

Impossible ecologies: Interaction networks and stability of coexistence in ecological communities

Highlights

- We analyze stability of coexistence in all small networks of ecological interactions
- Stable coexistence is non-trivially impossible in very rare “impossible” ecologies
- Equally rare “irreducible” ecologies determine the possibility of stable coexistence
- The probability of stable coexistence depends hugely on interaction network details

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In brief

Stability of coexistence in ecological communities follows classical trends based on the proportions of mutualistic, competitive, and predator-prey interactions. Meng et al. show that it also depends so strongly on the detailed network structure of these interactions that these trends can be broken. This reveals curious “impossible” and “irreducible” ecologies.



Article

Impossible ecologies: Interaction networks and stability of coexistence in ecological communities

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SUMMARY

Does an ecological community allow stable species coexistence? Identifying the general effects of competitive, mutualistic, and predator-prey interactions on stability remains a central problem of systems ecology because established approaches cannot account for the full network arrangement of these interactions. Here, we therefore analyze all interaction networks of $N \leq 5$ species with Lotka-Volterra dynamics by combining exact results and numerical exploration. We find that a very small subset of these networks is “impossible ecologies,” in which stable coexistence is non-trivially impossible. We prove that the possibility of stable coexistence is determined by similarly rare “irreducible ecologies.” Statistical sampling shows that this probability varies over orders of magnitude even in ecologies that differ only in the network arrangement of identical interactions. Thus, our approach reveals that the full network structure of interactions can influence stability of coexistence more than the established effect of interaction-type proportions. A record of this paper’s transparent peer review process is included in the supplemental information.

INTRODUCTION

Nigh on a century ago, Lotka and Volterra analyzed a minimal model of two-species predator-prey dynamics.¹ With extensions to competitive or mutualistic interactions and to interactions among $N \geq 2$ species, together with multitudinous further generalizations, this became the generic description of an ecological community now known as the Lotka-Volterra model.^{2,3} It is within such models that theoretical ecology can answer the paradigmatic question of stability: what are the general principles that determine the possibility of stable ecological coexistence?

While the analysis of two-species incarnations of the Lotka-Volterra model is textbook material,² not much analytical progress is possible for larger communities. Most of the understanding of these general principles therefore relies on the approach pioneered by May,⁴ who linked the statistics of stable coexistence to the eigenvalue distribution of a random matrix. Contrary to the “conventional wisdom of natural historians,”⁵ this suggests that species diversity begets instability. Over the ensuing decades,⁶ a large body of work has therefore explored how actual ecological communities overcome the stability limitations of May’s simple random model.⁴ This started with work pointing to the role of feasibility of coexistence^{5,7,8} and to the differences between random

and actual ecological communities.^{9–12} In this context, very recent work^{13,14} noticed that replacing the linear growth assumed in the Lotka-Volterra model with sublinear growth can break May’s stability paradigm: stability can now increase with increasing number of species. Meanwhile, on the mathematical side, further ideas from random matrix theory were adopted into theoretical ecology,^{6,15,16} although the link between random matrix theory à la May and the Lotka-Volterra model has been made explicit only recently.¹⁵ In particular, this approach revealed generic effects of competitive, mutualistic, and predator-prey interactions in an ecological community on stability of coexistence^{17–19}; for example, increasing the proportion of predator-prey interactions stabilizes coexistence, while increasing that of competitive or mutualistic interactions is destabilizing,¹⁷ with mutualism being more destabilizing than competition.^{17,19}

The network of competitive, mutualistic, and predator-prey interactions in the community depends, however, not only on these proportions of different interaction types but also on the network arrangement of these interactions. Recent work has therefore explored statistically the impact of community modularity²⁰ and interaction hierarchies.²¹ Related work has revealed the effect on stability of coexistence of additional ecological structures or processes, including resource dynamics,^{22–24} subpopulation structures associated with phenotypic switching,^{25–27}



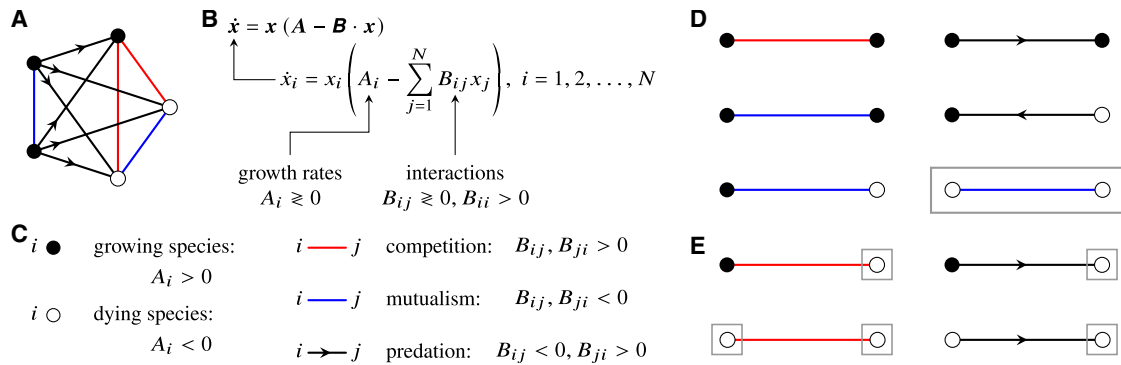


Figure 1. Lotka-Volterra ecological dynamics and impossible ecologies

(A) Example of a network topology on $N = 5$ species, defined below.

(B) Mathematical definition of the Lotka-Volterra model on N species: the dynamics of the vector $\mathbf{x}$ of the population abundances of the N species are determined by a vector $\mathbf{A}$ of growth rates and a matrix $\mathbf{B}$ of interaction strengths.

(C) The network topology or "ecology" is defined by the signs of $A_i \geq 0$ and $B_{ij} \geq 0$ for $j \neq i$, defining competitive, mutualistic, and directed predator-prey interactions between species.

(D) List of the six non-trivial network topologies on $N = 2$ species: one topology ("obligate mutualism," highlighted) is an "impossible ecology" in which stable and feasible coexistence is non-trivially impossible.

(E) List of the four trivial ecologies on $N = 2$ species: the highlighted species are dying on their own and have only deleterious interactions, prohibiting stable and feasible coexistence of all species.

dispersal,^{28,29} and self-regulation.³⁰ The full network structure of ecological interactions, although maybe the most fundamental aspect of the structure of an ecological community, has garnered less attention, however. This is perhaps partly because it does not allow the direct statistical description in large ecological communities that allows random matrix theory approaches.

Here, we reveal the huge effect of this network structure on stability of coexistence by taking a different approach, based on an exhaustive analysis of small ecological communities: we analyze all interaction networks of $N \leq 5$ species with Lotka-Volterra dynamics. Combining exact calculations for $N \leq 3$ species and numerical exploration, we discover that stable coexistence is non-trivially impossible in a very small subset of these networks, which we term "impossible ecologies". Somewhat conversely, we prove that any non-trivial network that contains a possible subecology is itself possible. The possibility of stable coexistence is therefore determined in general by the set of "irreducible ecologies" that are possible but do not contain a possible subecology. Strikingly, our results suggest that these constitute an exponentially small fraction of all ecologies. Finally, we compute the probability of stable coexistence for all ecologies of $N \leq 5$ species by random sampling of interaction strengths. Remarkably, these probabilities vary, even for these small ecologies, over many orders of magnitude. This is true even in ecologies that have the same counts of interaction types and hence differ only in the network structure of an identical set of ecological interactions. In this way, our results shift the stability paradigm partly from general stability principles to the detailed structure of the interaction networks.

RESULTS

To understand the effect of the structure of interaction networks on ecological stability, we consider the simplest ecological interactions between N species (Figure 1A) with Lotka-Volterra dy-

namics (Figure 1B): a vector $\mathbf{x} = (x_1, x_2, \dots, x_N)$ of population abundances satisfies

$$\dot{\mathbf{x}} = \mathbf{x}(\mathbf{A} - \mathbf{B} \cdot \mathbf{x}), \quad (\text{Equation 1A})$$

where $\mathbf{A}$ is a vector of growth rates, and $\mathbf{B}$ is a matrix of interaction strengths. In components, this becomes

$$\dot{x}_i = x_i \left(A_i - \sum_{j=1}^N B_{ij} x_j \right), \text{ for } i = 1, 2, \dots, N, \quad (\text{Equation 1B})$$

where $A_i > 0$ for a species i growing on its own, $A_i < 0$ for a species dying in the absence of inter-species interactions (Figure 1C), and $B_{ii} > 0$ defines the within-species competition of species i . The interactions between species are defined by $B_{ij} \geq 0$ for $j \neq i$ and may be of different types (Figure 1C): the interaction between species i and j is competitive if $B_{ij}, B_{ji} > 0$; it is mutualistic if $B_{ij}, B_{ji} < 0$; and it is a directed predation interaction, with i predating on j , if $B_{ij} < 0, B_{ji} > 0$. The signs of A_i and B_{ij} for $i, j = 1, 2, \dots, N$, and $j \neq i$ thus define the (network) topology of the ecological interactions. We will often refer to a topology as an "ecology."

Equations 1A and 1B have a single equilibrium of coexistence of all species, $\mathbf{x}_* = \mathbf{B}^{-1} \cdot \mathbf{A}$, which we term feasible if all population abundances at equilibrium are non-negative, i.e., $\min \mathbf{x}_* \geq 0$, and stable if the dynamics return to $\mathbf{x}_*$ upon an infinitesimal perturbation away from it, which is if and only if all eigenvalues of the Jacobian matrix $-\mathbf{x}_* \mathbf{B}$ have negative real parts.

We therefore asked the following question: how is the possibility of stable and feasible coexistence affected by network topology? To address this question statistically, we fixed a network topology, sampled its parameters, (i.e., the magnitudes of the growth rates and interactions strengths, independently and uniformly from a uniform distribution, $|A_i|, |B_{ij}| \stackrel{\text{iid}}{\sim} \mathcal{U}[0, 1]$), and computed the probability $\mathbb{P}$ of $\mathbf{x}_*$ being stable and feasible.

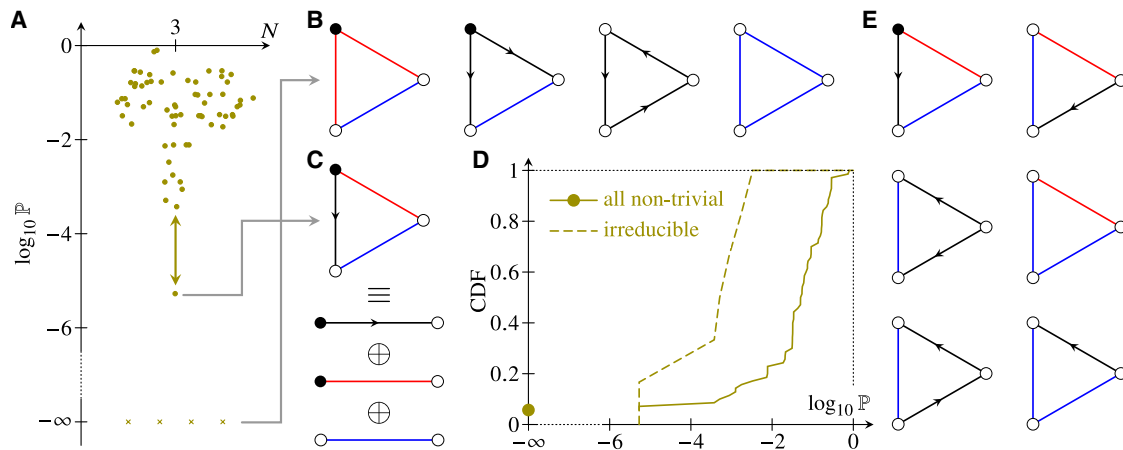


Figure 2. Three-species ecologies: Irreducible ecologies

(A) Swarm plot of the probability $\mathbb{P}$ of stable and feasible coexistence for all 70 non-trivial three-species ecologies. Impossible ecologies have $\log_{10} \mathbb{P} = -\infty$.
(B) List of the four impossible ecologies on three species.
(C) Example of an “irreducible ecology”, showing the decomposition ($\oplus$) into its three trivial or impossible two-species subecologies.
(D) Cumulative distribution function of $\mathbb{P}$ for all 70 non-trivial three-species ecologies and restricted to the 6 irreducible ecologies.
(E) List of the six irreducible ecologies on three species.

The choice of Lotka-Volterra dynamics may appear to restrict our analysis, but importantly, any dynamics reduce to the Lotka-Volterra dynamics (Equation 1A) in the vicinity of an equilibrium (STAR Methods). Our analysis thus covers general ecological dynamics close to coexistence.

Two-species ecologies: Impossible ecologies

We first deployed our framework on the simplest case, of $N = 2$ species. There are ten different ecologies on two species (Figures 1D and 1E). Each of the four topologies in Figure 1E has (at least) one species that dies on its own, highlighted in Figure 1E, and has only deleterious interactions with other species. The abundance of this species must decrease, so there cannot be stable and feasible coexistence of all species in these topologies. We call such ecologies trivial and call other topologies, in which each species is growing on its own or has a favorable interaction with another species, non-trivial. The remaining six ecologies on $N = 2$ species (Figure 1D) are thus non-trivial.

Interestingly, stable and feasible coexistence is only possible in five of them; in the final topology (“obligate mutualism” highlighted in Figure 1D), stable and feasible coexistence is non-trivially impossible, as proved in STAR Methods. We term such a topology an “impossible ecology”.

Three-species ecologies: Irreducible ecologies

Next, we considered the case of $N = 3$ species, for which there are 70 non-trivial ecologies (Figure S1). Sampling magnitudes of growth rates and interaction strengths as described above, we computed numerical estimates of the probability $\mathbb{P}$ of stable and feasible coexistence for each of these topologies (Figure 2A). These calculations suggested that $\mathbb{P}$ vanishes for four ecologies (Figure 2B). These ecologies are indeed impossible ecologies, as proved in STAR Methods. They include competition of a growing species with two obligate mutualists, facultative predation of a growing species on two obligate mutu-

alists, obligate cyclic predation, and obligate mutualism of three species.

Among the remaining 66 possible ecologies, one has a value of $\mathbb{P}$ that is lower by orders of magnitude (Figure 2C). Interestingly, the two-species subecologies of this ecology (Figure 2C) are either trivial or impossible. We therefore term this ecology an “irreducible ecology”: it allows stable and feasible coexistence even though stable and feasible coexistence is possible in none of its subecologies. This definition suggests that irreducible ecologies might have low probabilities of stable and feasible coexistence. Indeed, the cumulative probability density function (Figure 2D) is shifted to lower probabilities upon restriction to the six irreducible ecologies on three species shown in Figure 2E.

Extensions of ecologies

To understand the importance of these irreducible ecologies, we proved a partial converse of these observations. This requires two definitions formalizing our language: (1) we say that a topology is possible if it allows stable and feasible coexistence for some parameter values, and (2) we say that a topology is an extension of another topology if the second can be obtained from the first by removing one species and its interactions with the remaining species. With these definitions, we have the following result.

Theorem

Any non-trivial extension of a possible ecology is itself possible.

Its proof is given in STAR Methods, broken down into two cases: in the first case, the added extension species grows on its own; and in the second case, it does not.

This general result has the strong consequence that the possibility of stable and feasible coexistence in any network topology is determined completely by the subset of irreducible ecologies. In other words, to understand the possibility of stable and feasible coexistence, it suffices to classify the irreducible ecologies.

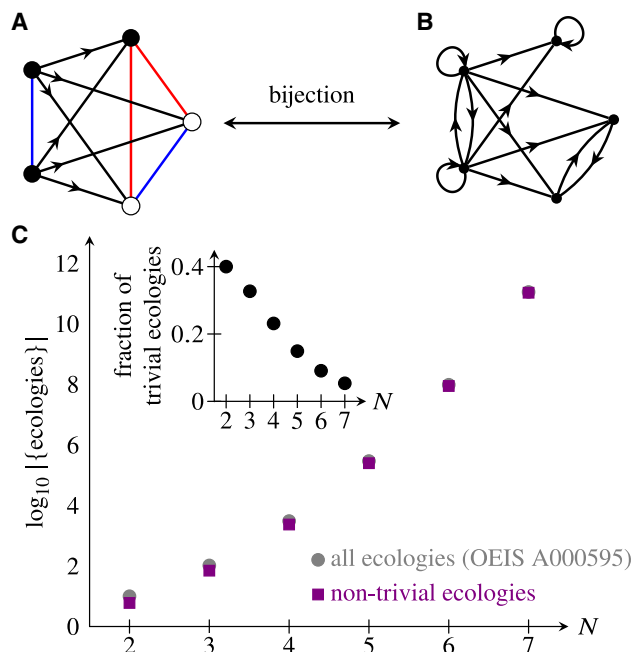


Figure 3. Enumeration of ecologies

(A) Example of a five-species ecology as a complete graph with two-colored nodes and four-colored edges.
(B) Image of this ecology under a bijection onto directed graphs with allowed self-loops. See text for definition of the bijection.
(C) Plot of the number of all and non-trivial ecologies against the number N of species, showing a combinatorial explosion. Inset: fraction of trivial ecologies plotted against N .

Larger ecologies

Armed with this observation, we sought to extend our results to network topologies with $N > 3$ species. First, we had to determine the non-trivial ecologies on N species. This amounts to enumerating the graphs (more technically, the complete directed acyclic graphs) on N two-colored nodes (corresponding to positive or negative growth rates of the N species) and with four-colored edges (corresponding to the competitive, mutualistic, and two directed predator-prey interactions), as illustrated in Figure 3A. However, there is currently no direct, efficient algorithm for enumerating such node-and-edge-colored graphs. We therefore transformed the problem by constructing a bijection between our ecologies and the set of directed graphs with allowed self-loops (Figure 3B): a node will have a self-loop in the image graph under this mapping if it is growing and no self-loop otherwise. Moreover, there are two edges between a pair of nodes in the image graph if the interaction between the corresponding species is mutualistic; there is no edge if it is competitive, and there is a single edge (directed toward the prey) if it is predation. By construction, an ecology is non-trivial if and only if each node in its image under this mapping has out-degree greater than zero. This mapping allows for computationally efficient enumeration of both all and non-trivial ecologies using the nauty library.³¹ Unsurprisingly, we found an extreme combinatorial explosion of the number of all and non-trivial ecologies alike (Figure 3C). The former is a known sequence recorded in the On-line Encyclopedia of Integer Sequences

(OEIS A000595),³² while the latter, following the same trend, does not yet appear there. Interestingly, the fraction of ecologies that are trivial quickly decreases as the number of species increases (Figure 3C, inset).

Since the number of non-trivial ecologies reaches into the hundreds of millions and hundreds of billions for six and seven species, respectively, we cannot feasibly sample these ecologies sufficiently to calculate the associated probabilities for stable and feasible coexistence. However, four- and five-species ecologies are within our grasp. Still, for these large-scale computations, we must use the eigen library for small matrix operations³³ liberally in our C++ code to make it sufficiently efficient (STAR Methods).

Four-species ecologies

We thus computed the probabilities of stable and feasible coexistence for all 2,340 non-trivial four-species ecologies (Figure 4A). It is remarkable that they vary over more than 12 orders of magnitude. In particular, we found 11 impossible ecologies and 18 irreducible ecologies (listed in Figure S2). We emphasize that the status of these 11 impossible ecologies rests only on our numerical observations; we do not have analytical proof of their impossibility to match those for two- and three-species ecologies. This number of 11 impossible ecologies therefore represents an upper bound on the number of impossible ecologies (while the number of 18 irreducible ecologies represents a lower bound). To provide further numerical support for our asserting these ecologies to be impossible, we also sampled feasible equilibria directly but not uniformly (STAR Methods), still without finding parameter instances for allowing stable and feasible coexistence.

Three examples of ecologies that we assert to be impossible are shown as insets in Figure 4A. One of these may be surprising as it is quite asymmetric. The other two are more symmetrical and exhibit structures that we also found in three-species impossible ecologies, such as obligate mutualism or a cycle of obligate predation. We conjecture that these examples extend to infinite families of impossible ecologies, but we do not have an analytical proof of this.

Five-species ecologies and the rareness of impossible and irreducible ecologies

Similarly, we computed the probabilities of stable and feasible coexistence for all 248,436 non-trivial ecologies on five species. The cumulative distribution function (CDF) of these probabilities is shifted toward lower probabilities, compared with that for three- and four-species ecologies (Figure 4B).

We call “non-extension ecologies” the non-trivial ecologies that do not contain a smaller possible subecology, so they are impossible or irreducible by our definitions and our theorem. It follows that the non-extension ecologies on N species are precisely the ecologies of which all the subecologies on $N - 1$ species are trivial or impossible. With this observation, our list of impossible four-species ecologies yields an upper bound of 83 non-extension ecologies on $N = 5$ species; these are listed in Figure S3. On sampling feasible equilibria directly again to identify possible and hence irreducible ecologies on this list (STAR Methods), this leads to an upper bound of 30 impossible ecologies (again listed in Figure S3; this contains the five-species realizations of the infinite families conjectured to be impossible

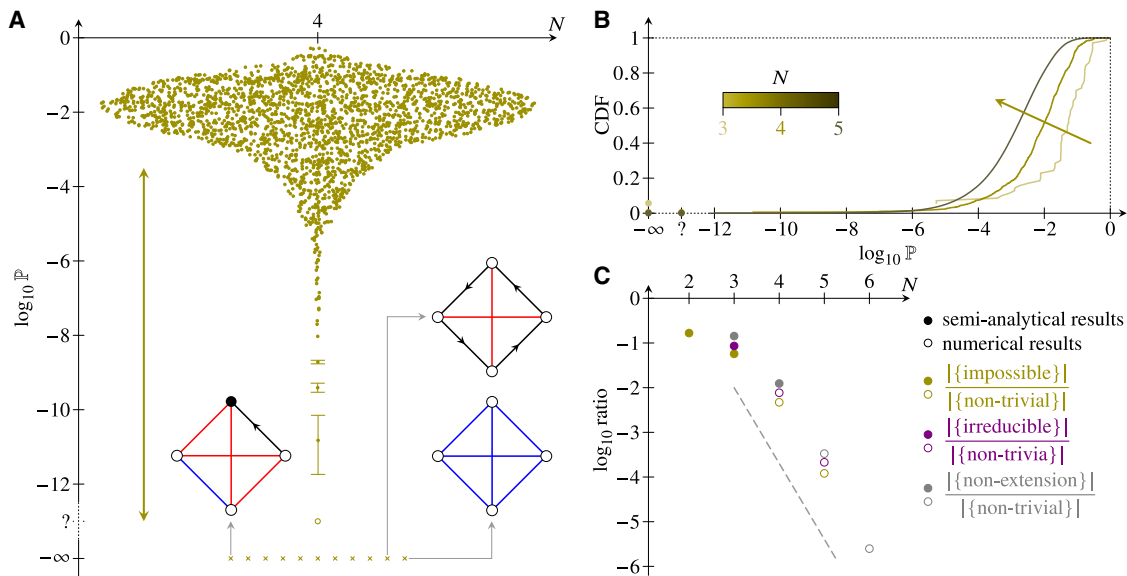


Figure 4. Four- and five-species ecologies and the rareness of impossible and irreducible ecologies

(A) Swarm plot of the probability $\mathbb{P}$ of stable and feasible coexistence for each of the 2,340 non-trivial four-species ecologies. Identification of impossible ecologies ($\log_{10} \mathbb{P} = -\infty$) is based on numerical results only; we have no analytical proof of their impossibility. The question mark (?) indicates ecologies for which direct, non-uniform sampling of feasible equilibria yielded parameter values allowing stable and feasible coexistence but for which no such parameter values could be found using uniform sampling, and hence $\mathbb{P}$ could not be computed. Error bars are 95% confidence intervals (STAR Methods) larger than the plot markers. The vertical arrow emphasizes that the probabilities vary over more than 12 orders of magnitude. Insets: three examples of impossible ecologies; all impossible ecologies are listed in Figure S2.

(B) Cumulative distribution function of $\mathbb{P}$ for three-, four-, and five-species ecologies. The arrow emphasizes the shift toward lower probabilities as the number N of species increases.

(C) Plot of the fraction of impossible, irreducible, and non-extension (i.e., irreducible or impossible) ecologies against N from semi-analytical and numerical computations. The dashed line suggests that these ratios decrease exponentially as N increases.

above). In turn, this list of impossible five-species ecologies yields an upper bound of only 220 non-extension topologies among the 88,124,470 non-trivial ecologies of $N = 6$ species.

Importantly, these numbers represent tiny fractions of the total number of non-trivial ecologies, and our numerical results actually suggest that these fractions decay exponentially as the number of species increases (Figure 4C). The possibility of stable and feasible coexistence is thus completely determined by an exponentially small fraction of all non-trivial ecologies.

Applications

These mathematical results provide the fundamental mathematical constraints on stable and feasible coexistence. We extended these results by applying our framework to three classical problems of theoretical ecology.

Application 1: Interplay of stability and network topology

First, we focused more specifically on the interplay between stability and feasibility of coexistence and network topology by analyzing our results for ecologies with $N = 5$ species in more detail. To this end, we separated the CDF of $\mathbb{P}$ (Figure 4B) according to the number of growing species in each network topology. The results in Figure 5A show that the resulting CDFs are shifted toward higher probabilities the more growing species there are. In other words, species growth tends to stabilize ecologies. We performed a similar analysis for the number of competitive interactions, mutualistic interactions, and predator-prey interactions (Figures 5B–D), which showed that

competition and mutualism tend to be destabilizing, while predation tends to be stabilizing. These observations recover results from random matrix theory for large ecological communities.¹⁷

Additionally, our results suggest that mutualism is only destabilizing if a large proportion of interactions are mutualistic. Indeed, the CDFs for small numbers of mutualistic interactions almost collapse on top of one another; only those for ecologies with a majority of mutualistic interactions are shifted toward low probabilities (Figure 5C).

More importantly, the distributions in Figures 5A–5D are wide, comparably so to the shift between the different distributions. This stresses the importance of the details of the interaction structure relative to the general stabilizing or destabilizing trends of species growth and interaction types.

To make this statement more quantitative, we noted that each ecology e on $N = 5$ species belongs to one and only one class of ecologies $\mathcal{E}(g, c, m)$, with precisely g growing species, c competitive interactions, and m mutualistic interactions, and hence with $p = N(N - 1)/2 - c - m$ predator-prey interactions. Ecologies belonging to the same class therefore have the same number of growing species and the same number of interactions of each type, so they differ only in the network arrangement of these growing species and interactions. We define

$$\varphi(g, c, m) = \left\{ \max \left\{ \frac{\mathbb{P}(e)}{\mathbb{P}(e')}, \frac{\mathbb{P}(e')}{\mathbb{P}(e)} \right\} \mid e \neq e' \in \mathcal{E}(g, c, m) \right\},$$

(Equation 2A)

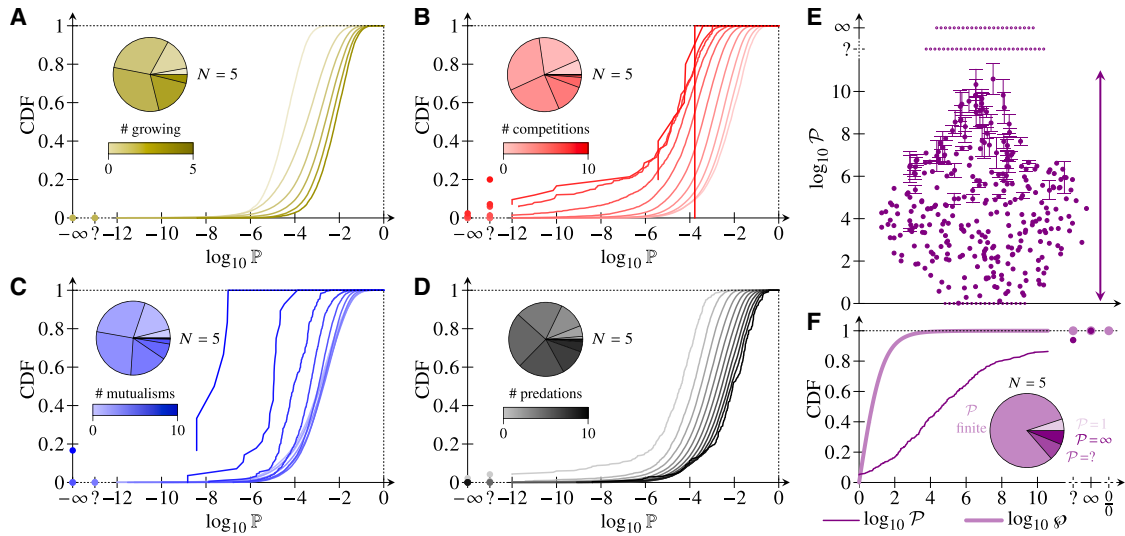


Figure 5. Interplay of stability and network topology, analyzed for all non-trivial ecologies with $N = 5$ species

(A) Cumulative distribution function (CDF) of the probability $\mathbb{P}$ of stable and feasible coexistence restricted to ecologies with g species growing on their own, for $g = 0, 1, \dots, N = 5$. $\log_{10} \mathbb{P} = -\infty$ corresponds to ecologies asserted to be impossible based on numerical calculations. The question mark (?) indicates ecologies for which direct, non-uniform sampling of feasible equilibria yielded parameter values allowing stable and feasible coexistence but for which no such parameter values could be found using uniform sampling, and hence $\mathbb{P}$ could not be computed. CDFs with more growing species are shifted to higher probabilities, showing that growing species are stabilizing. The pie chart inset shows the distribution of the number of growing species in the different ecologies. (B) Analogous plot of CDFs restricted to ecologies with c competitive interactions between species, for $c = 0, 1, \dots, N(N - 1)/2 = 10$, showing that competition is destabilizing. (C) Analogous plot of CDFs restricted to ecologies with m mutualistic interactions between species, for $m = 0, 1, \dots, N(N - 1)/2 = 10$, showing that high proportions of mutualistic interactions are destabilizing. (D) Analogous plot of CDFs restricted to ecologies with p predator-prey interactions between species, for $p = 0, 1, \dots, N(N - 1)/2 = 10$, showing that predation is stabilizing. (E) Swarm plot, for $N = 5$ species, of $\mathcal{P}$, defined in the text; this quantity measures the range of coexistence probabilities $\mathbb{P}$ for classes of ecologies that have the same number of growing species and the same number of mutualistic, competitive, and predator-prey interactions; so they differ only “purely topologically” in the network arrangement of these interactions and growing species. The vertical arrow emphasizes the many orders of magnitude over which $\mathcal{P}$ varies, even for $N = 5$ species. $\log_{10} \mathcal{P} = 0$ corresponds to singleton classes; $\log_{10} \mathcal{P} = \infty$ corresponds to classes containing an impossible ecology. The question mark (?) indicates classes containing one of the ecologies for which $\mathbb{P} \neq 0$ could not be computed. Error bars are 95% confidence intervals (STAR Methods) larger than the plot markers. (F) CDF of $\mathcal{P}$ and ϕ , defined in the text, for the ecological classes with $N = 5$ species. $\frac{0}{0}$ indicates undefined ϕ . Inset: proportion of classes with unit, finite, unknown, and infinite range, respectively.

the set of changes of probabilities of stable and feasible coexistence due to network rearrangements of an identical set of species and interactions between them. (We notice that $\phi(g, c, m)$ contains undefined elements if $\mathcal{E}(g, c, m)$ has more than one impossible ecology.) We also let

$$\mathcal{P}(g, c, m) = \max \phi(g, c, m) = \frac{\max_{e \in \mathcal{E}(g, c, m)} \mathbb{P}(e)}{\min_{e \in \mathcal{E}(g, c, m)} \mathbb{P}(e)}, \quad (\text{Equation 2B})$$

which thus quantifies the range of the probabilities of stable and feasible coexistence in each of these classes. Some classes are singleton classes, for which $\mathcal{P} = 1$ by definition, and classes containing an impossible ecology have $\mathcal{P} = \infty$ (Figures 5E and 5F). Strikingly, among the remaining classes that contain possible ecologies only, there are classes with $\mathcal{P} > 10^{10}$ (Figures 5E and 5F), and more than half have $\mathcal{P} > 10^4$ (Figure 5F), i.e., a range of more than four orders of magnitude, larger than the amount by which the medians of the distributions in Figures 5A–5D are shifted. This shows that even for these small ecologies with

only $N = 5$ species, the effect of structural details on stability of coexistence is humongous and can swamp the effect of the number of growing species or of interactions of different types. However, comparing the distributions of $\mathcal{P}$ and ϕ (Figure 5F) stresses that even within a class with a large range, not all network rearrangements lead to a large change in coexistence probability.

Application 2: Assembly of ecological communities

Next, we turned to the problem of assembly of ecological communities.^{34–41} By definition, the stable and feasible communities that cannot be assembled from a smaller stable and feasible subcommunity are precisely the irreducible ecologies. Their rareness implies, perhaps surprisingly, that the vast majority of communities can be assembled from smaller subcommunities.

More specifically, the proof of our theorem on extensions of ecologies, which is given in STAR Methods, shows that weak interactions between one species and the subcommunity formed by the other species are a sufficient condition for stable and feasible coexistence in the larger assembled community. However, weak interactions constitute but a tiny fraction of the space

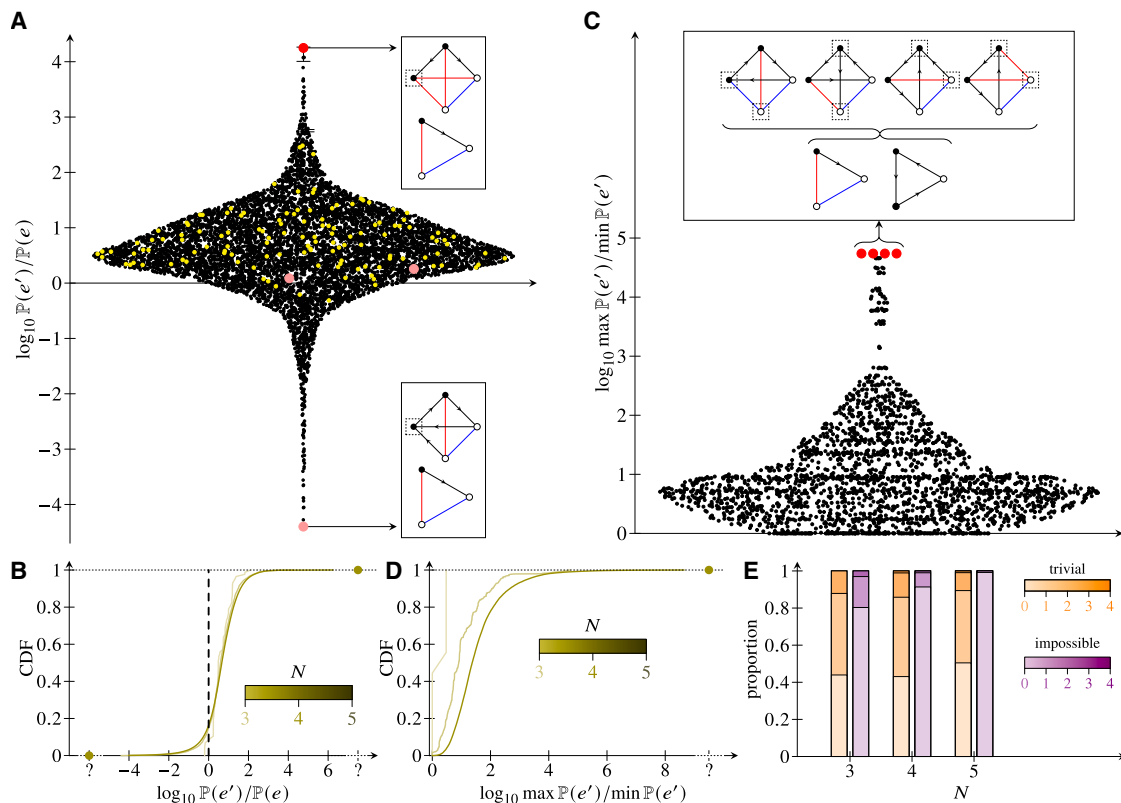


Figure 6. Assembly of ecological communities

(A) Swarm plot of the ratios $r(e', e) = \mathbb{P}(e')/\mathbb{P}(e)$ for all pairs (e', e) of possible ecologies e of $N = 4$ species and their possible subecologies $e' \subset e$ of $N - 1$ species. Ecologies with smaller $r(e', e)$ are “easier” to assemble from a subecology. Insets show the pairs (e', e) maximizing and minimizing $r(e', e)$, both of which contain the irreducible three-species ecology in Figure 2C. Dotted boxes in the insets surround the species to be removed from e to produce e' . Small yellow marks: other pairs (e', e) for which e' is the irreducible ecology in Figure 2C; large light red marks: pairs (e', e) for which e is the four-species ecology that minimizes $r(e', e)$. Error bars are 95% confidence intervals (STAR Methods) larger than the plot markers.

(B) Cumulative distribution function of $r(e', e)$ for $N = 3, 4, 5$. The distributions for different N almost collapse on top of one another. The dashed line highlights that $r(e', e) > 1$ on average. The question mark (?) indicates values for which $r(e', e)$ could not be computed.

(C) Swarm plot of the ratios $R(e) = \max \mathbb{P}(e')/\min \mathbb{P}(e')$ for all ecologies e of $N = 4$ species, where the extrema are taken over all their possible subecologies $e' \subset e$ of $N - 1$ species. The larger $R(e)$ is, the higher the importance of the assembly path. The ratio $R(e)$ reaches its maximal value (large red marks) for four different ecologies shown in the inset, corresponding to one pair of subecologies also shown in the inset. Dotted boxes in the inset again surround the vertices of e to be removed to produce one of these subecologies.

(D) Cumulative distribution function of R for three-, four-, and five-species ecologies. As the number of species increases, the distributions shift to larger values, so the assembly path becomes more important on average.

(E) Distribution, for possible ecologies of $N = 3, 4, 5$ species, of the number of subecologies of $N - 1$ species that are trivial or impossible.

of all interactions. In line with this, previous work has noted that coexistence in subcommunities of coexisting communities is unlikely.^{35,39}

How does the network of ecological interactions affect assembly? We could address this question using the coexistence probabilities $\mathbb{P}$ that we computed above.

First, for each pair (e, e') , in which e is a possible ecology of N species and $e' \subset e$ is a possible subecology of e of $N - 1$ species, we computed the ratios $r(e, e') = \mathbb{P}(e')/\mathbb{P}(e)$, to quantify the “cost” of adding a species to an ecological community. We plot the results in Figure 6A for $N = 4$. On average, $\log_{10} r(e, e') > 0$, i.e., $r(e, e') > 1$, which we expected because the probability of stable and feasible coexistence decreases on average with increasing number of species (Figure 4B). However, a large fraction of ecologies have

$r(e, e') < 1$; thus, they are comparatively “easy” to assemble from a subecology. The strong effect of the network of ecological interactions on assembly is emphasized not only by the wide range of values of $r(e, e')$, spanning more than 8 orders of magnitude for $N = 4$, but also by the fact that both the largest and the smallest values of $r(e, e')$ are associated with the same subecology e' (Figure 4A, insets), which, we note in passing, is the irreducible ecology that we highlighted in Figure 2C. Remarkably, the cost of adding a species remains the same as N increases (Figure 6B): the bulks of the CDFs of $r(e', e)$ appear to collapse on top of one another, although their tails become slightly heavier for larger N .

The cost of different assembly paths leading to the same ecology need not be the same of course, as illustrated in Figure 6A for the ecologies minimizing and maximizing $r(e, e')$, respectively. To

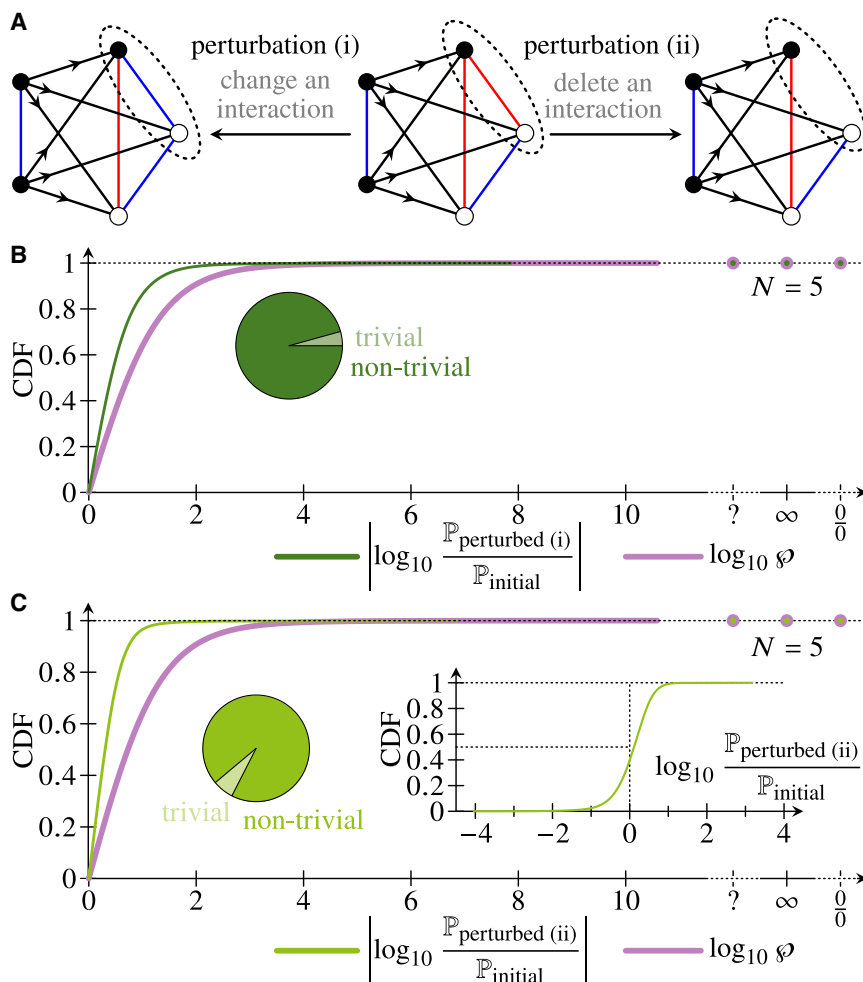


Figure 7. Minimal perturbations of ecologies

(A) Types of minimal perturbations: (i) change and (ii) deletion of an interaction.

(B) Cumulative distribution function (CDF) of the fold change of the probability of stable and feasible coexistence for all minimal perturbations of type (i) of ecologies of $N = 5$ species. CDFs are restricted to non-trivial perturbations; the insets show the proportion of trivial perturbations. Thick line: CDF of ϕ , reproduced from Figure 5F for comparison.

(C) Corresponding CDF for perturbations of type (ii). Additional inset: CDF of the ratio of the probability of stable and feasible coexistence of the perturbed ecology to the unperturbed one, highlighting the asymmetry of perturbations of type (ii). The question mark (?) indicates unknown values for perturbations involving ecologies for which $P \neq 0$ could not be computed; $\frac{0}{0}$ indicates perturbations for which the ratio of probabilities is undefined.

of the ecologies of $N \leq 5$ species that we have analyzed here contain at least one trivial subecology of $N - 1$ species (Figure 6E), and hence their number of possible assembly paths is not maximal.

Application 3: Minimal perturbations of ecologies

Finally, we considered perturbations of the network of ecological interactions that might result from environmental changes^{42,43} or evolutionary pressures. We focused on minimal perturbations that affect a single interaction. These come in two flavors (Figure 7A): (i) perturbations that change the competitive, mutualistic, or predator-prey interaction between any two species to a different one and (ii) perturbations that remove an ecological interaction.

First, for each perturbation of type (i), changing an initial ecology e of $N = 5$ species into a perturbed ecology e' , say, we computed the fold change of the probability of stable and feasible coexistence, $|\log_{10} P(e')/P(e)|$. This ratio is infinite if exactly one of the initial and perturbed ecologies is impossible; it is undetermined if both are trivial, but the fraction of such perturbations is minute (Figure 7B). Interestingly, the fraction of perturbations that result in a trivial ecology is also small (Figure 7B, inset). Importantly, the results reveal a certain robustness of coexistence to these perturbations, compared with network rearrangements of the initial species and their interactions; the distribution of the changes of coexistence probability due to such perturbations is narrower than that of the changes due to such rearrangements (Figure 7B).

Next, we turned to perturbations of type (ii). To analyze these, we needed to enumerate all incomplete networks of ecological interactions of $N = 5$ species. We did this using a mapping similar to the one that we used above to classify complete ecological networks (STAR Methods), finding that there are 569,364 network topologies of $N = 5$ species that are lacking a

quantify this effect, we computed, for each possible ecology e of N species, the ratio

$$R(e) = \frac{\max_{e' \in S(e)} P(e')}{\min_{e' \in S(e)} P(e')} \geq 1, \quad (\text{Equation 3})$$

where $S(e) = \{e' \in e | P(e') > 0\}$ is the set of possible subecologies of e of $N - 1$ species. These ratios vary over about 4 orders of magnitude even for small ecologies of $N = 4$ species (Figure 6C). In particular, the assembly paths maximizing $R(e)$ again involve the irreducible ecology highlighted in Figure 2C. Moreover, the CDFs (Figure 6D) shift toward higher values of R as N increases. In other words, the effect of different assembly paths becomes even stronger for larger communities.

Meanwhile, trivial and impossible ecologies of $N - 1$ species limit the assembly of communities of N species from smaller subcommunities by reducing the number of assembly paths. Because impossible ecologies are very rare, their effect on assembly paths is minute. This is reflected by the distribution of the number of impossible subecologies of N -species ecologies (Figure 6E). The proportion of trivial ecologies decreases more slowly, however (Figure 3C, inset). Correspondingly, about half

single edge. We then computed the probability of stable and feasible coexistence for each of these ecologies as we did for complete networks. Finally, for each complete network e and each incomplete network e' obtained by deletion of a single edge of e , we computed the fold change $|\log_{10} \mathbb{P}(e') / \mathbb{P}(e)|$. Again, this showed that the distribution of the changes of coexistence probability due to such perturbations is narrower than that of the changes due to such rearrangements (Figure 7C) and that only a small fraction of perturbations of type (ii) lead to trivial ecologies (Figure 7C, inset). These statements leave open the question of interest in the context of evolutionary or environmental pressures, whether specific perturbations are (more likely to be) stabilizing or destabilizing. Unlike the perturbations of type (i) that map complete networks to themselves, the perturbations of type (ii) are not symmetric, however. The CDF of the ratio $\mathbb{P}(e') / \mathbb{P}(e)$ displays this asymmetry (Figure 7C, inset), but it again emphasizes the importance of the details of the interaction network; on average, the probability of stable and feasible coexistence is slightly higher in the incomplete network, but this trend can be swamped in some ecologies in which the stable and feasible coexistence is much more likely in the complete network than in the perturbed one (Figure 7C, inset).

DISCUSSION

In this paper, we have analyzed the possibility of stable and feasible coexistence in all non-trivial interaction networks of $N \leq 5$ species. We found that a very small proportion of these are impossible ecologies, in which stable and feasible coexistence is non-trivially impossible. Somewhat conversely, we showed that the possibility of stable and feasible coexistence is completely determined by irreducible ecologies that constitute a similarly tiny proportion of all non-trivial ecologies. Finally, we applied our approach to classical problems of theoretical ecology: the interplay of stability and topology, assembly and disassembly of ecological communities, and perturbations of ecological interactions. In all three cases, we found that the details of the interaction network can have a huge influence on stability, which may swamp general trends.

In this way, our systematic, exhaustive analysis of “small” systems (still far beyond the reach of analytical approaches) complements random matrix theory à la May⁴ by allowing us to address these network details that do not admit a direct statistical description in large ecological communities. Beyond theoretical ecology, in the rather different context of Turing instabilities of reaction-diffusion systems, this kind of approach has previously yielded insights into the robustness of Turing instabilities and the diffusive threshold inherent in the mechanism.^{44,45} Still, it is meet to point out three current limitations of this approach that point toward directions for future work.

First, the probabilities that we have computed here quantify, to some extent, the robustness of stable and feasible coexistence to large environmental perturbations (i.e., large random parameter changes that move the ecology to a different part of parameter space). From this point of view, our results show that some network topologies (namely, those that have a high probability of stable and feasible coexistence, i.e., allow stable and feasible coexistence in large swathes of parameter space) are much more robust to such perturbations than others. The question

whether these topologies are also robust to small environmental perturbations relates instead to the shape of the subset of parameter space in which coexistence is stable and feasible and remains open. It is known, for example, that Turing instabilities, although common, are not robust to small perturbations.⁴⁴

Next, our numerical calculations sample parameters from “agnostic” uniform distributions, but the distributions selected by evolution, for example, through pruning of a larger pool of species,³⁷ are likely complex. The effect of the distribution has been emphasized in particular for the distribution of growth rates³⁸ to solve a conundrum about the stabilizing effect of feasibility.^{5,7,8} (We note in passing that this is likely the reason why our direct sampling of feasible equilibria allowed us to generate feasible and stable parameter sets for systems for which we did not find any such parameters by direct sampling.) It is also interesting to add that, somewhat conversely, the antisymmetric Lotka-Volterra equation (Equation 1A with $\mathbf{A} = \mathbf{0}$ and $\mathbf{B} = -\mathbf{B}^T$) admits “coexistence networks”⁴⁶ in which all species coexist permanently (albeit, trivially, not at steady state) irrespective of the interactions strengths $|\mathbf{B}|$. Similarly, it has been highlighted³⁸ that the distributions of species abundances are more even in stable communities than in those that are merely feasible.

Finally, our results concern linear stability of steady-state coexistence. It is important to acknowledge that this “local asymptotic stability,” although perhaps the most commonly used measure of stability, is only one possible measure of stability⁴⁷ that may even give ecologically misleading results.^{48–50} Extending our general results beyond local asymptotic stability, for example, to permanent coexistence in a limit cycle or more complex attractor, would require going beyond Lotka-Volterra dynamics. Indeed, this analysis would need to include non-linearities such as higher-order interactions, which are known to impact the stability of coexistence.^{51–54} This constitutes another important challenge for the future. Similarly, future work will also need to understand how the details of the network topology affect the transients that can allow unstable ecological communities to persist over long timescales.^{55,56} Additionally, recent work^{50,57} has revealed the effects on stability of adding time delays to the instantaneous interactions of the Lotka-Volterra models. Future work must therefore explore too how such time delays modulate our results.

Nevertheless, our results stress that the devil is in the details: for example, we have shown that the generic stabilizing or destabilizing trends of different interaction types^{17–19} can be swamped by the effect on stability and feasibility of coexistence of permutations of an identical set of competitive, mutualistic, and predator-prey interactions. Previous work⁵⁸ showed that for permutation tests of interaction topology and interaction strength correlations of food webs with predator-prey relationships, the effect of these correlations on stability dominates over that of the interaction topology. However, the regions of parameter space in which coexistence is stable and feasible may be very different for different network topologies; this effect cannot be captured by such permutation tests, so this does not contradict our findings. In this context, the interaction network of competitive, mutualistic, and predator-prey interactions sets the (signs of) all higher-order correlations between the entries of the interaction matrix. The fact that random matrix models, including some of these

higher-order correlations,⁵⁹ display rich additional stability behavior is thus consistent with our results.

Meanwhile, irreducible and impossible ecologies constrain crucial ecological processes. Irreducible ecologies restrict the paths of steady-state (dis)assembly of an ecological community toward stable and feasible coexistence.^{34–41} Impossible ecologies limit continued stable and feasible coexistence when the type of individual ecological interactions between species in a community changes due to environmental changes^{42,43} or evolutionary pressures. Although our analysis of all assembly paths and minimal perturbations gives, of course, a fuller description of these processes, the rareness of these impossible and irreducible ecologies ascribes a certain robustness to them. This says that impossible and irreducible ecologies are more than mere mathematical curios—they have real ecological meaning.

The results of our theoretical analysis can in principle be tested in two ways: first, one might hypothesize that the distribution of actual ecological communities with a given interaction network is proportional to the probability of stable and feasible coexistence that we predict. Unfortunately, it seems that the data that would allow testing of this hypothesis do not yet exist to our knowledge. For example, the “Web of Life” database⁶⁰ does not contain enough data on small ecological communities or indeed on ecological communities with any fixed number N of species to endow such analyses with statistical power. Alternatively, one might hypothesize that the long history of evolution of which actual ecological communities are the product has found ways to overcome the evolutionary cost of ending up at stable and feasible coexistence. From this point of view, the probabilities that we calculate quantify this evolutionary cost (including the infinite cost of impossible ecologies) and the large effect of topological details on this cost.

Our results thus emphasize that generic stability principles can but paint an incomplete picture of the stability of coexistence in general ecological communities, which is inextricably linked to the detailed structure of the network of ecological interactions in the community. However, these principles of course still hold true in an average sense. A fascinating question is therefore the following: in real ecological communities, has evolution led to interaction networks that satisfy these principles, or has it selected those that break them?

RESOURCE AVAILABILITY

Lead contact

Requests for further information should be directed to the lead contact, Pierre A. Haas (haas@pks.mpg.de)

Materials availability

This study did not generate new materials.

Data and code availability

- Network structure data have been deposited at Zenodo and are publicly available as of the date of publication. DOIs are listed in the [key resources table](#).
- All original code has been deposited at Zenodo and is publicly available as of the date of publication. DOIs are listed in the [key resources table](#).
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

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AUTHOR CONTRIBUTIONS

Y.M., C.D.M., and P.A.H. designed the study; Y.M., Sz.H., and P.A.H. wrote code and analyzed data; Sz.H. and P.A.H. derived analytical results; Y.M., C.D.M., and P.A.H. analyzed and interpreted results; Y.M. and P.A.H. wrote the initial draft of the paper; all authors contributed to the final draft of the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- [KEY RESOURCES TABLE](#)
- [METHOD DETAILS](#)
 - Lotka-Volterra equations near coexistence
 - Impossible ecologies of $N = 2$ species
 - Impossible ecologies of $N = 3$ species
 - Proof of the theorem on extensions of ecologies
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- [QUANTIFICATION AND STATISTICAL ANALYSIS](#)

SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
nauty	McKay and Piperno ³¹	N/A
Eigen (version 3.4.0)	eigen.tuxfamily.org	N/A
IGraph/M	Horvát et al. ⁶¹	https://doi.org/10.5281/zenodo.1134932
C++ source code	This paper	https://doi.org/10.5281/zenodo.15013702
MATLAB scripts	This paper	https://doi.org/10.5281/zenodo.15013702
Other		
ecological network data	This paper	https://doi.org/10.5281/zenodo.15013702

METHOD DETAILS

Lotka-Volterra equations near coexistence

Here, we prove that general population dynamics of N species linearise to Lotka-Volterra dynamics near a coexistence equilibrium; this result is probably folklore, but we could not find a reference. Consider general dynamics of a vector $\mathbf{x} = (x_1, x_2, \dots, x_N)$ of population abundances,

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}), \quad (\text{Equation 4})$$

or, in components, $\dot{x}_i = f_i(x_1, x_2, \dots, x_N)$ for $i = 1, 2, \dots, N$. We suppose that Equation 4 have a coexistence equilibrium $\mathbf{x}_* = (x_1^*, x_2^*, \dots, x_N^*)$ such that $x_i^* \neq 0$ for $i = 1, 2, \dots, N$. The Jacobian of Equations 4 at $\mathbf{x}_*$ is $\mathbf{J} = (J_{ij})$.

It now suffices to find $\mathbf{A}$ and $\mathbf{B}$ such that $\mathbf{x}_*$ is an equilibrium of the Lotka-Volterra equations (Equation 1A), and, by definition of linearisation, such that the Jacobians of Equation 1A and Equation 4 at $\mathbf{x}_*$ are equal. The first condition is satisfied by imposing $\mathbf{A} = \mathbf{B} \cdot \mathbf{x}_*$, while the second requires $-\mathbf{x}_* \mathbf{B} = \mathbf{J}$. This can be satisfied by choosing $B_{ij} = -J_{ij}/x_i^*$, which is well-defined by the above assumption on $\mathbf{x}_*$. This proves our claim. $\square$

Impossible ecologies of $N = 2$ species

Here, we prove that obligate mutualism of two species is an impossible ecology. The abundances of two such obligate mutualists obey

$$\dot{x} = x(-a - bx + cy), \quad \dot{y} = y(-d + ex - fy), \quad (\text{Equation 5})$$

where a, b, c, d, e, f are non-negative parameters. The coexistence equilibrium is

$$x_* = \frac{af + cd}{ce - bf}, \quad y_* = \frac{ae + bd}{ce - bf}. \quad (\text{Equation 6})$$

In particular, $x_*, y_* > 0$ for feasibility, which yields $ce > bf$. The Jacobian at this equilibrium is

$$\begin{pmatrix} -bx_* & cx_* \\ ey_* & -fy_* \end{pmatrix}. \quad (\text{Equation 7})$$

Stability requires its determinant to be positive,⁶² which implies $(bf - ce)x_*y_* > 0$. Since $x_*, y_* > 0$ for feasibility, this yields $bf > ce$, which is a contradiction. $\square$

Impossible ecologies of $N = 3$ species

Here, we prove that obligate mutualism of three species, obligate cyclic predation of three species, facultative predation on two obligate mutualists, and competition with two obligate mutualists are impossible ecologies.

Obligate mutualism

Consider obligate mutualism of three species, the abundances of which satisfy

$$\dot{x} = x(-a - bx + cy + dz), \quad (\text{Equation 8A})$$

$$\dot{y} = y(-e + fx - gy + hz), \quad (\text{Equation 8B})$$

$$\dot{z} = z(-i + jx + ky - lz), \quad (\text{Equation 8C})$$

wherein $a, b, c, d, e, f, g, h, i, j, k, l$ are non-negative parameters. The coexistence equilibrium (x_*, y_*, z_*) has

$$x_* = \frac{k(ah - de) - (agl + cel + ich + dg)}{D}, \quad (\text{Equation 9A})$$

$$y_* = \frac{j(de - ah) - (ble + afl + ibh + idf)}{D}, \quad (\text{Equation 9B})$$

where $D = bgl - bhk - cfl - chj - dfk - dgj$. Now assume feasibility. If $D > 0$, then $x_* > 0 \Rightarrow k(ah - de) > 0$, but $y_* > 0 \Rightarrow j(de - ah) > 0$, so $ah \geq de$, a contradiction. Hence $D < 0$. Now the characteristic polynomial of the Jacobian of Equations 8 at (x_*, y_*, z_*) is $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3$, with $a_3 = Dx_*y_*z_*$. One of the (necessary) Routh-Hurwitz conditions for stability is $a_3 > 0$.⁶² Since $D < 0$, this implies $x_*y_*z_* < 0$, contradicting feasibility. $\square$

Obligate cyclic predation

Consider three species with obligate cyclic predation, the abundances of which evolve according to

$$\dot{x} = x(-a - bx + cy - dz), \quad (\text{Equation 10A})$$

$$\dot{y} = y(-e - fx - gy + hz), \quad (\text{Equation 10B})$$

$$\dot{z} = z(-i + jx - ky - lz), \quad (\text{Equation 10C})$$

wherein $a, b, c, d, e, f, g, h, i, j, k, l$ are non-negative parameters. The coexistence equilibrium (x_*, y_*, z_*) has

$$x_* = \frac{g(di - al) - (ahk + cel + chi + dek)}{D}, \quad (\text{Equation 11A})$$

$$y_* = \frac{f(al - di) - (ahj + bel + bhi + dej)}{D}, \quad (\text{Equation 11B})$$

where $D = bgl + bhk + cfl - chj + dfk + dgj$. As in the case of obligate mutualism, $D < 0$ because $D > 0$ yields the contradiction $di \geq al$ from $x_*, y_* > 0$. The Routh-Hurwitz conditions for stability then imply $x_*y_*z_* < 0$ as in that case, contradicting feasibility again. $\square$

Facultative predation on two obligate mutualists

Consider facultative predation on two obligate mutualists, described by

$$\dot{x} = x(a - bx + cy + dz), \quad (\text{Equation 12A})$$

$$\dot{y} = y(-e - fx - gy + hz), \quad (\text{Equation 12B})$$

$$\dot{z} = z(-i - jx + ky - lz), \quad (\text{Equation 12C})$$

wherein $a, b, c, d, e, f, g, h, i, j, k, l$ are non-negative parameters. The coexistence equilibrium (x_*, y_*, z_*) has

$$x_* = \frac{g(al - di) - (ahk + cel + chi + dek)}{D}, \quad (\text{Equation 13A})$$

$$y_* = \frac{f(di - al) - (ahj + bel + bhi + dej)}{D}, \quad (\text{Equation 13B})$$

where $D = dgj + chj + dfk - bhk + cfl + bgl$. As in the previous cases, $D < 0$ because $D > 0$ yields the contradiction $al \geq di$ from $x_*, y_*, z_* > 0$. The Routh-Hurwitz conditions for stability then imply $x_* y_* z_* < 0$ as in those cases, contradicting feasibility once again. $\square$

It is remarkable that the seemingly worse case of obligate predation on two obligate mutualists allows stable and feasible coexistence, so is an irreducible ecology!

Competition with two obligate mutualists

Consider competition with two obligate mutualists, described by

$$\dot{x} = x(a - bx - cy - dz), \quad (\text{Equation 14A})$$

$$\dot{y} = y(-e - fx - gy + hz), \quad (\text{Equation 14B})$$

$$\dot{z} = z(-i - jx + ky - lz), \quad (\text{Equation 14C})$$

wherein $a, b, c, d, e, f, g, h, i, j, k, l$ are non-negative parameters. The coexistence equilibrium (x_*, y_*, z_*) has

$$y_* = \frac{d(ej - fi) - (afi + ahj + bel + bhi)}{D}, \quad (\text{Equation 15A})$$

$$z_* = \frac{c(fi - ej) - (afk + agj + bek + bgi)}{D}, \quad (\text{Equation 15B})$$

where $D = bgl - bhk - cfl - chj - dfk - dgj$. As in the previous cases, $D < 0$ because $D > 0$ yields the contradiction $ej \geq fi$ from $y_*, z_* > 0$. The Routh-Hurwitz conditions for stability then imply $x_* y_* z_* < 0$ as in those cases, contradicting feasibility once again. $\square$

Proof of the theorem on extensions of ecologies

Here, we prove the theorem on extensions of ecologies stated in the main text:

Theorem

Any non-trivial extension of a possible ecology is itself possible.

Proof

Let $N \geq 2$ be an integer. Consider a possible topology of $N - 1$ species, the abundances $\mathbf{x}_0$ of which follow

$$\dot{\mathbf{x}}_0 = \mathbf{x}_0(\mathbf{A}_0 - \mathbf{B}_0 \cdot \mathbf{x}_0),$$

with stable and feasible coexistence equilibrium $\mathbf{x}_0^* = \mathbf{B}_0^{-1} \cdot \mathbf{A}_0$, and associated Jacobian $\mathbf{J}_0 = -\mathbf{x}_0^* \mathbf{B}_0$ with stable eigenvalues $\mathcal{E}(\mathbf{J}_0)$. Choose $\varepsilon \ll 1$ such that

$$\min|\mathbf{A}_0|, \min|\mathbf{B}_0|, \min \mathbf{x}_0^*, \min|\text{Re}(\mathcal{E}(\mathbf{J}_0))| \gg \varepsilon. \quad (\text{Equation } \ddagger)$$

We extend this ecology non-trivially by adding species N , with abundance x_N . This extended ecology is described by the block equation

$$\dot{\mathbf{x}} = \mathbf{x} \left[\begin{pmatrix} \mathbf{A}_0 \\ a \end{pmatrix} - \begin{pmatrix} \mathbf{B}_0 & \mathbf{b} \\ \mathbf{c}^\top & d \end{pmatrix} \cdot \mathbf{x} \right], \text{ with } \mathbf{x} = \begin{pmatrix} \mathbf{x}_0 \\ x_N \end{pmatrix},$$

and where $a > 0$ if species N grows on its own, $a < 0$ if species N dies in the absence of inter-species interactions, and where $d > 0$ defines its within-species competition, and the vectors $\mathbf{b}, \mathbf{c}$ determine its interactions with the other species. We denote by $\mathbf{x}_*$ the corresponding coexistence equilibrium, and $\mathbf{J}$ the associated Jacobian. The proof now divides into two cases:

- (1) In the first case, $a > 0$, and we choose $a, d = O(1)$ and $\mathbf{b}, \mathbf{c} = O(\varepsilon)$, so that

$$\dot{\mathbf{x}} = \mathbf{x} \left[\begin{pmatrix} \mathbf{A}_0 \\ a \end{pmatrix} - \begin{pmatrix} \mathbf{B}_0 & O(\varepsilon) \\ O(\varepsilon) & d \end{pmatrix} \cdot \mathbf{x} \right].$$

We now use assumptions in Equation $\ddagger$ repeatedly to obtain, first,

$$\mathbf{x}_* = \begin{pmatrix} \mathbf{B}_0 & \mathbf{0} \\ \mathbf{0}^\top & d \end{pmatrix}^{-1} \cdot \begin{pmatrix} \mathbf{A}_0 \\ a \end{pmatrix} + O(\varepsilon) = \begin{pmatrix} \mathbf{x}_0^* \\ a/d \end{pmatrix} + O(\varepsilon),$$

and thence

$$\mathbf{J} = - \left(\frac{\mathbf{x}_0^*}{a/d} \right) \left(\begin{array}{c|c} \mathbf{B}_0 & \mathbf{0} \\ \hline \mathbf{0}^\top & d \end{array} \right) + O(\varepsilon) = \left(\begin{array}{c|c} \mathbf{J}_0 & \mathbf{0} \\ \hline \mathbf{0}^\top & -a \end{array} \right) + O(\varepsilon).$$

Thus $\mathbf{x}_*$ is feasible. Moreover, $\mathcal{E}(\mathbf{J}) = \{\mathcal{E}(\mathbf{J}_0), -a\} + O(\varepsilon)$, whence $\mathbf{x}_*$ is stable, too.

(2) In the second case, $a > 0$. Let $\mathbf{c} = (c_1, c_2, \dots, c_{N-1})$. Because the extension is non-trivial by assumption, there exists $i \in \{1, 2, \dots, N-1\}$ such that $c_i < 0$. Without loss of generality, $i = 1$ and we write $\mathbf{c} = (c_1, \mathbf{c}')$. We now choose $a = O(\varepsilon)$, $\mathbf{b} = O(\varepsilon)$, $c_1 = O(\varepsilon^{1/2})$, $\mathbf{c}' = O(\varepsilon)$, $d = O(1)$. Writing $c_1 = -\varepsilon^{1/2}\gamma$, where $\gamma = O(1)$ and $\gamma > 0$, we obtain

$$\dot{\mathbf{x}} = \mathbf{x} \left[\left(\frac{\mathbf{A}_0}{O(\varepsilon)} \right) - \left(\begin{array}{c|c} \mathbf{B}_0 & O(\varepsilon) \\ \hline -\varepsilon^{1/2}\gamma & O(\varepsilon) \end{array} \right) \cdot \mathbf{x} \right],$$

yielding the equilibrium condition

$$\left(\begin{array}{c|c} \mathbf{B}_0 & \mathbf{0}^\top \\ \hline -\varepsilon^{1/2}\gamma & \mathbf{0} \end{array} \right) \cdot \mathbf{x}_* = \left(\frac{\mathbf{A}_0}{0} \right) + O(\varepsilon).$$

We decompose

$$\mathbf{x}_* = \begin{pmatrix} \chi_* \\ x_N^* \end{pmatrix} + O(\varepsilon).$$

The first components of the equilibrium condition become

$$\mathbf{B}_0 \cdot \chi_* = \mathbf{A}_0 \Rightarrow \chi_* = \mathbf{B}_0^{-1} \cdot \mathbf{A}_0 = \mathbf{x}_0^*.$$

Writing $\mathbf{x}_0^* = (\xi^*, \xi'_*)$ with in particular $\xi^* > 0$, its final component then yields

$$-\varepsilon^{1/2}\gamma\xi^* + dx_N^* = 0 \Rightarrow x_N^* = \varepsilon^{1/2}\frac{\gamma\xi^*}{d}.$$

In particular, this shows that $\mathbf{x}_*$ is feasible. Moreover,

$$\begin{aligned} \mathbf{J} &= - \left(\frac{\mathbf{x}_0^*}{\varepsilon^{1/2}\gamma\xi^*/d} \right) \left(\begin{array}{c|c} \mathbf{B}_0 & \mathbf{0}^\top \\ \hline -\varepsilon^{1/2}\gamma & d \end{array} \right) + O(\varepsilon) \\ &= \left(\begin{array}{c|c} \mathbf{J}_0 & \mathbf{0} \\ \hline \mathbf{0}^\top & -\varepsilon^{1/2}\gamma\xi^* \end{array} \right) + O(\varepsilon), \end{aligned}$$

which has eigenvalues $\mathcal{E}(\mathbf{J}) = \{\mathcal{E}(\mathbf{J}_0), -\varepsilon^{1/2}\gamma\xi^*\} + O(\varepsilon)$, which are stable.

Stable and feasible coexistence is thus possible in the extended ecology in either case. This completes the proof of the theorem. $\square$

Numerical Methods

Numerical tolerances and cutoffs

To avoid numerical errors in the computation of deciding whether coexistence is stable and feasible for randomly sampled parameter values $|\mathbf{A}|$, $|\mathbf{B}|$, we replace, for numerical purposes, the exact feasibility and stability conditions with $\min \mathbf{x}_* > \tau$ and $\max \operatorname{Re}(-\mathbf{x}_* \mathbf{B}) < -\tau$, respectively, to which conditions we add $|\det \mathbf{B}| > \tau$. Our tests (not shown) show that, by choosing $\tau = 10^{-7}$, this avoids errors due to the entries of $\mathbf{x}_*$ varying by more than (machine precision) $^{-1}$.

Somewhat conversely, we declare systems with $|\min \mathbf{x}_*| \leq \tau$ or $|\max \operatorname{Re}(-\mathbf{x}_* \mathbf{B})| \leq \tau$ or $|\det \mathbf{B}| \leq \tau$ to be uncertain. Thus, after n samplings, of which c allowed stable and feasible coexistence and u were uncertain, we estimate the probability of stable and feasible coexistence to be $p = (c + u/2)/n$. We add 95% Wilson confidence intervals⁶³ to the endpoints of the interval $[c/n, (c + u)/n]$ to obtain an interval I that defines the error bars reported in Figures 4, 5, and 6.

Probabilities were computed by sampling random parameter values until the relative uncertainty $e = |I|/p$ of our probability estimate satisfied $e \leq e_{\text{stop}} = 0.01$, or $n > n_{\text{max}}$. We took $n_{\text{max}} = 10^{11}$ for $N = 4$ or $n_{\text{max}} = 10^{10}$ for $N = 5$.

Direct sampling of feasible equilibria

Feasible equilibria of a non-trivial ecology can be sampled directly (but non-uniformly in parameter space) by the following algorithm:

```
input:  interaction_signs[N,N], growth_signs[N]
output: x[N], A[N], B[N,N]

for i = 1..N:
    x[i] = random
for j = 1..N:
    B[i,j] = interaction_signs[i,j]*random
    A = B*x    # matrix product
for i such that growth_signs[i] == +:
    d = A[i] - B[i,i]*x[i]
    if d < 0:
        B[i,i] = (-d+random)/x[i]
for i such that growth_signs[i] == -:
    find j such that interaction_signs[i,j] == -
    d = A[i] - B[i,j]*x[j]
    if d > 0:
        B[i,j] = (-d-random)/x[j]
```

This algorithm generates a feasible equilibrium $\mathbf{x}_*$ and samples a random matrix of interaction strengths $\mathbf{B}$ consistent with the topology. It then adjusts one term in each row of $\mathbf{B}$, while keeping it consistent with the topology, to ensure that $\mathbf{A} = \mathbf{B} \cdot \mathbf{x}_*$ is consistent with the topology; we stress that the `find` instruction in the final loop must return a result because the topology is non-trivial by assumption.

This choice of algorithm is not of course unique, but we found that it allowed us to find parameter values allowing stable and feasible coexistence for topologies for which we were unable to find such parameter values by uniform sampling of parameters.

To prove that certain ecologies are possible by exhibiting parameter values giving stable and feasible coexistence, we sampled up to $n_{\max} = 10^{12}$ ($N = 4, 5$) systems. Systems for which no such parameter values had been found after $n_{\max}$ samplings were declared to be impossible (Figures S2B and S3B).

Enumeration of (non-extension) ecologies

By our theorem on extensions of ecologies, an ecology on N species is a non-extension ecology if and only if all its non-trivial subecologies on $N - 1$ species are impossible.

To classify non-extension ecologies on N species using `nauty`³¹ and the bijection discussed in the main text, we therefore first generate all non-trivial ecologies using `geng N | directg | vcolg -m2 -o | pickg - ~ d0` in which the final pipe removes graphs that have vertices with zero out-degree, hence are trivial. We obtain all non-trivial subecologies by piping the result to the `nauty` command `delpthg -m1`, of which we modified the output format to track which ecology each subecology in the resulting list arises from. We then generated adjacency matrices of all impossible ecologies on $N - 1$ species and their permutations, and converted them to `digraph`⁶ format using the `nauty` tool `amtog -z`, which we piped to `uniq` to remove repeats. Because of the small number of impossible ecologies, we could then find the impossible subecologies on $N - 1$ species and hence the non-extension ecologies on N species by brute force.

Enumeration of ecologies with deleted edges

To generate all networks of ecological interactions, not only the complete networks, we made use of a similar one-to-one mapping of ecologies to directed graphs as described in the main text. However, in this case, two nodes will have no connection if there is no ecological interaction between them, and both competitive and mutualistic interactions are mapped to a reciprocal pair of directed edges. Mutualistic and competitive interactions are then disambiguated by colouring the reciprocal edge pair with one of two colours. All unidirectional edges are assigned a third colour.

To implement this mapping, we first generated all directed graphs on N nodes using the `nauty`³¹ command `geng -c N | directg | vcolg -m2 -o`.

Then, for each directed graph, we used the `IGraph/M` software package⁶¹ to colour its R reciprocal edge pairs as mutualistic or competitive in all 2^R possible ways, and eliminated isomorphic duplicates between these colourings by pairwise testing using the VF2 algorithm⁶⁴ implemented in the `IGVF2IsomorphicQ` function of `IGraph/M`.

QUANTIFICATION AND STATISTICAL ANALYSIS

The only statistical analysis performed is the calculation of error bars on individually computed probabilities. These error bars are shown in [Figures 2A, 4A, 5E, 6A, and 6C](#) when they are larger than the plot markers. We calculate these error bars by using 95% Wilson confidence intervals,⁶³ augmented with a correction for systems that are numerically uncertain, as introduced in [method details](#).

All probabilities were computed by sampling n random parameter values until the length e of these confidence intervals satisfied $e \leq e_{\text{stop}} = 0.01$, or $n > n_{\text{max}}$. We took $n_{\text{max}} = 10^{11}$ for $N = 4$ or $n_{\text{max}} = 10^{10}$ for $N = 5$.