqrt{3}/2 \approx 0.886\sigma$: typically, interactions will be larger than in the normal case. What are the consequences for stability? We begin by computing τ . For a predator-prey matrix whose elements are taken from the uniform distribution above, the expected product of the interaction strengths of two interacting species is $\overline{M_{ij}M_{ji}} = -\frac{3}{4}\sigma^2$ and thus $\tau = -\frac{3}{4}$. This means that the stability criterion for uniform predator-prey becomes $\sigma\sqrt{SC} < 4d$: the uniform predator-prey matrices are much more likely to be stable than their normal counterpart. The uniform random and mixture cases trivially follow. For the uniform random, $\sigma\sqrt{SC} < d$: exactly as in the normal case. For the uniform mixture, $\sigma\sqrt{SC} < 4d/7$, less than in the normal case. To summarize, for the uniform distribution (where we expect stronger interactions than in the normal case), we observe an increase in stability for the predator-prey case and a decrease for the mixture case. The random case is unaltered.

To further prove that weak interactions stabilize the mixture and destabilize the predator-prey cases, we analyzed the effect of taking the magnitude of the coefficients from a gamma distribution. The gamma distribution takes two parameters, k (shape), and θ (scale). As above, we want to ensure that $\overline{M_{ij}} = 0$ and $\overline{M_{ij}^2} = \sigma^2$. This is accomplished, for arbitrary k , by choosing $\theta = \sigma\sqrt{\frac{1}{k(k+1)}}$. For such a gamma distribution, $E[X] = \sigma\sqrt{\frac{k}{k+1}}$. For example, for $k = 0.7$, $E[X] \approx 0.642\sigma$ (less than in the normal case), while for $k = 3$, $E[X] \approx 0.866\sigma$ (more than in the normal case, and exactly as in the uniform case). Computing τ for the predator-prey case, we find $\tau = -k/(k+1)$ and thus the stability criterion becomes $\sigma\sqrt{SC} < (k+1)d$. This means a higher likelihood of stability, compared to the normal case, whenever $k+1 > \pi/(\pi-2)$ (approximately, $k > 1.75$). Thus, when we extract the magnitude of the coefficients from a gamma distribution, increasing k will increase the expectation, and this in turn will result in more stability for the predator-prey case and less for the mixture (criterion: $\sigma\sqrt{SC} < d(2k+1)/(k+1)$). For the random case the situation is unaltered.

Our analytical predictions are confirmed by plotting the density of the eigenvalues (Figure 6) and drawing stability profiles (Figure 7) for all the distributions described above.

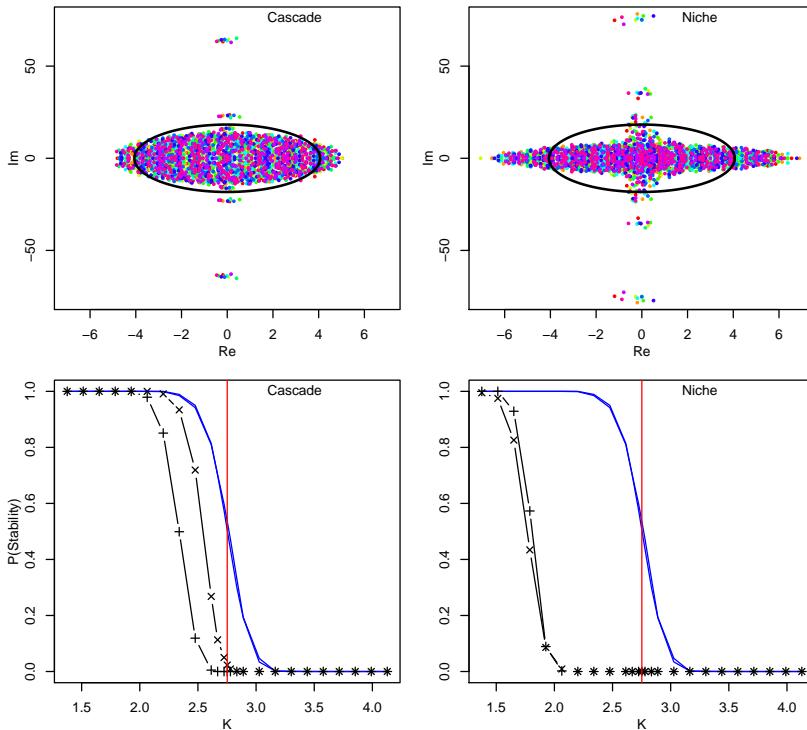


Figure 3: Top: Distribution of the eigenvalues for cascade and niche models, with the same values used in Figure 1. In both cases we observe extreme, largely imaginary eigenvalues. Accordingly, the theoretical ellipse for the predator-prey case (black) does not contain all the remaining eigenvalues, decreasing the probability of stability. This effect is more pronounced in the niche case. Bottom: Stability profiles obtained using the same values as Figure 1 (unstructured predator-prey case). We report the unstructured predator-prey profile (blue) for comparison. Note that, contrary to the unstructured model, in the cascade and niche matrices increasing C or σ yields different effects (separation between the two lines). This is because the row (column) sum scales linearly with C and σ , while K scales sublinearly with C .

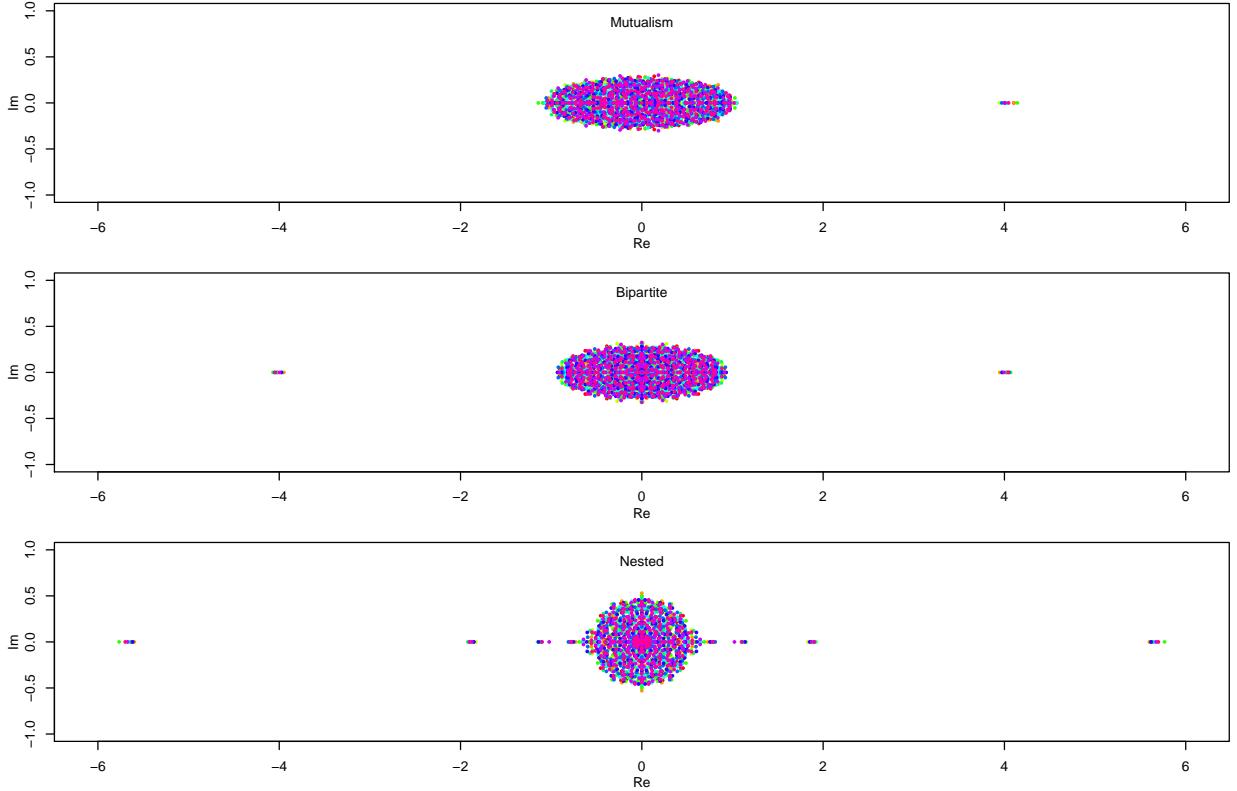


Figure 4: Distribution of the eigenvalues for the unstructured mutualism, bipartite mutualism and nested mutualism. In all cases, $S = 250$, $\sigma = 0.1$, $C = 0.2$ and $d = 0$. Note that the bipartite case does produce extreme negative real eigenvalues coupled with positive ones, but the row sum (and thus the dominant eigenvalue) is similar to that of the unstructured mutualistic case. The nested matrices, in which generalist species yield (on average), larger row and column sums, display larger dominant eigenvalues. Thus, nestedness should produce matrices that are less likely to be stable compared to the other two cases.

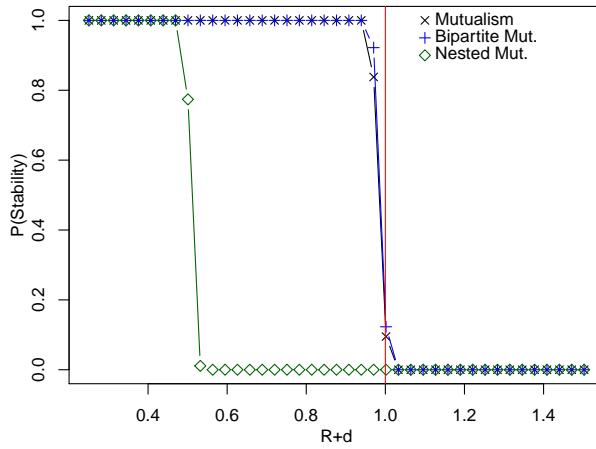


Figure 5: Stability profile for the mutualistic cases, for $S = 250$, $\sigma = 0.025$, $d = 1$. We vary C so that the critical value $(S - 1)C\sigma\sqrt{2/\pi} = R + d$ (x-axis) spans $[0.2, 1.2]$. The critical value is reached for $(S - 1)C\sigma\sqrt{2/\pi} = 1$ (red line). Note that, as expected from Figure 4, nested matrices are much less stable than the other two types of matrices.

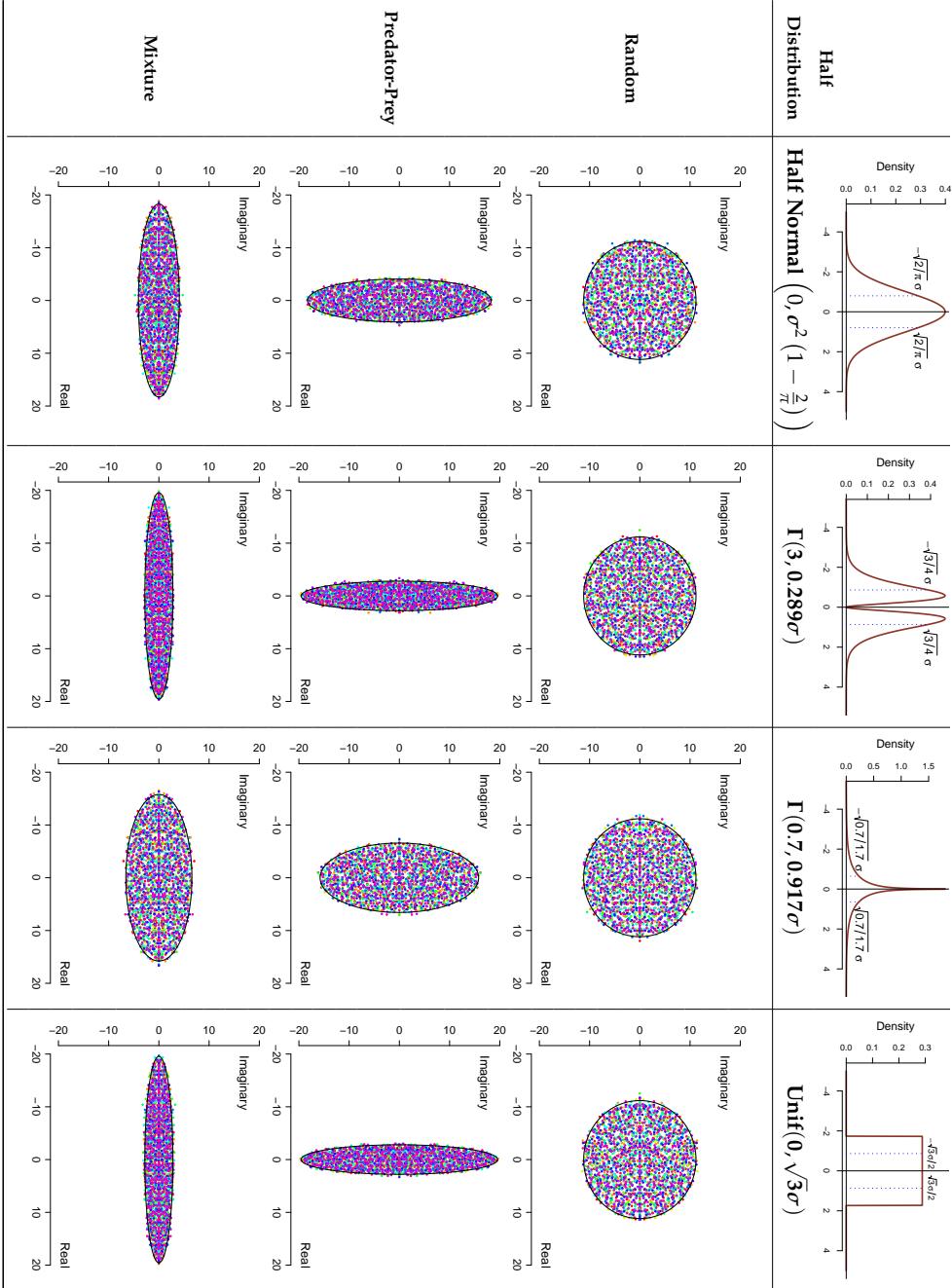


Figure 6: Distribution of the eigenvalues for random, predator-prey and mixture of competition and mutualism matrices (rows) for different distributions (top row). For $S = 250$, $C = 0.25$ and $\sigma = 1$, we plot the eigenvalues of 10 matrices (colors) with 0 on the diagonal. For the off-diagonal elements, the magnitudes are taken from an half-normal (first column), gamma (second and third columns) or uniform (fourth column) distributions, while the signs are assigned according to the types of matrices. The distributions are parametrized in a way such that $\overline{M_{ij}} = 0$ and $\overline{M_{ij}^2} = \sigma^2$. The ellipses are derived in the Appendix.

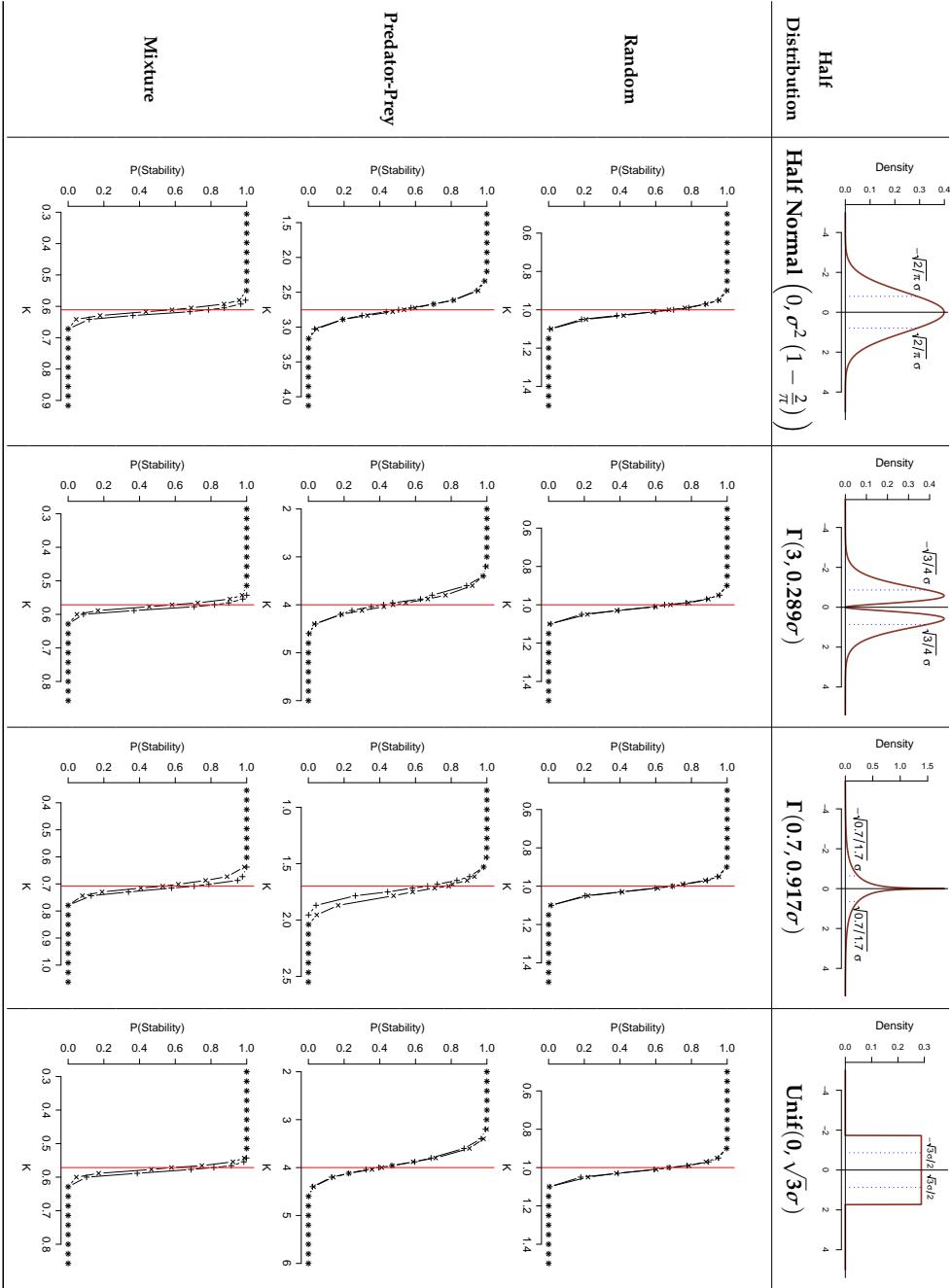


Figure 7: Stability profiles for the combinations of matrix type and distribution illustrated in Figure 6. For the random and mixture cases, starting from $S = 250$, $C = 0.5$, $\sigma = 0.1$ and $d = 1$, we systematically varied C (\times) or σ ($+$) in order to obtain $K = \sigma\sqrt{SC}$ spanning $[0.5, \dots, 1.0, \dots, 1.5]$ of the critical value for stability (indicated in red, 1 in the case of random matrices). The profiles were obtained computing the probability of stability out of 1000 matrices. The predator-prey case is as the random but with $\sigma = 0.3$ for the half-normal and $\Gamma(0.7, 0.917\sigma)$, while $\sigma = 0.5$ for the uniform and $\Gamma(3, 0.289\sigma)$ cases. The adjustment of σ is necessary as it would otherwise lead to $C > 1$.