Species segregation in a model of interacting populations

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We investigate segregation and spatial organization in a one-dimensional system of N competing species forming a cyclic food chain. For $N < 5$, the system organizes into single-species domains, with an algebraically growing typical size. For $N = 3$ and $N = 4$, the domains are correlated and they organize into "superdomains" which are characterized by an additional length scale. We present scaling arguments as well as numerical simulations for the leading asymptotic behavior of the density of interfaces separating neighboring domains. We also discuss statistical properties of the system such as the mutation distribution and present an exact solution for the case $N = 3$.

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I. INTRODUCTION

Coarsening underlies numerous natural processes including phase separation, grain growth, soap bubbles, and species segregation. It is generally believed that coarsening systems exhibit dynamical scaling [1], *i.e.*, the typical domain size grows algebraically with time, $\ell(t) \sim t^{\alpha}$. The exponent α is usually independent of many details of the system such as the spatial dimension. However, little is known on coarsening in systems with more than two equilibrium phases. In this study, we investigate species segregation and reveal the two-length scaling instead of the ordinary single-length scaling.

Lotka-Volterra model of interacting populations "living" on a one-dimensional lattice is the simplest system which exhibits species segregation. The case where N species form a food chain is especially well suited for studying species segregation. We assume that every species plays the role of prey and predator simultaneously. The food chain is arranged in a cyclic manner. For example, when $N = 3$, A eats B, B eats C, and C eats A. "Eating" events involve nearest neighbors and lead to duplication of the winner and elimination of the loser, corresponding to the following reaction scheme

$$A + B \to 2A, \quad B + C \to 2B, \quad C + A \to 2C. \qquad (1)$$

Here and throughout this study we restrict ourselves to random and symmetric initial conditions, where the average initial species densities are all equal $1/N$. Despite the nonconserving nature of the process, the average densities remain constant in the thermodynamic limit.

II. SEGREGATION IN ONE DIMENSION

For a large number of species, most pairs of species do not interact and the system quickly reaches a frozen state. Previous studies [2,3] have mainly concentrated on establishing the upper bound for N above which the system does not coarsen. It has been proved rigorously that the marginal chain length is $N_c = 5$ [2,3]. For $N \geq N_c$ each site quickly reaches a final frozen state, while for $N < N_c$, the state of each site changes an infinite number of times. However, theoretical understanding of the kinetic behavior and the coarsening properties of the system is still incomplete [3,4]. In this study, we illuminate the rich kinetic behavior of the system by analyzing the density of interfaces separating different single-species domains.

For $N = 2$, this system is equivalent to the voter model [5,6] which can be solved exactly [7]. In terms of interfaces, the $N = 2$ model is equivalent to an ensemble of annihilating random walks. The system separates into single species domains. The average domain size ℓ exhibits a diffusive growth law $\ell(t) \sim \sqrt{t}$.

Consider now the $N = 3$ case. There are two types of interfaces: right moving (AB, BC, and CA) and left moving (BA, CB, and AC), denoted by R and L, respectively. The interface dynamics and consequently, the coarsening kinetics are sensitive to the microscopic realization of the reaction process. For parallel dynamics (all bonds are updated simultaneously) only opposite moving interfaces annihilate, $R + L \to \emptyset$, while for sequential dynamics (bonds are updated one at a time) interfaces moving in the same direction react as well, $R + L \to \emptyset$, $R + R \to L$, and $L + L \to R$. Hence, for the 3-species model with parallel dynamics the interface reaction process is equivalent to the well-known two-velocities ballistic annihilation process [8] and the interface density, $M(t)$, decays as $t^{-1/2}$. This behavior can be understood by arguing that in a linear region of size $\mathcal{L}$, the imbalance between the number of left and right moving interfaces is of order $\Delta \sim \sqrt{c_0 \mathcal{L}}$. After a time $t = \mathcal{L}/v_0$ only this residual fluctuation remains and as a result the concentration decay $M(t) \sim \Delta/\mathcal{L} \sim (c_0/v_0 t)^{1/2}$ follows.

The above heuristic picture suggests a special domain pattern. The system organizes into ballistically growing superdomains. Each superdomain contains interfaces moving in the same direction, while neighboring superdomains are separated by opposite moving interfaces. Do-

mains inside each superdomain are arranged cyclically ($ABCABC$ or $CBACBA$). In addition to the average size of superdomains, one can define the average distance between two adjacent similar velocity interfaces. We define these two typical length scales using an illustrative configuration:

$$B\overbrace{AABBB\underbrace{CCCC}_{\ell}AAABBCCC}^{\mathcal{L}}B. \qquad (2)$$

The corresponding coarsening exponents, α and β, are defined via $\ell \sim t^{\alpha}$ and $\mathcal{L} \sim t^{\beta}$, respectively. For $N = 3$ with parallel dynamics we thus have $\alpha = 1/2$ and $\beta = 1$. Computation of $\ell_n(t) = \langle x^n \rangle^{1/n}$, the moments of the domain distribution, reveals a richer spatial structure than that anticipated by Eq. (2). Namely, a variety of scales is found [9]: $\ell_n(t) \sim 1$ when $n < 1/2$ and $\ell_n(t) \sim t^{1-1/2n}$ when $n > 1/2$. However, only the two extreme scales, the ballistic scale $\mathcal{O}(t)$ and the scale $\mathcal{O}(1)$ characterizing the initial conditions seem to be important. All other scales, including the average length of a domain $\ell = \ell_1$, should be interpreted as effective scales arising as the result of the competition between the two extreme scales present in this system.

In the complementary sequential dynamics case, interfaces perform a biased random walk and thus, the ballistic motion is now supplemented by diffusion. The system again organizes into domains of right and left moving interfaces. Inside a domain, interfaces moving in the same direction can now annihilate via a diffusive mechanism, unlike the case of parallel dynamics (more precisely, collision of say two right moving interfaces gives birth to a left moving interface which is soon annihilated with the nearest right moving interface). Similar single-species annihilation with convective-diffusive transport has been investigated in Ref. [10] where the concentration decay $M(t) \sim t^{-3/4}$ has been established. This prediction is consistent with numerical simulations. The simulations also indicate that the system slowly approaches the asymptotic behavior $\ell(t) \sim t^{3/4}$ [11].

The resulting spatial structure is thus similar to the parallel case, Eq. (2). However, while the larger length scale remains unchanged, $\mathcal{L} \sim t$, the smaller length scale is now a geometric average of a diffusive and a ballistic scale. We conclude that the coarsening patterns are characterized by two length scales, and the coarsening kinetics are sensitive to the details of the dynamics. We anticipate that a variety of scales would appear from the moments $\ell_n(t)$, and they should be interpreted as effective scales resulting from the competition between the ballistic $\mathcal{O}(t)$ and diffusive $\mathcal{O}(\sqrt{t})$ scales.

In the $N = 4$ case, there are static interfaces denoted by S (AC, BD, CA, and DB), in addition to the right and left moving interfaces, (AB, BC, CD, DA) and (BA, CB, DC, AD), respectively. For sequential dynamics, interfaces react upon collision according to $R + L \to \emptyset$, $R + S \to L$, $R + R \to S$, $L + L \to S$, and $S + L \to R$. Under the assumption that neighboring interfaces are uncorrelated, the interface densities evolve according to the following rate equations

$$\begin{aligned} \dot{R} &= -2R^2 - 2RL - RS + SL, \\ \dot{L} &= -2L^2 - 2RL - SL + RS, \\ \dot{S} &= R^2 + L^2 - RS - SL. \end{aligned} \qquad (3)$$

Solving these equations subject to the initial conditions $R(0) = L(0) = S(0) = 1/4$ gives

$$M(t) = \frac{1}{4+4t}, \quad S(t) = \frac{1}{\sqrt{4+4t}} - \frac{1}{4+4t}. \qquad (4)$$

In the above, $M(t) = R(t) = L(t)$ is the density of moving interfaces. According to the rate equation theory, the typical distance between two static interfaces, $\ell \sim t^{1/2}$, grows slower than the distance between two moving interfaces, $\mathcal{L} \sim t$. A nontrivial spatial organization occurs in which large "superdomains" contain many domains of alternating noninteracting (AC or BD) species. Similar to the $N = 3$ case, there are two relevant growing length scales as in the following illustration

$$B\overbrace{AACCCAAA\underbrace{CCCC}_{\ell}AACCAAACCC}^{\mathcal{L}}D. \qquad (5)$$

Numerical simulations agree qualitatively with this picture. However, the quantitative predictions for the coarsening exponents fail.

In the following, we use heuristic arguments to obtain the exponent values. Numerical simulations indicate that parallel and sequential dynamics are asymptotically equivalent and thus, we restrict ourselves to the former simpler case. The annihilation reaction $R + L \to \emptyset$ is supplemented by the exchange reaction $R + S \to L$ and $L + S \to R$. According to the rate theory as well as the simulations $M(t) \ll S(t)$, and thus, we assume an alternating spatial structure of "empty" regions (with no more than one moving interface) and "stationary" regions (with many stationary interfaces inside any such region). If the interface densities obey scaling, then the size of the empty and the stationary regions should be comparable. The typical size of an empty or a stationary region is therefore of the order of M^{-1}. The typical number of stationary interfaces inside a stationary region is of the order of S/M. The evolution proceeds as follows: a moving interface hits the least stationary particle and bounces back. Then this interface hits the least stationary particle of the neighboring stationary region, and bounces back again. This "zig-zag" process continues until one of these stationary regions "melts", thereby giving birth to a larger empty region. If there is a moving particle inside merging empty region, the two moving particles quickly annihilate. Otherwise, the moving particle continues to eliminate stationary interfaces. The typical time τ for a stationary region to melt

is $\tau = M^{-1} \times S/M = S/M^2$. This melting time τ is also the typical time for annihilation of a moving interface and thus,

$$\dot{M} \sim -\frac{M}{\tau} \sim -\frac{M^3}{S}. \tag{6}$$

Using $M(t) \sim \mathcal{L}(t)^{-1} \sim t^{\alpha}$ and $S(t) \sim \ell(t)^{-1} \sim t^{\beta}$, the exponent relation $2\beta - \alpha = 1$ emerges. A second independent exponent relation, $\alpha + \beta = 1$, will be presented in the discussion of the mutation distribution below. Combining these two relations we find that $\alpha = 1/3$ and $\beta = 2/3$. These values are in good agreement with parallel as well as sequential simulations.

As in the previously discussed $N = 3$ case the spatial organization occurs on two different length scales. On the other hand, for $N = 4$, the coarsening kinetics are independent of the details of the dynamics, in contrast with the $N = 3$ behavior.

For the 5-species cyclic Lotka-Volterra model, it is known that the system approaches a frozen state [2,3]. Nevertheless, it is useful to consider the interface dynamics for the $N = 5$ case, where there are two types of stationary interfaces, S_R (AC, BD, CE, DA, EB) and S_L (AD, BE, CA, DB, EC), in addition to the right and left moving interfaces, R (AB, BC, CD, DE, EA) and L (BA, CB, DC, AD, AE). The reaction process is symbolized by $R + L \to \emptyset$, $R + S_L \to L$, $R + S_R \to S_L$, $S_R + L \to R$, $S_L + L \to S_R$, $R + R \to S_R$, and $L + L \to S_L$. It is straightforward to generalize the rate equations (3) to this case as well, and we merely quote the results. According to these equations, the static interfaces approach a final nonzero value $S(t) \to S_\infty$, and the mobile interfaces decay exponentially, $M(t) \sim \exp(-S_\infty t)$, as $t \to \infty$.

Interestingly, the rate equations correctly predict the marginal number of species $N_c = 5$. However, for the 5-species cyclic Lotka-Volterra model (similarly to the previously discussed cases of $N = 2, 3, 4$) only the qualitative predications of the rate equations are correct, but the quantitative predictions fail. To derive a correct asymptotic behavior we first observe that the density of mobile interfaces rapidly decreases while the density of stationary interfaces remains finite. This allows us to ignore collisions between mobile interfaces in the large time limit. We should estimate the survival probability of a mobile interface in a sea of stationary ones. There are two reactions in which moving interfaces survive although they change their type, $R + S_L \to L$ and $L + S_R \to R$. Thus, a moving interface is long lived in the following environment: $\cdots S_R S_R S_R S_R M S_L S_L S_L S_L \cdots$. Clearly, in such configurations the zig-zag reaction process takes place. The moving interface travels to the right during a time $t_0 = (c_0 v_0)^{-1}$, eliminates a stationary interface and travels to the left a time of order $2t_0$, eliminates an interface and travels back to the right, *etc.* Thus, to eliminate N_s interfaces, the moving interface should spend a time of order $t \simeq t_0 \sum_{i=1}^{N_s} i = t_0 N_s(N_s + 1)/2$. Therefore, the number of stationary interfaces $N_s(t)$ eliminated by a moving interface scales with time as $N_s(t) \sim \sqrt{c_0 v_0 t}$. Special configuration of length N_s are encountered with probability $\propto \exp(-N_s)$, and thus, the density of moving interfaces exhibits a stretched exponential decay, $M(t) \propto \exp(-\sqrt{c_0 v_0 t})$. Hence, the approach towards the frozen state is slowed down due to spatial fluctuations.

It was pointed out recently that nontrivial behavior underlies low-activity or persistent sites in coarsening systems [12,13]. It is useful to consider the mutation distribution, $P_n(t)$, defined as the fraction of sites that have mutated (changed their state) exactly n times during the time interval $[0 : t]$. Mutation kinetics and coarsening kinetics are intimately related. Let $\langle n(t) \rangle = \sum_n n P_n(t) \sim t^{\nu}$ be the average number of mutations. Since every motion of an interface contributes to an increase in the number of mutations in one site, the mutation rate equals the density of moving interfaces, $d\langle n(t) \rangle / dt = M(t)$. Using $M(t) \sim t^{-\mu}$ one has $\nu = 1 - \mu$. In the closely related voter model [5–7] (corresponding to $N = 2$), it was found that the mutation distribution $P_n(t)$ obeys scaling [6]

$$P_n(t) = \frac{1}{\langle n(t) \rangle}\, \Phi\left(\frac{n}{\langle n(t) \rangle}\right). \tag{7}$$

The scaling function has the following limiting behaviors

$$\Phi(z) \sim \begin{cases} z^{\gamma} & z \ll 1; \\ \exp(-z^{\delta}) & z \gg 1 \end{cases} \tag{8}$$

The behavior in the small argument limit reflects the decay of persistent sites. For the voter model $P_0(t) \sim t^{-\theta}$ with $\theta = 3/8$ [14]. If this power-law decay holds generally, then the exponent relation $\theta = \nu(\gamma + 1)$ should hold. The large z limit describes ultra-active sites. A convenient way to estimate the fraction of such sites is to consider sites which make of the order of one mutations per unit time. At time t, the fraction of these rapidly mutating sites is exponentially suppressed, $P_t(t) \propto \exp(-t)$. It is therefore natural to assume a quasi-exponential form $\Phi(z) \sim \exp(-z^{\delta})$ for the tail of the scaling distribution, thereby implying an additional exponent relation $\delta = 1/(1 - \nu)$.

The mutation distribution can be exactly calculated for the $N = 3$ case with parallel dynamics. Since the initial $\pm v_0$ interface velocities are uncorrelated, the interface ballistic annihilation process can be mapped into a random walk problem. As a result, the interface density is found from first passage properties of a random walk. Similarly, the mutation distribution can be shown to be equivalent to the probability that the minimum of a t-step random walk is exactly n (for details, see [11]). Using the definition of Eq. (7), and the average number of mutations $\langle n(t) \rangle \sim \sqrt{4t/3}$, the exact scaling distribution can be written

$$\Phi(z) = \frac{4}{\sqrt{\pi}}\, e^{-z^2}\, \mathrm{Erf}(z), \tag{9}$$

with $z = n/\langle n(t) \rangle$. The limiting behaviors of this scaling function agree with the predictions of Eq. (8), and the

scaling exponents $\theta = 1$, $\nu = 1/2$, $\delta = 2$, and $\gamma = 1$, satisfy the predicted scaling relations.

The knowledge of the mutation distribution suggests that we can compute the autocorrelation function, $A(t) = \sum_{n\geq 0} P_{3n}(t)$, as well. Making use of the above scaling form is not enough – one finds rather trivial long-time behavior, $A(t) \to 1/3$. To determine a correction to the final value, a combinatorial approach is somewhat inconvenient. Thus, we reconsider the problem by assuming that interfaces are distributed on a continuous line; the long-time behavior should be the same both in this continuum version and in the original lattice version. The continuum version turns out to be simpler and we have found *exact* cumbersome expressions [9] for all $P_n(t)$ in terms of the modified Bessel functions. This solution is then used to find that $A(t) - 1/3 \simeq -2/(9\pi t)$ as $t \to \infty$. This implies that the autocorrelation exponent λ [15] defined via $A(\mathcal{L}) - 1/3 \sim \mathcal{L}^{-\lambda}$ is given by $\lambda = 1$. Note that this value agrees with bounds on λ, $d/2 \leq \lambda \leq d$, proposed by Fisher and Huse [15] for phase ordering systems with nonconservative dynamics in d dimensions.

Having discussed the mutation distribution that quantifies the temporal history of species replacements we turn to the *age distribution* $P(\tau, t)$ defined as the probability that an individual which has been born at time τ and survives up to time t. The average age of the population is then given by $T = \langle t - \tau \rangle = \int_0^t d\tau (t-\tau) P(\tau, t)$. This probability distribution can be calculated for $N = 3$ [16] and we found that the the average age of the population grows linearly with time according to $T \simeq (1 - 2/\pi)t$. The age distribution obeys the scaling form $P(\tau, t) \simeq t^{-1}\Psi(\xi)$ in the limit $t \to \infty$ and $\tau \to \infty$ with $\xi = \tau/t$. The scaling function reads $\Psi(\xi) = (2/\pi)(1-\xi^2)^{-1/2}$.

We now return now to the 4-species Lotka-Volterra model. According to the above discussion, the zig-zag reactions $R + S \to L$ and $L + S \to R$ dominate over the annihilation reaction $R + L \to \emptyset$ in the long-time limit. We therefore consider a simpler solvable case where a single mobile interface is placed in a regular sea of static interfaces to evaluate the scaling function $\Phi(z)$ defined in Eq. (7). This interface moves one site to the right, two to the left, three to the right *etc.* Similar to the above discussion on the survival probability in the $N = 5$ case, at time t this interface has eliminated $N_s \sim (t/t_0)^{1/2}$ static interfaces, with $t_0 = (c_0 v_0)^{-1}$. The origin is visited $N_s t_0$ times, site 1 is visited $(N_s - 1)t_0$, site -1 is visited $(N_s - 2)t_0$, *etc.* This implies that the mutation distribution is $P_n(t) = \langle n \rangle^{-1} \Phi(n/\langle n \rangle)$, with $\langle n \rangle \sim N_s t_0$ and $\Phi(z) = 1$ for $z < 1$ and $\Phi(z) = 0$ for $z > 1$. Therefore, $\gamma = 0$. This approximation is inappropriate for predicting the tail of $\Phi(z)$ which is sensitive to annihilation of the moving interfaces. However, in the small z limit the annihilation process should be negligible, and thus $\gamma = 0$. The fraction of unvisited sites is equivalent asymptotically to the survival probability of a stationary interface and thus $\theta = \alpha$. Using the previously established relations $\nu = 1 - \mu$, $\theta = \nu(\gamma + 1)$, and $\mu = \beta$, we obtain the second independent exponent relation $\alpha + \beta = 1$ which was used to obtain the asymptotic behavior of the mobile and the static interfaces.

III. EXTENSIONS

The cyclic lattice Lotka-Volterra model can be generalized in a number of directions. A natural generalization is to higher dimensions. Two-dimensional case seems to be especially interesting from the point of view of mathematical biology [17]. In the exactly solvable $N = 2$ case (the voter model), coarsening occurs for $d \leq 2$ [5], for the marginal dimension $d = 2$, the density of interfacial bonds decays logarithmically, $c(t) \sim 1/\ln t$ [18], while for $d > 2$, no coarsening occurs and the system reaches a reactive steady state. In two dimensions, our numerical simulations indicate that there is no coarsening, *i.e.* the density of reacting interfaces saturates at a *finite* value. For sufficiently large number of species the fixation is expected but we could not determine the threshold value, at least up to $N = 10$ we have not seen fixation.

Another extension concerns a different interaction rule. Previously, we investigated the cyclic Lotka-Volterra model with *asymmetric* interactions. To learn how the coarsening kinetics depend on the interaction rules it is useful also to consider a *symmetric* interaction rule where both of the reaction channels $A + B \to 2A$ and $A + B \to 2B$ are allowed. In this case, asymptotically exact results can be obtained. We discuss only the $N = 4$ case since the $N = 2$ and $N = 3$ cases reduce to the voter model (see [6]). Denote the static interfaces (AC, CA, BD, DB) by S and moving interfaces by M. The symmetric "eating" rule implies that moving interfaces perform simple random walks. Interfaces react according to $M + M \to S$, and $M + S \to M$ or $M + S \to S$ depending on the local environment. Moving interfaces undergo diffusive annihilation and thus, $M(t) \sim t^{-1/2}$. The fraction of surviving stationary interfaces is proportional asymptotically to the fraction of sites which have not been visited by mobile interfaces up to time t, $S(t) \sim P_0(t) \sim t^{-3/8}$. We should also take into account creation of stationary interfaces by annihilation of moving interfaces. This process produces new stationary interfaces with rate of the order $-dM/dt$. Thus, the stationary interface density satisfies the rate equation $\dot{S} = \dot{P}_0 - \dot{M}$. Combining this equation with $P_0(t) \sim t^{-3/8}$ [14] and $M(t) \sim t^{-1/2}$, we find that the surviving interfaces provide the dominant contribution while those created in the process $M + M \to S$ contribute only to a correction of the order $t^{-1/8}$. Thus a two-scale structure similar to Eq. (5), with $\ell \sim t^{3/8}$ and $\mathcal{L} \sim t^{1/2}$, emerges. Hence, it is seen that the coarsening exponents can be sensitive to the details of the interaction rules.

We also looked at the cyclic Lotka-Volterra model with unequal initial concentrations. We have seen rich kinetics [11] but mention just one example here: For the

4-species system with one majority species, say species A, and other species having the same concentrations, $b_0 = c_0 = d_0$, the system approaches a frozen state with $a_{\rm frozen} = 1/4$ and $c_{\rm frozen} = 3/4$.

IV. SUMMARY

We investigated coarsening in a one-dimensional model of competing species. Interestingly, the coarsening properties of this model may depend on the details of the dynamics. The spatial patterns are characterized by the existence of two characteristic length scales, the average length of the single-species domains, $\ell(t) \sim t^{\alpha}$, and the average length of superdomains, $\mathcal{L}(t) \sim t^{\beta}$ (the corresponding coarsening and mutation exponents are summarized in Table 1).

N	α	β	θ
3 (parallel)	1/2	1	1
3 (sequential)	3/4	1	1
4	1/3	2/3	1/3
4 (symmetric)	3/8	1/2	3/8

Table 1: Coarsening ($\ell \sim t^{\alpha}$ and $\mathcal{L} \sim t^{\beta}$) and persistence ($P_0(t) \sim t^{\theta}$) exponents in 1D.

Thus simple dynamical scaling is violated for the one-dimensional Lotka-Volterra models. Violations of scaling have been reported in a few recent studies of coarsening in one- and two-dimensional systems [19–25]. To the best of our knowledge, however, in previous work violations of dynamical scaling have been seen only in some systems with vector and more complex order parameter. In contrast, Lotka-Volterra models can be interpreted as systems with *scalar* order parameter, although the number of equilibrium states N generally exceeds two, the characteristic value for Ising-type systems.

Finally we note that presence of only two length scales exemplifies the mildest violation of classical single-size scaling. Generally, if scaling is violated one expects the appearance of an infinite number of independent scales, *i.e.*, multiscaling [19]. Surprisingly, we found no evidence of multiscaling. Similar two-length scaling has been observed in the simplest one-dimensional system with vector order parameter, namely in the XY model [22], and in the single-species annihilation with combined diffusive and convective transport [10]. Indications of the three-length dynamical scaling have been reported in the context of coarsening [24] and chemical kinetics [26].

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