# Coexistence of many species in random ecosystems

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#### Abstract

Rich ecosystems harbor 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 to obtain the stable coexistence of large communities. 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.

8 Here we compute the distribution of the number of species that can coexist when we 9 start from a pool of species interacting randomly, and show that even in this case we 10 can observe rich, stable communities. Interestingly, our results show that, once stability 11 conditions are met, network structure has very little influence on the level of biodiversity 12 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.

Lotka<sup>1</sup> and Volterra<sup>2</sup> first attempted to mathematize the population dynamics of interacting species, and their model has been eviscerated and refined by countless studies<sup>3</sup>. Analyzing models that include more than a handful of interacting populations has however

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proven remarkably difficult, despite the fact that ecosystems harbor hundreds of populations,
interacting through complex networks encompassing consumption, competition, and mutualism<sup>4</sup>.

In Lotka-Volterra and similar models, it is exceedingly improbable to obtain the coex-22 istence of all species in a large community without fine-tuning the parameters  $5^{-9}$ , and such 23 fine-tuning is questionable at best for biological systems<sup>10</sup>. Consider however that in natu-24 ral communities the extant species we observe are a selected portion of a much larger pool, 25 which has then been pruned by population dynamics  $^{7,11}$ . Therefore, to understand the estab-26 lishment and maintenance of natural communities we need to change our focus: rather than 27 asking what is the probability that all species in a community coexist, here we attempt to 28 predict the number of extant species we obtain when starting from a species pool of n species, 20 and let the dynamics unfold. As a limiting case, we study the behavior of ecological models 30 in which the parameters are randomly drawn from fixed distributions, meaning that species 31 have not had time to co-adapt or co-evolve. While many studies have investigated, numeri-32 cally<sup>12–19</sup> or analytically<sup>20</sup>, the effect of particular parameterizations and network structure 33 on the average number of coexisting species, here we derive the full distribution. 34

We start by studying coexistence in random ecological communities, and, having derived the behavior 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<sup>4,8,21-24</sup>, has instead very little effect on coexistence, once stability conditions are met.

The idea of studying random ecological communities was pioneered by  $May^5$ , who de-40 termined the local stability properties of large ecosystems through an application of random 41 matrix theory. His work was generalized and refined  $^{25,26}$ , so that we can now characterize the 42 stability of ecological networks displaying hierarchical<sup>22</sup> or modular<sup>23</sup> structure. Similarly, 43 "structural stability" (i.e., the range of conditions leading to positive equilibria in ecological 44 systems) has been investigated by letting the growth rate of the species<sup>8,9</sup>, or the interactions 45 between species<sup>27</sup> vary randomly. Clearly, to have robust coexistence we need a combination 46 of the two: species densities must be positive, while a stable attractor is needed to allow 47 densities to rebound when perturbed. 48

# 49 **Results**

<sup>50</sup> Our goal is to compute the probability of observing k species stably coexisting when starting <sup>51</sup> with a pool of n interacting populations and random parameters. For example, take the <sup>52</sup> generalized Lotka-Volterra (GLV) system

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

and sample parameters at random: how many species coexist once the dynamics have elapsed? 53 We first analyze the case closest to the spirit of May's contribution, which can be taught 54 of as a caricature of a food web: some species can grow in isolation (e.g., producers, with 55 positive intrinsic growth rates), while other species can grow only thanks to their interactions 56 (e.g., consumers, with negative growth rates); all species establish random interactions with 57 each other. More specifically, we sample the intrinsic growth (death) rates  $(r_i)$  and the 58 inter-specific interactions  $(A_{ij}, i \neq j)$  from distributions (not necessarily the same) that are 59 symmetric around zero (such that P(x) = P(-x)). For example, we could sample all these 60 entries from a Normal distribution with mean zero. We set the intra-specific interactions  $(A_{ii})$ 61 by summing a mean-zero symmetric random variable and a constant  $d_i$  (not necessarily the 62 same for all i). Note that in this way, about half of the species would grow in isolation, while 63 the rest rely on "consumption" for their survival. 64

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 (i.e., 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 S2). Our proof extends previously known mathematical results<sup>28</sup>, confirming the conjecture put forward by Goh & Jennings forty years ago<sup>13</sup>.

<sup>71</sup> Clearly, feasibility is only necessary, but not sufficient for coexistence. To study coexis-<sup>72</sup> tence, we make the stronger assumption that the matrix  $A + A^T$  is negative definite. This <sup>73</sup> property implies Lyapunov diagonal stability, and is a strong form of stability routinely as-<sup>74</sup> sumed in studies of feasibility<sup>8,9</sup> that can be always attained by choosing suitable large and <sup>75</sup> negative  $d_i$ . Under these conditions, a GLV model has a single, globally attractive equilibrium,

called the non-invasible solution (also called saturated rest point  $^{29}$ ): k species have positive 76 density at equilibrium, while all the other n-k species cannot invade this community, and 77 will go extinct irrespective of initial conditions. Surprisingly when we sample the parameters 78 at random as specified above, the non-invasibility and feasibility conditions for each subset 79 of species balance out, such that each species has probability 1/2 of being included in the 80 non-invasible, globally attractive solution. Hence, the probability P(k|n) of finding k species 81 coexisting when we start with n follows the binomial distribution B(n, 1/2) (Fig. 1 and Sup-82 plementary Information S2). This beautifully simple result means that if we were to start 83 with a strongly stable (i.e., with  $A + A^T$  negative definite) random matrix of interactions and 84 random growth rates, about half of the species would coexist, irrespective of the choice of n. 85 Remarkably, this is exactly what we would expect if species were not to interact with each 86 other at all (i.e.,  $d_i < 0$  for all i and  $A_{ij} = 0$  for all  $i \neq j$ ). 87

Extending May's results, Allesina & Tang<sup>25</sup> 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  $\rho$ , then stability is enhanced by choosing a negative correlation. When analyzing 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 S2).

So far, we have assumed that every species interacts with every other. To study the effect 95 of network structure, we set most of the interactions to zero, and choose the position of the 96 nonzero coefficients according to the adjacency matrix of a) an Erdős-Rényi random graph, 97 b) a random graph with power-law degree distribution, c) a graph displaying modular, or d) 98 bipartite structure. Irrespective of the choice of network structure, we always recover the same 99 distribution for the number of coexisting species k (Fig. 1 and Supplementary Information S2). 100 This is interesting, because network structure strongly influences stability  $^{22-25}$ . However, 101 because in our analysis stability is assumed, we find that the exact location of the nonzero 102 interactions has no effect on coexistence. 103

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 (e.g., contribution of prey to the growth of predators) on average counterbalance negative ones (e.g., effects of <sup>107</sup> predators on prey). Of course this needs not to be the case in natural communities, and <sup>108</sup> therefore we examine the mathematically much more challenging case in which the entries <sup>109</sup> have mean nonzero.

To this end, we consider a simple model of interacting competitors: we set all inter- and 110 intra-specific interactions to be negative, and consider the case of random growth rates. In this 111 case we assume that all species in the pool are sampled from a common habitat, and therefore 112 have growth rates with a well-defined average value. In particular, we sample the intrinsic 113 growth rates from a Normal distribution with mean  $\gamma$ , and, for simplicity, we construct A 114 by setting all inter-specific interaction to be competitive,  $A_{ij} = \mu = \hat{\mu}/n < 0$ , and all intra-115 specific effects to  $A_{ii} = d_i = \alpha < 0$ . Numerical simulations presented below show that our 116 results well-approximate the case in which the elements of A are variable (e.g., when the 117 nonzero elements are arranged in a network). 118

Again, we consider matrices for which  $\alpha$  is sufficiently strong to yield Lyapunov diagonal 119 stability  $(\alpha < \mu < 0)$ . When we sample the growth rates from a Normal distribution, then the 120 equilibrium point  $X = -A^{-1}r$  is described by a multivariate Normal distribution. Exploiting 121 this fact, we are able to express the probability that k species form a non-invasible and 122 feasible subset as a double integral that can be used to compute the size of the non-invasible 123 community (see Supplement). The double integral can be approximated, for large n, via a 124 saddle-point technique to obtain an accurate analytical approximation for the distribution 125  $P(k|n;\alpha,\hat{\mu},\gamma)$ . Note that in this setting, growth rates need to be positive for species to 126 survive, and therefore we only consider the case of  $\gamma \geq 0$ . We also show (Supplementary 127 Information S7) that the results remain qualitatively unchanged when rates are drawn from 128 a truncated Gaussian distribution, which forces all rates to remain strictly positive. 129

The results (Fig. 2) show that a nonzero mean  $\gamma$  in growth rates can yield a larger (red area of parameter space) or smaller (blue) number of coexisting species, compared to the mean-zero case. If

$$\frac{\alpha\gamma}{\hat{\mu}} > \frac{1}{\sqrt{2\pi}},\tag{2}$$

averages are larger than expected in the mean-zero case (and conversely). The distribution  $P(k|n; \alpha, \hat{\mu}, \gamma)$  is not binomial anymore, but still retains a strong central tendency. Importantly, the mode of the number of species can be estimated analytically (Supplementary Information S6).

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 well-describes coexistence in all cases (Fig. 3).

In summary, we have computed the distribution of the number of coexisting species under 141 the assumptions of random parameters and strong stability. We have two cases: a) when inter-142 specific interactions have mean zero, the number of coexisting species follows the binomial 143 distribution with probability 1/2, and network structure has no influence whatsoever—in fact, 144 we would recover the same result if species were not to interact at all; b) when the inter-specific 145 interactions have mean nonzero, the distribution is not binomial anymore, and we can expect 146 either a larger or smaller proportion of populations to survive, depending on the choice of 147 parameters. Also in this case, however, network structure has a very modest effect. 148

# 149 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.

The study of the stability of large ecological communities started by considering completely random matrices of interactions<sup>5</sup>; further studies included more realistic models in which interactions were paired<sup>25</sup> and organized in patterns<sup>22,23</sup>. 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 also the values of the nonzero coefficients are 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) effect<sup>22</sup>. Similarly, arranging the strong/weak competitive interactions in modules or in a nested fashion can greatly influence stability<sup>24</sup>. 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 however shed light on mechanisms of coexistence involving for example limit cycles or chaotic attractors. Recently, Bunin<sup>20</sup> 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 Sigmund<sup>7</sup>, "Mother Nature does not assemble her networks by 175 throwing n species together in one go". Understanding the process of assembly in which com-176 munities are built one species at a time is perhaps the greatest challenge ahead for theoretical 177 community ecology  $^{30}$ . In the Supplementary Information (S9) we show that, although some 178 of our non-invasible communities cannot be built by a sequential assembly, the probability 179 of finding such cases decreases rapidly with the size of the community. We conjecture that, 180 asymptotically, the probability of finding an assembly sequence for communities built in this 181 way converges to one. 182

In the last few decades, ecologists have compiled ever more detailed interaction networks<sup>31</sup>. 183 documenting the intricate relationships occurring in ecosystems<sup>32,33</sup>. These networks display 184 interesting patterns, such as broad degree distributions<sup>34</sup>, modular organization of interac-185 tions<sup>35</sup>, hierarchical structure<sup>36</sup>, and nestedness<sup>37,38</sup>. One of the main questions in community 186 ecology is therefore to determine whether these network properties have some bearing for the 187 robust coexistence of ecological communities. In this context, our results provide a baseline 188 for species coexistence under Lotka-Volterra dynamics—one can use these reference points to 189 prove that certain features of empirical communities promote or hinder coexistence. 190

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# 288 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. the supplement; C.A.S. drew the figures; all authors edited the manuscript.

# <sup>292</sup> Competing financial interests

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Figure 1. Number of coexisting species when interactions and intrinsic growth 296 rates are randomly sampled from the standard Normal distribution. For each panel, 297 histograms show the number of coexisting species out of  $2 \cdot 10^5$  simulations, when starting from 298 a different number of species n (colors) and interaction matrices A that are strongly stable. 299 Binomial distributions B(n, 1/2) are reported as crosses. In the three rows, different network 300 structures are used to set the positions of the nonzero coefficients (as exemplified by the 301 adjacency matrices on the right); top: complete graphs, middle: Erdős-Rényi graphs; bottom: 302 Power-law graphs; the results for other network structures are presented in Fig. S1. Sampling 303 the off-diagonal coefficients of matrix A independently ( $\rho = 0$ , center), or in correlated pairs 304  $(A_{ij}, A_{ji})$   $(\rho \neq 0)$ , has no effect on the expected number of coexisting species. 305



Figure 2. Number of coexisting species for competitive interactions. When species 306 interact competitively, the histograms deviate from the binomial distribution, but can still 307 be computed using a double integral (crosses, see Eq. S38). Here the interactions are set to 308  $A_{ij} = \hat{\mu}/n < 0$ , intra-specific competition to  $A_{ii} = \alpha$ , and intrinsic growth rates are normally-309 distributed with mean  $\gamma$ . The expected value of the ratio k/n, E(k/n), is drawn on the left 310 in the relevant parameter space: we chose two points (A, C) for which predictions in the 311 nonzero mean case match closely those for mean zero (E(k/n) = 1/2); in case B the number 312 of species coexisting exceeds that for the mean-zero case; for point D the expectation is lower. 313 The analytical prediction in equation (2) is also shown (line). 314



Figure 3. Effect of network structure on coexistence for the case of nonzero 315 means. The position of the nonzero coefficients is chosen according to one of four structures 316 (shape), and for two levels of connectance (proportion of nonzero coefficients, colors). Because 317 most of the coefficients are zero, one needs to calculate a "rescaled"  $\hat{\mu}$  (x-axis in upper panels, 318 see Supplement) in order to contrast the results of the simulations (point) with our analytical 319 approximation for the fully-connected case (line, see Supplement, Eq. (S87)). The four panels 320 show that, although both the interaction strength  $\hat{\mu}$  and the mean intrinsic growth rate  $\gamma$ 321 interacts with connectance and network structure in nontrivial ways, the overall effect is very 322 modest. 323

# <sup>324</sup> Supplementary Information

#### 325 S1 Problem statement

We consider *n* interacting populations, whose dynamics are defined by a system of Generalized Lotka-Volterra (GLV) equations:

$$\frac{dX_i(t)}{dt} = X_i(t) \left( r_i + \sum_j A_{ij} X_j(t) \right) , \qquad (S1)$$

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 **X** and **r**, respectively.

A vector  $\boldsymbol{x}^{\star}$  is a fixed point (equilibrium) of the system if

$$0 = x_i^{\star} \left( r_i + \sum_j A_{ij} x_j^{\star} \right) \quad \text{for } i = 1, 2, ..., n.$$
 (S2)

Since  $x_i^{\star} = 0$  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

$$\boldsymbol{r} = -\boldsymbol{A}\boldsymbol{x}^{\star}.\tag{S3}$$

337 If A is invertible, then

$$\boldsymbol{x}^{\star} = -\boldsymbol{A}^{-1}\boldsymbol{r}.\tag{S4}$$

#### <sup>338</sup> S1.1 Global stability and non-invasible fixed points.

In the following, we assume that A is negative definite, and in particular that the matrix  $A + A^T$  has only negative eigenvalues<sup>39</sup>. A matrix A is Lyapunov diagonally stable if there exists a positive diagonal matrix D such that  $DA + A^TD$  is negative definite<sup>40</sup>. 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 (S1) that is globally 344 attractive: irrespective of the (positive) initial conditions, dynamics always converge to the 345 same fixed point<sup>41</sup>. This globally stable fixed point has k positive entries and n - k entries 346 equal to zero. We define the support  $\{S\}_k$  as the set of k persistent species (i.e., those for 347 which at equilibrium  $x_i^* > 0$  and  $\{N\}_{n-k} = \{S\}_n \setminus \{S\}_k$  as the set of n-k species with zero 348 abundance. The  $i^{\text{th}}$  entry of the globally stable fixed point  $x^{\star}$  is equal to zero if  $i \in \{N\}_{n-k}$ 349 and equal to  $x_i > 0$  if  $i \in \{S\}_k$ , where  $\boldsymbol{x} = (x_i)$  is a k-dimensional (column) vector with 350 positive components. We define the  $k \times k$  matrix  $A^{(s)}$  as the submatrix of A obtained by 351 considering only rows and columns belonging to  $\{S\}_k$ . Similarly, we define the  $(n-k) \times (n-k)$ 352 matrix  $\mathbf{A}^{(n)}$  by considering rows and columns in  $\{N\}_{n-k}$ , the  $k \times (n-k)$  matrix  $\mathbf{A}^{(sn)}$  by 353 considering rows in  $\{S\}_k$  and columns in  $\{N\}_{n-k}$ , and the  $(n-k) \times k$  matrix  $A^{(ns)}$  by 354 considering rows in  $\{N\}_{n-k}$  and columns in  $\{S\}_k$ . Finally, the entries of the intrinsic growth 355 rate vector can be split into two subvectors  $r^{(s)}$ , a k-dimensional (column) vector with same 356 components of  $\boldsymbol{r}$  for the entries in  $\{S\}_k$ , and  $\boldsymbol{r}^{(n)}$ , a (n-k)-dimensional (column) vector 357 with entries corresponding to  $\{N\}_{n-k}$ . 358

If we rearrange the indices of the vectors such that the k persistent species occupy the first k entries, the globally stable fixed point  $\mathbf{x}^{\star}$  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

$$\boldsymbol{A} = \left( \begin{array}{c|c} \boldsymbol{A}^{(s)} & \boldsymbol{A}^{(sn)} \\ \hline \boldsymbol{A}^{(ns)} & \boldsymbol{A}^{(n)} \end{array} \right) \,. \tag{S5}$$

 $_{363}$  The abundance of the k persistent species is therefore a solution of the equation

$$\boldsymbol{A}^{(s)}\boldsymbol{x} = -\boldsymbol{r}^{(s)} \ . \tag{S6}$$

Since we are considering only diagonally stable matrices, this point is also not invasible by any of the remaining n - k species (i.e., none of the species in  $\{N\}_{n-k}$  can invade when the system is resting at the equilibrium point)<sup>41</sup>. 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

$$\boldsymbol{r}^{(n)} + \boldsymbol{A}^{(ns)}\boldsymbol{x} < 0 \ . \tag{S7}$$

In the case of diagonally stable matrices, the combination of  $\{S\}_k$  and x is unique. It is the only one for which the solution x of equation (S6) has positive components and, simultaneously, equation (S7) holds.

#### 373 S1.2 Distribution of non invasible 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 r. More precisely, only the direction of the vector 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 r. In particular, we parameterize the entries of A as the sum of a deterministic and a random matrix:

$$A_{ij} = (\alpha - \mu)\delta_{ij} + \mu + B_{ij} , \qquad (S8)$$

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  $\alpha$ , while the off-diagonal entries have mean  $\mu$ . Similarly, we consider

$$r_i = \gamma + b_i , \qquad (S9)$$

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

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

$$\mathcal{P}(\{S\}_k|n) := \mathbb{E}(\mathcal{P}(\{S\}_k|\mathbf{A})) .$$
(S10)

<sup>387</sup> The probability that the support has cardinality k is simply

$$P(k|n) := \sum_{\{S\}_k} \mathcal{P}(\{S\}_k|n) .$$
(S11)

In section (S2) we focus on the case  $\mu = 0$  and  $\gamma = 0$ , showing that if the distributions of the entries **B** and **b** are symmetric around zero

$$P(k|n) = \binom{n}{k} \frac{1}{2^n} .$$
(S12)

In section (S3) we provide an integral formula for  $\mathcal{P}(\{S\}_k | \mathbf{A})$  in case of a arbitrary matrix  $\mathbf{A}$ and in section (S4) we exploit this results to compute explicitly P(k|n) in the case of  $\mu \neq 0$ ,  $\gamma \neq 0$ ,  $\mathbf{B} = 0$  and normally distributed entries of  $\mathbf{b}$ .

<sup>393</sup> S2 Mean zero

#### <sup>394</sup> S2.1 Toy model: uncoupled logistic equations

Suppose that A is a diagonal matrix, and therefore that species do not interact with each other. For stability, we need  $A_{ii} < 0$  for all i (self-regulation). Let  $p_i$  be the probability of  $r_i > 0$ . Then, the probability that a solution x with k positive components  $\{S\}_k$  is noninvasible is  $\prod_{i \in \{S\}_k} p_i \prod_{i \notin \{S\}_k} (1-p_i)$ .

When the distribution of  $r_i$  is symmetric around zero,  $p_i = \frac{1}{2}$  irrespective of the distribution of  $A_{ii} < 0$ , and thus the probability of non-invasibility is  $\frac{1}{2^n}$  for any particular subsystem. Therefore, the binomial distribution with parameters n and  $\frac{1}{2}$  describes the the number of persistent species.

#### 403 S2.2 Feasibility

In this and the following section, we show that when the entries of matrix B and vector r are random variables whose distribution is symmetric around 0, and that any n element subset of the columns of B and r are linearly independent (which holds almost surely if the entries of Band r are sampled from a continuous probability distribution function and are independent of each other), then the probability P(k|n) is still described by the binomial distributions with parameters n and  $\frac{1}{2}$ —exactly what we found for non-interacting species. Note that this holds true both for the case in which the coefficients  $B_{ij}$  are sampled independently, and for the case in which these coefficients are sampled in pairs  $(B_{ij}, B_{ji})$ , and the pairs are sampled independently from a bivariate distribution symmetric around (0, 0).

First we show that  $P(n|n) = \frac{1}{2^n}$ . The proof amounts to showing that, of all the possible  $2^n \operatorname{sign}(+, -)$  patterns for the entries of a solution to equation (S4), each of them is equally probable.

Let  $x^*$  be an arbitrary solution of equation (S4), and define the matrix  $D_k = ((-1)^{\delta_{ik}} \delta_{ij})$ . Then,  $D_k x^*$  satisfies  $(D_k A D_k) D_k x^* = -D_k r$ . Because of the symmetry assumption, we have that  $D_k A D_k$  has the same distribution<sup>1</sup> as A, and similarly for  $D_k r$  and r. Since  $D_k$ just flips the sign of the  $k^{\text{th}}$  component of  $x^*$ , by repeating this operation a sufficient number of times we can connect any two sign patterns of solutions to equation (S4), and thus the conclusion follows.

#### 422 S2.3 Persistent species

As noted before, in the regime of diagonally stable matrices, the final state of the system is the 423 non-invasible (also called saturated) fixed point of the system<sup>41</sup>. With the same assumptions 424 of the previous section the distribution for the number of persistent species follows naturally: 425 the probability of having a non-invasible solution x with k positive components (with support 426  $\{S\}_k$  is the joint probability of the conditions expressed in equations (S6) and (S7), which 427 can be written as  $\mathcal{P}(\{S\}_k|n) = P(k|k)[1 - P_{inv}(\{S\}_n \setminus \{S\}_k|\{S\}_k)]$ , where  $P_{inv}$  denotes the 428 probability of being invasible by any of the remaining species given that x > 0. Let z =429  $r^{(n)} + A^{(ns)}x$ . By following the same procedure illustrated in the previous section (applying 430 the appropriate change of signs to A and r), one can show that any sign pattern for z is 431 equally likely, therefore  $1 - P_{inv}(\{S\}_n \setminus \{S\}_k | \{S\}_k) = \frac{1}{2^{n-k}}$ . As a consequence,  $\mathcal{P}(\{S\}_k | n) = \frac{1}{2^n}$ . 432 Because of the uniqueness of this type of solution for a given interaction matrix  $\boldsymbol{A}$  and a vector 433 of rates r, the binomial distribution with parameters n and  $\frac{1}{2}$  describes the distribution of 434 the number of species having positive density at the globally stable equilibrium. 435

<sup>&</sup>lt;sup>1</sup>This transformation also has the property of preserving the eigenvalues of the matrix, which allows this argument to hold also if we condition on Lyapunov diagonally stable matrices.

#### 436 S2.4 Adding Structure

Let G be the adjacency matrix of an undirected graph, and consider the matrix  $M = G \circ A$ , 437 where  $\circ$  represents the Hadamard (entry-wise) product between G and A. Because this 438 type of product is commutative with respect to the multiplication by a diagonal matrix, i.e., 439  $D(G \circ A)D = G \circ (DAD)$  for D diagonal, the arguments used in the previous two sections 440 still hold. This means that the distribution of M is invariant to  $D_k M D_k$  (even when G is 441 also a random matrix) and by restricting ourselves to diagonally stable matrices the linear 442 independence assumption is assured (the matrix is invertible). Consequently, adding a network 443 structure in this way does not change the probability of feasibility nor the distribution of 444 persistent species. 445

#### 446 S3 Calculating the distribution of persistent species

If we integrate the GLV dynamics starting from an interaction matrix A, a vector of intrinsic growth rates r, and an arbitrary (positive) initial condition with n species, we end up with kspecies with density different from zero and n - k species with density equal to zero. If the matrix A is diagonally stable, the end point of the dynamics always correspond to a fixed point  $x^*$ , irrespective of the initial conditions.

The goal of this section is to provide a formula for the probability P(k|n) of finding k persisting species out of n, for an arbitrary matrix A, under the assumption that A is diagonally stable. We assume that the entries of r are drawn from a Normal distribution with mean  $\gamma$  and unit variance. This choice of a variance does not affect the generality of out results, since the coexistence properties of the Generalized Lotka-Volterra equations are independent of the norm of r: rescaling all growth rates by a constant simply rescales all equilibrium abundances by the same constant, with no impact on feasibility or stability.

459 We define the vector  $\boldsymbol{z}$  with n - k components as

$$\boldsymbol{z} := \boldsymbol{r}^{(n)} + \boldsymbol{A}^{(ns)}\boldsymbol{x}.$$
(S13)

<sup>460</sup> On the other hand, we have equation (S6), that defines  $\boldsymbol{x}$ . By imposing feasibility and non-<sup>461</sup> invasibility —equation (S7)—, it must hold that  $\boldsymbol{x} > 0$  and  $\boldsymbol{z} < 0$ . <sup>462</sup> Using the probability density of the growth rates,

$$P(\mathbf{r}) = \frac{1}{\sqrt{(2\pi)^n}} \exp\left(-\sum_{i=1}^n \frac{(r_i - \gamma)^2}{2}\right) = \frac{1}{\sqrt{(2\pi)^n}} \exp\left(-\frac{1}{2} \|\mathbf{r}^{(s)} - \gamma \mathbf{1}_k\|^2 - \frac{1}{2} \|\mathbf{r}^{(n)} - \gamma \mathbf{1}_{n-k}\|^2\right),$$
(S14)

where  $\mathbf{1}_k$  stands for a k-dimensional column vector whose entries are all equal to one. Introducing equation (S6) and (S13), we can write the joint probability density as

$$f(\boldsymbol{x}, \boldsymbol{z}|\boldsymbol{A}) = \frac{|\det \boldsymbol{\Lambda}|}{(2\pi)^{n/2}} \exp\left(-\frac{1}{2} \|\boldsymbol{A}^{(s)}\boldsymbol{x} + \gamma \boldsymbol{1}_k\|^2 - \frac{1}{2} \|\boldsymbol{z} - \boldsymbol{A}^{(ns)}\boldsymbol{x} - \gamma \boldsymbol{1}_{n-k}\|^2\right), \quad (S15)$$

where  $\Lambda$  is the Jacobian matrix obtained from the change of variables  $r \to (x, z)$ . According to equations (S6) and (S13), it is simple to observe that  $\Lambda$  as the following structure:

$$\boldsymbol{\Lambda} := \begin{pmatrix} \frac{\partial \boldsymbol{r}^{(s)}}{\partial \boldsymbol{x}} & \frac{\partial \boldsymbol{r}^{(s)}}{\partial \boldsymbol{z}} \\ \frac{\partial \boldsymbol{r}^{(n)}}{\partial \boldsymbol{x}} & \frac{\partial \boldsymbol{r}^{(n)}}{\partial \boldsymbol{z}} \end{pmatrix} = \begin{pmatrix} \boldsymbol{A}^{(s)} & \boldsymbol{0} \\ \hline \boldsymbol{A}^{(ns)} & \boldsymbol{I}_{n-k} \end{pmatrix},$$
(S16)

<sup>467</sup>  $I_{n-k}$  being the (n-k)-dimensional identity matrix. Therefore  $|\det \Lambda| = |\det A^{(s)}|$ . <sup>468</sup> The first term appearing in the exponential in equation (S15) can be written as

$$\|\boldsymbol{A}^{(s)}\boldsymbol{x} + \gamma \boldsymbol{1}_k\|^2 = (\boldsymbol{x} - \boldsymbol{\xi})^T \boldsymbol{G}(\boldsymbol{x} - \boldsymbol{\xi}) , \qquad (S17)$$

469 where

$$\boldsymbol{\xi} = -\gamma (\boldsymbol{A}^{(s)})^{-1} \boldsymbol{1}_k , \qquad (S18)$$

470 and

$$\boldsymbol{G} = (\boldsymbol{A}^{(s)})^T \boldsymbol{A}^{(s)} . \tag{S19}$$

471 We obtain therefore

$$f(\boldsymbol{x}, \boldsymbol{z} | \boldsymbol{A}) = \frac{|\det \boldsymbol{A}^{(s)}|}{(2\pi)^{n/2}} \exp\left(-\frac{1}{2}(\boldsymbol{x} - \boldsymbol{\xi})^T \boldsymbol{G}(\boldsymbol{x} - \boldsymbol{\xi}) - \frac{1}{2} \|\boldsymbol{z} - \boldsymbol{A}^{(ns)} \boldsymbol{x} - \gamma \boldsymbol{1}_{n-k}\|^2\right).$$
(S20)

The probability  $\mathcal{P}(\{S\}_k | A)$  of observing the globally stable fixed point with support  $\{S\}_k$ , can be obtained from the joint probability in equation (S15) by imposing the feasibility condition for the k species (x > 0) and the non-invasibility condition for the other n - k species 475  $(\boldsymbol{z} < 0)$ . The equation reads

$$\mathcal{P}(\{S\}_k | \boldsymbol{A}) \equiv \int d^k \boldsymbol{x} \left( \prod_{i=1}^k \Theta(x_i) \right) \int d^{n-k} \boldsymbol{z} \left( \prod_{j=k+1}^n \Theta(-z_j) \right) f(\boldsymbol{x}, \boldsymbol{z} | \boldsymbol{A}) .$$
(S21)

### 476 S4 Mean non zero

In this section we consider a simplified interaction matrix A whose diagonal coefficients are all equal to  $\alpha$ , and all the off-diagonal elements are set to a fixed value  $\mu$ :

$$\boldsymbol{A} = (\alpha - \mu)\boldsymbol{I}_n + \mu \boldsymbol{1}_n \boldsymbol{1}_n^T .$$
(S22)

Since the matrix A is a deterministic matrix, in this case  $\mathcal{P}(\{S\}_k|A) = \mathcal{P}(\{S\}_k|n)$ . By introducing equation (S22) in equation (S20) and using equation (S21), we obtain

$$\mathcal{P}(\{S\}_{k}|n) = \frac{|\det \mathbf{A}^{(s)}|}{(2\pi)^{n/2}} \int d^{k} \boldsymbol{x} \prod_{i=1}^{k} \Theta(x_{i}) \int d^{n-k} \boldsymbol{z} \prod_{j=k+1}^{n} \Theta(-z_{j}) \\ \times \exp\left\{-\frac{1}{2} \left(\boldsymbol{x} - \boldsymbol{\xi}^{(k)} \mathbf{1}_{k}\right)^{T} \boldsymbol{G}\left(\boldsymbol{x} - \boldsymbol{\xi}^{(k)} \mathbf{1}_{k}\right) - \frac{1}{2} \|\boldsymbol{z} - (\mu(\mathbf{1}_{k}^{T} \boldsymbol{x}) + \gamma) \mathbf{1}_{n-k}\|^{2}\right\}, \quad (S23)$$

where we used the fact that, with the parameterization of equation (S22),  $\boldsymbol{\xi} = \boldsymbol{\xi}^{(k)} \mathbf{1}_k$ , where

$$\xi^{(k)} = -\frac{\gamma}{\alpha + (k-1)\mu} . \tag{S24}$$

482 Again, using equation (S22) together with equation (S19), we have

$$\boldsymbol{G} = (\alpha - \mu)^2 \boldsymbol{I}_k + \left[ k\mu^2 + 2\mu(\alpha - \mu) \right] \boldsymbol{1}_k \boldsymbol{1}_k^T .$$
(S25)

483 We change variables to  $x_i' = x_i - \xi^{(k)}$  to get

$$\mathcal{P}(\{S\}_{k}|n) = \frac{|\det \mathbf{A}^{(s)}|}{(2\pi)^{n/2}} \int d^{k} \boldsymbol{x} \prod_{i=1}^{k} \Theta(x_{i} + \xi^{(k)}) e^{-\frac{1}{2}\boldsymbol{x}^{T}} \boldsymbol{G} \boldsymbol{x} \times \int d^{n-k} \boldsymbol{z} \prod_{j=k+1}^{n} \Theta(-z_{j}) e^{-\frac{1}{2} ||\boldsymbol{z} - [\gamma + k\mu\xi^{(k)} + \mu(\mathbf{1}_{k}^{T}\boldsymbol{x})] \mathbf{1}_{n-k}||^{2}}.$$
 (S26)

484 We now write  $z_j' = z_j - \gamma - k \mu \xi^{(k)}$  and obtain

$$\mathcal{P}(\{S\}_k|n) = \frac{|\alpha - \mu|^{k-1}|\alpha + (k-1)\mu|}{(2\pi)^{n/2}} \int d^k \boldsymbol{x} \prod_{i=1}^k \Theta(x_i + \xi^{(k)}) e^{-\frac{1}{2}\boldsymbol{x}^T \boldsymbol{G} \boldsymbol{x}} \\ \times \int d^{n-k} \boldsymbol{z} \prod_{j=k+1}^n \Theta(-z_j - \gamma - k\mu\xi^{(k)}) e^{-\frac{1}{2}\|\boldsymbol{z} - \mu(\mathbf{1}_k^T \boldsymbol{x})\mathbf{1}_{n-k}\|^2} , \quad (S27)$$

485 where we used

$$|\det \mathbf{A}^{(s)}| = |\alpha - \mu|^{k-1} |\alpha + (k-1)\mu|$$
 (S28)

By introducing the expression for G obtained in equation (S25), we get

$$\mathcal{P}(\{S\}_k|n) = \frac{|\alpha - \mu|^{k-1}|\alpha + (k-1)\mu|}{(2\pi)^{n/2}} \int d^k x \prod_{i=1}^k \Theta(x_i + \xi^{(k)}) \times \int d^{n-k} z \prod_{j=k+1}^n \Theta(-z_j - \gamma - k\mu\xi^{(k)}) e^{g(x,z)}$$
(S29)

487 where

$$g(\boldsymbol{x},\boldsymbol{z}) = -\frac{1}{2} \Big[ (\alpha - \mu)^2 \boldsymbol{x}^T \boldsymbol{x} + \Big[ n\mu^2 + 2\mu(\alpha - \mu) \Big] (\boldsymbol{1}_k^T \boldsymbol{x})^2 - 2\mu(\boldsymbol{1}_k^T \boldsymbol{x}) (\boldsymbol{1}_{n-k}^T \boldsymbol{z}) + \boldsymbol{z}^T \boldsymbol{z} \Big].$$
(S30)

We can express this probability as a double integral by introducing two new variables thanks to a Hubbard-Stratonovich transformation: if b > 0 and c > 0, it holds that

$$e^{-bd^2/c^2 - de/c} = \frac{c}{2\pi} \int_{-\infty}^{\infty} dy \int_{-\infty}^{\infty} dw \, e^{-(by^2 + ey + idw - icwy)}.$$
 (S31)

for any real d and e numbers. Similarly, for b > 0 and c > 0,

$$e^{-bd^2/c^2 + de/c} = \frac{c}{2\pi} \int_{-\infty}^{\infty} dy \int_{-\infty}^{\infty} dw \, e^{-(by^2 + ey + idw + icwy)}.$$
 (S32)

In our case [cf. equations (S25) and (S30)], we choose  $d = \mathbf{1}_k^T \boldsymbol{x}$  and  $e = \mathbf{1}_{n-k}^T \boldsymbol{z}$  and identify the exponents of the l.h.s. of equations (S31) or (S32) with the terms in (S30). If  $\mu > 0$ , we find  $\frac{1}{c} = \mu$  and use equation (S32). If  $\mu < 0$ , we set  $\frac{1}{c} = |\mu|$  and consider equation (S31). In both cases, we set  $\frac{b}{c^2} = \frac{1}{2}[n\mu^2 + 2\mu(\alpha - \mu)]$ . In general, we can choose  $c = \frac{1}{|\mu|}$  and  $b = \frac{1}{2}[n + 2(\frac{\alpha}{\mu} - 1)]$ . To ensure diagonal stability, all the eigenvalues of matrix  $\boldsymbol{A}$  must be <sup>496</sup> negative. This implies the conditions  $\alpha - \mu < 0$  and  $\alpha - \mu + n\mu < 0$ . If  $\mu > 0$ , the second <sup>497</sup> restriction can be violated for *n* sufficiently large. Therefore we limit the discussion to the <sup>498</sup>  $\mu < 0$  case (competitive communities) and use equation (S31). In this case we have  $\alpha < \mu < 0$ <sup>499</sup> (hence  $|\alpha| > |\mu|$ ) and  $\frac{\alpha}{\mu} - 1 + n > 0$  (hence b > 0 and we can apply the Hubbard-Stratonovich <sup>500</sup> transformation). Therefore

$$\mathcal{P}(\{S\}_{k}|n) = \frac{|\alpha - \mu|^{k-1}|\alpha + (k-1)\mu|}{(2\pi)^{n/2+1}|\mu|} \int_{-\infty}^{\infty} dy \int_{-\infty}^{\infty} dw \, e^{-\frac{1}{2}\left[n+2\left(\frac{\alpha}{\mu}-1\right)\right]y^{2}+i\frac{yw}{|\mu|}} \int d^{k}x \prod_{i=1}^{k} \Theta(x_{i}+\xi^{(k)}) \\ \times \int d^{n-k}z \prod_{j=k+1}^{n} \Theta(-z_{j}-\gamma - k\mu\xi^{(k)})e^{-\frac{1}{2}(\alpha-\mu)^{2}x^{T}x-i\left(\mathbf{1}_{k}^{T}x\right)w}e^{-\frac{1}{2}z^{T}z-\left(\mathbf{1}_{n-k}^{T}z\right)y}.$$
(S33)

501 We complete squares and obtain

$$\mathcal{P}(\{S\}_k|n) = \frac{|\alpha - \mu|^{k-1} |\alpha + (k-1)\mu|}{(2\pi)^{n/2+1} |\mu|} \int_{-\infty}^{\infty} dy \int_{-\infty}^{\infty} dw \, e^{-\frac{1}{2} \left[n+2\left(\frac{\alpha}{\mu}-1\right)\right] y^2 + i\frac{yw}{|\mu|}} e^{-\frac{k}{2(\alpha-\mu)^2} w^2 + \frac{1}{2}(n-k)y^2} \\ \times \left[ \int dx \Theta(x+\xi^{(k)}) e^{-\frac{1}{2}(\alpha-\mu)^2 \left(x+\frac{iw}{(\alpha-\mu)^2}\right)^2} \right]^k \left[ \int dz \Theta(-z-\gamma-k\mu\xi^{(k)}) e^{-\frac{1}{2}(z+y)^2} \right]^{n-k}.$$
 (S34)

Denoting the cumulative distribution function of the standard Normal distribution N(0,1) as  $\Phi(x) = \frac{1}{2} \left[ 1 + \operatorname{erf}\left(\frac{x}{\sqrt{2}}\right) \right]$  we can write

$$\mathcal{P}(\{S\}_k|n) = \frac{|\alpha - \mu|^{k-1}|\alpha + (k-1)\mu|}{2\pi|\mu||\alpha - \mu|^k} \int_{-\infty}^{\infty} dy \int_{-\infty}^{\infty} dw \, e^{-\frac{1}{2}\left[k+2\left(\frac{\alpha}{\mu}-1\right)\right]y^2 + i\frac{yw}{|\mu|} - \frac{k}{2(\alpha-\mu)^2}w^2}} \times \left[1 - \Phi\left(\frac{iw}{|\alpha - \mu|} - |\alpha - \mu|\xi^{(k)}\right)\right]^k \left[\Phi\left(y - \gamma - k\mu\xi^{(k)}\right)\right]^{n-k}, \quad (S35)$$

504 and therefore we find

$$\mathcal{P}(\{S\}_k|n) = \frac{1}{2\pi} \left| k + \frac{\alpha}{\mu} - 1 \right| \int_{-\infty}^{\infty} dy \int_{-\infty}^{\infty} dw \, e^{-\frac{1}{2} \left[ k + 2\left(\frac{\alpha}{\mu} - 1\right) \right] y^2 + i \left| \frac{\alpha}{\mu} - 1 \right| yw - \frac{1}{2} kw^2} \\ \times \left[ 1 - \Phi \left( iw - |\alpha - \mu| \xi^{(k)} \right) \right]^k \left[ \Phi \left( y - \gamma - k\mu \xi^{(k)} \right) \right]^{n-k}.$$
(S36)

Note that  $\gamma + k\mu\xi^{(k)} = \gamma \left(1 - \frac{k\mu}{\alpha + (k-1)\mu}\right) = \frac{\gamma(\alpha - \mu)}{\alpha + (k-1)\mu}$ . We define  $s := \frac{\alpha}{\mu} - 1$  (which satisfies s > 0 to ensure diagonal stability) and

$$v := \frac{\gamma(\alpha - \mu)}{\alpha - \mu + k\mu} = \frac{\gamma s}{k + s}.$$
(S37)

Then, given that  $\alpha < \mu$ , it holds that  $|\alpha - \mu| \xi^{(k)} = -\frac{\gamma |\alpha - \mu|}{\alpha + (k-1)\mu} = v$  and we can express the probability in its final form as

$$\mathcal{P}(\{S\}_k|n) = \frac{k+s}{2\pi} \int_{-\infty}^{\infty} dy \int_{-\infty}^{\infty} dw \, e^{-\frac{1}{2}(k+2s)y^2 + isyw - \frac{1}{2}kw^2} [1 - \Phi(iw - v)]^k [\Phi(y - v)]^{n-k}.$$
(S38)

In this formula, the integration over w must be performed in the complex plane. An alternative way to express it is to consider a path  $\Gamma$  in the complex plane such that  $\Gamma = \{w' \in \mathbb{C} | w' = iw + x_0\}$  and then reducing the result to the limit  $x_0 \to 0$ , so that the integral over the imaginary axis is well defined. Therefore, an equivalent form of writing this equation is

$$\mathcal{P}(\{S\}_k|n) = \frac{k+s}{2\pi i} \int_{-\infty}^{\infty} dy \int_{\Gamma} dw \, e^{-\frac{1}{2}(k+2s)y^2 + syw + \frac{1}{2}kw^2} [1 - \Phi(w-v)]^k [\Phi(y-v)]^{n-k}, \quad (S39)$$

<sup>513</sup> where the integral in w has to be evaluated over the contour  $\Gamma$  and then take the limit  $x_0 \to 0$ . <sup>514</sup> Note that for the case k = 0 the probability density of x = 0 being non-invasible is simply

$$f(\boldsymbol{z}) = \frac{1}{(2\pi)^{n/2}} e^{-\frac{1}{2}(\boldsymbol{z} - \gamma \boldsymbol{1}_n)^T (\boldsymbol{x} - \gamma \boldsymbol{1}_n)}$$
(S40)

and the condition for non-invasibility reduces to

$$\mathcal{P}(\emptyset|n) = P[z_1 < 0, \dots, z_n < 0] = \frac{1}{(2\pi)^{n/2}} \int d^n \boldsymbol{z} \prod_{i=1}^n \Theta(-z_i) e^{-\frac{1}{2}(\boldsymbol{z} - \gamma \mathbf{1}_n)^T (\boldsymbol{x} - \gamma \mathbf{1}_n)} = [\Phi(-\gamma)]^n.$$
(S41)

In addition, for k = 1 the integral over w can be actually calculated. Using that

$$\int_{-\infty}^{\infty} dw \, e^{-\frac{1}{2}w^2 - iaw} [1 - \Phi(iw)] = \sqrt{2\pi} \Theta(-a) e^{-\frac{1}{2}a^2} \tag{S42}$$

517 we get

$$\mathcal{P}(\{S\}_1|n) = \frac{s+1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} dy \,\Theta(sy+v) e^{-\frac{1}{2}(s+1)^2 y^2} [\Phi(y-v)]^{n-1},\tag{S43}$$

518 or, alternatively,

$$\mathcal{P}(\{S\}_1|n) = \frac{1}{\sqrt{2\pi}} \int_{-\gamma}^{\infty} dy \, e^{-\frac{1}{2}y^2} \left[ \Phi\left(\frac{\mu y}{\alpha} - v\right) \right]^{n-1}.$$
(S44)

### 519 S4.1 Numerical evaluation of the double integral

Equation (S38) can be evaluated numerically via a Fast Fourier Transform (FFT). We can express it as

$$\mathcal{P}(\{S\}_k|n) = \frac{k+s}{2\pi} \int_{-\infty}^{\infty} dy \, e^{-\frac{1}{2}(k+2s)(y^2+2vy)+svy} [\Phi(y)]^{n-k} \widehat{F}(-s(y+v)-kv;k) \tag{S45}$$

where  $\widehat{F}(x;k)$  is the Fourier transform over w of the complex function

$$F(w;k) = e^{-\frac{1}{2}kw^2} [1 - \Phi(iw)]^k$$
(S46)

and the Fourier Transform of the function F(t;k) is defined as  $\hat{F}(x;k) := \int_{-\infty}^{\infty} dt f(t;k) e^{-itx}$ . Then we first calculate  $\hat{F}(x;k)$  via a FFT algorithm. For that purpose, we assume that f(t)is approximately equal to zero outside the interval (-T/2, T/2) and sample t at m equally spaced points separated a distance  $\delta = T/m$  (m is even), so that  $t_j = (j - m/2)\delta$ ,  $0 \le j < m$ . Then

$$\widehat{F}(x_{\ell};k) = \int_{-\infty}^{\infty} dt \, F(t;k) e^{-itx_{\ell}} \approx \int_{-T/2}^{T/2} dt \, F(t;k) e^{-itx_{\ell}} \approx \delta \sum_{j=0}^{m-1} F(t_j;k) e^{-itx_{\ell}}.$$
(S47)

If  $x_{\ell} = 2\pi(\ell - m/2)/T = 2\pi(\ell - m/2)/(m\delta)$ , the last expression can be written in terms of the Discrete Fourier Transform,  $D_{\ell}(\{z_j\}) = \sum_{j=0}^{m-1} z_j e^{-2\pi i j \ell/m}$ , as

$$\widehat{F}(x_{\ell};k) = \delta e^{i\pi(\ell - m/2)} \sum_{j=0}^{m-1} F(t_j;k) e^{i\pi j(1 - 2\ell/m)} = (-1)^{\ell - m/2} \delta D_{\ell} \Big[ \{(-1)^j F(t_j;k)\} \Big]$$
(S48)

where  $0 \leq \ell < m$ . Once we have calculated  $\widehat{F}(x_{\ell};k)$  over the set of sampling points, we interpolate to evaluate numerically the transform at an arbitrary point [see equation (S45)]. For numerical evaluation over a finite interval, equation (S45) is more conveniently expressed 533 by changing to the variable  $z = \Phi(y)$  as

$$\mathcal{P}(\{S\}_k|n) = \frac{k+s}{\sqrt{2\pi}} \int_0^1 dz \,\widehat{F}\Big(-s\Big[\Phi^{-1}(z)+v\Big] - kv; k\Big) e^{-\frac{1}{2}\big[\Phi^{-1}(z)\big]\big\{2v(k+s) + \big[\Phi^{-1}(z)\big](k-1+2s)\big\} + (n-k)\log z}.$$
(S49)

For k = 1 from (S44) we derive the expression

$$\mathcal{P}(\{S\}_1|n) = (s+1) \int_{\Phi(-\gamma)}^1 dz \, e^{-\frac{1}{2}(s+1)^2 \left[\Phi^{-1}(z)+v\right]^2 + \frac{1}{2} \left[\Phi^{-1}(z)\right]^2 + (n-1)\log z}.$$
 (S50)

#### 535 S4.2 Probability of coexistence

Assuming diagonal stability, the probability of observing k species in stable coexistence out of a pool of n species is given by

$$P(k|n) = \binom{n}{k} \mathcal{P}(\{S\}_k|n), \tag{S51}$$

with  $\mathcal{P}(\{S\}_k|n)$  given by equation (S39). We now approximate  $\mathcal{P}(\{S\}_k|n)$  for large n in order to obtain an analytical formula for the distribution, as well as the mode of the distribution  $k^*$ .

We use the saddle point technique from statistical mechanics to evaluate integrals of the form  $\int d^n u e^{-nh(u)} k(u)$  for *n* large. We define *q* through k = qn and regard *q* as a continuous, finite variable such that  $0 \le q \le 1$ . Then equation (S39) can be written as

$$\mathcal{P}(\{S\}_k|n) = \frac{k+s}{2\pi i} \int_{-\infty}^{\infty} dy \int_{\Gamma} dw \, e^{-sy^2 + syw} e^{-n\hat{h}(y,w;q,v)},\tag{S52}$$

544 where

$$\hat{h}(y,w;q) = \frac{q}{2} \left( y^2 - w^2 \right) - q \log[1 - \Phi(w-v)] - (1-q) \log \Phi(y-v).$$
(S53)

In the limit  $n \to \infty$ , we assume q to take a fixed value (which will be associated to any possible value that k can take in the range  $0 \le k \le n$ ). To calculate the limit correctly, at this point we assume that interactions scale with n as  $\mu = \hat{\mu}/n$ . In this way, the total interaction strength for any species is independent of n. Otherwise, since  $\mu$  only enters in equation (S52) through the combination  $s = \frac{\alpha}{\mu} - 1$ , if we do not assume the scaling in the limit for  $n \to \infty$  any dependence on interaction strengths will be lost for n large. Therefore we write s = nu - 1, where  $u := \alpha / \hat{\mu}$  and equation (S52) becomes

$$\mathcal{P}(\{S\}_k|n) = \frac{k+nu-1}{2\pi i} \int_{-\infty}^{\infty} dy \int_{\Gamma} dw \, e^{y^2 - yw} e^{-nh(y,w;\sigma)},\tag{S54}$$

where we use the shorthand  $\boldsymbol{\sigma} := (q, u, v)$  and

$$h(y,w;\boldsymbol{\sigma}) = \frac{q}{2} \left( y^2 - w^2 \right) - q \log[1 - \Phi(w - v)] - (1 - q) \log \Phi(y - v) + uy^2 - uyw.$$
(S55)

In this limit of large n, the exponential function  $e^{-nh(y,w;\sigma)}$  is very peaked around the global minimum of the real part of  $h(y,w;\sigma)$ . Then we can evaluate the integral by approximating the exponent up to second order around the minimum. Note also that w is a complex variable and h is an analytic function of w. Then the Cauchy-Riemann condition holds (i.e., the real part of h satisfies the Laplace equation) and the minimum of  $\Re(h)$  calculated along the integration path  $\Gamma$  is given by the maximum of  $\Re(h)$  when w is regarded as a real variable. Then we expect a saddle point in the real (y, w) plane.

The conditions for the critical point form a coupled system of non-linear equations for yand w as functions of  $\sigma$ :

$$\begin{aligned} \frac{\partial h}{\partial y} &= qy - (1-q)\frac{\Phi'(y-v)}{\Phi(y-v)} + 2uy - uw = qy - (1-q)\frac{e^{-(y-v)^2/2}}{\sqrt{2\pi}\Phi(y-v)} + 2uy - uw = 0,\\ \frac{\partial h}{\partial w} &= -qw + q\frac{\Phi'(w-v)}{1-\Phi(w-v)} - uy = -qw + q\frac{e^{-(w-v)^2/2}}{\sqrt{2\pi}[1-\Phi(w-v)]} - uy = 0. \end{aligned}$$
(S56)

This system can be solved numerically for each tuple  $\boldsymbol{\sigma} = (q, u, v)$ , yielding the functions  $y^{\star}(\boldsymbol{\sigma})$  and  $w^{\star}(\boldsymbol{\sigma})$  as the coordinates of the critical point. We now expand  $h(y, w; \boldsymbol{\sigma})$  around these coordinates point up to second order. Using that  $\Phi''(y - v) = -(y - v)\Phi'(y - v)$  and the conditions (S56), we find

$$\frac{\partial^{2}h}{\partial y^{2}}\Big|_{\substack{y=y^{\star}\\w=w^{\star}}} = 2u + q + (1-q)\Big[y - v + \frac{\Phi'(y-v)}{\Phi(y-v)}\Big]\frac{\Phi'(y-v)}{\Phi(y-v)}\Big|_{\substack{y=y^{\star}\\w=w^{\star}}} = 2u + q + (2uy^{\star} + qy^{\star} - uw^{\star})\Big(-v + \frac{y^{\star} - u(w^{\star} - 2y^{\star})}{1-q}\Big), \\
\frac{\partial^{2}h}{\partial w^{2}}\Big|_{\substack{y=y^{\star}\\w=w^{\star}}} = -q + q\Big[-w + v + \frac{\Phi'(w-v)}{1-\Phi(w-v)}\Big]\frac{\Phi'(w-v)}{1-\Phi(w-v)}\Big|_{\substack{y=y^{\star}\\w=w^{\star}}} = -q + (uy^{\star} + qw^{\star})\Big(v + \frac{uy^{\star}}{q}\Big), \tag{S57}$$

$$\frac{\partial^{2}h}{\partial y\partial w}\Big|_{\substack{y=y^{\star}\\w=w^{\star}}} = -u.$$

In Section S5 we show that the critical point obtained by solving the coupled system (S56) is precisely a saddle point, as stated above. Therefore, up to second order around the saddle point,

$$h(y,w;\boldsymbol{\sigma}) \approx h(y^{\star},w^{\star};\boldsymbol{\sigma}) + \frac{1}{2} \left. \frac{\partial^2 h}{\partial y^2} \right|_{\substack{y=y^{\star}\\w=w^{\star}}} (y-y^{\star})^2 + \frac{1}{2} \left. \frac{\partial^2 h}{\partial w^2} \right|_{\substack{y=y^{\star}\\w=w^{\star}}} (w-w^{\star})^2 + \frac{\partial^2 h}{\partial y \partial w} \right|_{\substack{y=y^{\star}\\w=w^{\star}}} (y-y^{\star})(w-w^{\star}).$$
(S58)

Substituting the expansion into equation (S54) and transforming the integral over  $\Gamma$  back into an integral over a real variable yields, up to first order in the asymptotic expansion of the exponent in powers of 1/n, the following approximation for the probability  $\mathcal{P}(\{S\}_k|n)$  that the support of the globally stable fixed point is  $\{S\}_k$ :

$$\mathcal{P}(\{S\}_k|n) = \frac{n(q+u)-1}{\sqrt{K(\boldsymbol{\sigma},n)}} e^{-nh(y^\star,w^\star;\boldsymbol{\sigma})+y^\star(y^\star-w^\star)},\tag{S59}$$

573 with

$$K(\boldsymbol{\sigma}, n) := (nu-1)^2 + n^2 \left[ -q + (uy^* + qw^*) \left( v + \frac{uy^*}{q} \right) \right] \\ \times \left[ \frac{2}{n} - 2u - q - (2uy^* + qy^* - uw^*) \left( -v + \frac{y^* - u(w^* - 2y^*)}{1 - q} \right) \right].$$
(S60)

 $_{574}$  We can write equation (S59) as

$$\mathcal{P}(\{S\}_k|n) = \frac{n(q+u) - 1}{\sqrt{K(\boldsymbol{\sigma}, n)}} e^{nH(\boldsymbol{\sigma}) + G(\boldsymbol{\sigma})}$$
(S61)

575 where

$$H(\boldsymbol{\sigma}) := \frac{q}{2} \left( w^{\star 2} - y^{\star 2} \right) + (1 - q) \log[\Phi(y^{\star} - v)] + q \log[1 - \Phi(w^{\star} - v)] - uy^{\star 2} + uy^{\star}w^{\star},$$
  

$$G(\boldsymbol{\sigma}) := y^{\star}(y^{\star} - w^{\star}).$$
(S62)

576 We now use the Stirling approximation to get

$$\binom{n}{qn} \approx \frac{e^{-n[q\log q + (1-q)\log(1-q)]}}{\sqrt{2\pi q(1-q)}}.$$
(S63)

577 According to equation (S51), our approximation for the probability of coexistence is

$$P(k|n) = \frac{n(q+u) - 1}{\sqrt{2\pi q(1-q)K(\boldsymbol{\sigma}, n)}} e^{nF(\boldsymbol{\sigma}) + G(\boldsymbol{\sigma})},$$
(S64)

578 where

$$F(\boldsymbol{\sigma}) := \frac{q}{2} \Big( w^{\star 2} - y^{\star 2} \Big) + (1 - q) \log[\Phi(y^{\star} - v)] + q \log[1 - \Phi(w^{\star} - v)] \\ - uy^{\star 2} + uy^{\star}w^{\star} - q \log q - (1 - q) \log(1 - q), \quad (S65)$$

In the discrete distribution given by equation (S64) we have to set k = qn for  $0 \le q \le 1$  (i.e.,  $0 \le k \le n$ ). We can reproduce the original parameterization with non-scaled interspecific interactions ( $\mu$ ) by changing  $\hat{\mu}$  back to  $n\mu$ , i.e, replacing the constant u by  $\frac{\alpha}{n\mu}$ .

# 582 S5 Classification of the critical point

In order to prove that the critical point  $(y^*, w^*)$  obtained as the solution of Eq. (S56) is a saddle point, we only have to show that the discriminant satisfies

$$D(y^{\star}, w^{\star}) = \left(\frac{\partial^2 h}{\partial y^2}\right) \left(\frac{\partial^2 h}{\partial w^2}\right) - \left(\frac{\partial^2 h}{\partial y \partial w}\right)^2 < 0,$$
(S66)

where all the derivatives are evaluated at the critical point. From Eq. (S57) we observe that

$$D(y^{\star}, w^{\star}) = \left(\frac{\partial^2 h}{\partial y^2}\right) \left(\frac{\partial^2 h}{\partial w^2}\right) - u^2.$$
(S67)

We now show that  $\frac{\partial^2 h}{\partial y^2} \ge 0$  and  $\frac{\partial^2 h}{\partial w^2} \le 0$  at the critical point for any combination of parameters  $\sigma = (q, u, v)$ . This will complete the proof.

First, consider the expression in (S57) for  $\frac{\partial^2 h}{\partial y^2}$ . Since u > 0 (recall that we study the case  $\alpha < \mu < 0$  and  $u = \alpha/\hat{\mu} = \alpha/(n\mu) > 0$ ) and  $0 \le q \le 1$ , we can write

$$\left. \frac{\partial^2 h}{\partial y^2} \right|_{\substack{y=y^*\\w=w^*}} \ge (2uy^* + qy^* - uw^*) \left( -v + \frac{y^* - u(w^* - 2y^*)}{1 - q} \right).$$
(S68)

<sup>590</sup> This product is positive or zero. On the one hand, according to (S56),

$$2uy^{\star} + qy^{\star} - uw^{\star} = \frac{1 - q}{\sqrt{2\pi}} \frac{e^{-(y^{\star} - v)^2/2}}{\Phi(y^{\star} - v)},$$
(S69)

which is obviously a non-negative quantity. On the other hand,  $y^* - u(w^* - 2y^*) = (1 - q)y^* + 2uy^* + qy^* - uw^*$ , hence

$$-v + \frac{y^{\star} - u(w^{\star} - 2y^{\star})}{1 - q} = y^{\star} - v + \frac{e^{-(y^{\star} - v)^2/2}}{\sqrt{2\pi}\Phi(y^{\star} - v)} = f_1(y^{\star} - v),$$
(S70)

where we have defined the function  $f_1(x) = x + \frac{e^{-x^2/2}}{\sqrt{2\pi}\Phi(x)}$ . It increases monotonically and, as  $x \to -\infty, f_1(x) \approx -\frac{1}{x} > 0$ . Therefore  $f_1(x) > 0$  for all x and we have shown that  $\frac{\partial^2 h}{\partial y^2} \ge 0$ . Now, from (S56) we obtain

$$uy^{\star} + qw^{\star} = \frac{q}{\sqrt{2\pi}} \frac{e^{-(w^{\star} - v)^2/2}}{1 - \Phi(w^{\star} - v)}.$$
 (S71)

<sup>596</sup> Therefore we can express the term  $v + uy^*/q$  that appears in Eq. (S57) as

$$v + \frac{uy^{\star}}{q} = -(w^{\star} - v) + \frac{e^{-(w^{\star} - v)^2/2}}{\sqrt{2\pi}[1 - \Phi(w^{\star} - v)]}.$$
 (S72)

597 Let us define the function

$$f_2(x) = \frac{e^{-x^2/2}}{\sqrt{2\pi}[1 - \Phi(x)]}.$$
(S73)

 $_{598}$  Using the three equations above into (S57) we find

$$\frac{\partial^2 h}{\partial w^2} \bigg|_{\substack{y=y^*\\w=w^*}} = -q\{1 + f_2(w^* - v)[w^* - v - f_2(w^* - v)]\}.$$
(S74)

599 Now we observe that the function

$$f_3(x) := 1 + f_2(x)[x - f_2(x)]$$
(S75)

is equal to the derivative of  $f_4(x) = x - f_2(x)$  with respect to x,  $f_3(x) = f'_4(x)$ . Therefore, to show that  $\frac{\partial^2 h}{\partial w^2} \leq 0$  it is sufficient to see that  $f_4(x)$  is a monotonically increasing function (hence  $f_3(x) > 0$  and  $\frac{\partial^2 h}{\partial w^2} = -qf_3(w^* - v) < 0$ ). A simple graphical analysis for  $f_4(x)$  proves that this is indeed the case. As a consequence,

$$D(y^{\star}, w^{\star}) = \left(\frac{\partial^2 h}{\partial y^2}\right) \left(\frac{\partial^2 h}{\partial w^2}\right) - u^2 \le -u^2 < 0$$
(S76)

and  $(y^{\star}, w^{\star})$  is a saddle pont.

In summary, we have shown that the solution  $(y^*, w^*)$  of Eq. (S56) is a saddle point for the function  $h(y, w; \boldsymbol{\sigma})$  defined in Eq. (S55), when w is regarded as a real variable. This implies, by the Cauchy-Riemman condition, that the real part of h has a minimum along the imaginary w axis (i.e, along the integration contour  $\Gamma$ ). Since the saddle point is unique, it yields a global minimum for the exponent in the probability (S54) of finding the globally stable fixed point with support  $\{S\}_k$ .

#### <sup>611</sup> S6 Mode of the distribution for large number of species

For large n, the mode of the distribution (S64) is recovered at a  $q^*$  value such that F takes its maximum value. We now calculate this  $q^*$  in the limits  $\alpha/\hat{\mu} \gg 1$  (the mode has to be close to 1/2) and the ecological case  $\alpha/\hat{\mu} \ll 1$ .

First recall that, by definition [cf. equation (S37)],  $v = \frac{\gamma s}{k+s}$ . In the limit of large n,  $v = \frac{\gamma u}{q+u}$  is a function of q, so we have to take into account this implicit dependence on q. We take the derivative with respect to q on equation (S65),

$$\frac{\partial F}{\partial q} = \frac{1}{2} \Big( w^{*2} - y^{*2} \Big) + q \Big( w^{*} w^{*\prime} - y^{*} y^{*\prime} \Big) - \log \Phi(y^{*} - v) + \log(1 - \Phi(w^{*} - v)) + (w^{*} - 2y^{*}) uy^{*\prime} \\ + uy^{*} w^{*\prime} + (1 - q) \Big( y^{*\prime} - v' \Big) \frac{\Phi'(y^{*} - v)}{\Phi(y^{*} - v)} - q \Big( w^{*\prime} - v' \Big) \frac{\Phi'(w^{*} - v)}{1 - \Phi(w^{*} - v)} + \log \frac{1 - q}{q}.$$
(S77)

<sup>618</sup> Now, according to equation (S56),

$$\frac{\Phi'(y^{\star}-v)}{\Phi(y^{\star}-v)} = \frac{qy^{\star}+2uy^{\star}-uw^{\star}}{1-q},$$
  
$$\frac{\Phi'(w^{\star}-v)}{1-\Phi(w^{\star}-v)} = \frac{uy^{\star}+qw^{\star}}{q},$$
 (S78)

so the derivative with respect to q simplifies to

$$\frac{\partial F}{\partial q} = \frac{1}{2} \left( w^{\star 2} - y^{\star 2} \right) - v(w^{\star} - y^{\star}) - \log \Phi(y^{\star} - v) + \log(1 - \Phi(w^{\star} - v)) + \log \frac{1 - q}{q}.$$
 (S79)

620 Setting the derivative to zero yields the condition

$$(1 - q^*)e^{w^{*2}/2 - vw^*}[1 - \Phi(w^* - v)] = q^*e^{y^{*2}/2 - vy^*}\Phi(y^* - v),$$
(S80)

where the functions  $y^{\star}(\boldsymbol{\sigma})$ ,  $w^{\star}(\boldsymbol{\sigma})$  and v(q) are evaluated at  $q = q^{\star}$ . On the other hand,

$$\frac{\Phi'(y^* - v)}{\Phi(y^* - v)} = \frac{qy^* + 2uy^* - uw^*}{1 - q} = \frac{e^{-(y^* - v)^2/2}}{\sqrt{2\pi}\Phi(y^* - v)},$$
  
$$\frac{\Phi'(w^* - v)}{1 - \Phi(w^* - v)} = \frac{uy^* + qw^*}{q} = \frac{e^{-(w^* - v)^2/2}}{\sqrt{2\pi}[1 - \Phi(w^* - v)]},$$
(S81)

622 hence

$$(1-q)e^{-(y^{\star}-v)^{2}/2} = \sqrt{2\pi}\Phi(y^{\star}-v)(qy^{\star}+2uy^{\star}-uw^{\star}),$$
  
$$qe^{-(w^{\star}-v)^{2}/2} = \sqrt{2\pi}[1-\Phi(w^{\star}-v)](uy^{\star}+qw^{\star}).$$
 (S82)

Substituting these expressions into equation (S80) yields, after some algebra, this simple condition for the mode of the distribution,  $q^*$ :

$$y^{\star}(q^{\star}, u, v(q^{\star})) = w^{\star}(q^{\star}, u, v(q^{\star})).$$
(S83)

<sup>625</sup> Then, if this condition is satisfied, equation (S79) reduces to  $\log \frac{1-\Phi(y^{\star}-v)}{\Phi(y^{\star}-v)} = \log \frac{q^{\star}}{1-q^{\star}}$ , which <sup>626</sup> implies

$$\Phi(y^* - v) = 1 - q^*.$$
(S84)

627 From this we get

$$y^{\star}(q^{\star}, u, v(q^{\star})) = v(q^{\star}) + \sqrt{2} \text{erf}^{-1}(1 - 2q^{\star}).$$
 (S85)

Finally we take into account the last expression and use equation (S83) into equation (S56) to obtain  $\left[-\frac{1}{2}\left(x-x\right)\right]^{2}$ 

$$\sqrt{2\gamma u} + 2(q^* + u) \operatorname{erf}^{-1}(1 - 2q^*) = \frac{e^{-\left[\operatorname{erf}^{-1}(1 - 2q^*)\right]^2}}{\sqrt{\pi}}$$
(S86)

which is a transcendental equation that determines the mode of the distribution  $q^* = \frac{k^*}{n}$  as a function of interaction strengths and growth rates. Equivalently, the transcendental condition for the mode can be expressed as

$$\frac{\alpha}{\hat{\mu}} = \frac{e^{-\left[\Phi^{-1}(1-q^{\star})\right]^2/2} - \sqrt{2\pi}q^{\star}\Phi^{-1}(1-q^{\star})}{\sqrt{2\pi}[\Phi^{-1}(1-q^{\star})+\gamma]},$$
(S87)

with  $\Phi^{-1}(q) = \sqrt{2} \text{erf}^{-1}(2q-1)$ . A simple relation arises for the curve that separates left- and right-skewed distributions by choosing the mode to be  $q^* = \frac{1}{2}$ :

$$\frac{\alpha\gamma}{\hat{\mu}} = \frac{1}{\sqrt{2\pi}}.$$
(S88)

<sup>635</sup> In terms of the original (non-scaled) parameterization, this expression becomes

$$\frac{\alpha\gamma}{\mu} = \frac{n}{\sqrt{2\pi}} \tag{S89}$$

<sup>636</sup> via the substitution  $\hat{\mu} \to n\mu$ .

In the limit of small interaction strengths ( $\hat{\mu} \ll \alpha$ ) of the mean zero case ( $\gamma = 0$ ), condition (S87) reduces to

$$\frac{k^{\star}}{n} \approx \frac{1}{2} - \frac{1}{2\pi} \frac{\hat{\mu}}{\alpha} + \frac{1}{4\pi} \left(\frac{\hat{\mu}}{\alpha}\right)^2,\tag{S90}$$

<sup>639</sup> which reproduces the expected (binomial) behavior.

#### 640 S7 Truncated-Gaussian distributed rates

<sup>641</sup> In this section we analyze the case that growth rates are drawn from a from a truncated<sup>642</sup> Gaussian distribution,

$$P(\mathbf{r}) = \frac{1}{Z_n} \exp\left(-\sum_{i=1}^n \frac{(r_i - \gamma)^2}{2}\right) \prod_{j=1}^n \Theta(r_j) , \qquad (S91)$$

so that every rate  $r_j > 0$  for j = 1, ..., n ( $Z_n$  is a suitable normalization constant). Then we can express the probability  $\mathcal{P}(\{S\}_k | \mathbf{A})$  of observing the globally stable fixed point with support  $\{S\}_k$  in a simple form:

$$\mathcal{P}_{T}(\{S\}_{k}|\boldsymbol{A}) \equiv \int d^{k}\boldsymbol{x} \left(\prod_{i=1}^{k} \Theta(x_{i})\right) \int d^{n-k}\boldsymbol{z} \left(\prod_{j=k+1}^{n} \Theta(-z_{j})\right) f_{T}(\boldsymbol{x},\boldsymbol{z}|\boldsymbol{A}) .$$
(S92)

646 where

$$f_T(\boldsymbol{x}, \boldsymbol{z} | \boldsymbol{A}) = \frac{|\det \boldsymbol{A}^{(s)}|}{Z_n} \exp\left(-\frac{1}{2}(\boldsymbol{x} - \boldsymbol{\xi})^T \boldsymbol{G}(\boldsymbol{x} - \boldsymbol{\xi}) - \frac{1}{2} \|\boldsymbol{z} - \boldsymbol{A}^{(ns)} \boldsymbol{x} - \gamma \boldsymbol{1}_{n-k}\|^2\right) \\ \times \prod_{i=1}^k \Theta\left(-(\boldsymbol{A}^{(s)} \boldsymbol{x})_i\right) \prod_{j=k+1}^n \Theta\left(z_j - (\boldsymbol{A}^{(ns)} \boldsymbol{x})_j\right).$$
(S93)

We focus on the rank-one competitive case:  $\mathbf{A}^{(s)} = (\alpha - \mu)\mathbf{I}_k + \mu \mathbf{1}_k \mathbf{1}_k^T$ ,  $\mathbf{A}^{(ns)} = \mu \mathbf{1}_{n-k} \mathbf{1}_k^T$ for  $\alpha < \mu < 0$ . Then

$$(\boldsymbol{A}^{(s)}\boldsymbol{x})_i = (\alpha - \mu)x_i + \mu(\boldsymbol{1}_k^T\boldsymbol{x}) = \alpha x_i + \mu \sum_{\substack{s=1\\s\neq i}}^k x_s.$$
 (S94)

Since Eq. (S92) forces that  $x_i > 0$ , and  $\alpha$  and  $\mu$  are both negative, we find that  $-(\mathbf{A}^{(s)}\mathbf{x})_i$  is always positive, i.e., it holds that

$$\Theta\left(-(\boldsymbol{A}^{(s)}\boldsymbol{x})_i\right)\Theta(x_i) = \Theta(x_i).$$
(S95)

On the other hand,  $\mu(\mathbf{1}_k^T \boldsymbol{x}) < 0$  and we can express

$$\Theta\left(z_j - (\boldsymbol{A}^{(ns)}\boldsymbol{x})_j\right)\Theta(-z_j) = \Theta\left(z_j - \mu(\boldsymbol{1}_k^T\boldsymbol{x})\right) + \Theta(-z_j) - 1.$$
(S96)

Now, we apply the same changes of variable leading to Eq. (S27). Then we can write

$$\mathcal{P}_{T}(\{S\}_{k}|n) = \frac{|\alpha - \mu|^{k-1}|\alpha + (k-1)\mu|}{Z_{n}} \int d^{k}\boldsymbol{x} \prod_{i=1}^{k} \Theta(x_{i} + \xi^{(k)}) e^{-\frac{1}{2}\boldsymbol{x}^{T}} \boldsymbol{G}\boldsymbol{x}$$

$$\times \int d^{n-k}\boldsymbol{z} \prod_{j=k+1}^{n} \Big[ \Theta(-z_{j} - \gamma - k\mu\xi^{(k)}) + \Theta(z_{j} - \mu(\mathbf{1}_{k}^{T}\boldsymbol{x}) + \gamma) - 1 \Big] e^{-\frac{1}{2}\|\boldsymbol{z} - \mu(\mathbf{1}_{k}^{T}\boldsymbol{x})\mathbf{1}_{n-k}\|^{2}} .$$
(S97)

Let  $\mathcal{K} = \{1, \dots, n-k\}$ . Expanding the product we get

$$\prod_{j=k+1}^{n} \left\{ \Theta(-z_{j} - \gamma - k\mu\xi^{(k)}) + \left[ \Theta(z_{j} - \mu(\mathbf{1}_{k}^{T}\boldsymbol{x}) + \gamma) - 1 \right] \right\} \\
= \sum_{\ell=0}^{n-k} \sum_{\substack{p \in C_{\ell}^{n-k} \\ b = \mathcal{K} \setminus p}} \prod_{j=1}^{\ell} \Theta(-z_{p(j)+k} - \gamma - k\mu\xi^{(k)}) \prod_{i=1}^{n-k-\ell} \left[ \Theta(z_{b(i)+k} - \mu(\mathbf{1}_{k}^{T}\boldsymbol{x}) + \gamma) - 1 \right], \quad (S98)$$

where  $p = (p(1), \ldots, p(\ell))$  is a combination of  $\ell$  elements taken from  $\mathcal{K}, p \in C_{\ell}^{n-k}$ , and b is formed by the remaining elements of the set,  $b = \{1, \ldots, n-k\} \setminus p$ . Without loss of generality, since integrals are invariant under changes of indices in variable z, we can decompose

$$\mathcal{P}_{T}(\{S\}_{k}|n) = \frac{|\alpha - \mu|^{k-1}|\alpha + (k-1)\mu|}{Z_{n}} \int d^{k}\boldsymbol{x} \prod_{i=1}^{k} \Theta(x_{i} + \xi^{(k)}) e^{-\frac{1}{2}\boldsymbol{x}^{T}}\boldsymbol{G}\boldsymbol{x}$$

$$\times \sum_{\ell=0}^{n-k} \binom{n-k}{\ell} \prod_{j=k+1}^{\ell+k} \int dz_{j} \Theta(-z_{j} - \gamma - k\mu\xi^{(k)}) e^{-\frac{1}{2}[z_{j} - \mu(\mathbf{1}_{k}^{T}\boldsymbol{x})]^{2}}$$

$$\times \prod_{i=\ell+k+1}^{n} \int dz_{i} \Big[\Theta(z_{i} - \mu(\mathbf{1}_{k}^{T}\boldsymbol{x}) + \gamma) - 1\Big] e^{-\frac{1}{2}[z_{i} - \mu(\mathbf{1}_{k}^{T}\boldsymbol{x})]^{2}}.$$
(S99)

657 Note now that

$$\int_{-\infty}^{\infty} dz \Big[\Theta(z-\mu(\mathbf{1}_k^T \boldsymbol{x})+\gamma)-1\Big] e^{-\frac{1}{2}\left[z-\mu(\mathbf{1}_k^T \boldsymbol{x})\right]^2} = -\sqrt{2\pi} \Phi(-\gamma).$$
(S100)

Therefore we can decompose  $\mathcal{P}(\{S\}_k|n)$  as the sum

$$\mathcal{P}_T(\{S\}_k|n) = \frac{(2\pi)^{n/2}}{Z_n} \sum_{\ell=0}^{n-k} \binom{n-k}{\ell} [-\Phi(-\gamma)]^{n-\ell-k} \mathcal{P}(\{S\}_k|\ell+k),$$
(S101)

where  $\mathcal{P}(\{S\}_k|n)$  is precisely the expression (S27) obtained for the non-truncated Gaussian distribution. According to Eq. (S39),

$$\mathcal{P}(\{S\}_k|\ell+k) = \frac{k+s}{2\pi i} \int_{-\infty}^{\infty} dy \int_{\Gamma} dw \, e^{-\frac{1}{2}(k+2s)y^2 + syw + \frac{1}{2}kw^2} [1 - \Phi(w-v)]^k [\Phi(y-v)]^\ell.$$
(S102)

<sup>661</sup> We introduce (S102) into (S101) and use the binomial expansion

$$\sum_{\ell=0}^{n-k} \binom{n-k}{\ell} [-\Phi(-\gamma)]^{n-\ell-k} [\Phi(y-v)]^{\ell} = [\Phi(y-v) - \Phi(-\gamma)]^{n-k}$$
(S103)

to get the probability  $\mathcal{P}_T(\{S\}_k|n)$  expressed as a double integral,

$$\mathcal{P}_{T}(\{S\}_{k}|n) = \frac{(2\pi)^{n/2-1}(k+s)}{i Z_{n}} \int_{-\infty}^{\infty} dy \int_{\Gamma} dw \, e^{-\frac{1}{2}(k+2s)y^{2}+syw+\frac{1}{2}kw^{2}} \times \left[1 - \Phi(w-v)\right]^{k} \left[\Phi(y-v) - \Phi(-\gamma)\right]^{n-k}.$$
 (S104)

Note that the only difference with Eq. (S39) is the term  $\Phi(-\gamma)$  that appears in the last factor of the integrand. Hence we can easily extend the saddle-point calculation for the truncated Gaussian case. The probability  $P_T(k|n) = \binom{n}{k} \mathcal{P}_T(\{S\}_k|n)$  that the support has cardinality k in this case can be written, up to a normalization factor and sub-leading corrections, as  $P_T(k|n) \sim e^{nF_T(\sigma)}$ , where

$$F_T(\boldsymbol{\sigma}) := \frac{q}{2} \left( w^{\star 2} - y^{\star 2} \right) + (1 - q) \log[\Phi(y^{\star} - v) - \Phi(-\gamma)] + q \log[1 - \Phi(w^{\star} - v)] - uy^{\star 2} + uy^{\star}w^{\star} - q \log q - (1 - q) \log(1 - q).$$
(S105)

We can compare the mode of the distribution for the truncated and the purely Gaussian cases. The calculation of the mode follows the same steps of the Gaussian case. The equations for the saddle point  $(y^*, w^*)$  are now

$$qy - (1 - q)\frac{\Phi'(y - v)}{\Phi(y - v) - \Phi(-\gamma)} + 2uy - uw = 0,$$
  

$$qw - q\frac{\Phi'(w - v)}{1 - \Phi(w - v)} + uy = 0.$$
(S106)

As can be easily checked, the condition  $\frac{\partial F_T}{\partial q} = 0$  to be satisfied by the mode  $q^*$  leads to the same constraint as in the Gaussian case,  $y^*(q^*, u, v(q^*)) = w^*(q^*, u, v(q^*))$ , see Eq. (S83). This implies that

$$\Phi(y^{\star} - v) = 1 - q^{\star} + q^{\star} \Phi(-\gamma), \qquad (S107)$$

which reduces to the Gaussian-case condition for the mode in the limit of large  $\gamma$ , where both the truncated and the Gaussian distributions tend to almost overlap. Finally, after the same algebraic manipulations in the condition above we obtain the following non-linear equation that determines the mode in the truncated-Gaussian case:

$$[1 - \Phi(-\gamma)] \Big[ \sqrt{2\gamma}u + 2(q^{\star} + u) \operatorname{erf}^{-1} (1 - 2q^{\star} + 2q^{\star} \Phi(-\gamma)) \Big] = \frac{1}{\sqrt{\pi}} e^{-\left[\operatorname{erf}^{-1} (1 - 2q^{\star} + 2q^{\star} \Phi(-\gamma))\right]^2}.$$
(S108)

Figure S1 shows the most probable number of coexisting species obtained for the Gaussian and the truncated Gaussian distributions as function of the parameters  $\gamma$  and  $\alpha/\hat{\mu}$ . We observe that the expected values for both cases are roughly the same for  $\gamma \gtrsim 1$ .



Fig. S1. Comparison between the modes for purely Gaussian and truncated-Gaussian distributed growth rates.

#### 684 S8 Final communities

Figure S2 shows the properties of the parameters of the communities found after the dynamical pruning, for an starting community of 1000 species, and a final community comprising 472 species. As proposed recently<sup>30</sup>, the matrix of interactions in the pruned community is a random subset of the original. On the other hand, the distribution of growth rates changes in a nontrivial way, with a larger mean and positive skewness. This change is related to the negative diagonal that we need to add to the matrix in order to ensure stability, pushing the r's values towards the right.



Fig. S2. Comparison between the properties of the original community with n = 1000 and 693 the final community, after dynamical pruning, comprising n = 472 species. The first row 694 shows the eigenvalue distribution of the matrix of interaction A; for a matrix in which the 695 entries are i.i.d. samples from a distribution, we expect the eigenvalues to be approximately 696 uniformly distributed in a circle in the complex plane, whose radius depends on the size of 697 the system and the variance of the distribution  $^{5,26}$ . In the second panel, we show that indeed 698 the distribution of the off-diagonal elements of A is the same before/after dynamics. Finally, 699 in the third panel we show that instead the distribution of growth rates changes non trivially. 700

#### 701 S9 Numerical simulations

In this section, we detail the numerical simulations we used to corroborate our argument, and extend it to cases in which a direct analytic computation is unfeasible. We start by illustrating the Lemke-Howson algorithm that can be used to efficiently search for the noninvasible solution. Applying this algorithm, we were able to determine the non-invasible solution of a system without the need to integrate the dynamics numerically. Then, we detail the parameters for the numerical simulations—how are the matrices constructed, and how the network structure is introduced.

#### 709 S9.1 Lemke-Howson algorithm

Because of the equivalence between the Lotka-Volterra and the replicator equation  $^{42}$ , the noninvasible solution in the diagonally stable regime *is* the *unique* symmetric Nash equilibrium for the replicator dynamics in which the last element of the solution is played with non-zero probability  $^{41}$  (this last element can be interpreted as "the environment" when moving from LV with *n* equations to a replicator system with n + 1 equations). We use the Lemke-Howson algorithm  $^{43}$  to find such a solution. This algorithm is based on exploring the vertices of the following polytope:

$$P = \{ \boldsymbol{z} \in \mathbb{R}^n | \boldsymbol{z} \ge \boldsymbol{0}, \boldsymbol{C}\boldsymbol{z} \le \boldsymbol{1} \},$$
(S109)

where C is a positive payoff matrix of an  $n \times n$  symmetric game—the positivity of the payoffs can be assumed without loss of generality, because adding a suitable constant to all the elements of the payoff matrix does not affect the dynamics. We say that  $z \in P$  has label k if  $z_k = 0$  and label -k if  $(Cz)_k = 1$ . Let us assume that P is simple (which holds almost surely in the cases we explore), that is, each vertex is adjacent to exactly n facets—a facet is defined by setting to equality one of the inequalities defining the polytope. Say that z represents strategy k if either it has label k or -k, then because of the simplicity assumption any z that represents all strategies is either **0** or the normalized vector  $\hat{z} = z / \sum_i z_i$  is a symmetric Nash equilibrium for the game.

In order to find the solution we move around the vertices of P starting from  $v_0 = 0$  using 726 a tableaux T: r = 1 - Cz with a slack variable r. Say that  $r_k$  is in the basis for a vertex 727  $v \in P$  if and only if v does not have label -k, and  $z_k$  is in the basis if and only if v does 728 not have label k. Then  $v_0$  has basis  $\{r_1, \ldots, r_n\}$ , bring  $z_n$  to the basis and by the min. ratio 729 rule—i.e., by looking at the ratio between the free variable (in this case 1) and the coefficients 730 of  $z_n$  in the tableaux—choose  $r_k$  to leave the basis and proceed to an adjacent vertex  $v_1$ . 731 In the next iteration bring  $z_k$  to the basis and move to an adjacent vertex  $v_2$ . We keep 732 repeating this process until we get to a vertex v which represents all strategies, that is, v is a 733 Nash equilibrium which moreover will have  $z_n$  in the basis (since by construction the process 734 will stop when the element leaving the basis is  $r_n$ ). Because of the simplicity assumption 735 the process is going to terminate, having to do in the worst case  $2^n$  iterations. As it often 736 happens, this worst-case scenario is never found in practice, making the algorithm efficient. 737

Let us illustrate this ideas by a simple example. Take the Lotka-Volterra system withinteractions

$$\boldsymbol{A} = \begin{pmatrix} -2 & 1\\ 1 & -2 \end{pmatrix}, \tag{S110}$$

740 and intrinsic growth rates:

$$\boldsymbol{r} = \begin{pmatrix} -1\\ 3 \end{pmatrix} \tag{S111}$$

<sup>741</sup> We build the payoff matrix:

$$C = \begin{pmatrix} -2 & 1 & -1 \\ 1 & -2 & 3 \\ 0 & 0 & 0 \end{pmatrix} \rightarrow \begin{pmatrix} 1 & 4 & 2 \\ 4 & 1 & 6 \\ 3 & 3 & 3 \end{pmatrix},$$
(S112)

where we have added a constant to all entries to make them all positive. At the beginning ofthe algorithm we have the following tableaux:

$$r_{1} = 1 - z_{1} - 4z_{2} - 2z_{3},$$

$$r_{2} = 1 - 4z_{1} - z_{2} - 6z_{3},$$

$$r_{3} = 1 - 3z_{1} - 3z_{2} - 3z_{3}.$$
(S113)

We now bring  $z_3$  into the basis, and by the min. ratio rule: the ratio of 1 and the coefficients of  $z_3$ ,  $r_2$  should leave the basis and the updated tableaux is:

$$r_{1} = \frac{2}{3} + \frac{1}{3}z_{1} - \frac{11}{3}z_{2} + \frac{1}{3}r_{2},$$

$$z_{3} = \frac{1}{6} - \frac{4}{6}z_{1} - \frac{1}{6}z_{2} - \frac{1}{6}r_{2},$$

$$r_{3} = \frac{1}{2} - z_{1} - \frac{5}{2}z_{2} + \frac{1}{2}r_{2}.$$
(S114)

Now  $z_2$  enters the basis, and in this case  $r_1$  leaves from the basis:

$$z_{2} = \frac{2}{11} + \frac{1}{11}z_{1} - \frac{3}{11}r_{1} + \frac{1}{11}r_{2},$$

$$z_{3} = \frac{3}{22} - \frac{15}{22}z_{1} + \frac{1}{22}r_{1} - \frac{2}{11}r_{2},$$

$$r_{3} = \frac{1}{22} - \frac{27}{22}z_{1} + \frac{15}{22}r_{1} + \frac{3}{11}r_{2}.$$
(S115)

<sup>747</sup> We bring  $z_1$  into the basis and then we are done because  $r_3$  leaves the basis in this case. So <sup>748</sup> the Nash equilibrium for this game has full support. The final state of the tableaux is :

$$z_{1} = \frac{1}{27} + \frac{15}{27}r_{1} + \frac{2}{9}r_{2} - \frac{22}{27}r_{3},$$

$$z_{2} = \frac{5}{27} - \frac{6}{27}r_{1} + \frac{1}{9}r_{2} - \frac{2}{27}r_{3},$$

$$z_{3} = \frac{1}{9} - \frac{1}{3}r_{1} - \frac{1}{3}r_{2} + \frac{15}{27}r_{3}.$$
(S116)

<sup>749</sup> By normalizing the free elements in the final tableaux we also get the values at equilibrium, <sup>750</sup> which in this case is (1/9, 5/9, 3/9). Because the last element is positive, then the two species <sup>751</sup> coexist, the second with an equilibrium value that is five times as large as the first.

#### 752 S9.2 Sampling the matrices and growth rates

In the following we give the details of the construction of the matrices and growth rates for the cases we explored. For each case we repeat the process  $2 \times 10^5$  times.

#### 755 S9.2.1 Mean zero

We sample the entries of  $\boldsymbol{B}$  in pairs,  $(B_{ij}, B_{ji})$  for  $j \neq i$  from a bivariate Normal distribution  $N(\mathbf{0}, \boldsymbol{\Sigma})$  where  $\boldsymbol{\Sigma}$  is a covariance matrix with diagonal 1 and off-diagonal  $\rho$ . The diagonal elements  $B_{ii}$  are chosen from a standard Normal distribution N(0, 1). We then calculate the leading eigenvalue of  $\boldsymbol{B} + \boldsymbol{B}^T$ :  $\lambda_M = \max_{\lambda}(\Re(\lambda(\boldsymbol{B} + \boldsymbol{B}^T)))$ . We define  $\boldsymbol{A} = \boldsymbol{B} - d\boldsymbol{I}$ , where d is a constant sufficient to make  $\boldsymbol{A} + \boldsymbol{A}^T$  negative definite. More precisely, we choose  $d = -\lambda_M - 10^{-6}$  (so that the matrix  $\boldsymbol{A} + \boldsymbol{A}^T$  is barely stable). The entries of  $\boldsymbol{r}$  are sampled from a standard Normal distribution N(0, 1).

#### 763 S9.2.2 Mean non zero

In this case, the entries of the matrix are fixed and we choose each entry of r from a Normal distribution  $N(\gamma, 1)$ .

#### 766 S9.2.3 Adding Structure

In order to include a network structure, we generate an adjacency matrix G with a desired 767 connectance level C (we used C = 0.1 and C = 0.25) and all diagonal elements set to one. In 768 the case of a power-law structure, we use the sample\_fitness\_pl function from the igraph 769 package in R with an exponent of 2. For the modular and bipartite structures we split the 770 matrix in two blocks, and arrange the connectance levels within and among them such that 771 one is higher than the other—in particular we require two parameters  $b_r$  and  $c_r$  that determine 772 the ratio of the size among the blocks and the ratio of the connectance within and among 773 blocks (e.g.  $c_r > 1$  for a modular structure). The values used were  $b_r = 1/3$  for both cases, 774 with  $c_r = 3$  for modular, and  $c_r = 1/3$  for bipartite. This adjacency matrix is then multiplied 775 element-wise to our original matrix. The results are presented in Figure 1 in the main text 776 as well as in Figure S3. 777

<sup>778</sup> In the mean-zero case the matrix is made negative definite by the same process described <sup>779</sup> above.

In the mean non-zero case the fully connected matrix is by construction negative definite  $(\alpha < \mu < 0)$  but when we add structure we need to restrict the values of  $\mu$  that keep the negative definiteness.

The prediction shown in Figure 3 of the main text is the mode of a fully connected system using the rescaled  $\mu$ :  $\hat{\mu} = n\mu C$ .



**Fig. S3.** As Figure 1 of the main text, but with modular (top) or "anti-modular" (i.e., close to bipartite, bottom) structures.

#### 788 S10 Assembly

So far, we have described the dynamical process associated with equation (S1) when starting 789 with all n species present. A different view of the problem is to take our original n-dimensional 790 system as a species pool, and from that derive the possible states to which one can arrive by 791 adding one species at a time. This define a directed graph in which the nodes are the feasible 792 states, and the edges represent invasion events connecting the two states (a subset of which 793 is shown for example in Fig. S2). In this section we present numerical evidence that suggests 794 that, in the regime of diagonal stability, one can find sets of persistent species satisfying 795 equation (S7) which cannot be assembled (Fig. S4). In such cases, our end-state with k796 species cannot be built by adding a species at a time. The probability of finding such a 797 case, however, decreases rapidly with k: when our final community has many species, the 798 probability of finding at least one assembly pathway to build the community approaches one 799 (Fig. S5). 800



Fig. S4. Assembling communities one species at a time. Top: we want to build the community with species 1, 2, ..., 7 present (darker shades for more speciose communities), by adding a species at a time. Starting from an empty system (state 0), we can try all assembly pathways in which we sequentially add one species at a time, let the dynamics unfold, and

reach a new state. In this case, an assembly path exists: by adding species 2, 5, 7, 3, 4, 6 and 1 one at a time, we always recover a feasible and stable community (dynamics are shown on the right). Bottom: again, we would like to build the community with all seven species present. In this case, no assembly path exist. For example, we can add sequentially 7, 6, 5, 3, and 2, reaching a stable community with five species. At this point, however, whenever we add one of the remaining species, we lose another—the state with all species present is unreachable, even when considering all possible assembly paths.



Fig. S5. Probability  $p_A$  of finding an assembly path when starting from n species. For different means and correlations of interactions strengths, sampled from a bivariate Normal with mean  $\mu$  (colors) and correlation  $\rho$  (columns), and for different values of mean intrinsic growth rates ( $\gamma$ , rows), we plot the probability of not finding an assembly path out of 10<sup>6</sup> simulations. While there is a nontrivial effect of all parameters (for example, for  $\rho = 0.5$  and

 $\gamma = 1$  we found an assembly path for all simulations), in all cases we found that for sufficiently large n, all communities could be built by sequential invasions.