Robust coexistence in ecological competitive communities

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Abstract

The notions of intraspecific competition and population self-regulation play a central role in ecological theory, leading to foundational concepts such as limiting similarity and niche differentiation[1–6]. They also are crucial for coexistence: for example, May[7] showed that ecological dynamics around a "feasible" equilibrium can be stabilized by imposing sufficiently strong self-regulation on all populations. For large random systems, the transition from instability to stability is sharp[7–9], and achieved beyond a critical value of intraspecific competition $\boldsymbol{d} > \boldsymbol{d_S}$. Here we show that, in ecological communities where competitive interactions are prevalent, the existence of a feasible state is guaranteed whenever $\boldsymbol{d} > \boldsymbol{d_F}$. We compute the probability of feasibility for a community of $\boldsymbol{n}$ populations given the level of intraspecific competition $\boldsymbol{d}$, and show that the transition to feasibility is smooth, contrary to what found for stability. We explore the relationship between the two critical levels, $\boldsymbol{d_S}$ and $\boldsymbol{d_F}$, and determine that, for large random ecological communities dominated by competition, $\boldsymbol{d_F} > \boldsymbol{d_S}$, that is, the existence of a feasible equilibrium implies its stability. This means that non-equilibrium coexistence via limit cycles or chaos[10, 11] is never observed in these large ecological systems. Dynamics always converge to an equilibrium in which a set of competitors robustly coexist, such that the community can recover from perturbations, be assembled from the bottom-up, and is resistant to invasions[12, 13]

Keywords: Feasibility, Stability, Lotka-Volterra, Random matrices

We study the Generalized Lotka-Volterra[14–17] (GLV) model for n interacting populations:

$$\dot{x}_i = x_i r_i \left(1 - \sum_j A_{ij} x_j\right), \tag{1}$$

where intrinsic growth rates are collected in the vector r and species interactions in the matrix A. Following May[7], we model A as the sum of two matrices $A = B + dI$, where B collects the inter-specific interactions as well as the baseline levels of intraspecific interactions, and $d \geq 0$ can be interpreted as the "excess" intraspecific competition in the system. We call these systems "competitive" whenever $r > \mathbb{0}$ (i.e., all populations can grow in isolation) and $\sum_j A_{ij} > 0$ for every species (i.e., each species has, on average, a negative effect on the growth of the other populations).

We say that Eq. 1 has a *feasible* (i.e., biologically attainable) equilibrium whenever there is a $x^\star > \mathbb{0}$ such that $\dot{x}_i = 0$ for all populations. For competitive systems, we compute a critical level $d = d_F$ such that the equilibrium $x^\star > \mathbb{0}$ exists, and further increasing $d > d_F$ retains the feasibility of the equilibrium. Interestingly, d_F is an eigenvalue of a matrix derived from that of interaction strengths, B (in analogy with d_S, which is the eigenvalue of another matrix derived from B[7–9]); we provide algorithms to compute d_F exactly, or to quickly approximate it to an arbitrary precision (SI, Sec. 1).

May[7] showed that whenever a feasible equilibrium $x^\star > \mathbb{0}$ exists, a sufficiently strong intraspecific competition $d > d_S$ guarantees that dynamics will approach $x^\star$ asymptotically. Here we compute d_S as the level of intraspecific competition that is sufficient to guarantee stability for any choice of $r > \mathbb{0}$, and show that, in competitive GLV systems this implies the global stability of a certain equilibrium[18] (SI, Sec. 2).

When $d > d_S$ and a feasible equilibrium exists, all populations coexist robustly, and dynamics return to the equilibrium after perturbations; if a feasible equilibrium does not exist, on the other hand, some populations go extinct, dynamics converge to an equilibrium containing the remaining populations, and the extinct populations cannot re-invade the system[12] (SI, Sec. 2). It is therefore important to determine the relationship between the two critical levels of intraspecific competition, d_S and d_F. For this, we turn to random ecological systems such as those studied by May[7, 8].

We take interactions to be sampled independently from a distribution with mean $\eta > 0$ and unit variance. We show that a) the exact value of $\eta > 0$ is inconsequential, and has no effect on either stability or feasibility (SI, Sec. 1), and b) both feasibility and stability are *universal*[19], meaning that any symmetric distribution with unit variance and mean $\eta > 0$ will yield the same results asymptotically (i.e., for $n \to \infty$). For each choice of n and d, the probability of feasibility $P(x^\star > \mathbb{0}|n, d)$ can be computed as:

$$P(x^\star > \mathbb{0}|n, d) = \Phi\left(\frac{\sqrt{n-1}}{n}\sqrt{d^2 - (n-1)}\right)^n \tag{2}$$

where $\Phi(\cdot)$ is the cumulative distribution function of the standard normal distribution (Figure 1, SI Sec. 2). In Figure 1, we numerically compute the probability of stability and feasibility as a function of d and overlay the theoretical curves. The transition to stability is sharp even for moderate n[9], and attained at $d_S = \sqrt{2n}$. On the contrary, the transition to feasibility is not, remaining visibly sigmoidal even for large n. Importantly, the probability of feasibility approaches zero when $d = d_S$ and the system is large: then, for a large system, whenever feasibility is attained, stability is ensured, i.e. $d_F > d_S$, and thus Eq. 2 measures the *probability of coexistence* for a large random competitive system.

This behavior is characteristic of large random communities: for an arbitrary system defined by r and B, we have that feasible equilibria can appear and disappear when increasing d (Figure 2, left). In any competitive system, however, a critical level

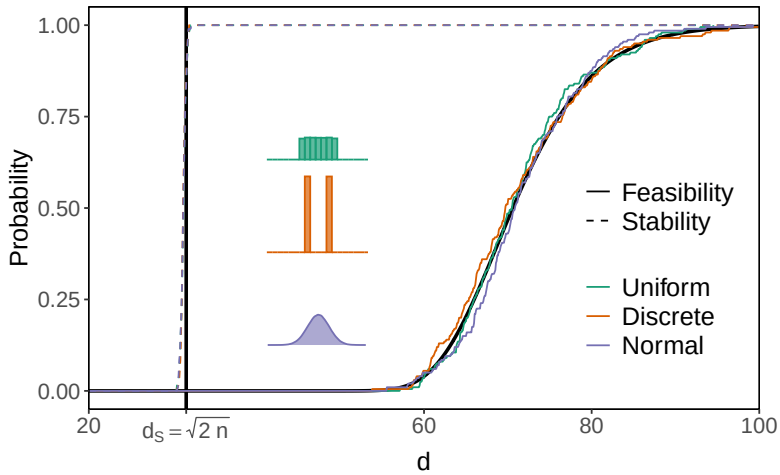

Fig. 1 Transition to stability (dashed) and feasibility (solid) for the GLV competitive system in Eq. 1, when interactions are sampled independently from a distribution, and the strength of intraspecific interaction d is increased. We perform simulations for $n = 500$, and sample parameters from different distributions, all with mean η and unit variance. Green: interactions sampled from the uniform distribution $\mathcal{U}[-\sqrt{3}+\eta, \sqrt{3}+\eta]$; Orange: coefficients are taken to be $\eta \pm 1$, with equal probability; Purple: interactions sampled from the normal distribution $\mathcal{N}(\eta, 1)$. On the x-axis, we report d, and on the y-axis the probability of stability (dashed line) and feasibility (solid line), computed by simulating 200 matrices for each distribution. The colored lines largely overlap, showing that the shape of the distribution does not influence the results, i.e., the curves are *universal*, as found for many other results in random matrix theory[19] The black solid lines represent the analytical expectations for $d_S = \sqrt{2n}$, and the probability of feasibility given d and n (Eq. 2).

d_F guarantees the existence of a feasible equilibrium for any $d > d_F$ (SI, Sec. 1). In random systems, the probability of obtaining feasibility for $d < d_F$ rapidly goes to zero when n increases (Figure 2, right). As such, for large random systems we expect to observe feasibility only when $d > d_F$.

These findings reinforce the notion that, in competitive systems, feasibility is difficult to achieve, and thus key for coexistence[5, 20–22]. In consumer-resource models[23], as well as in GLV models with symmetric interactions produced by niche overlap or species' similarity, stability is ensured, and thus feasibility determines coexistence. The high probability of stability given feasibility in competitive communities was first reported by Roberts[20], who maintained that conditioning the probability of stability on feasibility could resolve the debate on the relationship between stability and complexity. Several other studies expanded on these seminal results[21, 24];

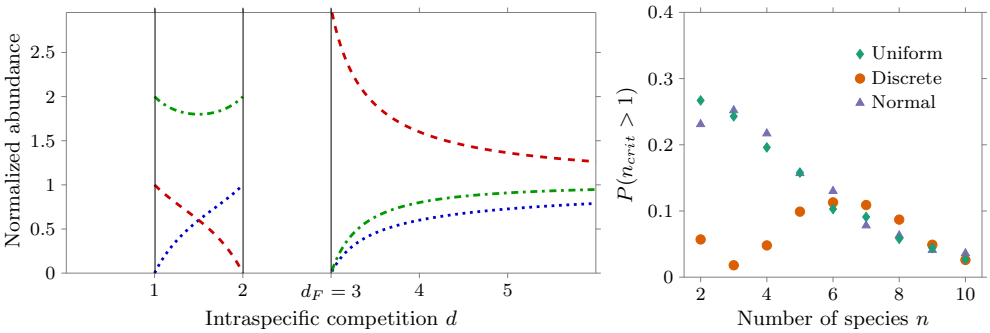

Fig. 2 Left: For a three-species competitive system (details provided in the SI), feasibility of the equilibrium can be achieved for different intervals of d (x-axis). For clarity, the y-axis reports the equilibrium abundances for the three species, normalized such that their average abundance is one. For this example, a feasible equilibrium exists whenever $1 < d < 2$, or $d > 3$. For any competitive system, feasibility is guaranteed whenever d exceeds a critical value, d_F (in the example, $d_F = 3$). Right: For systems with random interactions, the probability that a $d < d_F$ yields a feasible equilibrium decreases rapidly with system size, such that for large systems feasibility is found only for $d > d_F$.

more recently, it was shown that, when interactions are symmetric and one starts at a feasible, stable equilibrium, and interaction strengths are increased, feasibility is lost before stability[22]. We add to this mounting evidence, by showing that in large competitive communities feasibility is a synonym of coexistence, and by providing a way to compute its probability given the size of the system and the strength of intraspecific interactions.

These results have strong implications for dynamics. Competitive GLV systems can give rise to any type of dynamics, including limit cycles (for three or more populations) and chaos (when $n \geq 4$)[10, 11]. Importantly, non-equilibrium coexistence requires the existence of a feasible, unstable equilibrium. In random competitive systems however, feasibility generally implies stability, and therefore non-equilibrium coexistence is precluded.

One can go a step further, and imagine starting a large competitive system defined by $r > \mathbb{0}$, random interactions B, and a given level of intraspecific competition d (Figure 3). If $d > d_F > d_S$, then both the feasibility and global stability of the equilibrium are guaranteed, and thus populations coexist robustly, returning to equilibrium

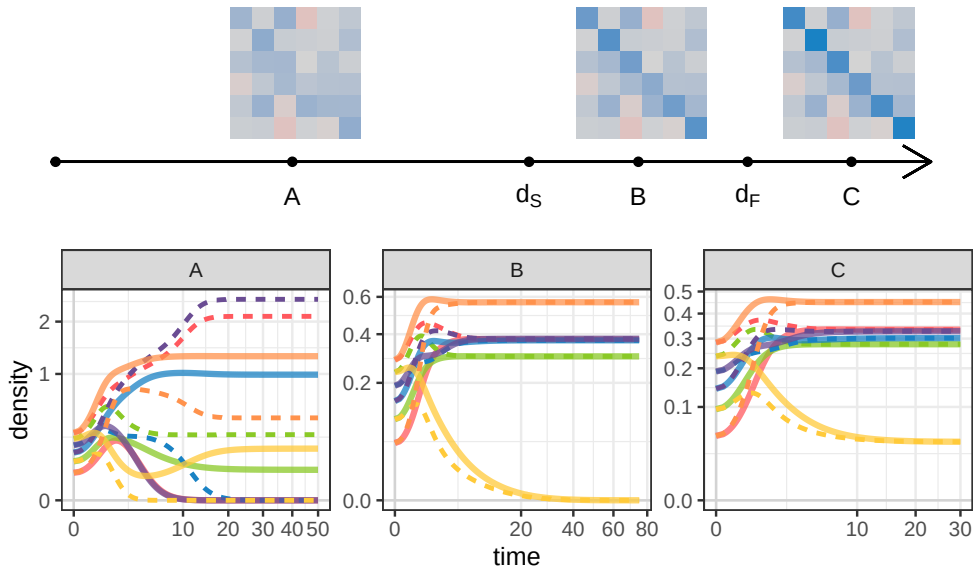

Fig. 3 Three scenarios for dynamics in random competitive communities. Top: we consider a small random B with independent entries and positive mean. We compute two critical values: d_S guarantees stability, and d_F guarantees feasibility for this system. We consider the dynamics for three different values of d, and when $A = dI + B$ in Eq. 1 (the three matrices are drawn above the line). C) when $d > d_F > d_S$, a feasible equilibrium exists, and is globally stable; when initializing the population densities (colors) at different values (e.g., dashed vs. solid lines), dynamics converge to the equilibrium. B) When $d_S < d < d_F$, the equilibrium is not feasible, but any feasible equilibrium for a sub-community is stable; then, the same species go extinct irrespective of initial conditions (in this case, the orange population), while the remaining populations converge to a stable equilibrium. A) Finally, when $d < d_S < d_F$, depending on the initial conditions, the set of coexisting species might differ (priority effects or alternative stable states; contrast dashed with solid lines); when extinctions ensue, however, both the value of d_F and d_S decrease, such that, after a sufficient number of extinctions, the system goes back to the dynamics found for case B).

after a perturbation (Figure 3C). When $d_F > d > d_S$, on the other hand, the lack of feasibility implies that some populations will go extinct (Figure 3B); however, because $d > d_S$, a) the same populations will go extinct irrespective of the (positive) initial conditions, and b) those that go extinct cannot re-invade the system (i.e., the equilibrium is *saturated*[12]). The most interesting case is obtained when $d < d_S < d_F$: because there is no feasible equilibrium, extinctions are guaranteed; however, because $d < d_S$ the identity of the populations that are bound to extinction depends on the initial conditions (Figure 3A); we thus can have priority effects and alternative stable states; once a population goes extinct, both d_S and d_F are reduced for the surviving

sub-community, while d is largely unaltered (because all species have, in expectation, the same d). Hence, as the number of extinction mounts, eventually d will cross d_S, and the system will settle at a saturated equilibrium. Thus, as long as the relationship $d_S < d_F$ is maintained as the populations go extinct (i.e., as long as the number of surviving species is large enough), the outcome is always qualitatively the same: a sub-set of the species pool will coexist robustly at an equilibrium that is characterized by $d_S < d_F < d$; the equilibrium is stable, and the last few species to go extinct (in the third case), or all the extinct species (in the second case) cannot re-invade the system.

In summary, we have shown that for large competitive communities the probability of non-equilibrium coexistence is negligible, and thus chaos or limit cycles will never be observed; moreover, the space for priority effects is greatly reduced: when considering the final set of species, we find that each population rebounds when set to extremely low values—the hallmark of robust coexistence [4, 6].

Supplementary information. Supplementary Information accompanies this work.

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1 Supplementary Information

1.1 Competitive Generalized Lotka-Volterra models

We consider the dynamics of competitive ecological communities composed on n interacting species, and following the Generalized Lotka-Volterra (GLV) model:

$$\dot{x}_i = x_i r_i \left(1 - \sum_j A_{ij} x_j\right), \tag{3}$$

where $x_i(t) \equiv x_i$ is the density of population i at time t, $\dot{x}_i \equiv dx_i(t)/dt$ its time derivative, $r_i > 0$ is the intrinsic growth rate of population i, achieved when growing in isolation at low abundance, and A_{ij} is the amount by which species j depresses the growth of population i.

We analyze cases in which, as stated, all populations can grow in isolation ($r > \mathbb{0}$), and, moreover, interactions are "mostly competitive" (defined below). Following May[7], we consider the case in which A is the sum of two matrices:

$$A = dI + B$$

with $d \geq 0$. Then, B collects all the inter-specific interactions, as well as the baseline levels of intraspecific interactions, and d can be interpreted as the "excess" intraspecific competition in the system.

We call the system *competitive* whenever $r > \mathbb{0}$, and $B^T \mathbb{1} = n\mu > \mathbb{0}$ (i.e., each column of B sums to a positive constant). While not *every* interaction needs to be competitive, each species must depresses the growth of the others, on average.

May[7] showed that choosing a value of d that exceeds a critical threshold ensures that dynamics of Eq. 3 are (locally) stable whenever a *feasible* equilibrium $x^\star > \mathbb{0}$ exists. Here we show that, for competitive GLV systems, whenever intraspecific competition exceeds a critical value, $d > d_F$, the existence of $x^\star > \mathbb{0}$ is guaranteed.

1.1.1 Effect of average interactions

In this section we show that, as long as interactions are (on average) competitive, then the actual strength of interaction has no effect on feasibility, i.e., on whether a positive equilibrium $x^\star > \mathbb{0}$ exists.

Take the matrix B to be the sum of two matrices: $B = \mathbb{1}\mu^T + C$, where $\mu = \frac{1}{n}B^T\mathbb{1}$ is the vector collecting the column means of B. Consequently, $C^T\mathbb{1} = 0$. We want to show that, as long as $\mu > \mathbb{0}$, the choice of specific values does not impact the feasibility of the equilibrium. Suppose that:

$$(C + dI)y = My = \mathbb{1}$$

has a unique solution $y^\star = (C + dI)^{-1}\mathbb{1} = M^{-1}\mathbb{1}$. Then, we can compute the solution $x^\star$ of the system $(B + dI)x = \mathbb{1}$ as a function of $y^\star$:

$$\begin{aligned}
(B + dI)x^\star &= \mathbb{1} \\
(M + \mathbb{1}\mu^T)x^\star &= \mathbb{1} \\
x^\star &= (M + \mathbb{1}\mu^T)^{-1}\mathbb{1} \\
x^\star &= \left(M^{-1} - \frac{1}{1 + \mu^T M^{-1}\mathbb{1}} M^{-1}\mathbb{1}\mu^T M^{-1}\right)\mathbb{1} \\
x^\star &= y^\star - \frac{\mu^T y^\star}{1 + \mu^T y^\star} y^\star \\
x^\star &= \frac{1}{1 + \mu^T y^\star} y^\star
\end{aligned}$$

where we have used the Sherman-Morrison formula to obtain the rank-one update of the inverse. This shows that, as long as $\mu > \mathbb{0}$, then $x^\star > \mathbb{0}$ if and only if $y^\star > \mathbb{0}$ (in fact, $y^\star \propto x^\star$, and the constant of proportionality is positive). Hence, without loss of generality, we can study whether $(dI + C)y = \mathbb{1}$ has a positive solution.

1.1.2 Effect of intraspecific competition on feasibility

In this section, we show that when we change the strength of intraspecific competition, d, we affect the feasibility of the equilibrium. As d changes, the feasibility of the equilibrium could be achieved or lost; however, there is a critical level of d beyond which feasibility is guaranteed. We call this critical value d_F.

A simple example motivates this discussion. We have a competitive system with three species, and, once we remove the average interactions as explained above (Section 1.1.1), we obtain the matrix C:

$$C = \begin{pmatrix} -1 & 1 & 0 \\ 1 & -2 & 0 \\ 0 & 1 & 0 \end{pmatrix}$$

We consider the system of equations $(C + dI)y = \mathbb{1}$, and solve for y:

$$y = \begin{pmatrix} \dfrac{d-3}{d^2-3d+1} \\ \dfrac{d-2}{d^2-3d+1} \\ \dfrac{(d-1)(d-3)}{d(d^2-3d+1)} \end{pmatrix} \tag{4}$$

Then feasibility for the GLV system is guaranteed whenever $y > \mathbb{0}$. We can see that for $d = \frac{1}{2}\left(3 \pm \sqrt{5}\right)$, the matrix $C + dI$ is singular, and thus values of y tend asymptotically to $\pm\infty$ around these points; otherwise $y > \mathbb{0}$ whenever either $1 < d < 2$, or $d > 3$. Figure 4 shows the trajectories of y_i as we increase d.

From this simple example, we can see that the effect of increasing d can be variable: we can move from an unfeasible system to a feasible equilibrium, and vice-versa. However, there is a critical value of d after which feasibility is guaranteed. This value, denoted d_F, is the focus of this study. In the next section, we show that, for a competitive GLV system, such a d_F always exists.

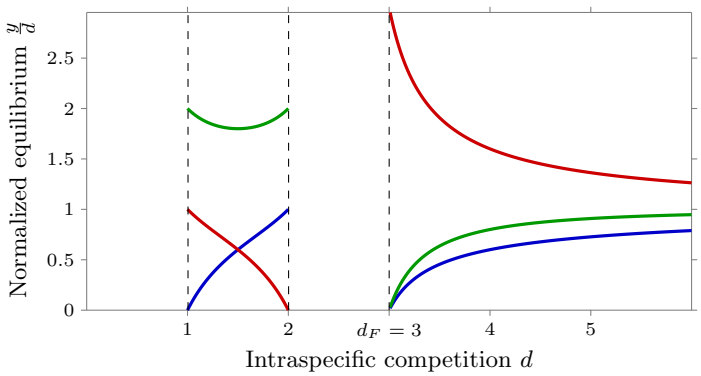

Fig. 4 Equilibrium values for y in Eq. 4 when d is increased from 0 to 6. The values on the y-axis are normalized for clarity: we plot y_i/d for each population (colors) such that the densities always sum to 3. The system is not feasible at $d = 0$. Feasibility is gained at the critical point $d = 1$ when the blue population becomes positive. At $d = 2$ the red population goes extinct, and the system looses feasibility. Feasibility is re-gained at $d = d_F = 3$, when both green and blue populations become positive. Feasibility is maintained for any $d > d_F$.

1.1.3 A sufficiently large d guarantees feasibility

We want to show that the system of equations $Ax = (dI + B)x = \mathbb{1}$ has a positive solution for d sufficiently large; moreover, further increasing d does not impact feasibility. In Section 1.1.1, we have shown that value of d needed to make the solution x positive is the same as that making y positive for $(dI + C)y = \mathbb{1}$, with the columns of C summing to zero. We are interested in the case in which $d > 0$; we can therefore divide all the equations:

$$\left(I + \frac{1}{d}C\right) y = \frac{1}{d}\mathbb{1}$$

Finally, we define $z = \frac{d}{n}$ y, obtaining:

$$\left(I + \frac{1}{d}C\right) z = \frac{1}{n}\mathbb{1}$$

Clearly, $z > \mathbb{0}$ implies $y > \mathbb{0}$ and therefore $x > \mathbb{0}$ in Eq. 3. Then, we have:

$$\mathbb{1}^T \left(I + \frac{1}{d}C\right) z = \frac{1}{n}\mathbb{1}^T\mathbb{1}$$

$$\mathbb{1}^T z = 1$$

Therefore, we can write:

$$\left(I + \frac{1}{d}C\right) z = \frac{1}{n}\mathbb{1}$$
$$\left(I + \frac{1}{d}C\right) z = \frac{1}{n}\mathbb{1}\mathbb{1}^T z$$
$$\left(\frac{1}{n}\mathbb{1}\mathbb{1}^T - \frac{1}{d}C\right) z = z$$
$$Q(d)z = z$$

Thus, z is a right eigenvector of $\frac{1}{n}\mathbb{1}\mathbb{1}^T - \frac{1}{d}C = Q(d)$, associated with the eigenvalue $\lambda_1 = 1$. The left eigenvector of $Q(d)$ associated with eigenvalue 1 is $\mathbb{1}$, given that all columns sum to one. Thus, $Q(d)$ has always a positive left eigenvector, and has a positive right eigenvector whenever $z > \mathbb{0}$ (i.e., when the GLV system in Eq. 3 is feasible).

The Perron-Frobenius theorem states that a matrix with all positive coefficients has a real, positive eigenvalue λ_1 that is larger than any other eigenvalue (in modulus), i.e., λ_1 is the spectral radius of the matrix; moreover, the eigenvalue is associated with an eigenvector in which all the components have the same sign.

Consider $Q(d) = \frac{1}{n}\mathbb{1}\mathbb{1}^T - \frac{1}{d}C$, and choose $d = d_m > \max C_{ij} n$; then all the coefficients of $Q(d_m)$ are positive. Moreover, all the columns sum to one, and therefore $\lambda_1 = 1$ is the spectral radius of the matrix $Q(d_m)$; then $Q(d_m)$ follows the Perron-Frobenius theorem and $z > \mathbb{0}$.

Importantly, further increasing d leaves the matrix $Q(d)$ positive, and thus feasibility is ensured for any $d > d_m$.

While d_m is an overly loose bound for most matrices, it is sufficient to prove that for d large, feasibility is ensured, and that once feasibility is achieved in this way, it cannot be lost by further increasing the strength of intraspecific competition. To show that a smaller d_F would be sufficient to guarantee $z > \mathbb{0}$ for each $d > d_F$, we turn to the theory of eventually positive matrices [25, 26].

1.1.4 Eventually positive matrices and feasibility

A matrix $\mathcal{A}$ is called *eventually positive* if there exists an integer k_0 such that

$$\left(\mathcal{A}^k\right)_{ij} > 0 \quad \forall i, j \quad k \geq k_0$$

Eventually positive matrices also have the Perron-Frobenius property: $\mathcal{A}v = \lambda_1 v$ with $\lambda_1 > 0$ being an eigenvalue of $\mathcal{A}$ which is also its spectral radius, and $v > \mathbb{0}$. Moreover, an eventually positive matrix also has the Perron-Frobenius property for its left eigenvector: $\mathcal{A}^T w = \lambda_1 w$ with $w > \mathbb{0}$. Finally, suppose that $\lambda_1 = 1$ and choose the eigenvectors v and w such that $w^T v = 1$. Then, one can prove[27] that:

$$\lim_{k\to\infty} \mathcal{A}^k = vw^T$$

We are going to use these properties to prove that, whenever $z > \mathbb{0}$, and $d > \rho(C)$ (the spectral radius of C), then $Q(d)$ is eventually positive, its spectral radius is 1, and $\mathbb{1}$ and z are its left and right Perron eigenvectors, respectively.

The strategy is as follows: a) we write z using the Neumann series; b) we take powers of $Q(d)$ and show that in the limit of $k \to \infty$, the powers converge to $z\mathbb{1}^T$; hence $Q(d)$ is eventually positive whenever $z > \mathbb{0}$.

We want to solve:

$$\left(I + \frac{1}{d}C\right) z = \frac{1}{n}\mathbb{1}$$

for z. If the spectral radius of C, $\rho(C) < d$, we can express z as a power series (Neumann series):

$$
\begin{aligned}
z &= \frac{1}{n}\sum_{k=0}^{\infty}\left(-\frac{1}{d}C\right)^k \mathbb{1} \\
&= \frac{1}{n}\left(I - \frac{1}{d}C + \frac{1}{d^2}C^2 - \frac{1}{d^3}C^3 + \cdots\right)\mathbb{1} \\
&= \frac{1}{n}\left(\mathbb{1} - \frac{1}{d}C\mathbb{1} + \frac{1}{d^2}C^2\mathbb{1} - \frac{1}{d^3}C^3\mathbb{1} + \cdots\right)
\end{aligned}
$$

We now take increasing powers of $Q(d)$:

$$
\begin{aligned}
Q(d) &= \left(\frac{1}{n}\mathbb{1}\mathbb{1}^T - \frac{1}{d}C\right) \\
Q^2(d) &= \frac{1}{n}\left(\mathbb{1} - \frac{1}{d}C\mathbb{1}\right)\mathbb{1}^T + \frac{1}{d^2}C^2 \\
Q^3(d) &= \frac{1}{n}\left(\mathbb{1} - \frac{1}{d}C\mathbb{1} + \frac{1}{d^2}C^2\mathbb{1}\right)\mathbb{1}^T - \frac{1}{d^3}C^3 \\
&\cdots \\
Q^k(d) &= \frac{1}{n}\left(\sum_{j=0}^{k-1}\left(-\frac{1}{d}C\right)^j \mathbb{1}\right)\mathbb{1}^T + (-1)^k\frac{1}{d^k}C^k
\end{aligned}
$$

The series converges whenever $\rho(C) < d$, leading to:

$$
\lim_{k\to\infty} Q^k(d) = z\mathbb{1}^T
$$

Thus, whenever $z > \mathbb{0}$, and $d > \rho(C)$ the matrix $Q(d)$ is eventually positive, and has spectral radius 1.

1.1.5 Further increasing intraspecific competition

The goal of this section is to show that, whenever $z > \mathbb{0}$ and $d > \rho(C)$ (i.e., for the conditions derived in the previous section), further increasing d maintains feasibility. In practice, we want to show that the solution z' of the system:

$$\left(I + \frac{1}{d+\epsilon}C\right) z' = \frac{1}{n}\mathbb{1}$$
$$\left((d+\epsilon)I + C\right) z' = \frac{d+\epsilon}{n}\mathbb{1}$$

where $\epsilon > 0$ is small, is still feasible. For this derivation, we use techniques for iteratively solving linear systems, and consider that we have found a sufficiently large d such that

$$(dI + C)\, z = \frac{d}{n}\mathbb{1} \qquad z > \mathbb{0}$$

The system $\mathcal{A}x = g$ with $\mathcal{A}$ invertible can be solved iteratively by defining the matrix splitting:

$$\mathcal{A} = \mathcal{M} - \mathcal{N}$$

with $\mathcal{M}$ invertible, and such that the spectral radius of $\rho(\mathcal{M}^{-1}\mathcal{N}) < 1$. Then:

$$\mathcal{A}x = g$$
$$\mathcal{M}x = \mathcal{N}x + g$$
$$x = \mathcal{M}^{-1}(\mathcal{N}x + g)$$

The iterative procedure for finding x is as follows: one chooses a starting point x_0, and then iterates:

$$x_{k+1} = \mathcal{M}^{-1}(\mathcal{N}x_k + g)$$

until convergence, which is guaranteed from any starting condition if the assumptions above are met.

We write

$$
\begin{aligned}
((d+\epsilon)I + C)\, z' &= \frac{d+\epsilon}{n}\mathbb{1} \\
(dI + C)\, z' &= -\epsilon I z' + \frac{d+\epsilon}{n}\mathbb{1} \\
\mathcal{M} z' &= \mathcal{N} z' + \frac{d+\epsilon}{n}\mathbb{1}
\end{aligned}
$$

where we have chosen $\mathcal{M} = (dI+C)$ and $\mathcal{N} = -\epsilon I$. Note that $\rho(\mathcal{M}) = d$, and $\rho(\mathcal{N}) = \epsilon$ and therefore $\rho(\mathcal{M}^{-1}\mathcal{N}) = \frac{\epsilon}{d} < 1$ as long as $\epsilon < d$. Then, choosing $z_0 = \mathbb{1}$, we obtain:

$$
\begin{aligned}
z_1 &= -\epsilon \mathcal{M}^{-1}\mathbb{1} + \frac{d+\epsilon}{n}\mathcal{M}^{-1}\mathbb{1} \\
z_1 &= \left(1 - \frac{(n-1)\epsilon}{d}\right) z
\end{aligned}
$$

Whenever $\epsilon < d/(n-1)$ we have that the first approximation of z', z_1 is still positive; moreover, the approximation should be accurate for small ϵ. But then, by continuity, we can repeat the calculation, and keep increasing d to higher values without foregoing feasibility.

1.1.6 d_F is an eigenvalue

In this section, we show that d_F is an eigenvalue of a matrix derived from the matrix of interactions. Consider the system:

$$
(C + dI)y = \mathbb{1}
$$

For any solution y, we have:

$$
dy_i = 1 - \sum_j C_{ij} y_j
$$

Whenever we are at a critical value d such that feasibility is gained or lost, at least one of the components of y, y_k, is exactly zero, while all the other components are nonnegative. This means that the sub-community in which population k is excluded can achieve a feasible equilibrium (or that reducing the community even further leads to a feasible equilibrium). Then, for y_k we have:

$$1 = \sum_{j \neq k} C_{kj} y_j$$

while for the other components, we have:

$$dy_i = 1 - \sum_{j \neq k} C_{ij} y_j$$

For the derivation below, it is convenient to have $k = n$, i.e., the focal population whose equilibrium is exactly zero is in the last position. If this is not the case, one can reorder the equations such that $k = n$. We partition the matrices C and I, and the vector y as:

$$C = \begin{pmatrix} \widetilde{C} & a \\ b^T & c \end{pmatrix} \quad I = \begin{pmatrix} \widetilde{I} & \mathbb{0} \\ \mathbb{0}^T & 1 \end{pmatrix} \quad y = \begin{pmatrix} \widetilde{y} \\ 0 \end{pmatrix}$$

i.e., the matrices and vectors denoted by the tilde are obtained by removing the last row and column (for matrices) or the last component (for vectors) from the corresponding variable. Importantly for the derivation below, notice that, because $C^T \mathbb{1} = \mathbb{0}$, then necessarily $\widetilde{C}^T \mathbb{1} = -b$.

With this notation, the equations above can be written as:

$$\begin{cases} (\widetilde{C} + d\widetilde{I})\widetilde{y} = \mathbb{1} \\ b^T \widetilde{y} = 1 \end{cases}$$

But then:

$$\begin{aligned} (\widetilde{C} + d\widetilde{I})\widetilde{y} &= \mathbb{1} b^T \widetilde{y} \\ (\widetilde{C} + d\widetilde{I} - \mathbb{1} b^T)\widetilde{y} &= \mathbb{0} \\ (\widetilde{C} - \mathbb{1} b^T)\widetilde{y} &= -d\widetilde{y} \\ (\mathbb{1} b^T - \widetilde{C})\widetilde{y} &= d\widetilde{y} \end{aligned}$$

i.e., the critical d is an eigenvalue of $\mathbb{1}b^T - \widetilde{C}$, corresponding to the positive eigenvector $\widetilde{y}$. Note that this derivation requires knowing which one of the populations is zero at equilibrium (y_k, made y_n by reordering). However, the formula above is sufficient to devise an algorithm to find the value of d_F precisely.

1.1.7 Finding d_F via eigendecomposition

For each index i in $1, \ldots, n$, we can form the corresponding matrix $\widetilde{C}(i)$ and vector $b(i)$ by:

$$\begin{cases} \widetilde{C}(i) = C^{(-i,-i)} \\ b^T(i) = C^{(i,-i)} \end{cases}$$

where $C^{(-i,-j)}$ is the matrix C with row i and column j removed, and $C^{(i,-j)}$ is the ith row of C with component j removed.

For each choice of i, we compute the eigenvalues of $\mathbb{1}b^T(i) - \widetilde{C}(i)$, indexed $\lambda_1(i), \lambda_2(i), \ldots, \lambda_{n-1}(i)$, and the corresponding right eigenvectors $v_1(i), v_2(i), \ldots, v_{n-1}(i)$.

Suppose that the matrix has a real eigenvalue $\lambda_k(i)$ with a corresponding eigenvector $v_k(i)$ that has all components of the same sign. Then, consider $\widetilde{y}(i) = \frac{1}{b^T(i)v_k(i)} v_k(i)$: if $\widetilde{y} \geq \mathbb{0}$, then it is a nonnegative solution of the system:

$$\begin{cases} (\widetilde{C}(i) + \lambda_k(i)\widetilde{I})\widetilde{y}(i) = \mathbb{1} \\ b^T(i)\widetilde{y}(i) = 1 \end{cases}$$

This means that by choosing $d(i) = \lambda_k(i)$, we would obtain a solution y of the system $(C + d(i)I)y = \mathbb{1}$ with $y_i = 0$, and all other components nonnegative.

If the matrix has no real, positive eigenvalue associated with a nonnegative $\widetilde{y}(i)$, then either it is impossible to make $y_i = 0$ by choosing a $d \geq 0$ (when there are no positive eigenvalues), or, whenever $y_i = 0$, some other components are negative (when

$\widetilde{y}(i) \not\geq \mathbb{0}$). If none of the matrices satisfy the conditions above, then $d_F = 0$; otherwise $d_F = \max_i(d(i))$.

To illustrate the algorithm, consider the matrix presented in Section 1.1.2:

$$C = \begin{pmatrix} -1 & 1 & 0 \\ 1 & -2 & 0 \\ 0 & 1 & 0 \end{pmatrix}$$

for which feasibility of $(dI + C)y = \mathbb{1}$ is ensured for $1 < d < 2$, and $d > 3$, and thus $d_F = 3$. We can find this value by considering the matrices $\mathbb{1}b^T(i) - \widetilde{C}(i)$ obtained for each choice of i. Choosing $i = 1$, we have:

$$\widetilde{C}(1) = C^{(-1,-1)} = \begin{pmatrix} -2 & 0 \\ 1 & 0 \end{pmatrix} \quad b^T(1) = C^{(1,0)} = \begin{pmatrix} -1 & 1 \end{pmatrix}$$

The matrix

$$\mathbb{1}b^T(1) - \widetilde{C}(1) = \begin{pmatrix} 1 & 0 \\ 1 & 0 \end{pmatrix} - \begin{pmatrix} -2 & 0 \\ 1 & 0 \end{pmatrix} = \begin{pmatrix} 3 & 0 \\ 0 & 0 \end{pmatrix}$$

has eigenvalues $\lambda_1(1) = 3$ and $\lambda_2(1) = 0$; the first eigenvalue is associated with $v_1(1) = (1, 0)^T$, from which we obtain:

$$\widetilde{y}(1) = \frac{1}{b^T(1)v_1(1)} v_1(1) = \begin{pmatrix} 1 \\ 0 \end{pmatrix}$$

This means that, when we choose $d = d(1) = 3$, we obtain a solution for $(C + dI)y = \mathbb{1}$ in which population 1 has density zero, and populations 2 has density 1, and population 3 has also density zero positive: $y = (0, 1, 0)^T$.

The same can be repeated for $i = 2$ (i.e., trying to find a value of d for which $y_2 = 0$); we have that

$$\widetilde{C}(2) = \begin{pmatrix} -1 & 0 \\ 0 & 0 \end{pmatrix} \quad b^T(2) = \begin{pmatrix} 1 & 0 \end{pmatrix}$$

the matrix

$$\mathbb{1}b^T(2) - \widetilde{C}(2) = \begin{pmatrix} 2 & 0 \\ 1 & 0 \end{pmatrix}$$

has a positive eigenvalue $\lambda_1(2) = 2$ associated with a positive eigenvector, yielding $\widetilde{y}(2) = (1, \frac{1}{2})^T$. That is, choosing $d = d(2) = 2$ implies that the community rests at $y = (1, 0, \frac{1}{2})$.

Finally, choosing $i = 3$, we have:

$$\widetilde{C}(3) = \begin{pmatrix} -1 & 1 \\ 1 & -2 \end{pmatrix} \quad b^T(3) = \begin{pmatrix} 0 & 1 \end{pmatrix}$$

The matrix

$$\mathbb{1}b^T(3) - \widetilde{C}(3) = \begin{pmatrix} 1 & 0 \\ -1 & 3 \end{pmatrix}$$

has eigenvalues $\lambda_1(3) = 3$ and $\lambda_2(3) = 1$; the first eigenvalue appeared already for $\mathbb{1}b^T(1) - \widetilde{C}(1)$. When we choose $d = d(3) = 1$, we obtain $y = (2, 1, 0)^T$. Thus, the algorithm would choose $d_F = \max(1, 2, 3) = 3$, which is the correct solution.

Code implementing this algorithm accompanies this work.

1.1.8 Finding d_F via power iteration

We have shown that d_F is an eigenvalue of the matrix $\mathbb{1}b^T - \widetilde{C}$, obtained by choosing one of the populations, and partitioning the matrix of interactions C accordingly. While the algorithm above returns the correct value for d_F, it requires calculating the eigenvalues and eigenvectors of n matrices—a computationally expensive task when the matrix of interactions is large.

If we assume that eigenvalue d of matrix $\mathbb{1}b^T - \widetilde{C}$ associated with the eigenvector $\widetilde{y}$ is the spectral radius of the matrix, then we can approximate $\widetilde{y}$ by the power method: a) we choose a starting condition (for example, $y_0 = \mathbb{1}$); b) we iterate:

$$y_k = \left(\mathbb{1}b^T - \widetilde{C}\right) y_{k-1}$$

If the eigenvalue associated with $\widetilde{y}$ is indeed the spectral radius, and provided that our initial choice y_0 has a nonzero projection on the dominant eigenvector, the method is guaranteed to converge to $\widetilde{y}$. One can normalize the approximate eigenvector appropriately at each step, if desired.

If we choose $y_0 = \mathbb{1}$, the first few iterations are:

$$\begin{aligned}
&y_0 = \mathbb{1} \\
&y_1 = \left(\mathbb{1}b^T - \widetilde{C}\right)\mathbb{1} = (b^T\mathbb{1})\mathbb{1} - \widetilde{C}\mathbb{1} = \beta\mathbb{1} - \widetilde{C}\mathbb{1} \\
&y_2 = \beta^2\mathbb{1} - (b^T\widetilde{C}\mathbb{1})\mathbb{1} + \widetilde{C}^2\mathbb{1} \\
&\dots
\end{aligned}$$

where we have defined $\beta = b^T\mathbb{1}$.

To find the corresponding (approximate) eigenvalue, we consider:

$$\begin{aligned}
\left(\mathbb{1}b^T - \widetilde{C}\right)\widetilde{y} &= d\widetilde{y} \\
\widetilde{y}^T\left(b\mathbb{1}^T - \widetilde{C}^T\right)\left(\mathbb{1}b^T - \widetilde{C}\right)\widetilde{y} &= d^2\widetilde{y}^T\widetilde{y} \\
\frac{\widetilde{y}^T\left(b\mathbb{1}^T - \widetilde{C}^T\right)\left(\mathbb{1}b^T - \widetilde{C}\right)\widetilde{y}}{\widetilde{y}^T\widetilde{y}} &= d^2
\end{aligned}$$

Given that $\widetilde{C}^T\mathbb{1} = -b$, we can rewrite:

$$\left(b\mathbb{1}^T - \widetilde{C}^T\right)\left(\mathbb{1}b^T - \widetilde{C}\right) =$$
$$b\mathbb{1}^T\mathbb{1}b^T - \widetilde{C}^T\mathbb{1}b^T - b\mathbb{1}^T\widetilde{C} + \widetilde{C}^T\widetilde{C} =$$
$$(n-1)bb^T + bb^T + bb^T + \widetilde{C}^T\widetilde{C} =$$
$$(n+1)bb^T + \widetilde{C}^T\widetilde{C}$$

To remove the dependency of $\widetilde{C}$ on b, we can define the matrix $Z = \widetilde{C} + \frac{1}{n-1}\mathbb{1}b^T$ such that $Z^T\mathbb{1} = \mathbb{0}$. But then $\widetilde{C}^T\widetilde{C} = Z^TZ + \frac{1}{n-1}bb^T$. With these simplifications, we obtain:

$$d^2 = \frac{\widetilde{y}^T(\frac{n^2}{n-1}bb^T + Z^TZ)\widetilde{y}}{\widetilde{y}^T\widetilde{y}} \tag{5}$$

A numerical algorithm can be therefore developed in which, for each population, a) one forms $\widetilde{C}(i)$ and the corresponding $b(i)$, b) approximates $\widetilde{y}(i)$ using the power method, c) whenever $\widetilde{y}(i) > \mathbb{0}$, compute $d(i)$ using Eq. 5; d) return the maximum $d(i)$, thereby approximating d_F.

The algorithm is effective only when certain assumptions are met: a) $d(i)$ is the spectral radius of the matrix $\mathbb{1}b^T(i) - \widetilde{C}(i)$, b) the initial condition has a projection on $\widetilde{y}(i)$, c) the number of iterations is sufficient. Despite these limitations, the algorithm has a much lower computational complexity than the exact one (and thus is much faster for large matrices), lends itself well to analytical calculations, and, as we will show below, works extremely well for large random matrices.

Code implementing this algorithm accompanies this work.

1.2 Random competitive interactions

Having derived a number of results for a generic matrix $A = dI + B$, we now study the case in which B is a random matrix of the type studied by May[7], and Allesina & Tang[8]. In particular, we take the elements of B to be independent, identically distributed random variables with mean η and unit variance:

$$B_{ij} \sim \eta + \mathcal{Q}(0,1)$$

where $\mathcal{Q}$ is a probability distribution parameterized by the mean (here taken to be zero) and the variance (here taken to be 1). The exact shape of the distribution is inconsequential, because, as shown in the main text, our results appear to be *universal*.

The goals of this section are: a) show that, for large n, the probability of feasibility when $d = 0$ is exceedingly small; b) use the algorithm based on the power method to derive an approximation of d_F for random matrices; c) use this approximation to compute the approximate probability of feasibility for a random matrix B of size $n \times n$ and a given d; d) show that for these systems feasibility implies stability, with important consequences on the type of dynamics one can observe.

1.2.1 Probability of feasibility when $d = 0$

We want to compute the probability that $(dI + C + 1\mu^T)x = \mathbb{1}$ has a positive solution when $d = 0$. Since the columns of C sum to 0 (see Sec 1.1.1), the mean of C_{ij} is exactly zero, and its variance is one.

We multiply the system of equations by the transpose of C:

$$\begin{aligned}
(C + \mathbb{1}\mu^T)x &= \mathbb{1} \\
Cx &= (1 - \mu^T x)\mathbb{1} \\
C^T Cx &= (1 - \mu^T x)C^T \mathbb{1} \\
C^T Cx &= \mathbb{0}
\end{aligned}$$

Given that the matrix C is obtained from a random matrix, we can assume it has rank $n - 1$, and therefore $C^T C$ is positive semi-definite. Then, solving the system of equations above is equivalent to solving $Cy = \mathbb{0}$, i.e., y is a right eigenvector of C associated with the zero eigenvalue. Thus, y is defined up to a constant of proportionality. We partition C and y as:

$$C = \begin{pmatrix} \widetilde{C} & a \\ b^T & c \end{pmatrix} \quad y = \begin{pmatrix} \widetilde{y} \\ 1 \end{pmatrix}$$

where $c = -\sum_{j=1}^{n-1} a_j$. We can therefore write $n-1$ independent equations:

$$\widetilde{C}\widetilde{y} = -a$$
$$\widetilde{y} = -\widetilde{C}^{-1}a$$

For feasibility, we need all $\widetilde{y} > \mathbb{0}$ (because we have chosen a positive y_n). To compute the probability that $\widetilde{y} > \mathbb{0}$ exactly, we need to make a further assumption: that the probability of observing a given C_{ij} (or the density of the distribution at C_{ij}, when the distribution is continuous), $P(C_{ij}) = P(-C_{ij})$, for all i; which in this context amounts to having chosen a distribution $\mathcal{Q}(0,1)$ (which we have used to sample the interactions B_{ij}) that is symmetric about its mean.

Then we can follow the approach of Serván *et al.*[28], and define the diagonal matrices $K_i = D(s_i)$, where the s_i are the 2^n distinct vectors of length n containing either 1 or -1: $s_1 = (1,1,1,\ldots,1)^T$, $s_2 = (1,-1,1,\ldots,1)^T$, $s_3 = (-1,-1,1,\ldots,1)^T$, $s_4 = (1,1,-1,\ldots,1)^T$, …, $s_{2^n} = (-1,-1,-1,\ldots,-1)^T$. We partition these matrices as well:

$$K_i = \begin{pmatrix} \widetilde{K_i} & \mathbb{0} \\ \mathbb{0}^T & \sigma_i \end{pmatrix}$$

Because of symmetry, we have $P(C) = P(CK_i)$, as multiplying C by $K_i = D(s_i)$ simply changes the signs of all the coefficients in the columns corresponding to negative signs in s_i.

Finally, we write:

$$\widetilde{C}\widetilde{K}_1\widetilde{y} = -\sigma_1 a$$
$$\widetilde{y} = -\sigma_1\widetilde{K}_1\widetilde{C}^{-1}a$$

Where we have used the fact $K_1 = I$. Now notice that by exchanging K_1 with K_i, we can change the signs of the components of $\widetilde{y}$; then, for each possible pattern of signs of $-\widetilde{C}^{-1}a$ there are exactly two choices of K_i that make the vector $\widetilde{y}$ all positive (one solution with $K_j = D(s_j)$, and the other with $K_l = D(-s_j)$). Given that the probability $P(CK_i) = P(CK_j)$, the probability of feasibility is exactly $2/2^n = 1/2^{n-1}$.

Thus, while for a random system of two species we have probability $1/2$ of obtaining a feasible equilibrium when we sample competition coefficients from a distribution that is symmetric about its (positive) mean, the probability rapidly decreases, so that we we have less than one in a thousand chance to find a feasible equilibrium for $n = 11$ and less than one in a million for $n = 21$.

1.2.2 Approximating d_F for large random systems

We want to use Eq. 5 we have obtained through the power method to approximate the value of d_F when we have chosen interactions strengths at random. To this end, we set each of the variables to their expectation.

In a random system of the type we are studying, all populations have exactly the same statistics. Then, the average $\widetilde{y}_i$ must be a constant, and thus we set $\widetilde{y} = \mathbb{1}$ (given that constants of proportionality cancel in Eq. 5). The approximation then reduces to:

$$d^2 \approx \frac{\mathbb{1}^T(\frac{n^2}{n-1}bb^T + Z^TZ)\mathbb{1}}{\mathbb{1}^T\mathbb{1}} = \frac{n^2}{(n-1)^2}(b^T\mathbb{1})^2 + \frac{\mathbb{1}^TZ^TZ\mathbb{1}}{n-1} = \frac{n^2}{(n-1)^2}\beta^2 + \frac{\mathbb{1}^TZ^TZ\mathbb{1}}{n-1}$$

where, as before, we have defined $\beta = b^T\mathbb{1}$. We need to compute the expectation for $\mathbb{1}^TZ^TZ\mathbb{1}$, which can be seen as the sum of the squared row sums of Z; defining $g = Z\mathbb{1}$, we have $\mathbb{1}^TZ^TZ\mathbb{1} = \sum_j g_j^2$.

Given that Z was obtained from a random matrix with identically distributed coefficients, and has $\mathbb{E}(Z_{ij}) = 0$ and $\mathbb{E}(Z_{ij}^2) \approx 1$, we can assume that, for sufficiently large systems ($n \gg 1$), g_i is approximately normally distributed $g_i \sim \mathcal{N}(0, (n-1))$, i.e.,

a normal distribution with mean zero and variance $(n-1)$ (the sum of the variances). Given that $\mathbb{E}(\alpha^2) = \mathbb{E}(\alpha)^2 + \mathbb{V}(\alpha)$ (where $\mathbb{V}$ denotes the variance), we have that $\mathbb{E}(g_i^2) = (n-1)$, and therefore $\mathbb{E}(\mathbb{1}^T Z^T Z \mathbb{1}) = (n-1)^2$. With these approximations, we obtain:

$$d^2 \approx \frac{n^2}{(n-1)^2}\beta^2 + (n-1) \tag{6}$$

Finally, we know that d_F is obtained by considering a *specific* population, i.e., the one that is exactly zero at the critical point d_F, yielding the largest value for the associated d. It therefore makes sense to take β to be the maximum among the n possible choices—i.e., assume that the population with the lowest abundance is the one experiencing the strongest inter-specific competition.

Each population i is associated with a certain $\mathbb{1}^T b(i) = \sum_{j \neq i} C_{ij}$, and we want to derive the distribution for $\max \mathbb{1}^T b(i)$. Each $\mathbb{1}^T b(i)$ is the sum of $n-1$ random variables, each with mean zero and unit variance. Therefore, we can assume that $\mathbb{1}^T b(i) \sim \mathcal{N}(0, (n-1)) = \sqrt{n-1}\mathcal{N}(0,1)$. The $b(i)$ are also independent; as such, the probability that $\max \mathbb{1}^T b(i) < \gamma$ is the joint probability that all $\mathbb{1}^T b(i) < \gamma$. Denoting as $\Phi(\cdot)$ the cumulative distribution function for a standard normal distribution, we have

$$P(\max \mathbb{1}^T b(i) < \gamma) = P(\beta < \gamma) = \prod_{i=1}^{n} \Phi\left(\frac{\gamma}{\sqrt{n-1}}\right) = \Phi\left(\frac{\gamma}{\sqrt{n-1}}\right)^n$$

and thus the probability density function for β is simply:

$$P(\beta) = \frac{n}{\sqrt{n-1}}\phi\left(\frac{\beta}{\sqrt{n-1}}\right)\Phi\left(\frac{\beta}{\sqrt{n-1}}\right)^{n-1}$$

where $\phi(\cdot)$ is the probability distribution function for the standard normal distribution.

Solving Eq. 6 for d, we obtain:

$$d \approx \sqrt{\frac{n^2}{(n-1)^2}\beta^2 + (n-1)} \tag{7}$$

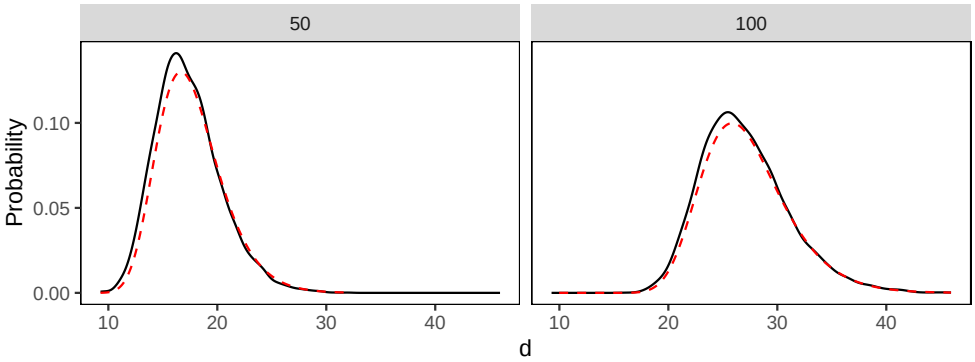

Fig. 5 Theoretical (red dashed line, Eq. 8) and empirical (black) density function for d, obtained by computing d numerically for 1000 matrices of size $n = 50$ (left) and 100 (right).

and thus the probability density function for d is approximately:

$$P(d|d > \sqrt{n-1}) = \frac{1}{\Theta}\frac{n}{\sqrt{n-1}}\phi\left(\frac{\sqrt{(d^2-(n-1))(n-1)}}{n}\right)\Phi\left(\frac{\sqrt{(d^2-(n-1))(n-1)}}{n}\right)^{n-1} \tag{8}$$

Where $\Theta > 0$ is a normalization constant stemming from the fact that the density function is well-defined only for $d > \sqrt{n-1}$ (i.e., when the assumption that d is the spectral radius of the matrix $\mathbb{1}b^T - \widetilde{C}$, which is key for our calculations, holds). The constant can be obtained by integrating the unnormalized density function between $\sqrt{n-1}$ and ∞. Figure 5 shows that this is a good approximation of the distribution of d obtained by simulating.

1.2.3 Probability that $d < d_F$ guarantees feasibility

As we have shown in Section 1.1.2, there might be values of $d < d_F$ that yield feasibility for the system. The approximation above is valid for d_F (as long as d_F is the spectral radius of $\mathbb{1}b^T - \widetilde{C}$ for the population with abundance zero), but not for cases in which $d < d_F$. We are therefore interested in counting how many transitions are found for random systems, i.e., how many $d(i)$ values will be found by our exact algorithm.

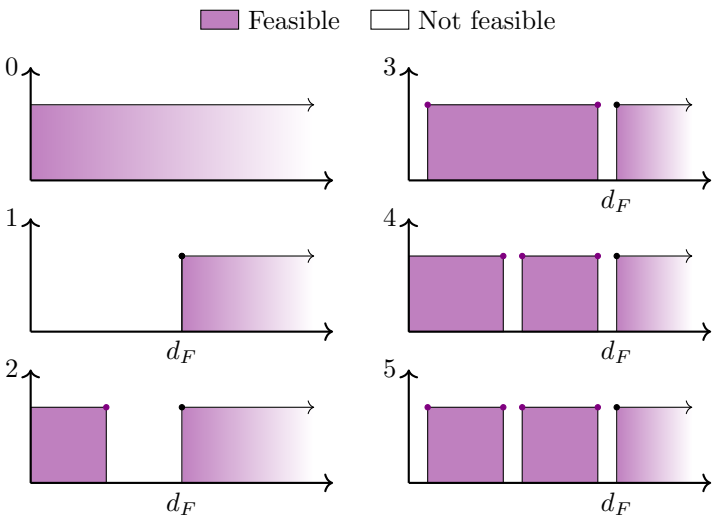

Fig. 6 Values for d (x-axis) in which the equilibrium is feasible (shaded) or not feasible (white). A system can have a variable number of critical points in which feasibility is lost or gained. From top left to bottom right: for some systems, feasibility is guaranteed for any value of $d > 0$, and as such we have zero critical points; if we have a single critical point, then it must be d_F; system with two critical points need to first lose feasibility and then gain it again at d_F—thus the system must be feasible at $d = 0$; this pattern generalizes to any number of transitions: whenever the number of transitions is even, $d = 0$ must be feasible; whenever it is odd the system cannot be feasible at $d = 0$.

Given that the last transition is given by d_F, and is always present (Section 1.1.3), and that at d_F the system should gain feasibility, we have that an even number of critical transition points implies that $d = 0$ is sufficient for feasibility, while an odd number of critical transitions implies that the system is not feasible at $d = 0$ (Fig. 6). Thus, the probability that we have an even number of critical transition points is exactly $1/2^{n-1}$ (Section 1.2.1). Therefore, for large n the number of critical transition points $d(i)$ is always odd.

For $n = 2$, the probability of having a single transition is necessarily $1/2$, and to determine how this probability changes with n, we performed simulations on random systems of increasing size. We find that the number of transitions tends to one as $n \to \infty$ (Fig. 7), and thus, for large random systems, d_F is the only transition point, and the calculations above apply.

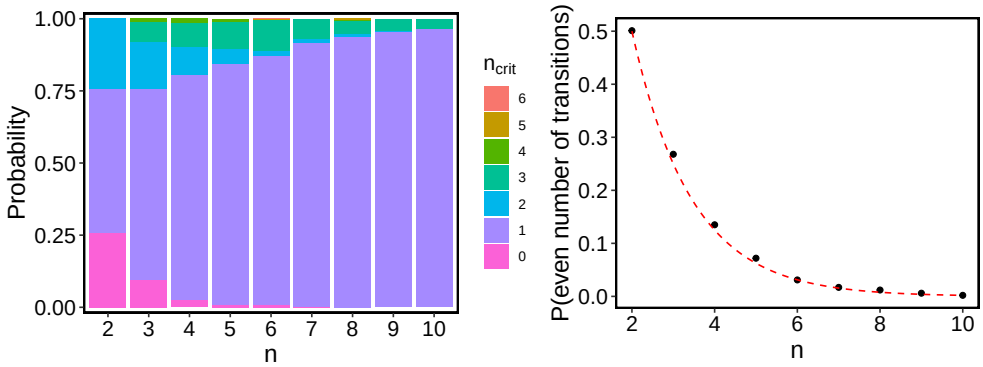

Fig. 7 Left: Number of critical transition points, i.e., values of d such that $(dI + C)y = \mathbb{1}$ has a solution with one component exactly zero, and all other components nonnegative. The number of transition points is zero if any $d \geq 0$ is sufficient to guarantee a feasible solution. When we increase the size of the system, n, the probability of having multiple transitions decreases rapidly, such that for large systems only d_F is present. Right: Because an even number of transition points implies that $d = 0$ yields feasibility, the probability of an even number of transitions should converge to $1/2^{n-1}$ (dashed line).

1.2.4 Probability of feasibility given n and d

We want to compute the probability that a given value of d is sufficient to provide feasibility for a random competitive system of size n. That is, we want t compute $P(x^\star > \mathbb{0}|n, d)$.

To this end, we solve Eq. 6 for β:

$$\beta = \frac{n-1}{n}\sqrt{d^2 - (n-1)} = \hat{\beta}(n, d)$$

Then, whenever $\beta < \hat{\beta}$ we have that the system is feasible. We can therefore compute the probability of feasibility for a given d and n as:

$$P(x^\star > \mathbb{0}|n, d) = P(\beta < \hat{\beta}(n, d)) = \Phi\left(\frac{\hat{\beta}(n, d)}{\sqrt{n-1}}\right)^n = \Phi\left(\frac{\sqrt{n-1}}{n}\sqrt{d^2 - (n-1)}\right)^n \tag{9}$$

which is the equation we report in the main text.

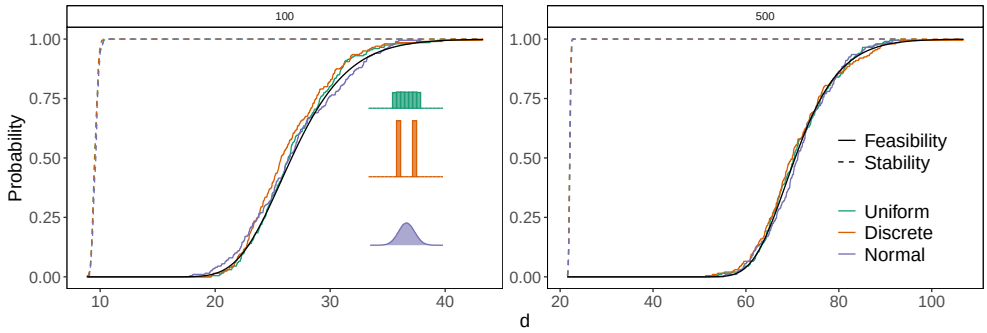

Fig. 8 Probability of feasibility (solid) when coefficients are sampled from different distributions (colors), and from analytical prediction (black), for two values of n (100, 500). Probability of stability is shown in dashed lines.

1.2.5 Stability in random competitive GLV

In this section, we show that there exists a critical value of $d = d_S$ for which stability of any feasible sub-community is guaranteed.

We start by discussing local stability of a feasible equilibrium. Suppose that a feasible equilibrium for Eq. 3 exists; then, dynamics can be linearized around the equilibrium, and the equilibrium is asymptotically locally stable if the Jacobian matrix for the system, evaluated at $x^\star$ (called the *community matrix*), has all eigenvalues with negative real part [7, 8]. For Eq. 3, the community matrix at $x^\star$ is simply :

$$J|_{x^\star} = -D(x^\star \circ r)A$$

where we use $\circ$ to denote the Hadamard (i.e., element by element) product. Whenever $A = dI + B$, we have that both A and $x^\star$ depend on d, while the vector r does not. We can write:

$$J|_{x^\star} = D(r)(-D(x^\star)A)$$

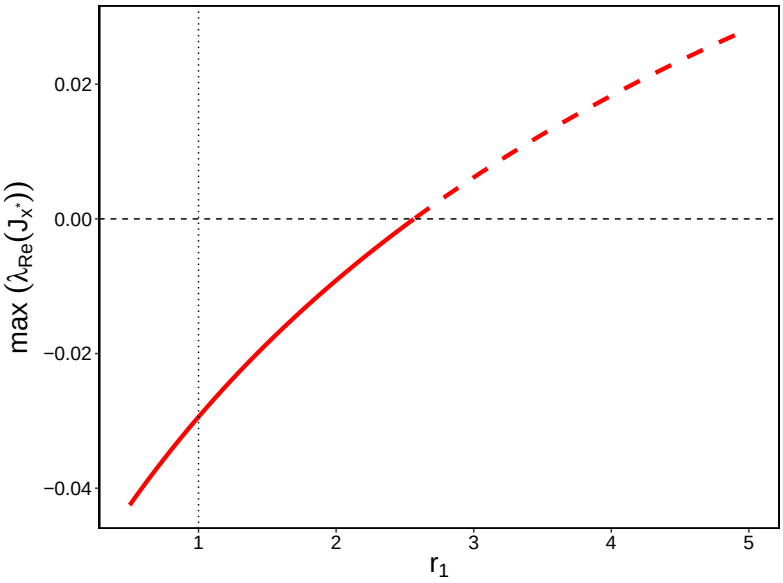

Fig. 9 Bifurcation diagram for varying growth rates for the three species system in Eq. 10. When the growth rates are chosen as $(r_1, 1, 1)$, the system experiences a transition from stability to instability as the maximum of $Re(\lambda(J|_{x^\star}))$ changes sign from negative to positive. The bifurcation occurs at about $r_1 = 2.57$ as r_1 is varied in the range $[1/2, 5]$, but the system remains feasible throughout.

to stress the fact that only the part in parenthesis is influenced by d. Importantly, we could have that $-D(x^\star)A$ has only eigenvalues with a negative real part, while $J|_{x^\star}$ does not. For example, take the competitive GLV system with:

$$A = \begin{pmatrix} 1 & 2 & 3 \\ 2 & 3 & 0 \\ 0 & 3 & 1 \end{pmatrix} \qquad x^\star = \frac{1}{17}\begin{pmatrix} 1 \\ 5 \\ 2 \end{pmatrix} \tag{10}$$

The system is feasible (for any choice of $r > \mathbb{0}$). However, the local stability of the equilibrium depends on the choice of r. For $r = \mathbb{1}$, we have that the eigenvalues of $J|_{x^\star}$ are $(-1, -\frac{1}{34}(1 \pm \mathbb{i}\sqrt{39}))$ and the equilibrium is thus locally stable. However, by increasing the value of r_1 we observe a bifurcation: the real part of the maximum eigen value becomes positive and the system loses stability, as shown in Figure 9.

Thus, in general the stability of the equilibrium might depend on the choice of r. However, if A is "sufficiently" stable, then the stability of any feasible equilibrium

is guaranteed for *any* choice of $r > \mathbb{0}$. In fact, one can go a step further and state that, whenever $A + A^T$ is positive definite, then a) dynamics will always converge to an equilibrium, $\bar{x}$; b) the equilibrium $\bar{x}$ is saturated, meaning that if any population goes extinct, it cannot re-invade the system when starting from low abundance; c) $\bar{x}$ is globally stable (i.e., for any choice of $r > \mathbb{0}$ and initial condition $x > \mathbb{0}$, dynamics asymptotically converge to $\bar{x}$).

We adapt the proof found for example in Hofbauer & Sigmund[12], because this result is important for our discussion on the dynamics of large competitive communities with random interactions.

We order the vector of densities of the species in Eq. 3 as $x = (y, z)^T$, where y are the densities of the (unknown) set of the k species that coexist at the saturated equilibrium, and z the densities of the $n - k$ populations that are extinct at the saturated equilibrium. Therefore $\bar{x} = (y^\star, \mathbb{0})^T$. We also consider a vector of positive weights $w > \mathbb{0}$, which we will use to prove stability. We partition the vector of growth rates, the vector of weights w, and the matrix of interactions according to whether the species belong to the set that coexists, or that that goes extinct:

$$w = \begin{pmatrix} u \\ v \end{pmatrix} > \mathbb{0} \quad r = \begin{pmatrix} a \\ b \end{pmatrix} > \mathbb{0} \quad A = \begin{pmatrix} \mathcal{A} & \mathcal{B} \\ \mathcal{C} & \mathcal{D} \end{pmatrix}$$

Next we consider the Lyapunov function[18]:

$$V(y, z) = \sum_i u_i \left(y_i - {y_i}^\star - {y_i}^\star \log \frac{y_i}{{y_i}^\star} \right) + \sum_l v_l z_l$$

The function is positive for any $y > \mathbb{0}$ and $z > \mathbb{0}$ (i.e., for any initial conditions), given that $u, v, y^\star$ are all positive. Moreover, the function is exactly zero at the saturated equilibrium $\bar{x} = (y^\star, \mathbb{0})^T$. We choose $u_i = 1/a_i$, and $v_l = 1/b_l$, and then differentiate with respect to time:

$$\frac{dV(y,z)}{dt} = \sum_i (y_i - {y_i}^\star)\left(1 - \sum_j \mathcal{A}_{ij} y_j - \sum_k \mathcal{B}_{ik} z_k\right) + \sum_l z_l \left(1 - \sum_j \mathcal{C}_{lj} y_j - \sum_k \mathcal{D}_{lk} z_k\right)$$

We define $\Delta y_i = y_i - {y_i}^\star$; noticing that $1 = \sum_j \mathcal{A}_{ij} {y_j}^\star$ we can write:

$$\frac{dV(y,z)}{dt} = -\sum_{i,j} \Delta y_i \mathcal{A}_{ij} \Delta y_j - \sum_{i,k} \Delta y_i \mathcal{B}_{ik} z_k - \sum_{l,k} z_l \mathcal{D}_{lk} z_k + \sum_l z_l \left(1 - \sum_j \mathcal{C}_{lj} y_j\right)$$

Now we add and subtract $\sum_l z_l \sum_j \mathcal{C}_{lj} {y_j}^\star$, thereby obtaining:

$$\begin{aligned}\frac{dV(y,z)}{dt} = &-\sum_{i,j} \Delta y_i \mathcal{A}_{ij} \Delta y_j - \sum_{i,k} \Delta y_i \mathcal{B}_{ik} z_k - \sum_{l,j} z_l \mathcal{C}_{lj} \Delta y_j \\ &- \sum_{l,k} z_l \mathcal{D}_{lk} z_k + \sum_l z_l \left(1 - \sum_j \mathcal{C}_{lj} {y_j}^\star\right)\end{aligned}$$

Thus, $dV(y,z)/dt$ is the sum of two parts. The first part can be rewritten as a quadratic form:

$$\begin{aligned}-\sum_{i,j} \Delta y_i \mathcal{A}_{ij} \Delta y_j - \sum_{i,k} \Delta y_i \mathcal{B}_{ik} z_k - \sum_{l,j} z_l \mathcal{C}_{lj} \Delta y_j - \sum_{l,k} z_l \mathcal{D}_{lk} z_k = \\ -\sum_{i,j} (x_i - \bar{x}_i) A_{ij} (x_j - \bar{x}_j) = \\ -(x - \bar{x})^T A (x - \bar{x}) = \\ -\frac{1}{2}(x - \bar{x})^T \left(A + A^T\right)(x - \bar{x})\end{aligned}$$

and is thus negative whenever $A + A^T$ is positive definite.

Finally, $(1 - \mathcal{C}y^\star)_j$ is positive only when population j can grow (and thus invade the system) when the system is resting at the saturated equilibrium. Hence, by the

definition of a saturated equilibrium, this term is also negative, and the proof is complete.

In summary, we have shown that, provided that $r > \mathbb{0}$ and that the symmetric part of A is positive definite, dynamics will always converge to an (unspecified) saturated equilibrium. This is a *sufficient* condition for dynamics converging to a saturated equilibrium, which can be made slightly more general. For example, whenever one can choose a positive vector $h > \mathbb{0}$ such that $D(h)A + A^T D(h)$ is positive definite, then the stability of dynamics is also ensured[18]. Because we are interested in an upper bound that is easy to calculate for random matrices, we just analyze the case in which $A + A^T$ is positive definite.

If the matrix $A = dI + B$, and B is a random matrix with independently sampled coefficients with the same positive mean and unit variance, then the eigenvalues of $\frac{1}{2}(B + B^T)$ are easy to compute[9]. In particular, if the mean is zero, the eigenvalues follow Wigner's semicircle distribution, and are approximately contained in the interval $[-\sqrt{2n}, \sqrt{2n}]$. If the mean μ is positive, an additional eigenvalue is located at approximately μn, as shown by the theory of perturbations of random matrices with matrices with small rank[29].

Hence, $A + A^T$ is positive definite (for large n) whenever $d > d_S = \sqrt{2n}$.

1.2.6 Feasibility implies stability in random competitive GLV

We then ask what is the probability of feasibility at the critical value for stability d_S.

$$P(x^\star > \mathbb{0}|n, d_S) = \Phi\left(\frac{\sqrt{n-1}}{n}\sqrt{d_S^2 - (n-1)}\right)^n = \Phi\left(\frac{\sqrt{n-1}}{n}\sqrt{n+1}\right)^n \approx \Phi\left(1\right)^n \approx 0.84^n \tag{11}$$

Thus, the probability of feasibility when $d = d_S$ decreases rapidly when the system increases in size. Asymptotically, the probability tends to zero.

1.2.7 Dynamical consequences

In the Section above, we have shown that, for large n, a random competitive system that is feasible is also stable. The competitive GLV system can give rise to all types of dynamics, including limit cycles (for $n \geq 3$) and chaos (for $n \geq 4$) [10, 11]. Non-equilibrium coexistence via limit cycles or chaos requires a *feasible, locally unstable* equilibrium[12], but we have just shown that whenever $d > d_F > d_S$, then the local stability of the equilibrium is ensured for any choice of $r > \mathbb{0}$. Hence, we conclude that limit cycles or chaos are going to be almost impossible to observe for large random competitive systems.

If the relationship $d_F > d_S$ is maintained for moderate sizes n as well, then the dynamical consequences are even more far-reaching. In a competitive GLV system, lack of feasibility guarantees that one or more populations will go extinct[12]. Suppose that we initialize a random competitive system with n populations at arbitrary initial conditions; this system will have a certain d (taken to be the difference between the mean diagonal element and the mean off-diagonal element). If $d > d_F$, the system is feasible and stable; trajectories will converge to the equilibrium, and if the equilibrium is perturbed, dynamics will return to it. If, on the other hand, $d < d_F$, then the system is not feasible, and therefore some populations will go extinct. There are two distinct cases:

Case a): $d_S < d$: the system will converge to a saturated equilibrium (as shown by the Lyapunov function in Section 1.2.5); the same species will go extinct irrespective of the (positive) initial conditions; the populations that go extinct cannot re-invade the system; the species that coexist do so stably, and when their densities are perturbed, the system will asymptotically return to the saturated equilibrium.

Case b): $d < d_S$: this is the most interesting case. Some populations will go extinct, because there is no feasible equilibrium. However, which species will go extinct *depends*

on the initial conditions. The system can therefore display priority effects and alternative stable states. Every time a species goes extinct, the system shrinks to $n-1$, $n-2$, etc. Accordingly, the threshold values d_S and d_F are also decreased, while the value of d is (substantially) unchanged. As such, provided that the d_S for the reduced system is still smaller than the corresponding d_F, the system will keep losing species until $d > d_S$, thus eventually attaining Case a).

Therefore, for large n (and provided that $d_S < d_F$ when species are lost), the ultimate result is always the same: the surviving populations coexist robustly at a globally-attractive equilibrium. Moreover, while the populations that went extinct at the onset of the dynamics could potentially re-invade the system (only when we start in Case b), the last few populations (i.e., those that went extinct once $d > d_S$) cannot.

Taken collectively, our results show that *robust, stable coexistence* (of a sub-community) *is the norm* for large random competitive communities. For large system with random parameters, dynamics will not display cycles or chaos. Moreover, the final community (i.e., that obtained once the dynamics have elapsed, and extinctions have occurred) is such that priority effects are excluded: if the final community contains k species, all sub-systems formed using these populations can coexist stably, and all remaining species can invade when they are rare. This means that the final community can be assembled from the ground-up by introducing one species at a time[13].

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