

Coexistence of many species in random ecosystems

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Rich ecosystems harbour thousands of species interacting in tangled networks encompassing predation, mutualism and competition. Such widespread biodiversity is puzzling, because in ecological models it is exceedingly improbable for large communities to stably coexist. One aspect rarely considered in these models, however, is that coexisting species in natural communities are a selected portion of a much larger pool, which has been pruned by population dynamics. Here we compute the distribution of the number of species that can coexist when we start from a pool of species interacting randomly, and show that even in this case we can observe rich, stable communities. Interestingly, our results show that, once stability conditions are met, network structure has very little influence on the level of biodiversity attained. Our results identify the main drivers responsible for widespread coexistence in natural communities, providing a baseline for determining which structural aspects of empirical communities promote or hinder coexistence.

Lotka¹ and Volterra² first attempted to mathematize the population dynamics of interacting species, and their model has been methodically analysed and refined by countless studies³. Analysing models that include more than a handful of interacting populations has, however, proved remarkably difficult, despite the fact that ecosystems harbour hundreds of populations, interacting through complex networks encompassing consumption, competition and mutualism⁴.

In the Lotka–Volterra model and similar models, it is exceedingly improbable to obtain the coexistence of all species in a large community without fine-tuning the parameters^{5–9}, and such fine-tuning is questionable at best for biological systems¹⁰. Consider, however, that in natural communities the extant species we observe are a selected portion of a much larger pool, which has then been pruned by population dynamics^{7,11}. Therefore, to understand the establishment and maintenance of natural communities we need to change our focus: rather than asking what is the probability that all species in a community coexist, here we attempt to predict the number of extant species we obtain when starting from a species pool of n species, and let the dynamics unfold. As a limiting case, we study the behaviour of ecological models in which the parameters are randomly drawn from fixed distributions, meaning that species have not had time to co-adapt or co-evolve. Although many studies have investigated, numerically^{12–19} or analytically^{20,21}, the effect of particular parameterizations and network structure on the average number of coexisting species, here we derive the full distribution.

We start by studying coexistence in random ecological communities, and, having derived the behaviour of random networks of interacting species, we probe the effect of particular network structures on coexistence. We find that network structure, which has been shown to have strong influence on the stability properties of ecological communities^{4,8,22–25}, has instead very little effect on coexistence, once stability conditions are met.

The idea of studying random ecological communities was pioneered by May⁵, who determined the local stability properties of large ecosystems through an application of random matrix theory.

His work has been generalized and refined^{26,27}, so that we can now characterize the stability of ecological networks displaying hierarchical²³ or modular²⁴ structure. Similarly, ‘structural stability’ (the range of conditions leading to positive equilibria in ecological systems) has been investigated by letting the growth rate of the species^{8,9}, or the interactions between species²⁸, vary randomly. Clearly, to have robust coexistence we need a combination of the two: species densities must be positive and a stable attractor is needed to allow densities to rebound when perturbed.

Results

Our goal is to compute the probability of observing k species stably coexisting when starting with a pool of n interacting populations and random parameters. For example, we take the generalized Lotka–Volterra system of equations

$$\frac{dX_i(t)}{dt} = X_i(t) \left(r_i + \sum_j A_{ij} X_j(t) \right) \quad (1)$$

and sample parameters at random and we want to determine how many species coexist once the dynamics have elapsed.

We first analyse the case closest to the spirit of May’s contribution, which can be thought of as a caricature of a food web: some species can grow in isolation (such as producers, with positive intrinsic growth rates), while other species can grow only as a result of their interactions (such as consumers, with negative growth rates); all species establish random interactions with each other. More specifically, we sample the intrinsic growth (death) rates r_i and the inter-specific interactions A_{ij} ($i \neq j$) from distributions (not necessarily the same) that are symmetric around zero (such that $P(x) = P(-x)$). For example, we could sample all these entries from a normal distribution with mean zero. We set the intra-specific interactions A_{ii} by summing a mean-zero symmetric random variable and a constant d_i (not necessarily the same for all i). We note that in this way, about

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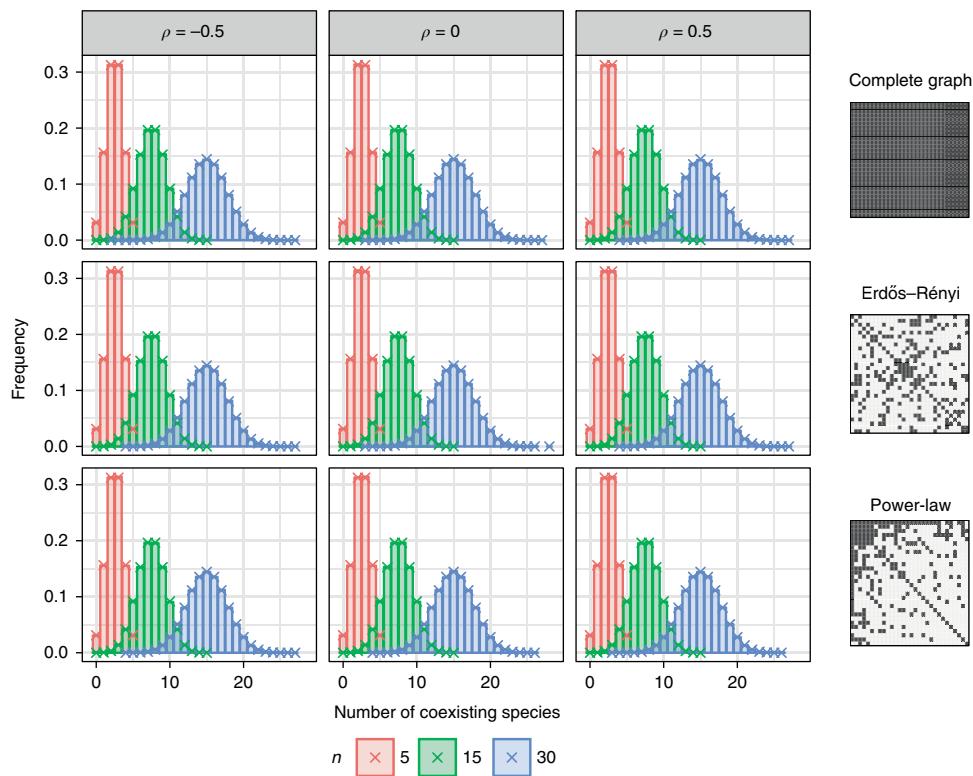


Fig. 1 | Number of coexisting species when interactions and intrinsic growth rates are randomly sampled from the standard normal distribution. For each panel, histograms show the number of coexisting species out of 2×10^5 simulations, when starting from a different number of species n (colours) and interaction matrices A that are strongly stable. Binomial distributions $B(n, 1/2)$ are reported as crosses. In the three rows, different network structures are used to set the positions of the nonzero coefficients (as exemplified by the adjacency matrices on the right): top, complete graphs; middle, Erdős-Rényi graphs; and bottom, power-law graphs. The results for other network structures are presented in Supplementary Fig. 3. Sampling the off-diagonal coefficients of matrix A independently ($\rho=0$, centre), or in correlated pairs (A_{ij}, A_{ji}) ($\rho \neq 0$), has no effect on the expected number of coexisting species.

half of the species will grow in isolation, while the rest rely on ‘consumption’ for their survival.

We start by presenting a result on the feasibility of equilibria. Under the conditions outlined above, the probability that a system composed of n species has a completely positive equilibrium point (in which all species have positive density) is $1/2^n$, irrespective of the choice of d_i , and the exact shapes of the distributions (Supplementary Information 1). Our proof extends previously known mathematical results²⁹, confirming the conjecture put forward by Goh and Jennings forty years ago¹³.

Clearly, feasibility is only necessary, but not sufficient, for coexistence. To study coexistence, we make the stronger assumption that the matrix $A + A^T$ is negative definite^{30,31}. This property implies Lyapunov diagonal stability, and is a strong form of stability routinely assumed in studies of feasibility^{8,9} that can be always attained by choosing suitable large and negative d_i . Under these conditions, a generalized Lotka–Volterra model has a single, globally attractive equilibrium, called the non-invasive solution (also known as the saturated rest point^{32,33}): k species have positive density at equilibrium, while all the other $n - k$ species cannot invade this community, and will go extinct irrespective of initial conditions. Surprisingly, when we sample the parameters at random as specified above, the non-invasibility and feasibility conditions for each subset of species balance out, such that each species has probability 1/2 of being included in the non-invasive, globally attractive solution. Hence, the probability $P(k|n)$ of finding k species coexisting when we start with n follows the binomial distribution $B(n, 1/2)$ (Fig. 1 and Supplementary Information 1). This beautifully simple result means that if we were to start with a strongly stable (that is, with $A + A^T$ negative definite) random matrix of interactions and

random growth rates, about half of the species would coexist, irrespective of the choice of n . Remarkably, this is exactly what we would expect if species were not to interact with each other at all (that is, $A_{ii} = d_i < 0$ for all i and $A_{ij} = 0$ for all $i \neq j$).

Extending May’s results, Allesina and Tang²⁶ showed how stability is strongly influenced by the correlation between the inter-specific interactions: if we sample interactions in pairs (A_{ij}, A_{ji}) from a bivariate distribution with mean zero and correlation ρ , then stability is enhanced by choosing a negative correlation. When analysing coexistence, breaking the independence among the inter-specific effects by sampling them in pairs from a bivariate distribution has no effect: we recover the same condition for feasibility, and the same distribution for the number of coexisting species (Fig. 1 and Supplementary Information 1).

So far, we have assumed that every species interacts with every other. To study the effect of network structure, we set most of the interactions to zero, and choose the position of the nonzero coefficients according to the adjacency matrix of (1) an Erdős–Rényi random graph, (2) a random graph with power-law degree distribution, (3) a graph displaying modular structure, or (4) a graph displaying bipartite structure. Irrespective of the choice of network structure, we always recover the same distribution for the number of coexisting species k (Fig. 1 and Supplementary Information 1). This is interesting, because network structure strongly influences stability^{23–26}. However, because in our analysis stability is assumed, we find that the exact location of the nonzero interactions has no effect on coexistence.

The results above hold when we sample the growth rates and the inter-specific effects from symmetric distributions with mean zero, meaning that positive effects (such as the contribution of prey to

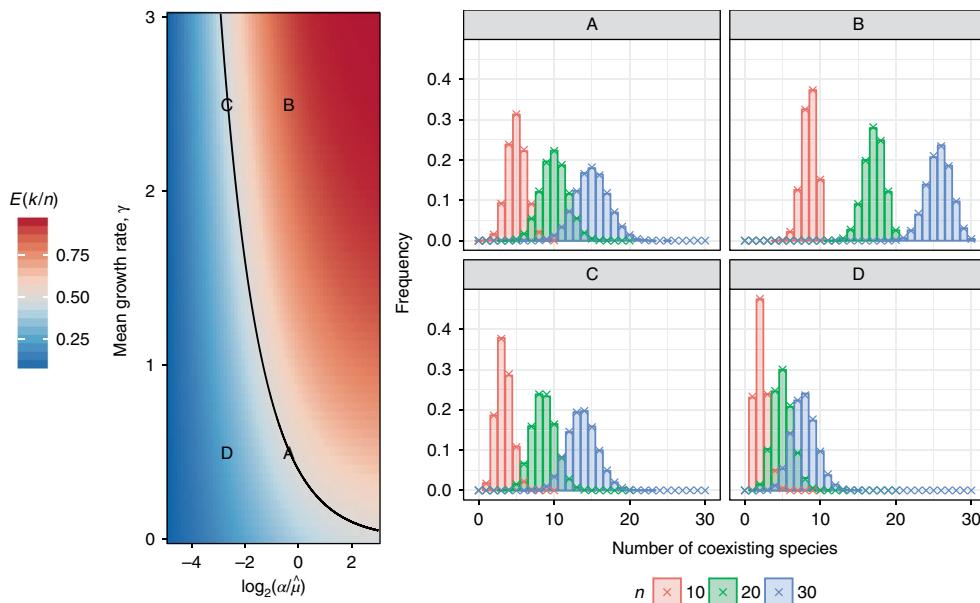


Fig. 2 | Number of coexisting species for competitive interactions. When species interact competitively, the histograms deviate from the binomial distribution, but can still be computed using a double integral (crosses, see Supplementary equation (38)). Here the interactions are set to $A_{ij} = \hat{\mu}/n < 0$, intra-specific competition to $A_{ii} = \alpha$, and intrinsic growth rates are normally distributed with mean γ . The expected value of the ratio k/n , $E(k/n)$, is drawn on the left in the relevant parameter space: we chose two points (A, C) for which predictions in the nonzero mean case match closely those for mean zero ($E(k/n) = 1/2$); in case B the number of species coexisting exceeds that for the mean-zero case; for point D the expectation is lower. The analytical prediction in equation (1) is also shown (line).

the growth of predators) on average counterbalance negative ones (such as the effects of predators on prey). Of course, this need not be the case in natural communities, and therefore we examine the mathematically much more challenging case in which the entries have mean nonzero.

To this end, we consider a simple model of interacting competitors: we set all inter- and intra-specific interactions to be negative, and consider the case of random growth rates. In this case we assume that all species in the pool are sampled from a common habitat, and therefore have growth rates with a well defined average value. In particular, we sample the intrinsic growth rates from a normal distribution with mean γ , and, for simplicity, we construct A by setting all inter-specific interactions to be competitive, $A_{ij} = \mu = \hat{\mu}/n < 0$, and all intra-specific effects to $A_{ii} = d_i = \alpha < 0$. The numerical simulations presented below show that our results approximate well the case in which the elements of A are variable (for example, when the nonzero elements are arranged in a network).

Again, we consider matrices for which α is sufficiently strong to yield Lyapunov diagonal stability ($\alpha < \mu < 0$). When we sample the growth rates from a normal distribution, then the equilibrium point $X = -A^{-1}r$ is described by a multivariate normal distribution. Exploiting this fact, we are able to express the probability that k species form a non-invasive and feasible subset as a double integral that can be used to compute the size of the non-invasive community (Supplementary Information). The double integral can be approximated, for large n , via a saddle-point technique to obtain an accurate analytical approximation for the distribution $P(k|n; \alpha, \hat{\mu}, \gamma)$. We note that in this setting, growth rates need to be positive for species to survive, and therefore we only consider the case of $\gamma \geq 0$. We also show (Supplementary Information 6) that the results remain qualitatively unchanged when rates are drawn from a truncated Gaussian distribution, which forces all rates to remain strictly positive.

The results (Fig. 2) show that a nonzero mean γ in growth rates can yield a larger (red area of parameter space in main panel) or

smaller (blue area) number of coexisting species, compared to the mean-zero case. If

$$\frac{\alpha\gamma}{\hat{\mu}} > \frac{1}{\sqrt{2\pi}} \quad (2)$$

averages are larger than expected in the mean-zero case (and conversely). The distribution $P(k|n; \alpha, \hat{\mu}, \gamma)$ is not binomial any more, but still retains a strong central tendency. Importantly, the mode of the number of species can be estimated analytically (Supplementary Information 5).

When we repeat the calculation but position the nonzero elements according to a network structure, we find results that are quite similar to the mean-zero case: though not all network structures yield the same exact distribution, the effect is very modest, such that our analytical approximation describes coexistence in all cases well (Fig. 3).

Thus we have computed the distribution of the number of coexisting species under the assumptions of random parameters and strong stability. We obtain two cases: first, when inter-specific interactions have mean zero, the number of coexisting species follows the binomial distribution with probability 1/2, and network structure has no influence whatsoever—in fact, we would recover the same result if species were not to interact at all; and second, when the inter-specific interactions have mean nonzero, the distribution is no longer binomial, and we can expect either a larger or smaller proportion of populations to survive, depending on the choice of parameters, and the network structure has a very modest effect.

Discussion

Our results show that large communities can stably coexist thanks to the selection imposed by the dynamical pruning of a large species pool. In practice, we can attain communities of any size (with no saturation) even when setting parameters at random—all we need is to start with a much larger species pool.

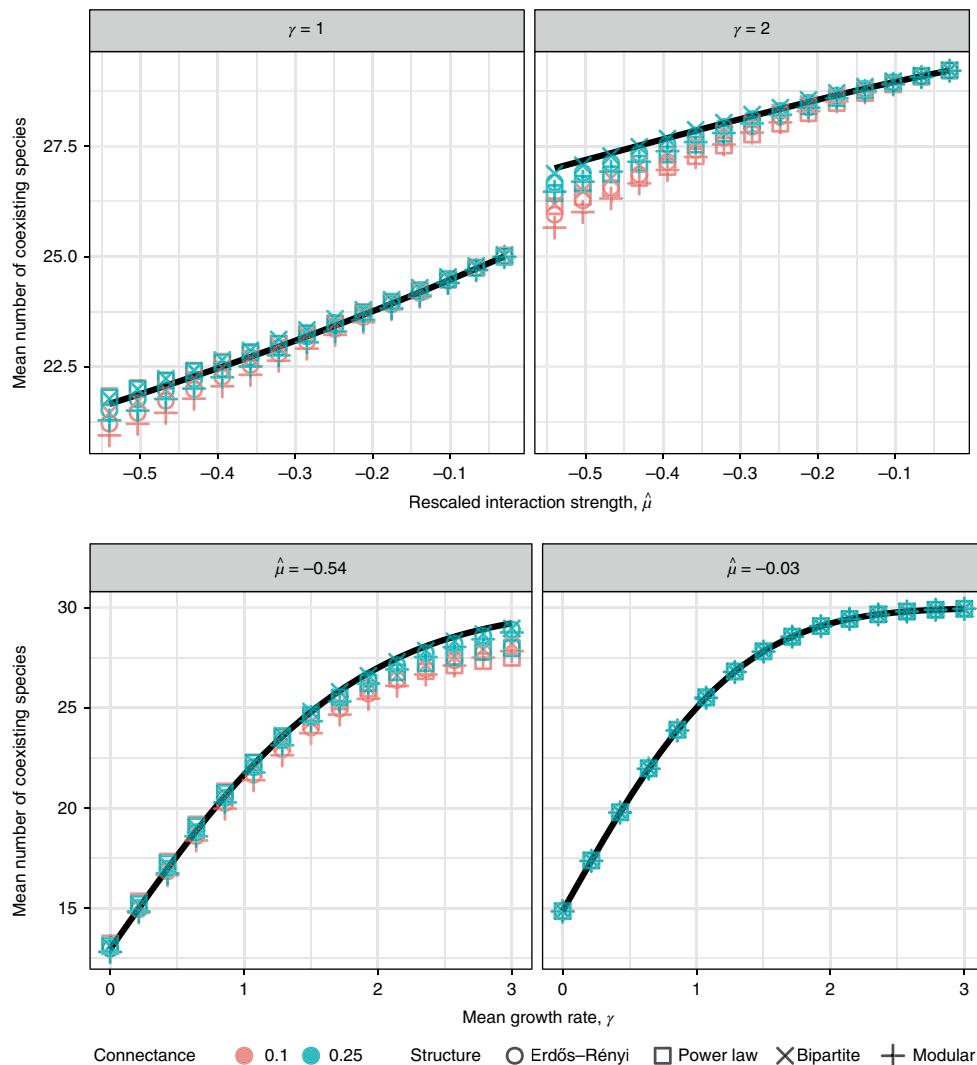


Fig. 3 | Effect of network structure on coexistence for the case of nonzero means. The position of the nonzero coefficients is chosen according to one of four structures (shapes), and for two levels of connectance (proportion of nonzero coefficients, colours). Because most of the coefficients are zero, one needs to calculate a ‘rescaled’ $\hat{\mu}$ (x axis in upper panels, see Supplementary Information) to contrast the results of the simulations (points) with our analytical approximation for the fully connected case (line, see Supplementary equation (87)). The four panels show that, although both the interaction strength $\hat{\mu}$ and the mean intrinsic growth rate γ interact with connectance and network structure in nontrivial ways, the overall effect is very modest.

When the growth (death) rates and the interactions are sampled from distributions that are symmetric about zero, we find that the number of coexisting species follows the binomial distribution. Given that this result holds for any distribution of interactions (provided it is symmetric about zero), it follows that the same should be found when interactions are all zero (when species do not interact), which can be thought of as a limiting case.

In our simple model of a food web, we sample growth (death) rates and interactions independently. As such, we could create species that have a negative growth rate (typical of consumers) and yet establish only negative interactions with the rest of the species (typical of producers). Such species will surely go extinct, resulting in a non-trivial correlation between the growth rates of the extant species and the type of interaction they can establish (that is, for the extant species, negative growth rates are possible only when they consume other species). This explains the shift in the distribution of growth rates found in the extant communities after pruning (Supplementary Fig. 2).

The picture is complicated considerably when interactions and growth rates can have nonzero mean: as found in the case of

feasibility⁹, nonzero means in growth rates and interactions can have a strong effect on the number of species that can coexist. For the competitive case studied here, this can enhance or depress biodiversity, depending on the parameterization.

Many studies have tracked the average number of species coexisting using simulations^{12–19}. Recently, much progress has been made analytically by borrowing methods from the physics of disordered systems^{20,21}. We add to this growing body of literature by focusing on the full distribution of the number of extant species. Our results can be applied to two cases of interest. First, when we have many local communities composed of subsets of the same pool of species, such as in metacommunities, our methods could model the distribution of the number of species found in local patches. Second, thanks to progress in molecular biology and imaging, it is now possible to assemble increasingly large microbial communities in the laboratory setting. Our methods could be used as a baseline distribution for the number of strains coexisting when randomly seeding communities with a subset of a microbial pool.

The study of the stability of large ecological communities started by considering completely random matrices of interactions⁵; further

studies included more realistic models in which interactions were paired²⁶ and organized in patterns^{23,24}. We believe that our results can be similarly extended, and we see three main directions that need to be explored.

First, we have considered here a ‘weak’ form of network structure: the location of the nonzero elements of the matrix is specified, but other than that the coefficient values are randomly determined. A stronger form of network structure would be one in which the values of the nonzero coefficients are also organized in a pattern. For example, a ‘cascade’ structure in which all the positive (negative) elements of the matrix A are confined to the upper (lower) triangular part has been shown to have a strong stabilizing (or destabilizing) effect²³. Similarly, arranging the strong/weak competitive interactions in modules or in a nested fashion can greatly influence stability²⁵. It would therefore be important to determine whether this ‘strong’ formulation of network structure can indeed influence coexistence as well as stability.

Second, we have determined coexistence under the assumption of strong stability (Lyapunov diagonal stability). Relaxing this constraint will be challenging, but could shed light on mechanisms of coexistence involving, for example, limit cycles or chaotic attractors. Recently, Bunin²⁰ studied coexistence in species pools with random (weak) interactions and identical growth rates, identifying the transitions between systems characterized by a single stable equilibrium, and those displaying multiple attractors. Though this study disregards other types of attractors, it shows that analytical progress in this area is possible.

Third, as pointed out by Sigmund⁷, “Mother Nature does not assemble her networks by throwing n species together in one go”. Understanding the process of assembly in which communities are built one species at a time is perhaps the greatest challenge ahead for theoretical community ecology³⁴. In Supplementary Information 9 we show that, although some of our non-invasive communities cannot be built by a sequential assembly, the probability of finding such cases decreases rapidly with the size of the community. We conjecture that, asymptotically, the probability of finding an assembly sequence for communities built in this way converges to one.

In the last few decades, ecologists have compiled ever more detailed interaction networks³⁵, documenting the intricate relationships occurring in ecosystems^{36,37}. These networks display interesting patterns, such as broad degree distributions³⁸, modular organization of interactions³⁹, hierarchical structure⁴⁰ and nestedness^{41,42}. One of the main questions in community ecology is therefore to determine whether these network properties have some bearing on the robust coexistence of ecological communities. In this context, our results provide a baseline for species coexistence under Lotka–Volterra dynamics, providing insights into which features of empirical communities promote or hinder coexistence.

Methods

Problem statement. We consider n interacting populations, for which the dynamics are defined by a system of generalized Lotka–Volterra equations:

$$\frac{dX_i(t)}{dt} = X_i(t) \left(r_i + \sum_j A_{ij} X_j(t) \right) \quad (3)$$

where $X_i(t)$ is the abundance of population i at time t , r_i is the intrinsic growth rate of species i , and A_{ij} is the per-capita effect of species j on the growth rate of species i . For notational convenience, we collect the coefficients A_{ij} into the interaction matrix A , and X_i and r_i into the (column) vectors \mathbf{X} and \mathbf{r} , respectively.

A vector \mathbf{x}^* is a fixed point (equilibrium) of the system if

$$0 = x_i^* \left(r_i + \sum_j A_{ij} x_j^* \right) \quad \text{for } i = 1, 2, \dots, n \quad (4)$$

Since $x_i^* = 0$ is always a possible solution, the system admits up to 2^n fixed points, corresponding to all the combinations of presence and absence of each species.

A fixed point is feasible if $x_i^* > 0$ for all i . If a feasible fixed point exists, it is the solution of

$$\mathbf{r} = -A\mathbf{x}^* \quad (5)$$

If A is invertible, then

$$\mathbf{x}^* = -A^{-1}\mathbf{r} \quad (6)$$

Global stability and non-invasive fixed points. In this study, we assume that A is negative definite, and in particular that the matrix $A + A^T$ has only negative eigenvalues. A matrix A is Lyapunov diagonally stable if there exists a positive diagonal matrix D such that $DA + A^T D$ is negative definite³¹. Our assumption therefore implies Lyapunov diagonal stability (corresponding to choosing D as the identity matrix).

If A is diagonally stable, then there exists a fixed point of equation (2) that is globally attractive: irrespective of the (positive) initial conditions, dynamics always converge to the same fixed point³³. This globally stable fixed point has k positive entries and $n - k$ entries equal to zero. We define the support $\{S\}_k$ as the set of k persistent species (those for which at equilibrium $x_i^* > 0$) and $\{N\}_{n-k} = \{S\}_n / \{S\}_k$ as the set of $n - k$ species with zero abundance. The i th entry of the globally stable fixed point \mathbf{x}^* is equal to zero if $i \in \{N\}_{n-k}$ and equal to $x_i > 0$ if $i \in \{S\}_k$, where $\mathbf{x} = (x_i)$ is a k -dimensional (column) vector with positive components. We define the $k \times k$ matrix $A^{(s)}$ as the submatrix of A obtained by considering only rows and columns belonging to $\{S\}_k$. Similarly, we define the $(n - k) \times (n - k)$ matrix $A^{(ns)}$ by considering rows and columns in $\{N\}_{n-k}$, the $k \times (n - k)$ matrix $A^{(sn)}$ by considering rows in $\{S\}_k$ and columns in $\{N\}_{n-k}$, and the $(n - k) \times k$ matrix $A^{(ns)}$ by considering rows in $\{N\}_{n-k}$ and columns in $\{S\}_k$. Finally, the entries of the intrinsic growth rate vector can be split into two subvectors $\mathbf{r}^{(s)}$, a k -dimensional (column) vector with the same components of \mathbf{r} for the entries in $\{S\}_k$, and $\mathbf{r}^{(n)}$, a $(n - k)$ -dimensional (column) vector with entries corresponding to $\{N\}_{n-k}$.

If we rearrange the indices of the vectors such that the k persistent species occupy the first k entries, the globally stable fixed point \mathbf{x}^* can be written as the vector $\begin{pmatrix} \mathbf{x} \\ \mathbf{0}_{n-k} \end{pmatrix}$, where $\mathbf{0}_{n-k}$ denotes a (column) vector with $n - k$ zero entries, the intrinsic growth rate vector becomes $\mathbf{r} = \begin{pmatrix} \mathbf{r}^{(s)} \\ \mathbf{r}^{(n)} \end{pmatrix}$, and the interaction matrix reads

$$A = \left(\begin{array}{c|c} A^{(s)} & A^{(sn)} \\ \hline A^{(ns)} & A^{(n)} \end{array} \right) \quad (7)$$

The abundance of the k persistent species is therefore a solution of the equation

$$A^{(s)}\mathbf{x} = -\mathbf{r}^{(s)} \quad (8)$$

Since we are considering only diagonally stable matrices, this point is also not invasive by any of the remaining $n - k$ species (that is, none of the species in $\{N\}_{n-k}$ can invade when the system is resting at the equilibrium point)³³. The condition of non-invasibility can be written by imposing that the growth rate of each of the $n - k$ species is negative for small densities. In the limit of small densities, the per-capita growth rates of the invaders become independent of their densities, and one obtains the following $n - k$ conditions

$$\mathbf{r}^{(n)} + A^{(ns)}\mathbf{x} < 0 \quad (9)$$

In the case of diagonally stable matrices, the combination of $\{S\}_k$ and \mathbf{x} is unique. It is the only one for which the solution \mathbf{x} of equation (8) has positive components and, simultaneously, equation (9) holds.

Distribution of non-invasive fixed points. Provided that A is diagonally stable, the number of coexisting species k is fully and uniquely determined by the vector of intrinsic growth rates \mathbf{r} . More precisely, only the direction of the vector \mathbf{r} , and not its norm, determines coexistence. Our goal is to determine $P(k|n)$, the probability of observing k coexisting species out of n , given a distribution for the entries of the matrix A and a distribution for the intrinsic growth rates \mathbf{r} . In particular, we parameterize the entries of A as the sum of a deterministic and a random matrix:

$$A_{ij} = (\alpha - \mu)\delta_{ij} + \mu + B_{ij} \quad (10)$$

where B is a random matrix, whose entries are random variables with mean zero, and $\delta_{ij} = 1$ if $i = j$ and 0 otherwise. As such, the entry A_{ii} (self-interaction) has mean α , while the off-diagonal entries have mean μ . Similarly, we consider

$$r_i = \gamma + b_i \quad (11)$$

where the entries of vector \mathbf{b} are random variables with mean zero.

We define $\mathcal{P}(\{S\}_k|A)$ as the probability (calculated over the growth rate vectors r) that the support of the globally stable fixed points is $\{S\}_k$. By averaging this quantity over the distribution of A , we obtain

$$\mathcal{P}(\{S\}_k|n) := \mathbb{E}(\mathcal{P}(\{S\}_k|A)) \quad (12)$$

The probability that the support has cardinality k is simply

$$P(k|n) := \sum_{\{S\}_k} \mathcal{P}(\{S\}_k|n) \quad (13)$$

The derivations are presented in the Supplementary Information. In particular, in Supplementary Information 1 we focus on the case $\mu=0$ and $\gamma=0$, showing that if the distributions of the entries of B and b are symmetric around zero

$$P(k|n) = \binom{n}{k} \frac{1}{2^n} \quad (14)$$

In Supplementary Information 2, we provide an integral formula for $\mathcal{P}(\{S\}_k|A)$ in case of an arbitrary matrix A and in Supplementary Information 3, we exploit this results to compute explicitly $P(k|n)$ in the case of $\mu \neq 0, \gamma \neq 0, B=0$ and normally distributed entries of B . Supplementary Information 4 and 5 use saddle-point techniques to provide the mode of the distribution of the number of coexisting species. In Supplementary Information 6, we present a derivation for the case in which growth rates are positive and sampled from a truncated Gaussian distribution. Supplementary Information 7 analyses the differences between the starting and final community, and Supplementary Information 8 details the numerical simulations. Finally, in Supplementary Information 9, we discuss the relationship between our model and the process of ecological assembly.

Reporting Summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this article.

Code availability. Code to replicate the findings presented above can be found at: github.com/StefanoAllesina/randomzoo.

Data availability. The results make use of no data.

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Author contributions

S.A. and C.A.S. devised the study; C.A.S. and K.E.M. solved the mean-zero case; J.A.C. and J.G. the nonzero-mean case; S.A. wrote the main text; J.A.C., C.A.S. and J.G. wrote the Supplementary Information; C.A.S. drew the figures; all authors edited the manuscript.

Competing interests

The authors declare no competing interests.

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