Survival of the Weaker

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We investigate extinction dynamics in the paradigmatic model of two competing species A and B that reproduce ($A \to 2A$, $B \to 2B$), self-regulate by annihilation ($2A \to 0$, $2B \to 0$), and compete ($A+B \to A$, $A+B \to B$). For a finite system that is in the well-mixed limit, a quasi-stationary state arises which describes coexistence of the two species. Because of discrete noise, both species eventually become extinct in time that is exponentially long in the quasi-stationary population size. For a range of asymmetry in the growth and competition rates, the paradoxical situation in which the smaller-population (weaker) species survives longer.

In the paradigmatic two-species competition model, a population is comprised of distinct species A and B, each of which reproduce and self regulate by intraspecies competitive reactions. In addition, *interspecies* competitive reactions occur, which are deleterious to both species [1]. For large, well-mixed populations, the evolution can be accurately described by deterministic rate equations. For finite systems, however, fluctuations in the numbers of individuals ultimately lead to extinction, in stark contrast to the rate equation predictions.

In this work, we investigate how *asymmetric* interspecies competition influences the extinction probability of each species. In a finite ecosystem, extinction arises naturally when multiple species compete for the same resources. In such an environment, one species often dominates, while the others become extinct [2–6], a feature that embodies the *competitive exclusion principle.* A related paradigm appears in the context of competing parasite strains that exploit the same host population, or in the fixation of a new mutant allele in a haploid population whose size is not fixed [7].

When the interspecies competition is asymmetric, we find that the *more numerous species may be more likely to become extinct.* This paradoxical situation arises, for example, when the growth rate of species A exceeds that of B, but As are more susceptible to competition than Bs. Consequently, the quasi-stationary population of species B may be smaller than A and yet B may be much less likely to become extinct—"survival of the weaker".

Model: Asymmetric competition of two species A and B is defined by the reactions:

$$
\begin{aligned}
&A \xrightarrow{1} A+A && B \xrightarrow{g} B+B\,,\\
&A+A \xrightarrow{1/K} 0 && B+B \xrightarrow{1/K} 0\,,\\
&A+B \xrightarrow{\epsilon/K} B && A+B \xrightarrow{\alpha\epsilon/K} A.
\end{aligned}
\tag{1}
$$

The first line accounts for reproduction, the second for intraspecies competition, and the last for interspecies competition. Here K is the environmental carrying capacity, which sets the size of the overall population, ϵ quantifies the severity of the competition, while g and α quantify the asymmetries in the growth and interspecies competition rates, respectively. In our presentation, we focus on the limit $K \gg 1$. While a general model should also contain asymmetry in the intraspecies competition rate, no new phenomena arise by this generalization; for simplicity, we study the model defined by Eqs. (1).

To probe extinction in two-species competition, we focus on $P_{m,n}(t)$, the probability that the population consists of $m \geq 0$ As and $n \geq 0$ Bs at time t. In the limit of a perfectly-mixed population, the stochastic reaction processes in (1) lead to $P_{m,n}(t)$ evolving by the master equation

$$
\begin{aligned}
\dot{P}_{m,n}(t) = \hat{H}P_{m,n} &= \left[\left(\mathbb{E}^{-1}-1\right)m + g\left(\mathbb{F}^{-1}-1\right)n\right]P_{m,n}\\
&+\left[\left(\mathbb{E}^{2}-1\right)\frac{m(m-1)}{2K} + \left(\mathbb{F}^{2}-1\right)\frac{n(n-1)}{2K}\right]P_{m,n}\\
&+\left[\frac{\epsilon}{K}\left(\mathbb{E}-1\right) + \frac{\alpha\epsilon}{K}\left(\mathbb{F}-1\right)\right]mnP_{m,n}\,.
\end{aligned}
\tag{2}
$$

Here $\mathbb{E}$ and $\mathbb{F}$ are the raising and lowering operators [8] for species A and B, respectively; viz. $\mathbb{E}^i P_{m,n} = P_{m+i,n}$ and $\mathbb{F}^j P_{m,n} = P_{m,n+j}$.

Deterministic Rate Equations: We focus on the average population sizes $\langle m\rangle = \sum_{m,n} mP_{m,n}$ and $\langle n\rangle = \sum_{m,n} nP_{m,n}$. From (2), the evolution of these quantities is given by

$$
\begin{aligned}
\dot{\langle m\rangle} &= \langle m\rangle\left(1-\frac{\langle m\rangle}{K} - \epsilon\frac{\langle n\rangle}{K}\right),\\
\dot{\langle n\rangle} &= \langle n\rangle\left(g-\frac{\langle n\rangle}{K} - \alpha\epsilon\frac{\langle m\rangle}{K}\right).
\end{aligned}
\tag{3}
$$

Here we neglect correction terms of the order of $1/K$ and, more importantly, neglect correlations by assuming that $\langle m^2\rangle = \langle m\rangle^2$, $\langle n^2\rangle = \langle n\rangle^2$, and $\langle mn\rangle = \langle m\rangle\langle n\rangle$. We restrict ourselves to the parameter range $\alpha\epsilon < g < 1/\epsilon$, which guarantees that the fixed point corresponding to coexistence of both species is stable. The four fixed points of the rate equations (3) are then:

$$
\begin{aligned}
(m^*, n^*) &= (0,0) && \text{unstable node,}\\
&= (K,0)\,,(0,Kg) && \text{saddles,}\\
&= \left(K\tfrac{1-g\epsilon}{1-\alpha\epsilon^2}, K\tfrac{g-\alpha\epsilon}{1-\alpha\epsilon^2}\right) && \text{stable node.}
\end{aligned}
\tag{4}
$$

If the initial populations of both species are non-zero, they are quickly driven to the stable fixed point (Fig. 1) on a *relaxation* time scale τ_r that is independent of K.

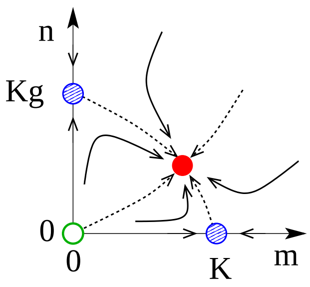

FIG. 1. Schematic flow diagram in asymmetric two-species competition for weak competition in the mean field. The unstable node, the saddles, and the stable node are shown as open, hatched, and solid, respectively.

Extinction: The mean-field picture is incomplete because fluctuations of the population sizes about their fixed-point values are ignored. For large populations (corresponding to carrying capacity $K \gg 1$), these fluctuations are typically small. Thus the populations achieve a *quasi-stationary* state where the two species coexist. This state is stable in the mean-field description (heavy dot in Fig. 1). However, an unlikely sequence of deleterious events eventually occurs that ultimately leads one population, and then the other, to extinction. After the first extinction, the remaining population settles into another quasi-stationary state around one of the single-species fixed points $(m^*, n^*) = (K, 0)$ or $(0, Kg)$. Eventually a large fluctuation drives the remaining species to extinction. This second extinction time is typically much longer [by a factor that scales as $\exp(\text{const.} \times K)$] than the first time, because the remaining species does not suffer inter-species competition. Once a species is extinct, there is no possibility of recovery since there is no replenishment mechanism.

The question that we address is: which species typically goes extinct first? The answer to this question is encoded in the dynamics of the two-species probability $P_{m,n}(t)$. During the initial relaxation stage, a quasi-stationary probability distribution is quickly reached. The probability distribution is sharply peaked at the stable fixed point of the mean-field theory. This probability slowly "leaks" into localized regions near each of the single-species fixed points $(m^*, n^*) = (K, 0)$ and $(0, Kg)$. Thus two sharply-peaked single-species distributions start to form. If the $(K, 0)$ peak grows faster then the B species is more likely to go extinct first. Similarly, a faster growing $(0, Kg)$ peak means A extinction is more likely. Eventually, the probability distribution that is localized at the two single-species fixed points slowly leaks toward the fixed point $(0, 0)$ that corresponds to complete extinction [9].

To determine extinction rates, it is helpful to define $\mathcal{P}_A$, $\mathcal{P}_B$, and $\mathcal{P}_\phi$ as the respective probabilities that species A is extinct, species B is extinct, or neither is extinct at time t [10]. (Being interested in times much shorter than the expected extinction time of *both* species, we can neglect the probability of the latter process.) By definition, these extinction probabilities are

$$\mathcal{P}_A = \sum_{n>0} P_{0,n}, \quad \mathcal{P}_B = \sum_{m>0} P_{m,0}, \quad \mathcal{P}_\phi = \sum_{m,n>0} P_{m,n}; \quad (5)$$

these satisfy $\mathcal{P}_A + \mathcal{P}_B + \mathcal{P}_\phi = 1$, up to an exponentially small correction that stems from the process where both species become extinct simultaneously. In the limit $K \gg 1$ and for times much greater than the relaxation time scale τ_r, the sums in Eqs. (5) are dominated by contributions from values of m and n that are close to the single-species and coexistence fixed points. Moreover, these extinction probabilities evolve according to a set of effective coupled equations

$$\begin{aligned} \dot{\mathcal{P}}_A &= R_A \mathcal{P}_\phi \,, \\ \dot{\mathcal{P}}_B &= R_B \mathcal{P}_\phi \,, \\ \dot{\mathcal{P}}_\phi &= -(R_A + R_B) \mathcal{P}_\phi \,, \end{aligned} \quad (6)$$

that define R_A and R_B as the respective extinction rates for species A and species B. Solving these equations yields the time dependence of the extinction probabilities

$$\mathcal{P}_A(t) = \frac{R_A}{\mathcal{R}}\left(1 - e^{-\mathcal{R}t}\right), \quad \mathcal{P}_B(t) = \frac{R_B}{\mathcal{R}}\left(1 - e^{-\mathcal{R}t}\right), \quad (7)$$

with $\mathcal{R} = R_A + R_B$. To determine R_A and R_B, we follow the evolution of the eigenstate of the master equation (2) that determines the leakage of probability from the vicinity of the coexistence point:

$$P_{m,n}(t) = \Pi_{m,n}\, e^{-\mathcal{R}t}, \qquad m, n > 0, \quad (8)$$

where

$$\hat{H}\, \Pi_{m,n} = -\mathcal{R}\, \Pi_{m,n}, \qquad m, n > 0, \quad (9)$$

and $\mathcal{R}$ is the *third*-lowest positive non-trivial eigenvalue of the operator $\hat{H}$. The two still-smaller positive non-trivial eigenvalues correspond to the much slower decay of quasi-stationary single-species states and play no role in the dynamics of the first extinction event. There is also a trivial eigenvalue that corresponds to the final state of complete extinction.

Combining Eq. (2) with (5)–(8), we obtain the following expression for the extinction rate of the A species:

$$R_A = \frac{1}{K} \sum_{n>0} \left(\epsilon n \Pi_{1,n} + \Pi_{2,n}\right). \quad (10a)$$

As expected, the extinction rate for As involves two processes: (i) elimination of the last remaining A via competition with Bs and (ii) annihilation of the last remaining pair of As. Similarly,

$$R_B = \frac{1}{K}\sum_{m>0}\left(\alpha\epsilon m\Pi_{m,1} + \Pi_{m,2}\right). \tag{10b}$$

To calculate R_A and R_B, we therefore need to evaluate the small-population-size tails of $\Pi_{m,n}$. This task can be achieved by applying a variant of Wentzel-Kramers-Brillouin (WKB) approximation, that was pioneered in Refs. [11–14], and was applied more recently to population extinction, in particular, for stochastic two-population systems [10, 15–22]. The WKB ansatz for $\Pi_{m,n}$ has the form

$$\Pi_{m,n} = e^{-KS(x,y)}, \tag{11}$$

where $x = m/K$ and $y = n/K$ are treated as continuous variables. Substituting Eq. (11) into (10a) and assuming $K \gg 1$, gives, to lowest order in $1/K$

$$R_A \sim e^{-KS_A}, \qquad R_B \sim e^{-KS_B}, \tag{12}$$

where $S_A = S(0, g)$ and $S_B = S(1, 0)$, (see Refs. [10, 15–17]). Thus as $K \gg 1$, the eventual extinction probabilities in (7) simply become (up to pre-exponential factors that depend on K), as

$$\mathcal{P}_A(t=\infty) = 1-\mathcal{P}_B(t=\infty) \simeq \frac{e^{-KS_A}}{e^{-KS_A}+e^{-KS_B}}. \tag{13}$$

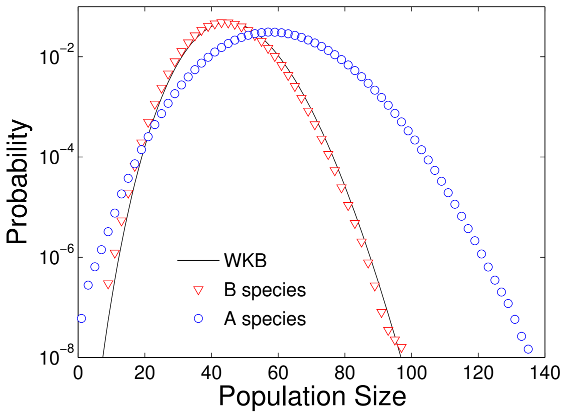

FIG. 2. Quasi-stationary probability distributions for species A, $P_m = \sum_n P_{m,n}$, and species B, $P_n = \sum_m P_{m,n}$. Parameters are $K = 100$, $\epsilon = 0.9$, $g = 0.45$, and $\alpha = 0$. Symbols are simulation results, while the solid curve is WKB approximation for the B species distribution.

To determine the extinction probabilities explicitly, we therefore need S_A and S_B. To this end, we substitute the WKB ansatz (11) in Eq. (9) and Taylor expand $S(x, y)$ to lowest order in $1/K$. After some algebra, we obtain an effective Hamilton-Jacobi equation $H(x, y, \partial_x S, \partial_y S) = -\mathcal{R}$, with the Hamiltonian

$$\begin{aligned} H(x, y, p_x, p_y) &= x(e^{p_x}-1) + gy(e^{p_y}-1) \\ &+\frac{x^2}{2}(e^{-2p_x}-1)+\frac{y^2}{2}(e^{-2p_y}-1) \\ &+ \epsilon xy(e^{-p_x}-1)+\alpha\epsilon xy(e^{-p_y}-1). \end{aligned} \tag{14}$$

Here $p_x = \partial_x S$ and $p_y = \partial_y S$ are the canonical momenta that are conjugate to the "coordinates" x and y. Correspondingly, $S(x, y)$ is the classical action of the system.

Since we expect that $-\mathcal{R}$ (which now has the meaning of energy in this Hamiltonian system) is expected to be exponentially small, we set it to zero. The Hamiltonian equations of motion $\dot{x} = \partial H/\partial p_x$, $\dot{p}_x = -\partial H/\partial x$, etc., have six finite zero-energy fixed points, and three more fixed points where one or both momenta are at minus infinity. Only three of the fixed points, however, turn out to be relevant for answering our question about which species typically goes extinct first. These are:

$$\begin{aligned} F_\phi &= \left(\frac{1-g\epsilon}{1-\alpha\epsilon^2}, \frac{g-\alpha\epsilon}{1-\alpha\epsilon^2}, 0, 0\right), \\ F_A &= (0, g, \ln(g\epsilon), 0), \\ F_B &= (1, 0, 0, \ln(\alpha\epsilon/g)). \end{aligned} \tag{15}$$

A straightforward way to determine S_A and S_B is by calculating the action along the *activation trajectories*. These are zero-energy, but non-zero-momentum trajectories of the Hamiltonian system (14) that go from F_ϕ to F_A, and from F_ϕ to F_B, respectively. These actions are

$$S_A = \int_{F_\phi}^{F_A} (p_x dx + p_y dy), \tag{16}$$

and similarly for S_B. In general, these activation trajectories—separatrices, or instantons—cannot be calculated analytically because of the lack of an integral of motion that is independent of the energy. However, for $\epsilon \ll 1$ a perturbative solution for these trajectories is possible.

As a preliminary, we outline how to calculate the action for the special case $\epsilon = 0$, which corresponds to two uncoupled species. Here the zero-energy activation trajectories can be easily found. For the $F_\phi \to F_A$ separatrix, the B species is unaffected by A extinction so (y, p_y), which correspond to the coordinates of the Bs, remains constant throughout the evolution. As a result, a parametric form of the $F_\phi \to F_A$ separatrix is

$$x = \frac{2(e^{p_x}-1)}{e^{-2p_x}-1}, \tag{17a}$$

with $y = g$ and $p_y = 0$ throughout. Similarly, for the $F_\phi \to F_B$ separatrix one obtains

$$y = \frac{2g(e^{p_y}-1)}{e^{-2p_y}-1}, \tag{17b}$$

with $x = 1$ and $p_x = 0$ throughout. Substituting the trajectories given in (17) into (16) and performing the integration by parts gives $S_A = 2(1 - \ln 2)$ and $S_B = 2g(1 - \ln 2)$ [23, 24].

For weak interspecies competition ($\epsilon \ll 1$), we can calculate the corrections to the actions to first order in ϵ. For this purpose, we split the Hamiltonian (14) into unperturbed and perturbed parts, $H = H_0 + \epsilon H_1$, and similarly expand the action as $S = S_0 + \epsilon S_1 + \ldots$. Following [15, 18, 25], the correction to the action is $S_1 = \int_{-\infty}^{\infty} H_1[x(t), y(t), p_x(t), p_y(t)]dt$, where the integral is evaluated along the *unperturbed* trajectories given by Eqs. (17). Performing this integral for S_1 yields the corrected actions

$$
\begin{aligned}
S_A &= 2(1 - \ln 2) - \epsilon(2g \ln 2)\,, \\
S_B &= 2g(1 - \ln 2) - \epsilon(2\alpha \ln 2)\,.
\end{aligned}
\tag{18}
$$

Equations (12) and (18) give the analytic expression for the extinction probabilities of each species for weak interspecies competition. Using Eq. (18) and imposing the condition $S_A = S_B$ from Eq. (13), we obtain the following condition for equal extinction probability for both species:

$$
g = \frac{1 + \alpha\, c\, \epsilon}{1 + c\, \epsilon}\,, \tag{19}
$$

where $c = \left[(\ln 2)^{-1} - 1\right]^{-1}$. The predictions of Eqs. (13) and (18) are in good agreement with our simulation results (Fig. 3).

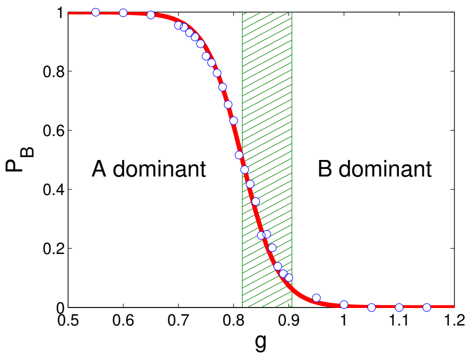

FIG. 3. Probability that species B first becomes extinct as a function of growth rate asymmetry g for $\alpha = 0$, $\epsilon = 0.1$, and $K = 40$. The curve is the prediction of Eq. (13) with actions given by (18) while circles are simulation results. In the hatched region, the quasi-stationary population of A exceeds B, but A is less likely to become extinct first.

Phase Diagram: From the stable fixed point of the rate equations given in (4), the populations of the two species are equal when $g = \frac{1+\alpha\epsilon}{1+\epsilon}$. Comparing this condition with (19), there is a finite region in the α-g parameter space where one species has a larger quasi-stationary population and yet a smaller probability to first become extinct. As an illustration, Fig. 3 shows the probability for B to become extinct first for fixed α and ϵ. We also produced analogous curves as Fig. 3 at many values of α. From the value of g at which the extinction probabilities are equal, we infer the phase diagram shown in Fig. 4. Simulations at larger values of ϵ yield the same qualitative phase diagram.

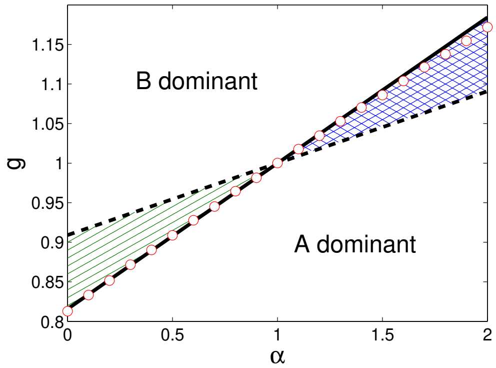

FIG. 4. Phase diagram for $\epsilon = 0.1$ showing loci of equal quasi-stationary population sizes (dashed) and equal extinction probabilities from Eq. (19) (solid). Circles indicate simulation results. In the hatched region, As are more numerous in the quasi-stationary state but are more likely to become extinct first. In the cross-hatched region Bs are more numerous but are more likely to become extinct first.

Conclusion: In two-species competition, interspecies competition asymmetry leads to an unexpected phenomenon of "survival of the weaker", in which the species with the smaller quasi-stationary population has a greater chance of long-term survival.

AG and SR gratefully acknowledge NSF grant DMR-0906504 and DMR-1205797 for partial financial support. BM was partially supported by the Israel Science Foundation (Grant No. 408/08), by the US-Israel Binational Science Foundation (Grant No. 2008075), and by the Condensed Matter Theory Visitors Program in the Boston University Physics Department.

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