

Competition and Cooperation in One-Dimensional Stepping-Stone Models

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Mutualism is a major force driving evolution and sustaining ecosystems. Although the importance of spatial degrees of freedom and number fluctuations is well known, their effects on mutualism are not fully understood. With range expansions of microbes in mind, we show that, even when mutualism confers a selective advantage, it persists only in populations with high density and frequent migrations. When these parameters are reduced, mutualism is generically lost via a directed percolation (DP) process, with a phase diagram strongly influenced by an exceptional symmetric DP (DP2) transition.

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Cooperation is at the heart of many complex systems [1,2]. On an organism level, gut bacteria help their hosts digest cellulose. On an ecosystem level, plants often rely on fungi to receive important nutrients. Even human societies are products of cooperation between individuals. Despite the apparent advantage and pervasiveness of mutualistic interactions, their existence is often difficult to explain by a naive application of Darwinian natural selection: Cooperation can succumb to cheating [1] and, as we show here, to number fluctuations.

To model complex interactions between individuals or species, Maynard Smith developed evolutionary game theory [2]. The central idea of game theory is that the fitness of an organism depends on the frequency of encounters with other organisms in the population. Evolutionary games are usually analyzed using mean-field-type approximations, which neglect both spatial correlations and number fluctuations. However, these simplifications are not appropriate for natural populations living in spatially extended habitats and can miss important stochastic aspects of population dynamics. In particular, the interplay of stochasticity and spatial degrees of freedom leads to spatial demixing of different species or genotypes in the population [3,4], which can significantly decrease the probability of mutualistic interactions.

Following pioneering work of Nowak and May [5], several studies have investigated the effects of space on evolutionary games [6,7] (and references therein) using simulations on a two-dimensional lattice with a single nonmotile individual per site. Although these studies underscored the significant effects of spatial structure on evolutionary dynamics, outstanding issues remain. First, the outcomes of these lattice simulations are very sensitive to the exact rules of birth and death updates and interaction pattern between nearest neighbors [7]; as a result, these studies do not smoothly connect with the well-understood dynamics in spatially homogeneous

(well-mixed) populations. Moreover, it is not clear whether a model with a single nonmotile organism per site and nearest neighbor interactions is a good description of any species. Second, such models do not allow systematic investigation of the role of migration and the magnitude of number fluctuations, which are important for the applications of the theory to natural and experimental populations. Third, closely related voter models in two spatial dimensions have very slow logarithmic coarsening [8]; 2D simulations typically do not explore the time scales on which spatial demixing of species becomes important.

Our Letter studies competition and cooperation in the stepping-stone model of population genetics [9]. This model preserves the dynamics of well-mixed populations locally, but includes migrations as well as number fluctuations, which are controlled by the population density. We focus on a one-dimensional model because stochastic effects are more pronounced in lower spatial dimensions [4]. More important, the spread of mutualism in two dimensions often occurs via a traveling reaction-diffusion wave, where the most important dynamics often occurs at a moving quasi-one-dimensional frontier [4]. We find that mutualism persists in a much smaller region of parameter space compared to well-mixed populations and that it is more susceptible to spatial demixing when the benefits to the interactants are unequal. The critical strength of mutualism required to sustain cooperation increases with migration rate and population density. As the strength of mutualism is reduced, the population undergoes a nonequilibrium phase transition in the universality class of either directed percolation (DP) or Z_2 symmetric directed percolation (DP2); see Ref. [10] for a comprehensive review of DP models.

The stepping-stone model [9,11] consists of demes (islands) arranged on a line, with spacing a . Each deme has N organisms, which can reproduce and migrate. During a generation time τ , organisms migrate to one of the nearest

neighbors with probability m . Reproduction occurs within a deme by selecting a random individual to die and another individual to reproduce. The probability to be selected for reproduction is proportional to an individual's fitness. We assume that the fitness is a sum of two contributions: a background reproduction rate, scaled to one for all organisms, and a benefit due to mutualistic interactions with other organisms in the same deme (e.g., due to exchanging nutrients). Let the benefit to the organism of type i from interacting with the organism of type j be a_{ij} . If the type's fractions within a deme are f_i , then the corresponding fitnesses w_i in a given generation are $w_i = 1 + \sum_j a_{ij} f_j$ because the increases in growth rate due to mutualism should be weighted by the density of cooperating organisms.

For simplicity, we consider only two cooperating species (or genotypes) and let the frequency of species 1 be $f(t, x)$, where t is time and x is position. The frequency of the other species is then $1 - f(t, x)$. In the limit $a_{ij} \ll 1$, $m \ll 1$, $N \gg 1$, we find a continuum description of this one-dimensional stepping-stone model in terms of a generalized stochastic Fisher equation [4]

$$\frac{\partial f}{\partial t} = sf(1-f)(f^* - f) + D_s \frac{\partial^2 f}{\partial x^2} + \sqrt{D_g f(1-f)} \Gamma(t, x), \quad (1)$$

where $\Gamma(t, x)$ is an Itô delta-correlated Gaussian white noise [11], $D_s = ma^2/(2\tau)$ is the spatial diffusion constant, and $D_g = 2a/(N\tau)$ is the strength of number fluctuations. The key parameters $s = (\alpha_1 + \alpha_2)/\tau$ and $f^* = \alpha_1/s$ are given in terms of $\alpha_1 = a_{12} - a_{22}$ and $\alpha_2 = a_{21} - a_{11}$, which characterize the relative benefit of interspecies versus intraspecies interactions. The selective advantage (or strength) of mutualism is given by s , while f^* is the equilibrium fraction of species 1 that would occur in a spatially homogeneous population without number fluctuations.

The usual mean-field treatment neglects spatial correlations and fluctuations. With the neglect of the last two terms, Eq. (1) becomes an ordinary differential equation, and its dynamics can be easily analyzed. There are four possible outcomes [11]. The population develops mutualism when α_1 and $\alpha_2 > 0$, one of the species outcompetes the other when $\alpha_1 \alpha_2 < 0$, and, when α_1 and $\alpha_2 < 0$, the population is bistable, with either species capable of outcompeting the other depending on the initial conditions.

Number fluctuations lead to local extinctions. In a finite well-mixed population, a stochastic treatment must account for absorbing boundary conditions at $f = 0$ and $f = 1$, when one of the two species goes extinct. The absorbing boundaries arise because there is a finite probability to find the population in any of its discrete states when the population size is finite. Therefore, after a sufficiently long time, the population will reach one of the

absorbing boundaries and become fixed. The splitting probabilities and fixation times can be calculated for this zero-dimensional problem with fluctuations using the Kolmogorov backward equations [11].

In a spatially extended population, however, local extinctions can be prevented or rescued through migration. Suppose, in particular, that migrations are frequent and mutualism is sufficiently strong to keep the population near the equilibrium fraction f^* . In this limit, we can extend the mean-field approximation to account for fluctuations and spatial degrees of freedom by replacing the nonlinear reaction term in Eq. (1) with a linear one:

$$\frac{\partial f}{\partial t} = sf^*(1-f^*)(f^* - f) + D_s \frac{\partial^2 f}{\partial x^2} + \sqrt{D_g f(1-f)} \Gamma(t, x). \quad (2)$$

If $f(t, x) \approx f^*$, the error we make should be small; more important, Eq. (2) can now be solved exactly. The solution is most easily obtained in terms of the average spatial heterozygosity $H(t, x)$, a two-point correlation function equal to the probability to sample two different species distance x apart:

$$H(t, x) = \langle f(t, 0)[1 - f(t, x)] + f(t, x)[1 - f(t, 0)] \rangle. \quad (3)$$

Using the Itô calculus, we derive the equation of motion for $H(t, x)$ from Eq. (2),

$$\frac{\partial H}{\partial t} = \left[2D_s \frac{\partial^2}{\partial x^2} - D_g \delta(x) \right] H + sH^*(H^* - H), \quad (4)$$

where $\delta(x)$ is the delta function, $H^* = 2f^*(1 - f^*)$, and we, for simplicity, assumed that $f(0, x) = f^*$. The stationary solution, valid at long times, reads

$$\frac{H(\infty, x)}{H^*} = 1 - \frac{e^{-x\sqrt{s f^*(1-f^*)/D_s}}}{1 + \sqrt{8s D_s H^*/D_g^2}}. \quad (5)$$

Since H^* is the heterozygosity of a well-mixed population with $f = f^*$, the fraction on the right-hand side is the correction to the mean-field analysis. Thus, we see that, for $s \ll D_g^2/D_s$, the probability of the two species coexisting at any particular point in space [given by $H(\infty, 0)$] becomes small, which is inconsistent with mutualism and our assumption that $f(t, x) \approx f^*$. Hence, we anticipate a critical value of s below which mutualism *must* give way to spatial demixing.

Although the hierarchy of moment equations does not close for the original nonlinear problem given by Eq. (1), the average spatial heterozygosity $H(t, x)$ is still useful for characterizing the behavior of the system. In particular, $H(t, 0)$ can be used to measure the local amount of mutualism. Equation (5) suggests that $H(t, 0)$ reaches a nonzero steady state value when $s \gg D_g^2/D_s$. However, when

$s = 0$, the exact solution of Eq. (1) reveals that instead of reaching a steady state, $H(t, 0)$ decays to zero as $t^{-1/2}$ [4]. When species do not coexist locally, mutualism is impossible. Hence, we can use the long time behavior of $H(t, 0)$ to distinguish between populations where mutualism can and cannot persist. See Ref. [11] for another quantity to distinguish the phases, similar to the susceptibility in equilibrium physics.

The phase diagram obtained from simulations is shown in Fig. 1(c). The region of parameters where mutualism can evolve is significantly reduced compared to the well-mixed prediction ($\alpha_1 > 0$ and $\alpha_2 > 0$). In particular, mutualism is impossible even for positive s , provided s is small. Fluctuations and spatial structure also favor *symmetric* mutualism, with $\alpha_1 \approx \alpha_2$, i.e., when the two species benefit equally from the interaction. The mutualistic phase [characterized by $\lim_{t \rightarrow \infty} H(t, 0) \neq 0$] is separated from the demixed phase [$\lim_{t \rightarrow \infty} H(t, 0) = 0$] by two lines of second order phase transitions that meet in a cusp: $\lim_{t \rightarrow \infty} H(t, 0)$ decreases continuously to zero as these lines are approached.

Nonequilibrium phase transitions from an active (mixed) to an absorbing (demixed) state have been studied extensively; see Ref. [10]. Generically, when the absorbing states are not symmetric, $\alpha_1 \neq \alpha_2$, the exit from mutualism belongs to the DP universality class. We can most readily see this for f^* close to an absorbing boundary, say, $f^* \ll 1$. For large s , species 1 then remains at low frequencies. As s decreased, some spatial regions stochastically lose species 1, but the more abundant species 2 persists. Local extinctions are opposed by the spread of species 1 from the nearby regions via Fisher waves. This dynamics is just that of DP in [10]. When $\alpha_1 = \alpha_2$, the absorbing states are symmetric and the local extinctions of either species are equally likely. As a result, this phase

transition belongs to DP2 universality class. We checked that our simulations are consistent with the DP2 “bicritical point” by calculating how $H(t, 0)$ decays for different values of s in a population that is initially well mixed [see Fig. 2(a)] and then collapsing these decay curves onto a unique scaling function using DP2 exponents as shown in Fig. 2(b). Equation (1) is also known to describe a DP2 transition for $f^* = 1/2$ [12]. Although the DP2 transition occurs only at a point, it influences a large portion of the phase diagram and governs the nonlinear shape of the DP transition lines near this “bicritical point.”

To understand how phase boundaries depend on the parameters of the model, it is convenient to measure distance in the units of D_s/D_g and time in the units of D_s/D_g^2 . For $\alpha_1 = \alpha_2 = 0$, the new time unit is proportional to the time of local demixing, and the new unit of distance to the size of domain boundaries [4,13]. When Eq. (1) is nondimensionalized, only two dimensionless parameters remain, f^* and $\tilde{s} = sD_s/D_g^2$. We confirm this data collapse in simulations; see Fig. 2(c).

Spatial structure and number fluctuations change not only the mutualistic region ($\alpha_1 > 0$ and $\alpha_2 > 0$), but also the whole phase diagram for well-mixed populations [11]. In particular, there is no bistable phase in 1D spatial populations. For almost all initial conditions, domains of species 1 or species 2 appear because of number fluctuations; the subsequent behavior can be analyzed in terms of the Fisher wave velocities of the domain boundaries. For $\alpha_1 > \alpha_2$, this velocity is directed from species 1 to species 2, and the direction is reversed for $\alpha_1 < \alpha_2$. As a result, one of the species takes over, much like an equilibrium first order phase transition proceeds through nucleation and growth.

When $\alpha_1 = \alpha_2$ and mutualism is unstable, the population segregates into single species domains, and the

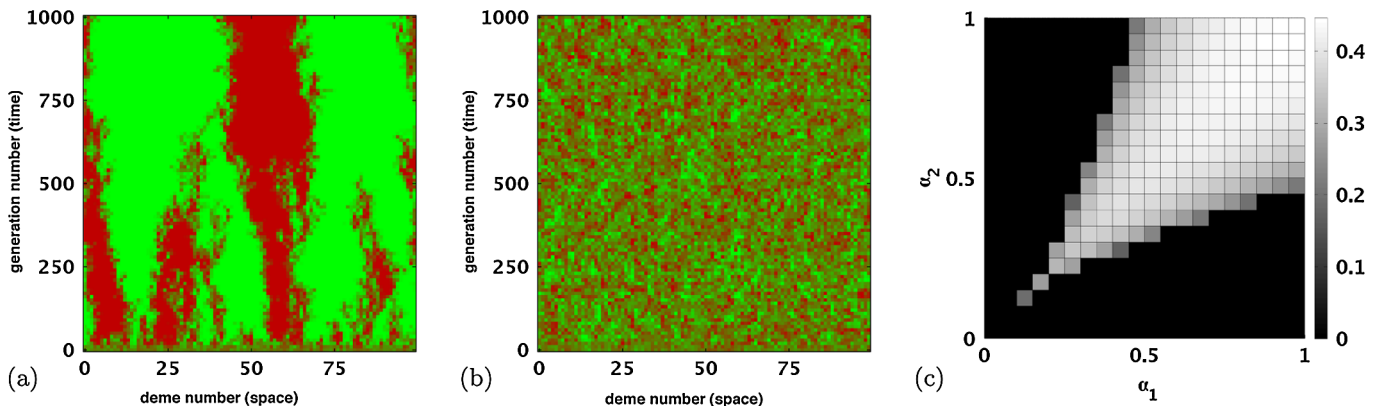


FIG. 1 (color online). Mutualism in the one-dimensional stepping-stone model [9,11]. The simulation parameters are chosen to mimic bacterial colonies growing in a Petri dish [14]. (a) Spatial demixing for $N = 30$, $mN = 1$, and no interspecies interactions, all $a_{ij} = 0$. Green (light gray) and red (dark gray) represent species 1 and 2, respectively. Every deme and every tenth generation are shown. (b) The same as in (a), but with strong mutualism $a_{12} = a_{21} = 0.5$. (c) Heat map of $H(4 \times 10^6, 0)$ from simulations with the same parameters as in (a), but with 10^4 demes and varying a_{12} and a_{21} .

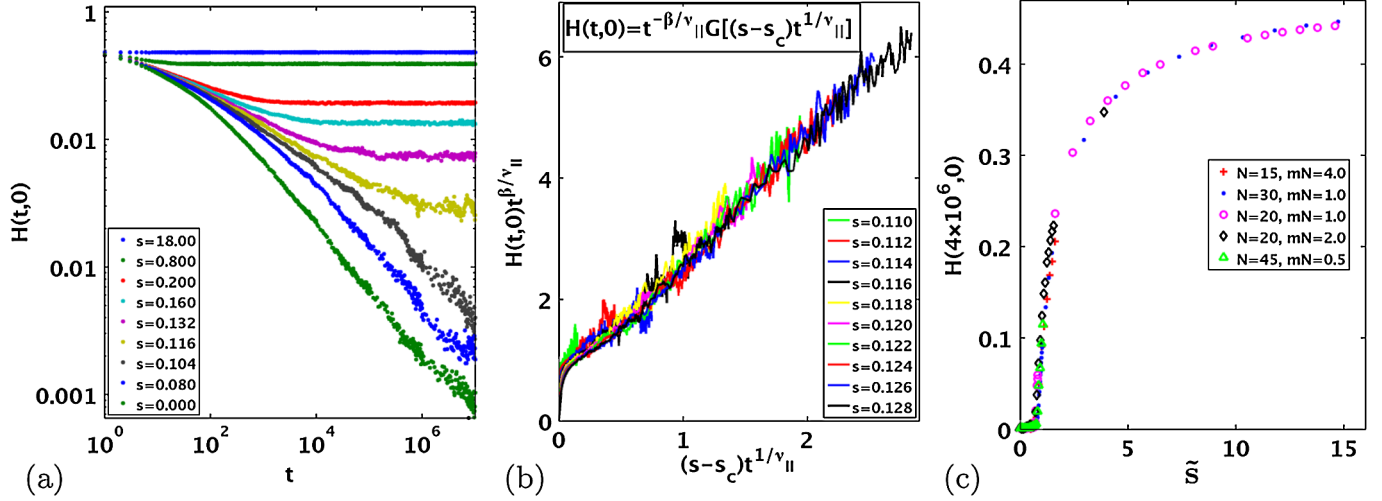


FIG. 2 (color online). Properties of the DP2 phase transition ($\alpha_1 = \alpha_2$) from simulations with the same parameters as in Fig. 1(c). (a) Decay of the local heterozygosity with time; lower values of the mutualism selective advantage s lead to faster decay. (b) The collapse of $H(t, 0)$ onto a universal scaling function shown in the inset with DP2 critical exponents for different s above the phase transition at $s_c = 0.109$. For the DP2 critical point, we expect $\beta = 0.92$ and $\nu_{\parallel} = 3.22$ [10]. (c) $H(t = 4 \times 10^6, 0)$ as a function of $\tilde{s} = sD_s/D_g^2$ for different values of m and N [11].

dynamics is driven by the random walks of domain boundaries. For $s > 0$ this demixing is slowed down by mutualism, but for $s < 0$ it is sped up initially due to the reaction term in Eq. (1). After domains form, however, more negative values of s lead to slower coarsening because the diffusion constant of domain boundaries decreases. Surprisingly, the exactly solvable limit of $\alpha_1 = \alpha_2 = 0$ undergoes the fastest demixing in the long time limit for large system sizes [11].

We have shown that number fluctuations can destroy mutualism. This prediction can be tested most easily in populations with weak migration and low effective population densities because the expected critical selective advantage of mutualism s_c is proportional to D_g^2/D_s . Although D_s and D_g are rarely known for natural populations, they have been estimated in bacterial colonies [14]. With some limitations [14], our theory should be directly applicable to these populations because the edge of a growing colony is a quasi-one-dimensional population, where the organisms not keeping up with the expansion are effectively dead. Indeed, the competition of two equally fit bacterial strains was accurately described by Eq. (1) with $s = 0$ [14]. For mutualistic versions of the two species *Escherichia coli* and *Pseudomonas aeruginosa* studied in Ref. [14], our theory predicts $s_c = 0.21$ and $s_c = 0.055$, respectively. Fitness differences of such magnitude can often be observed in microbial populations. More important, the relative strength of mutualism can be varied in the lab [15] allowing observation of the predicted phase transition.

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Note added.—Recently, we learned of work by Dall’Asta *et al.*, Ref. [16], that discusses symmetric cooperation in a similar model, corresponding to $f^{*} = 1/2$ and $\alpha_1 = \alpha_2$ in our terminology. Our work was constructed with experiments at microbial frontiers in mind; hence, it differs due to its focus on asymmetric interactions α_1 and α_2 of arbitrary sign and the large deme sizes in our simulations.

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