Robust coexistence in ecological competitive communities

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Abstract

Darwin already recognized that competition would be the fiercest among conspecifics. In time, intraspecific competition has become a centerpiece of ecological theory, yielding for example the notions of niche differentiation and limiting similarity. When considering the dynamics of ecological communities, one can show that a sufficiently strong level of intraspecific competition can buffer the effects of perturbations, such that populations stably coexist at a steady state—i.e., they return to it after disturbance. Here we analyze the effect of intraspecific competition on the *existence* of such a steady state, in large random ecological communities where competition is the prevalent mode of interaction. We show that, in analogy with stability, when a critical level of intraspecific competition is surpassed, the existence of the steady state is guaranteed. More importantly, we derive a general expression for the probability of feasibility for these systems, and show that the transitions to stability and feasibility always occur in the same order: stability first, feasibility second. Consequently, feasible systems will necessarily be stable. This result holds generally, even when the initial pool of species lacks a feasible equilibrium. That is, when dynamics play out, species extinctions affect the stability and feasibility threshold values but their ordering is maintained. This has profound consequences for ecological dynamics: a subset of the species pool will always coexist robustly at a stable equilibrium, and out-of-equilibrium coexistence via limit cycles or chaos, will never be observed—consistently with experimental results.

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

1 Introduction

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 can be stabilized by imposing sufficiently strong intraspecific competition, and that for large systems with random species interactions the stability transition is universal (independent of the probability distribution used to model interactions), and

sharp (always achieved at the same critical value of intraspecific competition). Importantly, the stability of an equilibrium requires its existence (feasibility) in the first place. In fact, results on stability can dramatically change when conditioned on feasibility. The first contribution on this topic[8]—a response to May's work on stability—showed that the probability of stability, given a feasible equilibrium, actually increases with system size, contrary to earlier expectations. Since then, significant advances have been gradually accumulating on the literature over decades [9–15] (SI, Sec. 3.2), but the question of feasibility and intraspecific competition enjoys only a fraction of the progress made on stability[16, 17]. Maturing our current theory of feasibility, to mirror the broader results we have for stability, is key to deepen our understanding of large random competitive systems and being able to answer important questions as: what type of ecological dynamics should we expect to observe generally?

Here, we compute the probability that a system would display a feasible equilibrium given its level of intraspecific competition, size, and the statistics on the random distribution of species interactions. We show that the transition to feasibility is universal, as in stability, but not sharp—thereby extending, generalizing and refining previous results[8, 9, 12, 14, 18–20]. More importantly, we show explicitly that the transition to stability almost invariably takes place before the one to feasibility[8, 9, 18], implying that feasibility guarantees stability. This result holds generally, even when the initial pool of species lacks a feasible equilibrium. That is, during ecological dynamics species extinctions will change the values of the stability and feasibility thresholds, but not their ordering. This has far-reaching consequences for the ecological dynamics: coexistence via limit cycles or chaos[21, 22] is precluded. Furthermore, the community always converges to an extremely robust equilibrium that (1) is resilient to any perturbation sort of extinction, (2) is resistant to invasions, and (3) can always be assembled from the ground-up[23, 24].

2 Stability and feasibility thresholds

We consider the Generalized Lotka-Volterra[25–28] (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 r_i are organized in the vector r, and interactions A_{ij} in the matrix A. Following May[7], we model A as the sum of two matrices, $A = \alpha I + B$, where B collects the inter-specific interactions, as well as the baseline levels of intraspecific interactions. I is the identity matrix, and $\alpha \geq 0$ can be interpreted as the "excess" intraspecific competition in the system. Now we consider increasing α from zero to an arbitrary large positive value, and track the effects of this change on coexistence. 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, and that such a feasible equilibrium is *stable* if dynamics return to it following a perturbation. We denote α_S as the level of intraspecific competition that is sufficient to guarantee the (global) stability of a feasible equilibrium (SI, Sec. 1.3). Here, we focus on the analogous critical level of intraspecific competition guaranteeing feasibility

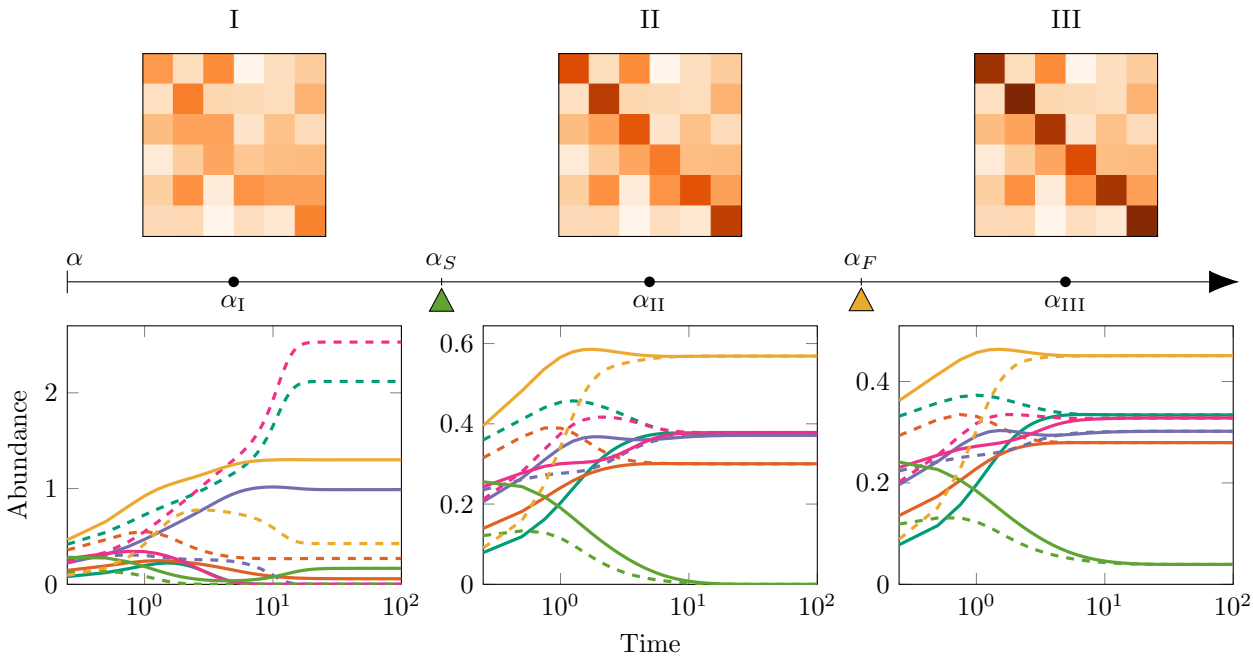

Fig. 1 Three dynamical scenarios of random competitive communities. We consider the dynamics for a system when $A = \alpha I + B$ (Eq. 1), B common to the three systems, and α takes three different values (α_{I}, α_{II}, and α_{III}). The three matrices, with the same off-diagonal coefficients and increasingly strong diagonal coefficients, are drawn above the arrow. By increasing α from I to III, we observe distinct dynamical behaviors. First (case I), initializing the population densities (colors) at different values (dashed vs. solid lines) leads to extinctions, and the set of coexisting populations differ (priority effects or alternative stable states): the equilibrium is not feasible nor stable, so we have not surpassed the stability and feasibility thresholds: $\alpha_{\mathrm{I}} < \alpha_S < \alpha_F$. Second (case II), the equilibrium is not feasible, but the same populations go extinct irrespective of initial conditions (in this case, the green population), while the remaining populations converge to a stable equilibrium (see Sect. 1.3), so that $\alpha_S < \alpha_{\mathrm{II}} < \alpha_F$. Third (case III), a feasible equilibrium exists, and is globally stable. Dynamics always converge to the same equilibrium irrespective of initial conditions, so we conclude that $\alpha_S < \alpha_F < \alpha_{\mathrm{III}}$.

(denoted α_F). Specifically, we ask if it exists (SI, Sec. 2.3), if it is unique, and what is its magnitude compared to that of α_S (Sec. 3). These questions have significant consequences for dynamics, as we illustrate below.

We start with a toy example; in Fig. 1, we illustrate the effect of increasing α on feasibility and stability. We first sample a baseline interaction matrix B, and growth rate vector $r > \mathbb{0}$. For that choice of B, we compute the thresholds for stability, α_S, and feasibility, α_F (SI, Secs. 1.3 and 2.4), marked in Fig. 1 with green and yellow triangles, respectively. Finally, we form three interaction matrices A with differing only in their values of intraspecific competition: α_{I}, α_{II}, and α_{III} (Fig. 1, top row). Once the three systems are initialized, we integrate the dynamics in Eq. 1 from two different initial conditions for each of the three systems (Fig. 1, bottom row, solid vs dashed lines), and observe three different dynamical behaviors. System I (Fig. 1, left panel) undergoes extinctions and displays alternative stable states, indicating that the equilibrium is not feasible nor globally stable (that is, neither stability nor feasibility thresholds have been surpassed, since $\alpha_{\mathrm{I}} < \alpha_S < \alpha_F$). System II (Fig. 1, middle panel), also undergoes extinctions (there is no feasible equilibrium), but starting from two different initial conditions no longer leads to different equilibria because the resulting equilibrium is globally stable ($\alpha_S < \alpha_{\mathrm{II}} < \alpha_F$). Finally, system III (Fig. 1, right panel), exhibits all populations coexisting stably, independent of initial conditions. That is, we have surpassed both the stability and feasibility thresholds ($\alpha_S < \alpha_F < \alpha_{\mathrm{III}}$).

The dynamics here illustrate two important features: (1) there is only one feasibility threshold, and (2) stability comes before feasibility ($\alpha_S < \alpha_F$). Next, we show that these two observations are invariably true for

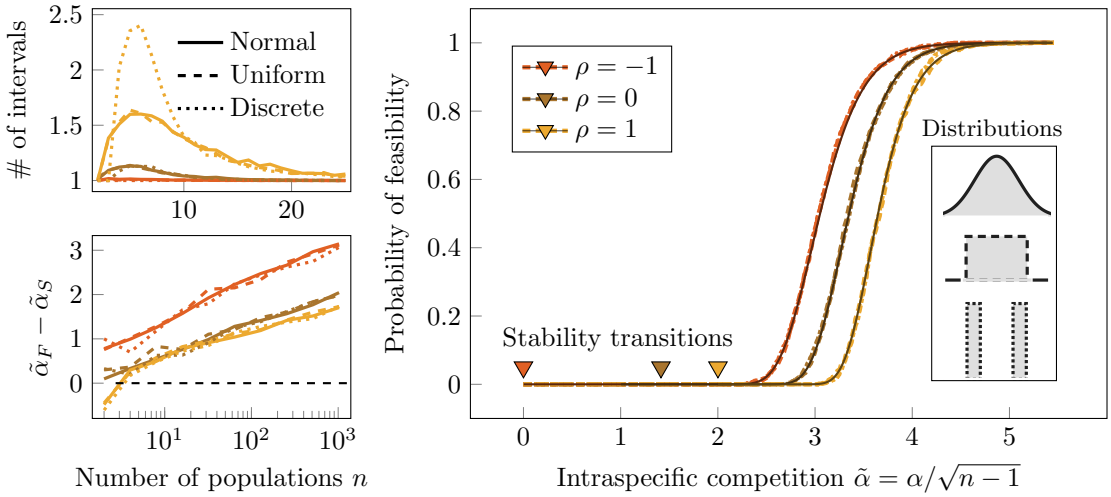

Fig. 2 Transition to feasibility for the GLV competitive system in Eq. (1) with random interactions. Top left: The number of intervals containing values of α that yield feasibility converges to one as n increases. Hence, these systems typically gain feasibility only at α_F, and maintain it for any larger α. The panel shows simulation results in which the interactions are sampled in pairs from a bivariate distribution with positive mean, unit variance, and correlation ρ (colors), and the number of disjoint intervals of α yielding feasibility are averaged (y-axis) for a given value of n (x-axis). To show that results are asymptotically the same irrespective of the choice of distribution, we sample entries from distributions (linetypes) whose marginals are either normal, uniform, or "discrete" (coefficients take positive or negative values with equal probability, SI Appendix A). Bottom left: as n increases (x-axis), the average α_F, i.e., the strength of intraspecific competition guaranteeing feasibility (y-axis, we track $\tilde{\alpha}_F = \alpha_F/\sqrt{n-1}$, and average over many realizations), grows faster than α_S (we track $\tilde{\alpha}_S = \alpha_S/\sqrt{n-1}$), such that for large n, we have that $\tilde{\alpha}_F - \tilde{\alpha}_S > 0$, and the difference grows with n. Right: probability of feasibility for a given level of intraspecific competition (we plot $\tilde{\alpha}$ to ease comparison across panels, x-axis) for systems of size $n = 1000$, and interactions sampled from different distributions (line types) and correlation values (colors). The curves for different distributions collapse to the same curve, showing that the probability of feasibility is asymptotically *universal* (i.e., the higher moments of the distribution have no effect). However, even for such large matrices, the effect of the correlation is noticeable. For each choice of correlation, the value $\alpha = \alpha_S$ at which the stability of a feasible equilibrium is guaranteed is marked by a triangle: note that negative ρ increases both the probability of feasibility and stability for any α, and a positive ρ decreases it[16]. Moreover the probability of feasibility at α_S is negligible. The black solid lines represent the analytical expectations obtained by approximating the variance using resolvents —Eqs. (3) and (4).

the large random ecological systems studied here (but see Sec. 2.3 for general results on arbitrary competitive systems).

3 Feasibility implies robust coexistence

We focus on the ensemble of random ecosystems where each pair of interactions (B_{ij}, B_{ji}) is sampled from *any* bivariate distribution with mean $\mu > 0$, unit variance, and correlation ρ (SI, Sec. 3.1). We call these systems *competitive* whenever $r > \mathbb{0}$ (i.e., all populations can grow in isolation), and $\sum_j B_{ij} > 0$ for every population i (i.e., each population has, on average, a negative effect on the growth of the other populations).

To study the transition to feasibility, we want to compute the probability p_F that a random system of size n, with interactions sampled as described above, will have a feasible equilibrium for a certain value of α. When $\alpha = 0$, such probability decays very rapidly as n increases (SI, Sec. 3.3); however, the previous example suggests that a sufficiently large $\alpha = \alpha_F$ ensures feasibility—we therefore track how the probability of feasibility varies as we increase α. First, we show that feasibility is typically gained only at the critical level α_F, and thus there is a single transition to feasibility for large n (Fig. 2, top left, and SI, Sec. 3.5). This is in contrast with smaller or arbitrary systems, for which several transitions can be observed (SI, Sec. 2.3).

Next, we approximate p_F given the level of intraspecific competition, the size of the system, and the statistics of the distribution of interaction strengths. We start by showing (Methods) that the feasibility of the

system in Eq. (1) is unchanged when we subtract to each column of B its mean, leading to a new interaction matrix C, whose columns sum to zero. This shows that the actual strength of competition does not influence feasibility——we can strengthen the competitive effect of certain populations on all others without affecting the feasibility of the equilibrium. Because infinitely many competitive matrices B will map into the same C, we focus on the feasibility of the following *canonical* competitive system:

$$\dot{y}_i = y_i r_i \left(1 - \alpha y_i - \sum_j C_{ij} y_j \right) . \tag{2}$$

For any model in which populations are *statistically equivalent* (i.e., there is no *a priori* structure making some populations behave differently from the rest), the distribution of the equilibrium values, $y^\star$, always has the same mean and correlation structure (Methods). Moreover, when n is large, we can approximate the components of $y^\star$ to be normally distributed[9] and uncorrelated (Methods, and SI Sec. 3.7). The probability of feasibility can then be expressed (SI, Sec. 3.7) as the cumulative distribution function of a standard normal:

$$p_F(\alpha) \approx \Phi \left(\frac{1}{\alpha \sigma_{y^\star}} \right)^n . \tag{3}$$

This simple expression highlights that models with random interactions different from the ones studied here (e.g., with higher-order correlations, with cyclical structure, etc.) will only affect the variance of $y^\star$. As such, computing the variance $\sigma^2_{y^\star}$ (which in general will depend on n, α, and ρ) is sufficient to approximate the probability of feasibility (black solid lines in Fig. 2, right panel). In our case, we use the theory of resolvents (see Sec. 3.8 for an alternative method based on iterative approximations to equilibrium populations) to approximate the variance for any ρ, obtaining

$$\frac{1}{(\alpha \sigma_{y^\star})^2} \approx \frac{\alpha^2 + \alpha \sqrt{\alpha^2 - 4\rho(n-1)}}{2(n-1)} - (1+\rho) . \tag{4}$$

Substituting this expression into Eq. (3), we obtain an extremely accurate analytical approximation of the probability of feasibility (Fig. 2, black curve). Expression (4) shows that the details of the distribution of interactions (Fig. 2, linetypes), once accounted for the mean, variance and correlation (Fig. 2, colors), are irrelevant when the system is large. This means that asymptotically (i.e., as $n \to \infty$), the curve describing the probability of feasibility is *universal*. Interestingly, exactly as a negative correlation between interaction strengths improves the chance of stability[16], it also increases the probability of feasibility[19]. Finally, contrary to current expectations[14], the effect of the pairwise correlation ρ on the probability of feasibility remains significant for large systems ($n = 1000$ in Fig. 2).

Note that, while the transitions to stability are sharp (Fig. 2, triangles), the feasibility ones are smooth. Importantly, we find that the probability of feasibility at the critical level for stability $p_F(\alpha_S)$ is negligible when n is large (as argued before[9, 14, 18]). Then, for any moderately large system (Fig. 2, bottom left),

whenever feasibility is attained, stability is almost surely guaranteed (i.e., $\alpha_S < \alpha_F$), and thus $p_F(\alpha)$ measures the *probability of coexistence* for a large, random competitive system. These results have profound 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 $n \geq 4$)[21, 22]. Importantly, however, non-equilibrium coexistence still requires the existence of a feasible equilibrium[23]. But we have seen that feasibility generically implies global stability, and therefore non-equilibrium coexistence is precluded.

When the system is not feasible, extinctions will ensue, pruning the original pool of species to a subsystem with different thresholds for feasibility (α_F) and stability (α_S). As such, in principle, any type of dynamics could arise. Next, we show that despite the change in values of α_S and α_F, their ordering is maintained; i.e., $\alpha_S < \alpha_F$. As a result, the dynamics still converge to stable equilibria even when feasibility is not guaranteed for the initial community.

4 Robust coexistence emerges through community dynamics

So far, we have investigated how coexistence is affected by increasing α. However, for a given community, the levels of intraspecific competition remain more or less constant over time. Thus, we start with an example where we sample a pool of n populations, fixing $\alpha < \alpha_S < \alpha_F$ (analogous to system I in Fig. 1), and consider "top-down assembly" (where all the species in the pool are introduced in the environment at the same time, Fig. 3, top panel). Since we are below the feasibility threshold, the community will undergo extinctions and, as a result, α_F and α_S will change. We re-compute their values every time an extinction occurs (plotted in Fig. 3), and find that their ordering is maintained; $\alpha_S < \alpha_F$ throughout assembly. Consequently, the initial species pool traverses the same dynamical states illustrated in Fig. 1: I $\rightarrow$ II $\rightarrow$ III, converging to a globally stable equilibrium after ecological dynamics have elapsed. Furthermore, we show (SI, Sec. 3.11) that the same equilibrium can always be achieved via "bottom-up assembly", through successive invasions[24].

To confirm that these observations are a generic feature, we plot the ratio α_F/α_S when we run the same simulation in the previous example for many draws of random systems with the same characteristics (Fig. 3, bottom panel). We see that it is always above one, implying that the relationship $\alpha_S < \alpha_F$ is maintained throughout the dynamics. This shows that the dynamical outcome of large random systems is always qualitatively the same: a sub-set of the species pool will coexist robustly at an equilibrium that is characterized by $\alpha_S < \alpha_F < \alpha$; the equilibrium is stable, and the last few populations to go extinct (if started in phase I), or all the extinct populations (if started in phase II) cannot re-invade the system.

5 Discussion

Ecological dynamics can be extremely complex, with populations' trajectories oscillating regularly or chaotically. The Generalized Lotka-Volterra model for multiple competitors embodies this complexity: for less than three competitors, trajectories always converge to steady states; for three or more species, one can observe cyclic dynamics; four or more competitors can coexist via nonperiodic, chaotic oscillations. Importantly, to

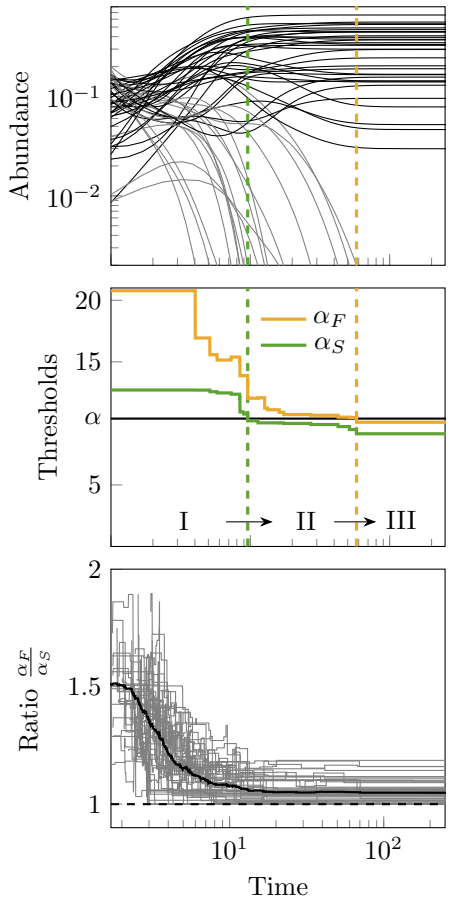

Fig. 3 Community dynamics lead to robust coexistence. We initialize an example community of 50 populations with random interactions, setting $\alpha = \alpha_F/2$ (black line, middle panel); then, there is no feasible equilibrium, and extinctions are guaranteed (grey lines, top panel); note that for this simulation we also have $\alpha < \alpha_S < \alpha_F$, and thus we are in case I. As populations are lost to extinction, the values of α_S and α_F (green and yellow lines respectively, middle panel) for the surviving sub-community change. As the number of extinctions mounts, α_S crosses α (dashed green line, top and middle panels), and thus the system transitions to case II. Extinctions continue until α_F falls below α (dashed yellow line), and the system transitions to case III. The extant populations coexist at a globally stable equilibrium, and those that went extinct since during case II cannot re-invade the system. The ratio $\frac{\alpha_F}{\alpha_S}$ is plotted (bottom) as a function of time for many random realizations (individual trajectories in gray, average in black) of the communities with the same statistics as in the example. The ratio is always above 1, meaning that the relationship $\alpha_F > \alpha_S$ maintains through the dynamics in all simulations.

ensure long-term coexistence of the species there must exist a *feasible* equilibrium: a choice of positive densities at which species, if unperturbed, could remain indefinitely. Here we ask what types of dynamics arise when the number of competitors is large and interactions are chosen at random: we derive the probability of feasibility, and in doing so, notice that stability always comes before feasibility. As a consequence, feasible systems will always be stable. This observation reinforces the notion that, in competitive systems, feasibility is key for coexistence[5, 8, 20, 29]. This is in analogy with consumer-resource models[30], as well as in GLV models with symmetric interactions produced by niche overlap or species' similarity[31], for which stability is guaranteed, and thus feasibility determines coexistence[24, 32].

Furthermore we show that, when the number of competitors is large, trajectories will always converge to stable steady states, ensuring the robust coexistence of the extant competitors. These findings are in line with empirical results: experimenting with organisms at the same trophic level (for which competition is believed to be the dominant mode of interaction) often results in equilibrium dynamics [33–37], while sustained cycles and chaos are typically associated with predator-prey systems and structured populations[38–43].

In summary, we have shown that, for large competitive communities with random coefficients, the probability of non-equilibrium coexistence is negligible because feasible systems are almost surely always stable, and thus chaos or limit cycles will not be observed; moreover, coexistence via stable equilibria emerges through community dynamics even when the initial system lacks feasibility. In conclusion, when considering the subset of coexisting populations, we find that each population rebounds from perturbations, and that the community can be built through successive invasions—the hallmark of robust coexistence [4, 6].

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Author contributions. SA conceived and designed the study. SA and PLA drafted the manuscript. PLA drafted the code and the figures. SA and JAC performed the derivations; JAC derived the approximation using resolvents; SA derived those based on iterative solutions and small-rank perturbations. All Authors contributed to the mathematical derivations, the implementation of the code, edited the manuscript, and discussed and interpreted the results.

Competing interests. The authors declare no competing interests.

Code availability. Code to reproduce all findings is available at
`https://github.com/StefanoAllesina/robust_coexistence`

Methods

A canonical form for competitive systems

We consider the competitive GLV system in Eq. (1), with $r > \mathbb{0}$, $A = \alpha I + B$ and $B^T \mathbb{1} > \mathbb{0}$. We can further decompose the matrix $A = \alpha I + C + \mathbb{1} m^T$, where C is the matrix obtained by subtracting from each column of B its (positive) mean, and m is a vector containing the column means. We can write the solution of $(\alpha I + C + \mathbb{1} m^T) x^\star = \mathbb{1}$ as a function of the solution of the simpler system $(\alpha I + C) y^\star = \mathbb{1}$ (SI, Sec. 2.1), finding:

$$x^\star = \frac{1}{1 + m^T y^\star} y^\star \quad .$$

Then, $x^\star$ and $y^\star$ are proportional to each other, and thus $x^\star > \mathbb{0}$ requires all the components of $y^\star$ to have the same sign. However, because the sum of all the components of $y^\star$ is positive (as seen when summing all the equations: $\mathbb{1}^T (\alpha I + C) y^\star = \alpha \mathbb{1}^T y^\star = n$), and $m > \mathbb{0}$ (because the system is competitive), then $x^\star$ is feasible if and only if $y^\star$ is feasible. Because infinitely many competitive matrices B will map into the same C, we say that this is the *canonical* matrix of interactions for the competitive system.

Intraspecific competition guaranteeing feasibility

One can show that, in competitive systems, there exists a level of intraspecific competition at which the feasibility of the equilibrium is guaranteed, and further strengthening intraspecific competition retains feasibility (SI, Sec. 2.2). We denote this critical level as α_F. To find this value for a given matrix of interaction strengths B, we consider the eigenvalues of several matrices derived from B (or, equivalently, C, SI Sec 2.3). In particular, consider the real, positive eigenvalues of $-C = \mathbb{1} m^T - B$, and call α_0 the largest value such that the components of the solution $(\alpha_0 I + C) y^\star = \mathbb{1}$ diverge to $\pm\infty$ (if it exists, otherwise $\alpha_0 = 0$). Then, we form n matrices Q_i, each of size $n - 1$. Each Q_i is obtained as the sum of two matrices, $Q_i = \mathbb{1} (b^{(i)})^T - B^{(i)}$, where $b^{(i)}$ is the ith row of matrix B with the ith element removed, and $B^{(i)}$ is the matrix B with the ith row and the ith column removed. Denote as α_i the maximum real eigenvalue of Q_i (if it exists, otherwise $\alpha_i = 0$). Finally, we have that the value α_F that guarantees the feasibility of the system is $\alpha_F = \max\{\alpha_0, \alpha_1, \alpha_2, \ldots, \alpha_n\}$.

Interestingly, the value of intraspecific competition sufficient to guarantee the global stability of any feasible equilibrium is also an eigenvalue, this time the largest positive eigenvalue of $-(B + B^T)/2$ (SI, Sec. 1.3).

Distribution of $y^\star$ for systems with random parameters

For random models in which populations are *statistically equivalent* (SI, Sec. 3.1), we have that the expectations $\mathbb{E}(y_i^\star) = \mathbb{E}(y_j^\star)$, the variances $\mathbb{V}(y_i^\star) = \mathbb{V}(y_j^\star) = \sigma^2_{y^\star}$, and the correlation $\mathbb{C}\mathrm{or}(y_i^\star, y_j^\star)$ is the same for all pairs. Note that the sum of the components of $y^\star$ is fixed: $\mathbb{1}^T y^\star = n/\alpha$, and therefore the mean correlation must be negative; because it has to be the same for all pairs, it is exactly $\mathbb{C}\mathrm{or}(y_i^\star, y_j^\star) = -1/(n-1)$, as shown also by calculating it explicitly (SI, Sec. 3.7). Moreover, if one approximates the distribution of $y^\star$ as a multivariate normal distribution, finding the unknown variance (which will depend on the exact definition of the model, the statistics of the distribution, etc.) is sufficient to approximate the probability, by either ignoring

the correlation between the components (because for large n it is negligible), or by computing an integral over the positive orthant (SI, Sec. 3.7).

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