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Nonlocal competition and front propagation in branching-coalescence systems

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The spatial invasion of a stable into an unstable phase is studied for the branching-coalescence process with nonlocal competition. Numerical experiments show that the threshold at the front leading edge, introduced by the discreteness of the reactants, allows for the nonlocal competition to affect the front velocity. However, the front still moves ballistically after a short transient period for any finite range competition length.

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I. INTRODUCTION

The logistic equation, first presented by Verhulst [1], served for centuries as the fundamental method for describing growth processes with saturation [2]. The equation was applied to such diverse processes as the growth of a bacterial colony on a petri dish [3], the spread of a favored gene in a population [4], and first order phase transitions in the absence of a metastable state [5]. Logistic growth on spatial domains, where the motion of the individual reactant is diffusive, was initially considered by Fisher [4], and independently by Kolomogoroff, Petrovsky, and Piscounoff [6]. The following represents its "mean-field" version:

$$\frac{\partial c(x,t)}{\partial t} = D\nabla^2 c(x,t) + ac(x,t) - bc(x,t)^2. \tag{1}$$

This version has been shown to support a stable front that propagates in constant velocity $v_F = 2\sqrt{Da}$. The velocity is independent of the saturation term b, since the front velocity is determined by its leading edge where the nonlinear competition is negligible. In such a "pulled front," the properties of the bulk, like the number of particles at saturation, do not affect the velocity of the leading edge [7].

Any realistic system is made of discrete reactants (e.g., atoms, molecules, animals, cells), and therefore must admit some sort of demographic stochasticity, related to the probabilistic nature of birth-death-diffusion processes, and to a "threshold," reflecting the fact that the particles' density cannot be less than unity. Equation (1), in that framework, should be considered as an approximation of an underlying master equation, where averages over higher moments are replaced by powers of the average. For such a pulled front, the corrections to Eq. (1) due to discretization are of great importance, since the velocity is determined in the diluted region. The effect of stochastic fluctuations induced by the discrete character of the individual reactants (e.g., animals, genes, molecules) was considered either in the strong stochasticity, low density limit [8–10], or in the "semiclassical" limit close to the mean field [11,12]. It turns out that the basic feature, namely, the ballistic propagation of the front, is robust to discretization, but the velocity of the front is affected by it. In general, as the discretization introduced a "cutoff" along the leading edge, the front velocity was lowered with respect to the mean-field predictions.

In many biological situations, e.g., where the invasion of a new species is considered, the offspring and its "parent" (or any other individual) compete for common resources. It is known, for example, that this type of competition decreases the chance of a seed to sprout close to an existing plant [13]. This situation may be incorporated into the logistic-diffusive description by the introduction of a nonlocal competition term,

$$\frac{\partial c(x,t)}{\partial t} = D\nabla^2 c(x,t) + ac(x,t) - c(x,t)\int_{-\infty}^{\infty} \gamma(x,y)c(y,t)dy, \tag{2}$$

where D is the diffusion coefficient, a is the growth rate, and $\gamma(x,y)$ is a kernel for the nonlocal interaction. This modified Fisher-Kolomogoroff-Petrovsky-Piscounoff (FKPP) equation is the subject of many current studies [14–20], where the main new feature considered is an instability of the homogenous solution that leads to the appearance of ordered [14–16,18–20] or disordered [14] steady-state spatial patterns on spatial domains.

A subject that remains quite unnoticed is the effect of nonlocal competition on the invasion process itself, and in particular on the velocity of the front. Clearly, since the FKPP front is a "pulled" one [5,7], the effect of the competition on the velocity in the "mean-field" framework should be negligible. As long as the competition kernel $\gamma(x,y)$ in Eq. (2) is finite, there is a region on the leading edge where its effect is negligible and the velocity of this region is still $v_F = 2\sqrt{Da}$. In the continuum approximation the only effect of the competition relates to the shape of the front, but its velocity remains untouched. Moreover, even the leading "semiclassical" correction to the front velocity due to discretization, obtained by [11], is the same for local and nonlocal competition. In fact, the derivation of [11] assumes that the cutoff associated with the discretization is deep in the low-density region, where the nonlinear interaction is irrelevant.

One may suspect, though, that the combined effect of the discreteness of the reactants and the nonlocal competition may alter the invasion characteristics. As explained, discreteness of the reactants implies some sort of threshold at the leading edge, and thus the effect of nonlocal competition may be large enough at this region. In fact, in a recent work by Young and Birch [19], the effect of agents' discretization with nonlocal interaction was considered numerically, and one of the results suggests that the front invasion into the unstable phase halts due to the combined effect of strong nonlocal competition and reactant discretization. These findings have motivated this study, where we have tried to consider this effect in detail and to see if, and under what conditions, it is possible to stop the propagation by nonlocal competition. Our study indicates that the front does not really stop, although its velocity is diminished significantly with the interaction strength and range. While discretization does affect the velocity of the Fisher front, the front still propagates linearly as long as the growth rate is larger than zero.

II. MODEL

There are several discrete reactant "microscopic" models that yield the FKPP equation as their continuous limit. One of the standard realizations is the branching-annihilation process, which involves the multiplication of an agent (**A**) divided into two reactants at rate α, and the mutual annihilation of two agents by each other at rate β. All the agents are diffusing with hopping rate D. Schematically, the branching-annihilation basic ingredients are

$$A \overset{\alpha}{\rightarrow} 2A,$$

$$A + A \overset{\beta}{\rightarrow} 0,$$

$$A_i \overset{D}{\rightarrow} A_{i\pm1}. \tag{3}$$

However, this model is inappropriate for our study, as the two basic processes yield an effective "death rate," due to the mutual exclusion of a particle with its offspring. The renormalized model, accordingly, admits an extinction transition at finite α/β, as shown by Grassberger and de la Torra [21] (see also the work of Cardy and Tauber [22]). In order to avoid the extinction transition at finite α, a branching-coalescence process is used here, where the basic reactions are

$$A \overset{\alpha}{\rightarrow} 2A,$$

$$A + A \overset{\gamma}{\rightarrow} A,$$

$$A_i \overset{D}{\rightarrow} A_{i\pm1}.$$

Nonlocal competition is modeled by introducing $\gamma(r)$, i.e., by allowing for nonlocal coalescence of agents, and the process elements are

$$A \overset{\alpha}{\rightarrow} 2A,$$

$$A + \{A_\Omega\} \overset{\gamma_{\{A_\Omega\}}}{\rightarrow} A,$$

$$A_i \overset{D}{\rightarrow} A_{i\pm1}.$$

Here, Ω is the set of neighbors (particles located in neighboring sites) that "compete" with a specific reactant, and the strength of the competition between two reactants is, in general, proportional to the distance between them.

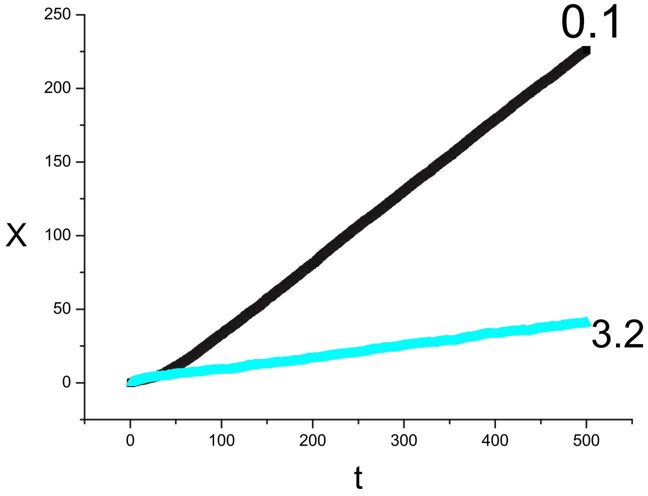

FIG. 1. (Color online) The location of the rightmost particle in a process described in the text, averaged over 40 different runs. The top hat competition is characterized by $L=5$, $D=0.25$, and the growth rate $\alpha=0.5$. The results are shown for weak $\gamma=0.1$ and strong $\gamma=3.2$ competition strength. Clearly, the front moves with constant velocity, but the velocity v is decreasing with γ.

From hereon, we will use the "top hat" kernel, as in [19], where $\gamma=\gamma_0$ if $|x_i-x_j|\leq L$, and where x_i is the location of the ith particle and L is the interaction range, for $|x_i-x_j|>L$, $\gamma=0$. The "strength" of the nonlocal interaction has to do with both γ_0 and L. The number of particles at a single site is not limited.

III. SIMULATION PROCEDURE AND RESULTS

We have run a Monte Carlo simulation of the branching-coalescence model described above on a one-dimensional array. Initially, only one site at the middle of the array is occupied by a single agent. The rates for either diffusion, birth, and the "per pair" coalescence are predetermined and kept constant along the simulation. At each time step, every particle is surveyed, the number of other particles that may perform "pair coalescence" with this individual is enumerated, and its chance to disappear is calculated. With that, the relative chances for the next event (e.g., yield of an offspring, migration, or coalescence) are calculated, and the event to happen is determined by "tossing" a weighted coin. If the event selected is migration or birth, one of the particles is chosen at random and migrates or yields an offspring. In a case of coalescence, the probability of a single particle to disappear is proportional to the number of particles in its L neighborhood.

Iterating this process and recording the location of the rightmost particle in the system, one gets the instantaneous location of the front. This noisy quantity has to be averaged over many realizations of other processes with the same parameters. The results, shown in Fig. 1, clearly indicate that, unlike its continuum approximation, the discrete process allows for the nonlinear competition term to affect the propa-

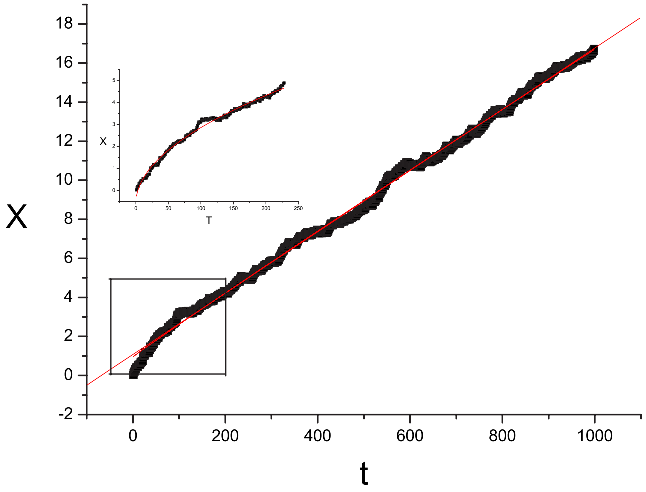

FIG. 2. (Color online) The average (over 200 samples) location of the front for top hat competition. At short time, the propagation is sublinear $x \sim t^{\alpha}$, while for long time the propagation is linear $x \sim t$. The simulation parameters are $D=0.5$, $\alpha=0.5$, and $\gamma=2$. The inset emphasizes the short time behavior.

gation velocity, so the front movement rate diminishes with the interaction growth. However, even for large competition, the front location still grows linearly with time, so the invasion is still ballistic, not diffusive or even superdiffusive.

The underlying mechanism beyond that result is related to the combination of diffusion and "escape" from the competition range. For any growth and competition parameters there is a finite probability that a newborn reactant will diffuse far enough to escape the competition length and give birth to another new reactant there. The event of birth and diffusing out of the interaction length has a typical time τ. This new time scale determines the effective growth rate, as now a reactant gives birth at a rate $a+1/\tau$ (rather than a in the case with local competition). Therefore the overall propagation mode turns out to be of a Fisher type, i.e., ballistic. Averaging over many samples, one indeed finds a sublinear displacement of the front, $x \sim t^{\alpha}$ with $\alpha < 1$, at short times. After some transient period, however, the propagation becomes linear in time $x \sim t$ as shown in Fig. 2.

The dependence of the linear velocity on the competition strength for top hat interaction is shown in Fig. 3. The functional dependence of v on γ is not trivial, and is clearly neither exponential nor a power law (see inset). We have also failed to fit the behavior to a stretched exponent. It seems that the velocity is determined by a few processes that interfere with each other. Among these, one can point out the reduction of the average density of particles, yielding larger corrections to the front velocity due to discretization [9,11], and the suppression of the growth rate for the leading particle by its neighbors along the front. It is interesting to note that the "break" between the two regions in the inset of Fig. 3 occurs when the average number of individuals at a site is of order unit [the number of individuals at site is $a/(L\gamma)$; for the parameters of Eq. (3) it is about one when $\gamma=0.1$].

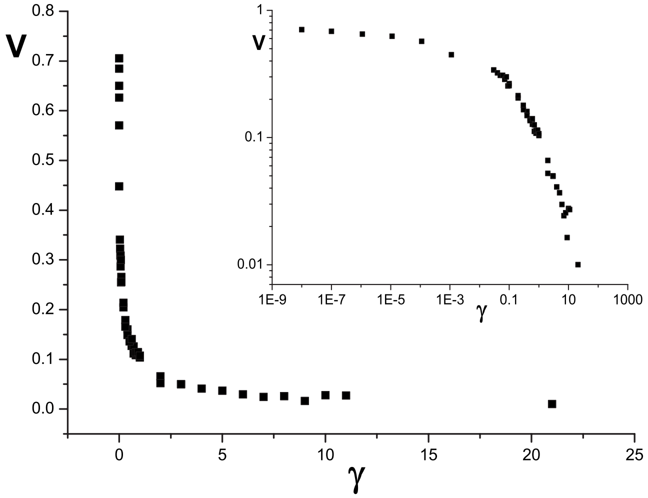

FIG. 3. Front velocity (arbitrary units) of the discrete Fisher process with long range competition vs the interaction strength γ. The kernel type is top hat ($L=5$), the diffusion coefficient is $D=0.25$, and growth rate is $\alpha=0.5$. In the inset, the same data are presented in log-log scale, indicating that the decay is faster than a simple power law. However, the decay is slower than exponential and does not fit to a simple stretched exponent. At the large concentration limit (small γ), the velocity converges to its mean-field value with the appropriate corrections coming from the spatial discretization as predicted by [23].

The effective growth rate depends, as explained before, on the competition strength (the chance for an offspring to diffuse out of the competition length before it undergoes coalescence), thus the nonlocal competition rescales the growth rate. Note that at the small γ limit the front velocity converges to its mean-field value and the front shape is similar to the shape observed in the continuum case (see Fig. 4).

To conclude, the branching-coalescence process with nonlocal coalescence of individual agents is mapped, in the mean-field approximation, to the FKPP equation with nonlo-

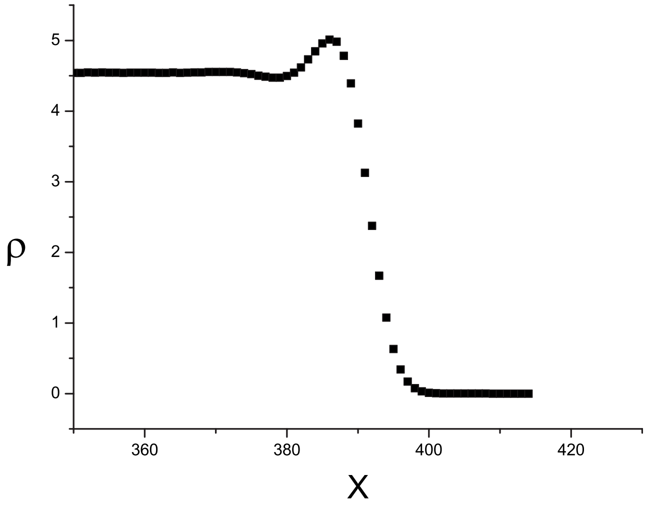

FIG. 4. The shape of a Fisher front (local density N in units of 10^6) close to the mean-field limit, i.e., where the number of individual reactants at saturation is large. The main features of the front, including its leading tail and the "overshoot" bump, correspond to the equivalent characteristics for the nonlocal FKPP model as shown in [14]. The simulation parameters are $a=0.5$, $D=0.25$, $L=5$, $\gamma=10^{-8}$.

cal competition. Our numerical analysis shows that, while the nonlocal competition may effect the invasion of the stable phase into the unstable region, it cannot change the fundamental characteristic of the front propagation, namely, its ballistic motion. Based on the general argument of renormalization of the growth rate by the escape time, we expect this feature to be valid as long as the nonlocal competition length is finite.

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